

Papéis Avulsos de Zoologia

Museu de Zoologia da Universidade de São Paulo

Volume 45(13):143-177, 2005

www.scielo.br/paz.htm

ISSN impresso: 0031-1049

ISSN on-line: 1807-0205

A MORPHOLOGY-BASED PHYLOGENY OF *PHYMATURUS* (IGUANIA: LIOLAEMIDAE) WITH THE DESCRIPTION OF FOUR NEW SPECIES FROM ARGENTINA

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ABSTRACT

Phylogenetic relationships within the liolaemid lizard genus Phymaturus were studied using parsimony analysis of morphological data. The data set includes 133 characters: 28 described in the literature as apomorphies of the three genera of Liolaemidae (Ctenoblepharys, Liolaemus, and Phymaturus), 21 published characters of allozymes and karyology, 53 characters taken from external morphology across all terminals of Phymaturus, and 31 from the skeletal anatomy. This data set includes representatives of 10 of the 12 species currently recognized in the literature plus twelve other terminals considered in this study and representing independent lineages assigned to patagonicus or palluma. Four of these terminals are described in the present study as new species, one belonging to the palluma group and the other three to the patagonicus group. We performed four analyses using different methods of coding binary polymorphic characters, and a new method for treating continuous characters. The traditional division of the genus in two groups is not supported here, with the patagonicus group resulting paraphyletic in some of the analyses. The palluma group is monophyletic and supported by many characters. A majority rule consensus tree of all runs recovers a reasonably well-resolved topology of the group. All analyses recovered a northern subclade within the palluma group, formed by species distributed in Argentina from northern of San Juan province (north to 30 degrees of latitude). In this analysis palluma from El Planchón (Chile) was found to be more closely related to this northern subclade than any other "palluma" form.

KEYWORDS: Liolaemidae; *Phymaturus*; new species; morphology; phylogenetic analysis.

INTRODUCTION

Phymaturus comprises a group of iguanian lizards inhabiting rocky places of Patagonia and both eastern and western mid- to high-elevation slopes of the Andes. This group of viviparous and herbivorous lizards reaches its northern limit in the Puna region of

Catamarca in northern Argentina. The southernmost-distributed species is *indistinctus*, living at the latitude of 45°30' South. According to Etheridge (1995) species of this clade of iguanians are characterized by having wide and flattened head and body, tail with a regular whorls of spinose scales, lateral nuchal skin folds with fat-filled pouches, a short interclavicular,

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among other characters that are exclusive and provide strong evidence of monophyly.

At the time of Donoso Barros (1964) and Peters and Donoso Barros (1970), the genus included only one species with two subspecies: *palluma palluma* (Molina) 1782, and *palluma patagonicus* (Koslowky) 1898. Most taxa recognized as species today were described during the 1970s-80s: *P. patagonicus payunae*, *P. p. somuncurensis*, *P. p. zapalensis*, *P. p. indistinctus*, and *P. p. nevadoi* by Cei & Castro (1973); *P. mallimaccii* by Cei (1980); *P. punae* by Cei *et al.*, (1983); and *P. antofagastensis* by Pereyra (1985). Despite publication of several systematic studies on the genus over the last 30 years (Cei & Lescure, 1985; Lescure & Cei, 1991; Pereyra, 1992a; among others), the phylogenetic relationships among *Phymaturus* species remain enigmatic. Pereyra (1992a) studied the external morphology, karyology, and allozymes of six species/populations of *Phymaturus*, but his study applied phenetic techniques (cluster analysis), which established phenetic distances among taxa but did not provide a genealogical reconstruction. Much of Pereyra's (1992a) information was included and reevaluated in the present study. Etheridge (1995) provided the first extensive study of genera now included in the Liolaemidae (*Phymaturus*, *Liolaemus*, and *Ctenoblepharys*), and proposed a cladistic taxonomy based on morphological characters. Within *Phymaturus* Etheridge (1995) recognized two groups of species, the *palluma* group with four species, and the *patagonicus* group formed by six species (formerly considered subspecies of *patagonicus* by Cei [1986]). Characters defining the *palluma* group were the non-imbricate superciliaries, five or more suboculars, three to four rows of lorilabials, mental narrower than rostral and usually in contact with sublabials, caudal spines well developed, and two annuli per segment. For the *patagonicus* group, Etheridge (1995) identified a splenial short and a fused Meckel's groove. However, Etheridge (1995) noted that these groups may not necessarily be monophyletic. Following this work, no additional studies were published that sought to recover the genealogical relationships within the genus, yet, many questions remain, like the validity and or monophyly of Etheridge's (1995) groups of species, and the phylogenetic relationships among species. Recently, Cei & Videla (2003) and Scolaro & Cei (2003) described two new species for the genus and discussed the unresolved problem of the identity of the true *palluma*, a lizard collected by Charles Darwin on his voyage on the *Beagle* and posteriorly described by Bell (1843). The latter issue remains a problem that needs to be resolved through the examination of populations on both sides

of the Andes, and compared to the type material deposited at the British Museum of Natural History.

The goal of this study is to provide a first comprehensive analysis of *Phymaturus*, using cladistic methods. We studied the external morphology and skeletons of an extensive sample of terminals and individuals. We examined and described more than 100 informative characters, most of them used in the systematics of *Phymaturus* for the first time, as well as other characters taken from the literature.

MATERIALS AND METHODS

For the phylogenetic analysis we were able to reexamine the type series of nine of the 12 currently recognized species (with the exception of *palluma*, *verdugo*, and *calcogaster*). Characters used in this study were obtained primarily from the skeleton, squamation, morphometry, and body patterns. The allozyme data set plus two chromosomal characters of Pereyra (1992a) were also included. Skeletal characters were visualized from cleared and stained material following Wassersug's (1976) technique, which allows differential staining of cartilage and bone. For some specimens (MVZ and SDSU dry skeletons) however, cartilaginous structures (larynx, trachea, and hyoid apparatus) were not available because they were prepared as dry skeletons. External characters were scored from formalin-preserved specimens stored in alcohol 70%. Characters for phylogenetic analysis were scored only from adults. Ontogenetic shift in external morphology between juveniles and adults was recorded and it is presented in a separated section. Scale terminology follows a previous study on the *Liolaemus chiliensis* group (Lobo, 2001), measurements were taken with digital calipers (± 0.01 mm) and following the definitions of Laurent (1984). Skeleton terminology follows previous studies (Lobo & Abdala, 2001, 2002). Museum numbers and localities for specimens included in this study are listed in Appendix I. We selected characters based on previous cladistic studies in *Liolaemus* (Lobo, 2001; Lobo & Abdala, 2001, 2002), or those described for *Phymaturus* (Cei, 1980, 1986, 1993; Cei & Castro, 1973); Cei *et al.*, 1983; Etheridge, 1995), and we reevaluated many of characters considered informative for the genus by Pereyra (1992a) (among meristic, allozyme, and karyological characters he studied). For a details and a list of characters see Appendix II. He found characters discriminating *payunae* and cf. *palluma* (CH) from the rest of species (morphometric characters in page 71, Table 18), head length, number of scales

on the dorsum of the head (equivalent to his LCI), and head width; from his meristic characters that he found useful for discriminating *payunae* and *mallimaccii* from other species (page 68, Table 17) we used number of scales in contact to mental, scales around mid-body, dorsals along the back included in a head length, and number of suboculars. Also we included his data set of allozymes (19 characters) and two from karyology (diploid chromosomal number and number of microchromosomes in females), which were available for four of our terminals (*P. antofagastensis*, *P. mallimaccii*, *P. palluma* from Mendoza, and *P. payunae*). We added diploid chromosomal number to two other terminals, *P. dorsimaculatus* (from Copahue, Neuquén Province) and *P. excelsus* (from Ojo de Agua, Rio Negro) following Morando *et al.*, (2001).

Phylogenetic analyses were conducted with parsimony software (TNT: Tree Analysis Using New Technology, vers. 1.0; Goloboff *et al.*, (2003). We choose TNT for our analysis because this is the only program that allows the analysis of continuous characters without first converting them in discrete characters (as proposed by Thiele, 1993). Data matrices are available at www.unsa.edu.ar/acunsa. There is more than one matrix because different coding methods were applied for binary polymorphic characters. The first block in matrix is comprised of continuous characters (26 for external morphology and 14 for skeletal anatomy), the same characters are included in the following block (characters 88-106; 109-113; 135-148). During searches we deactivate these characters if we use the range method for continuous, and the opposite to apply Thiele's gap-weighting method (Thiele, 1993). For TNT numeration of characters begins with the first block (with character "0" designating the first one), so the second block (traditional format) starts with character 40. The list of characters in text 0-132 are equivalent in TNT format of our matrices to 40-172. In our analysis we considered the following TNT characters non-additive 68-86 (allozyme characters: 28-46); 128 and 130 (throat pattern of males and females, dorsal pattern of tails: 88-90), 168 and 170 (128 and 130, "smooth pattern" and dorsal pattern black with two rows of ocelli); all remaining characters were additive. Binary polymorphic characters were analyzed in four different ways: any-instance (the polymorphic species is considered already having the novelty, so it is coded "1" as in species that this state is fixed), scaled (polymorphic species have an intermediate state "1" in an ordered series between species not having that derived state "0" and those having the derived state "2"), frequency bins (frequency of the presence of the derived state is

used to score each species, percentage ranges are divided by 0-9 states for TNT analysis), and missing (question mark for polymorphic species). For more details on these methods and performance of them in cladistic analysis see Wiens (2000) TNT uses Farris' optimization (Farris, 1970) to estimate distances and costs among ranges, when ranges between two terminals overlap, TNT assumes zero cost. In this study we entered ranges for continuous data to the program considering a mean \pm SD as a range for any continuous character, and we standardized all continuous characters dividing the ranges by the major data and multiplying this by ten. In this way the costs of the continuous characters are similar to the others.

For frequency bins we preferred not dividing by more states than 10 because the limited sample size we had of some species.

For rooting our trees we included the other two liolaemid genera, *Liolaemus* (three species: *L. kingii*, *L. tenuis*, and *L. pseudoanomalous*) and the monotypic *Ctenoblepharys*. Relationships among genera in Liolaemidae were once controversial (Frost & Etheridge, 1989; Etheridge, 1995), yet according to the last revision of intergeneric relationships (Etheridge, 1995), there are many synapomorphies supporting the monophyly of each of the three genera. Recent DNA analyses support a *Phymaturus*-*Liolaemus* sister-taxon relationship with *Ctenoblepharys adspersa* as the basal member of the family (Schulte *et al.*, 2003; Espinoza *et al.*, 2004).

RESULTS

1) Choice of terminal taxa

We included in the present study all recognized species of *Phymaturus* in literature (Etheridge & Espinoza, 2000) except the recently described *P. verdugo* Cei & Videla, 2003 and *P. calogaster* Scolaro & Cei, 2003: cf. *palluma*, *antofagastensis*, *mallimaccii*, *puna*, *patagonicus*, *nevadoi*, *payunae*, *zapalensis*, *indistinctus*, and *somuncurensis*. Also we included *spurcus*, a recently revalidated species (Lobo & Quinteros, in press). In addition to these species, we included twelve populations that are assigned to named species yet show morphological evidence of evolutionary isolation (likely representing independent lineages) from nominal forms. Four of these terminals are described below as new species. We follow Cei & Videla (2003) in recognizing that the issue of the provenance of *P. palluma* cannot be readily resolved (i.e., populations inhabiting the eastern and western slopes of the Andes exhibit morphological [this study],

karyological [Pereyra, 1992a], and DNA [R. Espinoza, unpubl. data] differences), so we use cf. *palluma*, rather than *P. palluma* in this study.

I—Description of four new species of *Phymaturus*

Of the twelve terminals added to this analysis to the currently recognized species, four exhibit obvious discriminating characters (squamation and patterns) that justify their description as new species.

Phymaturus dorsimaculatus sp. nov.

Holotype (Figure 1A and B): MCN 1573. Copahue, Dpto. Ñorquin. 37°49'S; 71°06'W. Neuquén, Argentina. Abdala, C.; Avila, L.; F. Lobo, & M. Morando, collectors. 13 January 1999.

Paratypes: MCN 1571-72, 1574-75. Same data as holotype. MCN 1568-69. Termas de Copahue, Dpto. Ñorquin, Neuquén, Argentina. 37°49'14"S; 71°05'12"W; 2050 m. 13 January 1999. MCN 1566-67. Copahue, Dpto. Ñorquin, Neuquén.

Diagnosis: *Phymaturus dorsimaculatus* belongs to the *palluma* group (sensu Etheridge, 1995) because it has square-shaped non-imbricate superciliaries, rugose dorsal scales of the tail, usually a fragmented subocular, and the subocular-supralabials separation is two or more scale rows. It is distinguishable from all other species in the group by its unusual dorsal pattern. Dorsal pattern from occiput to the posterior region of trunk with black transverse bands interrupted medially (Figure 1A). *Phymaturus verdugo* is a larger species (106-120 mm both sexes; Cei & Videla, 2003) than *dorsimaculatus* (76.1-92.6), has a different dorsal pattern, and a patternless tail (ringed in *dorsimaculatus*). This new species has a different karyotype number ($2n = 36$) versus $2n = 26$ of *P. verdugo* (Morando *et al.*, 2001; Cei & Videla, 2003). Adults of cf. *palluma* (PA) lack melanism on head and neck and all other members of the *palluma* group have patternless tails. *Phymaturus dorsimaculatus* never have a divided rostral scale as does many *punae*, *antofagastensis*, cf. *antofagastensis* SC (Sierra de Calalaste and Cuesta de Randolpho), and *punae* LR (La Rioja). Most specimens from northern Argentina of the *palluma* group exhibit a homogeneous and dense "spray" pattern on their dorsum (Figure 12C) and lack black reticulation or spots.

Description of holotype: Female. Snout-vent length (SVL) 92.6 mm. Head length 16.2 mm. Head width 16.8 mm.

Head height (at parietal) 8.8 mm. Axilla-groin 46.7 mm (50.4% of SVL). Tail length (complete, not regenerated) 83.3 mm (0.9 times SVL). Body moderately wide, trunk width: 40.2 mm (43.4% of SVL). Eighteen dorsal head scales. Dorsal head scales smooth, with scale organs more abundant in prefrontal region. Six, five, five, and four scale organs in each postrostral. Nasal scale not in contact with rostral, bordered by nine scales. Canthal separated from nasal by one scale. Loreal region flat. Seven enlarged supralabial scales with seventh upturned posteriorly, contacting subocular. Nine enlarged infralabials. Auditory meatus oval; auricular scale absent, three to four projecting scales on anterior margin of auditory meatus (both sides). Nine convex, juxtaposed, smooth temporals. Rostral undivided. Mental subpentagonal, in contact with six scales. Interparietal bordered by five scales, parietals of similar size. Frontal region without an azygous scale. Supraorbital semicircles incomplete posteriorly on both sides. No distinctly enlarged supraoculars. Twelve non imbricate subquadrangular superciliaries. Sixteen upper and thirteen lower ciliaries (right side). Subocular fragmented in two (left side) and three scales (right side), separated from supralabials by three to one row of lorilabials. Ten lorilabials. Preocular separated from lorilabial row by three scales. Postocular equal in length to preocular. Chinshields not enlarged (similar size of that of sublabials) forming a longitudinal row of five scales. Scales of throat round, flat, and juxtaposed. Seventy-four gulars between auditory meatus. Lateral nuchal folds well developed, with granular scales over longitudinal fold that are smaller than dorsals. Antehumeral pocket well developed. Fifty-six scales between auditory meatus and shoulder. In ventral view gular fold not well developed and posterior gular folds present with their anterior margins lacking enlarged scales on their borders. Dorsal scales round, smooth, juxtaposed. Thirty dorsal scales along midline of the trunk in a distance equivalent to head length. Scales around midbody 210. Mid-dorsal scales slightly enlarged, becoming smaller and granular on flanks and toward belly. Ventral scales larger than dorsals; 172. Between mental and preloacal area. No preloacal pores. Brachial and antebrachial scales smooth with round posterior margins. Supracarpals laminar, round, smooth. Subdigital lamellae of fingers with five keels (more conspicuous in proximal lamellae). Number of subdigital lamellae of fingers I: 9; II: 13; III: 17; IV: 19; V: 12. Claws moderately long. Supradigital lamellae convex, smooth, imbricate. Infracarpals and infratarsals with round margins and two to three obtuse keels. Supracarpals and supratarsals smooth, with round pos-

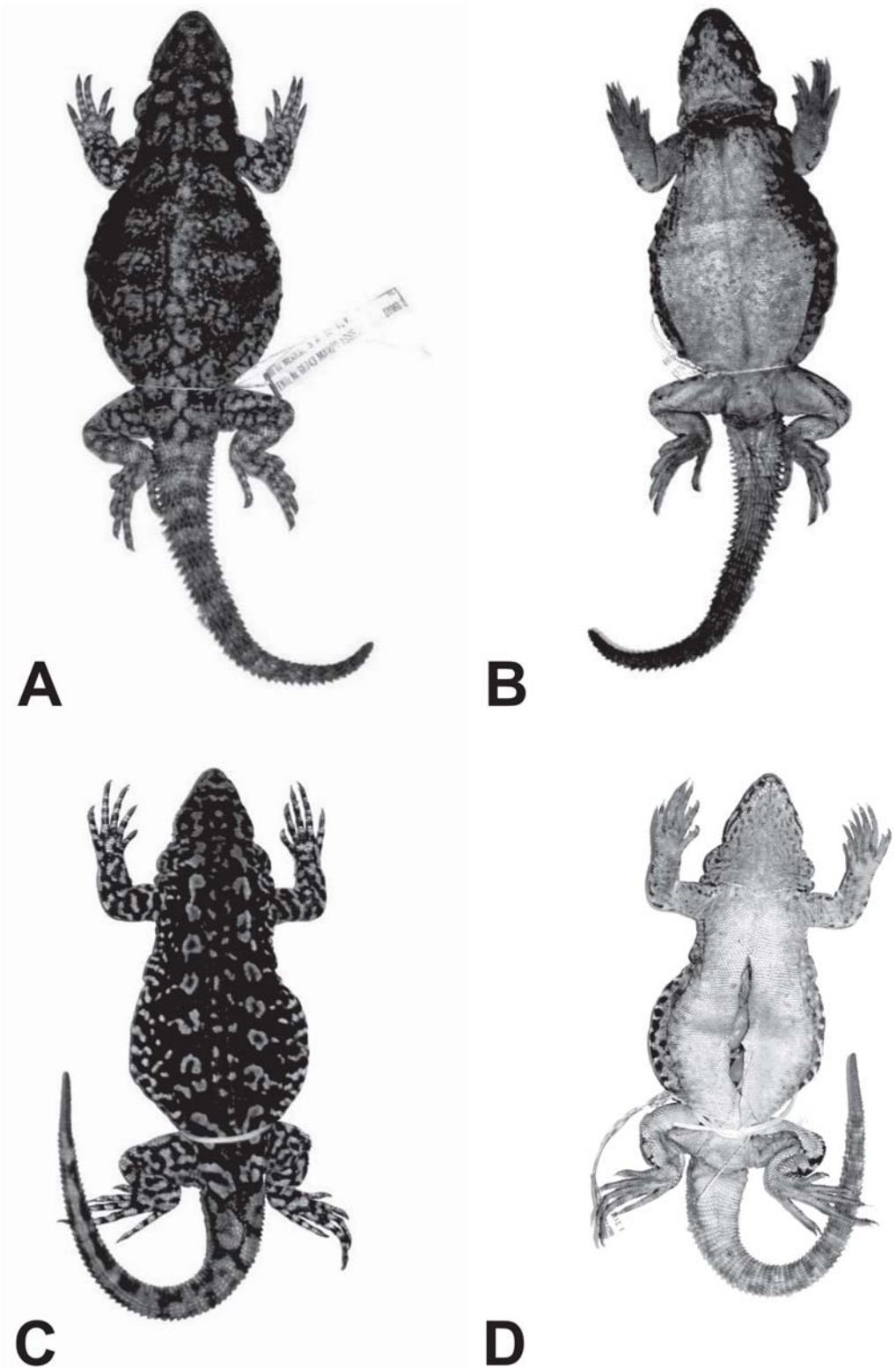


FIGURE 1. (A) Dorsal view of the holotype of *Phymaturus dorsimaculatus* sp. nov. (B) Ventral view of the same specimen. Snout-vent length = 92.6 mm. (C) Dorsal view of the holotype of *Phymaturus excelsus* sp. nov. (D) Ventral view of the same specimen. Snout-vent length = 82.5 mm.

terior margins. Subdigital lamellae of toes I: 8; II: 13; III: 20; IV: 23; V: 15.

Variation: Based on 15 specimens (4 females, 7 males, 2 juvenile females, and 2 juvenile males). Snout-vent length 62.2-92.6 mm (\bar{x} = 79.3; SD = 9.4). Head length 0.17-0.22% (\bar{x} = 0.20; SD = 0.01) of SVL. Tail length 0.81-1.04 (\bar{x} = 10.95; SD = 0.07) times SVL. Scales around midbody 200-256 (\bar{x} = 229.55; SD = 17.4). Dorsal head scales 17-24 (\bar{x} = 19.4; SD = 1.7). Ventrals 160-199 (\bar{x} = 176.5; SD = 11.3). Precloacal pores in males 5-10 (\bar{x} = 8.3; SD = 2.1). Scales surrounding interparietal 5-8 (\bar{x} = 6.5; SD = 0.9). Scales of neck along longitudinal fold from posterior border of auditory meatus to shoulder 62-87 (\bar{x} = 76.6; SD = 9.1). Gulars 55-86 (\bar{x} = 78.4; SD = 8.8). Scales between rostral and frontal 7-12 (\bar{x} = 9.3; SD = 1.6). Subdigital lamellae of fourth toe 20-24 (\bar{x} = 22.5; SD = 1.5). Dorsal pattern black-forked is typical in adult females and all juveniles, but less conspicuous or restricted to the region of the neck and shoulder in adult males. One male have completely melanic head.

Color of holotype in alcohol (Figure 1A and B): Dorsal background color brown with a distinct pattern in black extended from occiput to the posterior region of trunk forming transverse bands that are interrupted medially. Finer irregular black reticulation distributed along the vertebral region reaching the base of the tail. The tail is ringed with darker brown bands two scales wide. Forearms and hindlimbs with fine reticulation. Head not melanic. Throat gray-light brown with reticulate brown more evident below jaws. Chest black. Abdominal region variegated.

Color in life: Not available.

Etymology: The epithet refers to the conspicuous pattern of black spots over the neck, shoulders, and dorsum of the trunk of this new species. It is a compound name (originated from two latin words dorsum that means back and macula that means spot, mark).

Distribution: Only known from the type locality, Copahue, Neuquén province, Argentina, 37°49'14"S, 21°05'12"W; 2050 m elevation.

Phymaturus excelsus sp. nov.

Holotype: MCN 1582. Ruta prov. 6, 1 km NW of Ojo de Agua, Dpto. Ñorquinco, Rio Negro, Argentina. L.

Avila & M. Morando, collectors. 41°32'30"S; 69°51'33"W; 1141 m.

Paratypes: MCN 1386, 1388. Ojo de Agua. Ruta 6. Dpto. Ñorquinco, Rio Negro, Argentina. Abdala, C.; F. Lobo; I. Martínez Oliver; S. Quinteros. MCN 922 (CS), 1583-1586. Same data as holotype. MCN 1587-88. No data.

Diagnosis: *Phymaturus excelsus* belongs to the *patagonicus* group (sensu Etheridge, 1995) because it has flat imbricate superciliaries, non-rugose dorsal scales on tail, subocular usually not fragmented, and subocular-supralabials separated by one scale row. This new species differs from all other members of this group in its unique dorsal pattern, with a dorsal background in black and a pair of longitudinal series of white ocelli (fig. 1C). Similar patterns with a paired series of ocelli are found (but in different colors, shapes, and arrangements) in *payunae*, *zapatensis*, and *spectabilis* sp. nov. (described below). *Phymaturus payunae* and *P. zapatensis* are sexually dimorphic in dorsal patterns, whereas in *excelsus* there are no pattern differences between the sexes. Dominant colors in *excelsus* are black and white, whereas in *spectabilis* are brown and light brown, and ocelli in this latter species are much wider and more symmetrical.

Description of holotype: Male. SVL 82.5 mm. Head length 16.0 mm. Head width 14.2 mm. Head height (at parietal) 9.0 mm. Axilla-groin 41.9 mm (50.8% of SVL). Tail length (complete, not regenerated) 82.8 mm (1.00 times SVL). Trunk width: 35.6 mm (43.1% of SVL). Twenty one smooth dorsal head scales. Five, five, and four scale organs in each postrostral. Nasal scale not in contact with rostral (separated by one scale), bordered by eight scales. Canthal separated from nasal by two scales. Loreal region flat. Nine enlarged supralabial scales with the seventh upturned posteriorly, not contacting subocular (separated by one lorilabial). Seven enlarged infralabials. Auditory meatus oval; auricular scale absent, three to four projecting scales on anterior margin of auditory meatus (both sides). Eleven convex, juxtaposed, smooth temporals. Rostral undivided. Mental subpentagonal, in contact with four scales. Interparietal bordered by seven scales, parietals smaller. Frontal region without an azygous scale. Supraorbital semicircles incomplete posteriorly on both sides. No distinctly enlarged supraoculars. Nine distinctly imbricate superciliaries. Thirteen upper and twelve lower ciliaries (right side). Subocular elongate, longer than eye diameter, separated from supralabials

by a single row of lorilabials. Eleven lorilabials; tenth through eleventh contacting subocular. Preocular separated from lorilabial row by one scale. Chinshields forming a longitudinal row of seven or eight enlarged scales. Scales of throat round, flat, and juxtaposed. Seventy gulars between auditory meatus. Lateral nuchal folds well developed with granular scales over longitudinal fold that are smaller than dorsals. Antehumeral pocket well developed. Sixty-eight scales between auditory meatus and shoulder. In ventral view, gular fold absent, and posterior gular folds present with their anterior margins bordered by enlarged scales. Dorsal scales round, smooth, juxtaposed. Forty-three dorsal scales along midline of the trunk in a distance equivalent to head length. Scales around midbody 202. Mid-dorsal scales same size of those on flanks. Ventral scales larger than dorsals. Ventral scales between mental and preloacal pores 182. Eleven preloacal pores forming an interrupted row. Brachial and antibrachial scales smooth with round posterior margins. Supracarpals round and smooth. Subdigital lamellae of fingers with five to three keels, in number I: 11; II: 17; III: 24; IV: 25; V: 17. Claws moderately long. Supradigital lamellae convex and imbricate. Infracarpals and infratarsals trifid with round margins. Supracarpals and supratarsals smooth with round posterior margins. Subdigital lamellae of toes with three to five keels: I: 12; II: 19; III: 24; IV: 29; V: 19.

Variation: Based on 8 adult specimens (4 females and 4 males). SVL 77.0-89.7 mm (\bar{x} = 85.9; SD = 4.2). Head length 0.17-0.19% (\bar{x} = 0.18; SD = 0.01) of SVL. Tail length 1.0-1.07 (\bar{x} = 1.02; SD = 0.03) times SVL. Scales around midbody 178-223 (\bar{x} = 201.9; SD = 14.0). Dorsal head scales 17-22 (\bar{x} = 20.13; SD = 1.55). Ventrals 156-182 (\bar{x} = 168.25; SD = 8.4). Preloacal pores in males 9-11 (\bar{x} = 10; SD = 1.0). Scales surrounding interparietal 6-8 (\bar{x} = 7.0; SD = 0.8). Scales of neck along longitudinal fold from posterior border of auditory meatus to shoulder 62-92 (\bar{x} = 71.1; SD = 10.4). Gulars 60-88 (\bar{x} = 71.5; SD = 8.9). Scales between rostral and frontal 7-9 (\bar{x} = 8.4; SD = 0.7). Subdigital lamellae of fourth toe 26-28 (\bar{x} = 27.0; SD = 0.6).

Color of holotype in alcohol (Figure 1C and D): Dorsal background black on trunk, shoulder, neck, and head. A paired series of eight lateral white or cream ocelli are conspicuous from the occiput to the thighs. Between these two rows of ocelli are irregularly located small light-cream spots. Dorsum of limbs and tail variegated. Ventral coloration light gray to white, immaculate exhibiting small spots on the throat.

Color in life: see Figure 3. Dorsal background of trunk, head and limbs black, with light brown ocelli over the dorsum. A reticulate pattern in black and light brown over the head, limbs and dorsal surface of tail.

Etymology: *Phymaturus excelsus* is Latin for "distinguished," which describes the peculiar and distinct pattern exhibited by these lizards.

Distribution (Figure 5): *Phymaturus excelsus* is known only from its type locality, where it lives syntopically with *Phymaturus spurcus* a species described by Barbour (1921) from Estancia Huanuluan, 40 km to the north (straight line).

Phymaturus spectabilis sp. nov.

Holotype: MCN 1203. 28 km south of Ingeniero Jacobacci, Rio Negro province, Argentine (on Provincial Road 6). C. Abdala, F. Lobo, I. Martínez Oliver, and S. Quinteros, collectors.

Paratypes: MCN 1204-1215. Same data as holotype.

Diagnosis: *Phymaturus spectabilis* belongs to the *patagonicus* group (sensu Etheridge, 1995) because it has flat imbricate superciliaries, non-rugose dorsal scales of the tail, subocular unique usually not fragmented, and subocular-supralabials separation given for one row of scales. It is distinguishable of all other species of the genus by its unusual dorsal pattern (Figures 2 and 4). Phenetically the species more close to *P. spectabilis* is *P. excelsus*. The last one exhibit a general dorsal pattern black with smaller and more ocelli than *spectabilis* (7-8 among shoulder and the level of thighs versus 5-6) and several markings irregularly distributed on its vertebral field between the series of dorsal ocelli.

Description of holotype: Female. SVL 95.8 mm. Head length 16.6 mm. Head width 15.1 mm. Head height (at parietal) 8.6 mm. Axilla-groin 53.2 mm (55.5% of SVL). Tail length (complete, not regenerated) 98.9 mm (1.03 times SVL). Body moderately wide, trunk width 42.8 mm (44.7% of SVL). Twenty-two smooth dorsal head scales. Two, two, and four scale organs in each postrostral. Nasal not in contact with rostral, bordered by nine scales. Canthal separated from nasal by two scales. Loreal region flat. Ten enlarged supralabial scales with seventh upturned posteriorly but not contacting subocular. Nine enlarged infralabials. Auditory meatus oval; auricular scale absent, five projecting scales on

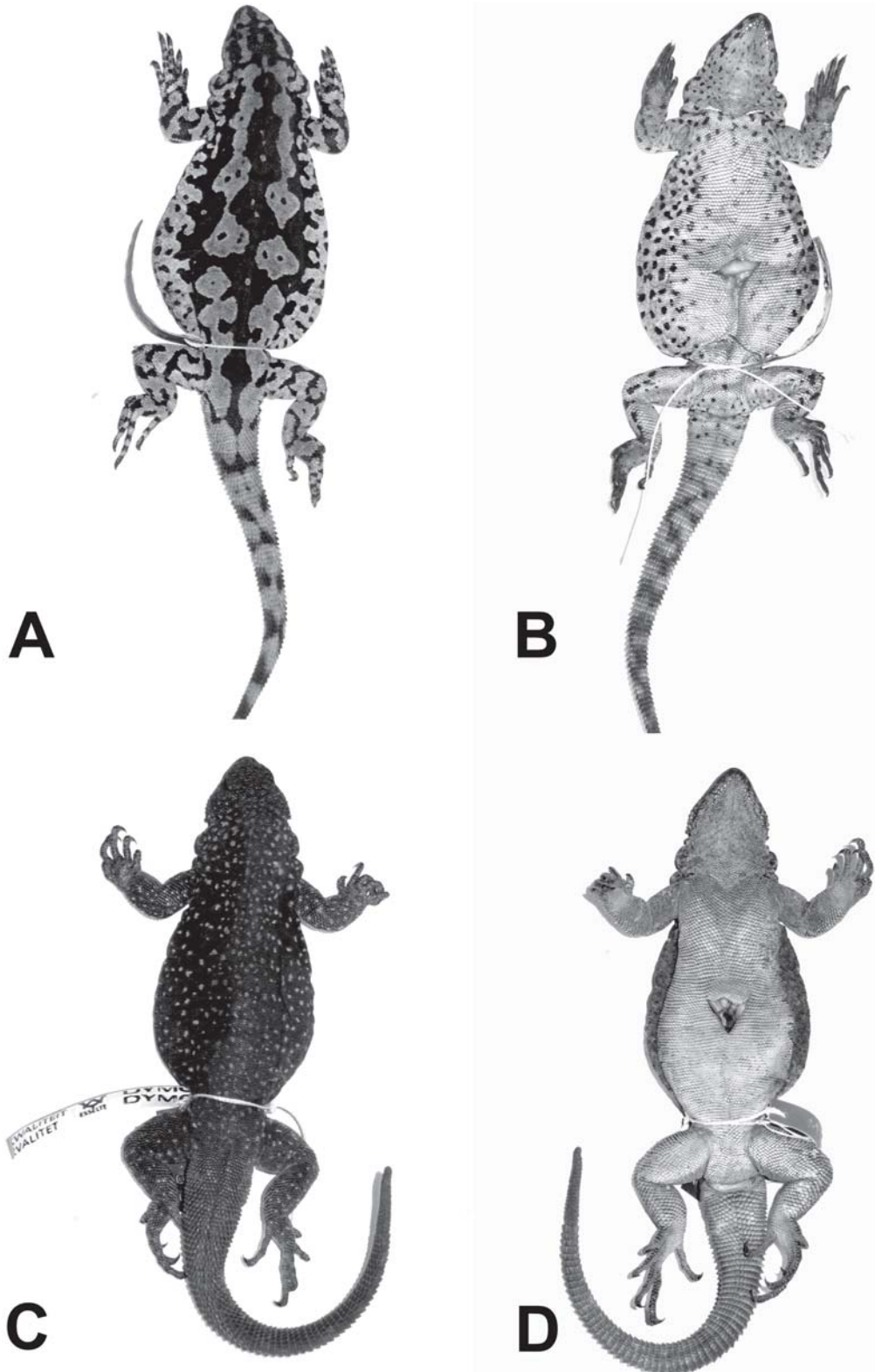


FIGURE 2. (A) Dorsal view of the holotype of *Phymaturus spectabilis* sp. nov. (B) Ventral view of the same specimen. Snout-vent length = 95.8 mm. (C) Dorsal view of the holotype of *Phymaturus tenebrosus* sp. nov. (D) Ventral view of the same specimen. Snout-vent length = 87.2 mm.

anterior margin of auditory meatus. Eleven smooth, convex, juxtaposed temporals. Rostral undivided. Mental subpentagonal, in contact with four scales. Interparietal bordered by six scales. Frontal region without an azygous scale. Supraorbital semicircles incomplete posteriorly on both sides. No distinctly enlarged

supraoculars. Seven imbricate flat superciliaries. Fifteenth upper ciliaries (right side). Subocular fragmented into two scales, separated from supralabials by one row of lorilabials. Eleven lorilabials, the tenth and eleventh contacting suboculars. Preocular separated from lorilabial row by one scale. Chinshields not en-



***Phymaturus spurcus* Barbour, 1921**



***Phymaturus excelsus* sp. nov.**

FIGURE 3. Live specimens of *Phymaturus* inhabiting western Rio Negro province. *Phymaturus spurcus* (MCN 1249 male, SVL = 8,5 mm); *Phymaturus excelsus* sp. nov. (MCN 1386 female, SVL = 90.0).

larged. Scales of throat round, flat, and juxtaposed. Sixty-nine gulars between auditory meatus. Lateral nuchal folds well developed, with granular scales over longitudinal fold that are smaller than dorsals. Antehumeral pocket well developed. Eighty-four scales between auditory meatus and shoulder. In ventral view

gular fold not well developed and posterior gular folds present with enlarged scales on their anterior margins. Dorsal scales round, smooth, juxtaposed. Forty-one dorsal scales along midline of the trunk in a distance equivalent to head length. Scales around midbody 224. Middorsal scales not enlarged in comparison to those



***Phymaturus spectabilis* sp. nov.**



***Phymaturus tenebrosus* sp. nov.**

FIGURE 4. Live specimens of *Phymaturus* from western Rio Negro province. *Phymaturus spectabilis* sp. nov. (MCN 1203 female holotype, SVL = 95.8 mm); *Phymaturus tenebrosus* sp. nov. (MCN 1271 male holotype, SVL = 87.2).

along flanks. Ventral scales larger than dorsals. Ventral scales between mental and the posterior bordering of the cloaca 169. No preloacal pores. Brachial and antebrachial scales smooth with round posterior margins. Supracarpals laminar, round, smooth. Subdigital lamellae of fingers with 3-5 keels (more conspicuous in proximal lamellae). Number of subdigital lamellae of fingers I: 12; II: 17; III: 24; IV: 25; V: 17. Claws moderately long. Supradigital lamellae convex, imbricate. Infracarpals and infratarsals with round margins and two to three obtuse keels. Supracarpals and supratarsals smooth, with round posterior margins. Subdigital lamellae of toes I: 13; II: 19; III: 23; IV: 29; V: 21.

Variation: Based on 7 adult specimens (5 females and 2 males). SVL 86.8-97.5 mm ($\bar{x} = 90.6$; SD = 4.3). Head length 0.16-0.18% ($\bar{x} = 0.17$; SD = 0.01) of SVL. Tail length 1.00-1.15 ($\bar{x} = 1.07$; SD = 0.06) times SVL. Scales around midbody 191-224 ($\bar{x} = 206.6$; SD = 10.3). Dorsal head scales 20-22 ($\bar{x} = 21.4$; SD = 0.8). Ventrals 145-178 ($\bar{x} = 164.8$; SD = 10.4). Nine preloacal pores in both males. One female with two preloacal pores. Scales surrounding interparietal 6-8 ($\bar{x} = 6.7$; SD = 0.8). Scales of neck along longitudinal fold from posterior border of auditory meatus to shoulder 70-87 ($\bar{x} = 78.0$; SD = 5.8). Gulars 61-91 ($\bar{x} = 78.4$; SD = 10.5). Scales between rostral and frontal 8-11 ($\bar{x} = 9.4$; SD = 0.9). Dorsal pattern of white ocelli numbering 7-8 between shoulder to the level of thighs, otherwise light brown over a black background in all but two adult specimens that lack ocelli, yet retain the general brown pattern. Five juveniles also with the same ocellated pattern.

Color of holotype in alcohol (Figure 2A and B): Dorsal background predominantly brown and black, six white and brown ocelli delimited in black and exhibiting one to two small black spots in the middle of each ocellation. Dorsal pattern of tail variegated. Beyond shoulders ocelli are fused reaching the parietal region of head. Central region of head black flanked by a pair of brown bands that reach the nasal region anteriorly. Ventral surfaces light gray, lateral margins of abdomen and chest with small black diffuse spots, throat with few very small spots, more conspicuous under jaws. This light gray coloration becomes light brown gradually along the flanks. Ventral surface of tail is light brown variegated with dark brown.

Color in life: See Figure 4. Similar pattern to that described for *excelsus*, with the light brown fields widely

extended (ocelli over dorsum and pattern of head, limbs and dorsal surface tailand).

Etymology: The epithet *spectabilis* is Latin and means "notable, showy" in reference to the distinct pattern of dorsal ocellations in this new species.

Distribution (Figure 5): Only known from the type locality, 28 km south of Ingeniero Jacobacci, Rio Negro, Argentina.

Phymaturus tenebrosus sp. nov.

Holotype: MCN 1271. 20 km south of Cerro Alto, National Road N° 40, Rio Negro, Argentina. C. Abdala, F. Lobo, I. Martínez Oliver, and S. Quinteros, collectors.

Paratypes: MCN 1264-1270, 1272-73. Same data as holotype.

Diagnosis: *Phymaturus tenebrosus* belongs to the *patagonicus* group (sensu Etheridge, 1995) because it has flat imbricate superciliaries, non-rugose dorsal scales on tail, subocular usually not fragmented, and subocular-supralabials separated by one scale row. The new species is distinguishable from all other species of the genus by its dorsal pattern: black in most specimens, some with very fine, sparse white spots (e.g., holotype). This melanism is dark brown in some specimens. The morphologically most similar species to *P. tenebrosus* are *P. zapalensis* and the recently described *P. calcogaster*, from which this new species can be readily distinguished. *Phymaturus zapalensis* has a more dense pattern of dorsal spots and very often a pattern of reticulation/occellation and obvious sexual dimorphism (females with variegated pattern) and *P. calcogaster*, which was described solely from the male holotype (Scolaro & Cei, 2003), which has a peculiar pattern not seen in *P. tenebrosus*: dorsum with larger and homogeneous white spots arranged in trasverse rows, a subocular fragmented into five scales (*P. tenebrosus* usually lacks subocular fragmentation), and the throat of *P. calcogaster* is variegated.

Description of holotype—Male. SVL 87.2 mm. Head length 16.2 mm. Head width 15.5 mm. Head height (at parietal) 9.2 mm. Axilla-groin 46.5 mm (53.3% of Snout-vent length). Tail length (complete, not regenerated) 81.1 mm (0.93 times SVL). Body moderately wide, trunk width: 33.3 mm (0.38% of SVL). Twenty-two

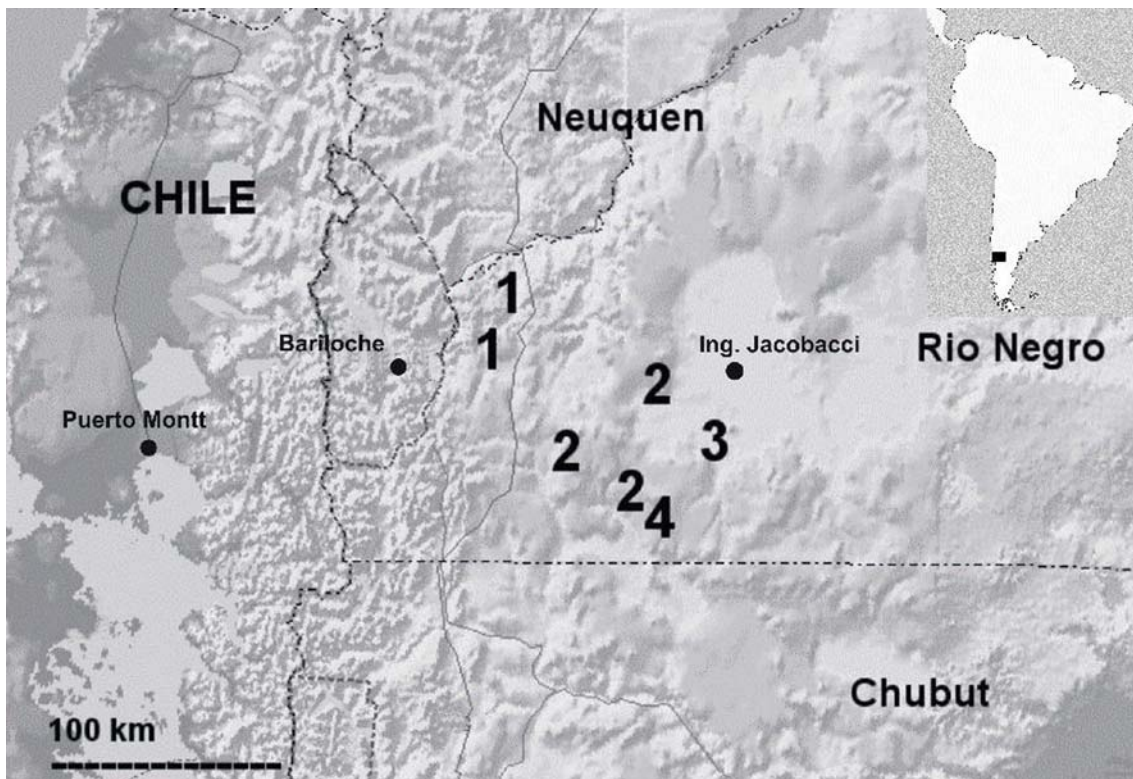


FIGURE 5. Map of the western region of Rio Negro province of Argentina showing known localities for the new species belonging to the *patagonicus* group described here plus *Phymaturus spurcus*. 1 *Phymaturus tenebrosus* sp. nov. (between Bariloche and Pilcaniyeu, 20 km south of Cerro Alto); 2 *Phymaturus spurcus* (Estancia Huanuluan, Alto El Escorial south of Las Bayas and Ojo de Agua); 3 *Phymaturus spectabilis* sp. nov. (28 km south of Ing. Jacobacci on Provincial Road 6); 4 *Phymaturus excelsus* sp. nov. (Ojo de Agua, in syntopy with *Phymaturus spurcus*).

smooth dorsal head scales. Seven, four, and seven scale organs in each postrostral. Nasal bordered by eight scales, not in contact with rostral. Canthal separated from nasal by two scales. Loreal region flat. Eight enlarged supralabial scales with seventh upturned posteriorly but not contacting subocular. Seven enlarged infralabials. Auditory meatus oval with five projecting scales on the anterior margin. Auricular scale absent. Nine convex, juxtaposed temporals. Rostral undivided. Mental subpentagonal, in contact with four scales. Interparietal bordered by seven scales. Frontal region without an azygous scale. Supraorbital semicircles incomplete posteriorly. No distinctly enlarged supraoculars. Nine imbricate flat superciliaries. Subocular unfragmented, separated from supralabials by one row of lorilabials. Nine lorilabials, the eight to ninth contacting subocular. Preocular separated from lorilabial row by two scales. Scales of throat round, flat, and juxtaposed. Eighty-one gulars between auditory meata. Lateral nuchal folds well developed, with granular scales over longitudinal fold. Antehumeral

pocket well developed. Eighty-one scales between auditory meatus and shoulder. In ventral view, gular fold not well developed and posterior gular folds present with their anterior margins with enlarged scales on their borders. Dorsal scales round, smooth, juxtaposed. Thirty-nine dorsal scales along midline of the trunk in a distance equivalent to head length. Scales around midbody: 202. Mid-dorsal scales not enlarged in comparison to those on flanks. Ventral scales larger than dorsals. Ventral scales between mental and preloacal pores: 170. Nine preloacal pores. Brachial and antebrachial scales smooth with rounded posterior margins. Supracarpals laminar, round, smooth. Subdigital lamellae of fingers with 3-5 keels (more conspicuous in proximal lamellae). Number of subdigital lamellae of fingers I: 11; II: 16; III: 22; IV: 24; V: 15. Claws moderately long. Supradigital lamellae convex, imbricate. Infracarpals and infratarsals with round margins and 2-3 obtuse keels. Supracarpals and supratarsals smooth, with round posterior margins. Subdigital lamellae of toes I: 13; II: 17; III: 18; IV: 23; V: 21.

Variation: Based on 16 adult specimens (12 females and 4 males from both known localities). SVL 85.0-107.5 mm ($x = 94.8$; $SD = 6.4$). Head length 0.15-0.19% ($x = 0.17$; $SD = 0.01$) of SVL. Tail length 1.00-1.41 ($x = 1.21$; $SD = 0.18$) times SVL. Scales around midbody 171-236 ($x = 199.2$; $SD = 20.2$). Dorsal head scales 16-25 ($x = 20.2$; $SD = 2.18$). Ventrals 149-185 ($x = 171.4$; $SD = 14.15$). Precloacal pores in males 7-9 ($x = 8.5$; $SD = 1.0$). Scales surrounding interparietal 5-8 ($x = 6.9$; $SD = 0.9$). Scales of neck along longitudinal fold from posterior border of auditory meatus to shoulder 58-88 ($x = 70.9$; $SD = 8.3$). Gulars 65-100 ($x = 77.8$; $SD = 9.3$). Scales between rostral and frontal 6-11 ($x = 8.7$; $SD = 1.3$). Dorsal and flank pattern in most specimens black, in some specimens with small and sparsely distributed white spots. Some specimens brown morph with conspicuous black spots on flanks (similar to that exhibited by specimens of *P. zapalensis*). Not all specimens have strong ventral coloration (orange in brown individuals, yet mustard or dark gray in black specimens), suggesting that this coloration may be related to season or physiological conditions.

Color of holotype in alcohol (Figure 2C and D): Dorsal background with black spots and small white markings that are smaller and more densely distributed middorsally. This pattern extends over the head and dorsal surfaces of the limbs. The tail is patternless. General coloration of ventral surfaces (throat, limbs, and tail) gray, with slight yellow color in the posterior region of abdomen continuous over the cloaca and thighs.

Color in life: See Figure 4. Dorsum black scattered with small white spots. Margins of ventral region gray and central areas of chest, abdomen, ventral surfaces of thighs and cloaca mustard. Females can exhibit their bellies light gray to orange.

Etymology: The epithet *tenebrosus* Latin word that means “dark, gloomy” in reference to the dark dorsal coloration of this new species.

Distribution (Figure 5): This new species is known to be found between Bariloche and Pilcaniyeu northward to 20 km south of Cerro Alto (National Road N° 40), Rio Negro, Argentina.

II – Other terminal taxa included in the analysis

Because its distribution (too far from type locality) and some meristic characters we analyzed as ter-

restrial taxon: *Phymaturus* cf. *punae* (Road to Laguna Brava, La Rioja province). Around 40% of specimens of cf. *punae* examined have their rostral scale divided like *Phymaturus punae* (San Guillermo, San Juan), number of scales around midbody are fewer in *Phymaturus punae* ($x = 179.6$; $SD = 10.9$; 168.0-196) than in *Phymaturus* cf. *punae* ($x = 205.8$; $SD = 13.7$; 188.0-234.0).

Phymaturus cf. *antofagastensis* (SC), from Cuesta de Randolpho and Sierra de Calalaste: according to Pereyra (1991) the type locality of *Phymaturus antofagastensis* is Los Nacimientos near Paso San Francisco. Both terminals (Paso San Francisco and Randolpho-Calalaste) have enlarged scales in the central area of chest, as described in the original description (Pereyra, 1985). Specimens from Cuesta de Randolpho and Sierra de Calalaste exhibit an undivided rostral and a homogeneous dense “spray” dorsal pattern of coloration (Figure 12C), whereas most specimens from Paso San Francisco have a divided rostral scale and an “aggregate dorsal” pattern of coloration (Figure 12D).

Phymaturus cf. *palluma* (CH): (Chillán, Chile): lizards from this population, as in *P. cf. dorsimaculatus* (Copahue, Neuquén province), have ringed tails but they lack the reticulate pattern typical of other *Phymaturus*. Females from this locality have immaculate throats, whereas all other *P. cf. palluma* have spotted or black throats. Specimens from this population also have lorilabials occasionally in contact with the subocular, which never occurs in other *P. cf. palluma*, and members of this population have fewer scales in contact with the nasal than in all other populations.

Phymaturus cf. *palluma* (EP): (El Planchón and San Pedro, Chile): females can exhibit precloacal pores (not found in other *P. cf. palluma*), temporal scales are protruded conical shaped not as in *dorsimaculatus* and *P. cf. palluma* (CH), anterior gular fold present (absent in *P. cf. palluma* of Payunia), the lorilabials never contact the subocular (as in *P. cf. palluma* of Chillán), there are no enlarged scales on the margins of posterior gular fold as in *P. cf. palluma* (ME). Specimens from El Planchón are quite similar of those from Maule (MVZ 232506-07).

Phymaturus cf. *palluma* (ME): differs from *P. cf. palluma* (PA) because adult specimens of the former have partially or completely black heads and neck foldings, sexual dimorphism in dorsal pattern, but never a divided rostral (which is common in *P. cf. palluma* PA). This population differs also in similar way from *P. cf. palluma* (LB) because this last population lacks sexual dimorphism, and temporal scales in adult specimens are strongly projected (spinose).

Phymaturus cf. *palluma* (LB) (Laguna Blanca): is smaller than *P. verdugo*: 86-110 mm, whereas in *P. verdugo*: 106-120 mm SVL. From *P. dorsimaculatus* sp. nov. because do not exhibit the same pattern of black transversal bars over their neck and shoulders and ringed pattern on tails (this last character discriminate it also from *P. cf. palluma* CH). Does not exhibit sexual dimorphism in pattern like *P. cf. palluma* (ME) (with both states aggregate and dense “spray” Figure 12). Is allopatrically distributed very far from the northern group of species (*P. punae*, *P. cf. punae* LR, *P. antofagastensis*, and *P. cf. antofagastensis* SC) and no individuals have a divided rostral.

Phymaturus cf. *palluma* (PA) (Payunia): these lizards are morphologically similar to those here called “Mendoza” but the adult specimens lack the distinct black head and neck present in other forms of “*palluma*”. This character discriminates this form from other members of the *palluma* group. It shares with northern species of the group the a divided rostral in many specimens.

Phymaturus cf. *patagonicus* (EC) (San Antonio del Cuy, Rio Negro): *Phymaturus* with a gray background coloration with white spots (like in *P. patagonicus* from Dolavon, Chubut province), spots are smaller and usually these lizards have a dark gray to black dorsolateral band. This dark band is also present in individuals of *P. tenebrosus* and most females of *P. zapalensis* (Figure 12A), but *P. patagonicus* (EC) lacks black and brown morphs and has a smaller body size.

2) Phylogenetic analysis of *Phymaturus* comparison of four matrices

The analysis applying the ANY INSTANCE coding method for binary polymorphic characters brought one most parsimonious tree of 522.48 steps (CI = 0.57; RI = 0.66) (Figure 6). This topology recovered *P. patagonicus* as the most basal species of the genus, the *patagonicus* group is paraphyletic, *P. payunae* is the sister taxon of a subclade formed by *P. somuncurensis*, *P. spectabilis*, and *P. spurcus*, this group is related to another formed by *P. indistinctus* as the most basal species, *P. cf. patagonicus* (EC), and *P. nevadoi* as sister taxon to the pair formed by *P. zapalensis* and *P. tenebrosus*. *Phymaturus excelsus* is related to the *palluma* group for which *P. dorsimaculatus* is the most basal species. The topology of the *palluma* group in this tree is unbalanced, with species subsequently related as follows: *P. cf. palluma* (CH), *P. cf. palluma* (LB), *P. cf. palluma* (ME), *P. cf. palluma* (EP), *P. cf. palluma* (PA), *P. punae*, *P. punae* (LR), *P. cf. antofagastensis* (SC), *P. antofagastensis*, and *P. mallimaccii*. Jackknifing recovered four nodes with

good support in the consensus tree: 52% for *P. tenebrosus*-*P. zapalensis*, 90% for *P. spectabilis*-*P. spurcus*, 94% for the *palluma* group, and 61% for the *palluma* group except *P. dorsimaculatus* and *P. cf. palluma* (CH).

Runs made applying the FREQUENCY BINS coding method for binary polymorphic characters brought one shortest tree of 978.63 steps (CI = 0.49; RI = 0.58) (Figure 6). In this analysis the *patagonicus* group is monophyletic with *P. indistinctus* as the most basal species, *P. excelsus* is the sister taxon to all remaining species, the subsequent node has *P. spurcus* as sister taxon to all the rest of the group. *P. spectabilis*, *P. tenebrosus*, and *P. nevadoi* are branching up the most terminal subclade formed by two groups, one formed by *P. cf. patagonicus* (EC) and *P. patagonicus*, and the other by *P. somuncurensis* sister taxon of the pair *P. payunae*-*P. zapalensis*. The *palluma* group is monophyletic with *P. dorsimaculatus* and *P. cf. palluma* (CH) as the most basal species of the group, two main subclades are formed in this hypothesis, one including *P. cf. palluma* (ME) sister taxon of the pair *P. cf. palluma* (PA)-*P. cf. palluma* (LB), and the other group including all northern species plus *P. cf. palluma* (EP). *Phymaturus* cf. *punae* (LR) is sister taxon of a clade formed by *P. cf. antofagastensis* (SC), *P. punae*, and *P. antofagastensis*, whereas *P. mallimaccii* is related to *P. cf. palluma* (EP). Jackknife values for this analysis include 99% for the *palluma* group, 53% all species of that group without *P. dorsimaculatus*, 53% for *P. cf. palluma* (PA)-*P. cf. palluma* (LB), and 52% for a node formed by *P. punae*, *P. antofagastensis*, and *P. cf. antofagastensis* (SC).

Phylogenetic analysis applying the SCALED coding method for binary polymorphic characters yielded one most parsimonious tree of 571.06 steps (CI = 0.56; RI = 0.65) (Figure 7). In this analysis the *patagonicus* group is monophyletic, formed by two main groups, one including *P. excelsus*, *P. indistinctus*, and *P. patagonicus*, and the other with *P. payunae* as the basal species, with *P. spectabilis*-*P. spurcus* as sister taxon of a subclade formed by *P. somuncurensis*, *P. cf. patagonicus* (EC), *P. nevadoi*, *P. tenebrosus*, and *P. zapalensis*. In the *palluma* group, *P. cf. palluma* (PA), and *P. cf. palluma* (LB) are sister taxa and basal-most subclade in the group. *Phymaturus dorsimaculatus* and *P. cf. palluma* (CH) are sister taxa, related to a central and northern clade that includes *P. mallimaccii* related to the pair *P. antofagastensis*-*P. cf. antofagastensis* (SC), and *P. cf. palluma* (EP) related to a group formed by *P. cf. palluma* (ME), *P. punae*, and *P. cf. punae* (LR). Jackknifing analysis of the consensus tree found support for six nodes, 64% for *P. spurcus*-*P. spectabilis*, 99% for the *palluma* group, 57% for all species of the *palluma* group except *P. dorsimaculatus* (not

recovered in the shortest tree), 86% for *P. cf. palluma* (PA)-*P. cf. palluma* (LB), 80% for the northern clade: *P. mallimacii*, *P. punae* (LR), *P. punae*, *P. antofagastensis*, and *P. cf. antofagastensis* (SC); *P. cf. palluma* (EP) and *P. cf. palluma* (ME) are not in this subclade in this consensus tree, 54% for *P. punae*, *P. antofagastensis*, and *P. cf. antofagastensis* (SC) (these two last taxa are related to *P. mallimacii* in the shortest tree, Figure 7).

The analysis applying the MISSING coding method for binary polymorphic characters recovered two equally parsimonious trees of 489.59 steps (CI = 0.60; RI = 0.68). In Figure 7 we show one of these trees. In this analysis the *patagonicus* group is not monophyletic, common to these trees are the pair formed by *tenebrosus* and *zapalensis*, and the subclade including *P. somuncurensis* sister taxon of *P. spurcus*-*P. spectabilis*. *Phymaturus dorsimaculatus* and *P. cf. palluma* (CH) are the basal subgroup in the *palluma* group, *P. cf. palluma* (LB) is the most basal species of a big clade formed by all remaining species. *Phymaturus cf. palluma* (PA) and *P. cf. palluma* (ME) are related to a group including *cf. palluma* (EP) and all northern species; *P. cf. punae* (LR) is basal to a couple of sister taxa, one including *P. punae* and *P. cf. antofagastensis* (SC) and the other *mallimacii* and *antofagastensis*. For this analysis Jackknifing reports eight nodes supported over 50% of frequency. The *palluma* group at 99%, *P. cf. palluma* (EP) plus all northern species: *P. punae*, *P. punae* (LR), *P. mallimacii*, *P. antofagastensis*, and *P. cf. antofagastensis* at 85%, all northern species at 83%, *P. cf. palluma* (LB)-*P. cf. palluma* (PA) at 81% (not found in both trees); the subclade formed by *P. punae* and *P. antofagastensis* (SC) at 79%, *P. spurcus*-*P. spectabilis* at 68%, all northern species without *P. punae* (LR) at 53% and a node not found in the two shortest trees formed by *P. antofagastensis*, *P. punae*, and *P. cf. antofagastensis* (SC) at 74%.

Supported group common in all analysis (4) was the *palluma* group (94, and three 99%), *P. cf. palluma* (PA)-*P. cf. palluma* (LB) in three analysis (53, 81, 86%) (not supported in the any instance analysis). In three runs also is recovered the node *P. spurcus*-*P. spectabilis* (not in the frequency bins analysis; 52, 64, 68%). *Phymaturus punae* is related to *antofagastensis* and *P. cf. antofagastensis* (SC) in three jackknife consensus trees (missing, scaled and frequency) (74, 54 and 52%). The northern subclade formed by *punae*, *punae* (LR), *P. mallimacii*, *P. antofagastensis*, and *P. cf. antofagastensis* (SC) have support in the missing and scaled analysis (80-83%). *Phymaturus dorsimaculatus* is the most basal species in two of the jackknife consensus trees (frequency and scaled analysis) (53-57%).

Consensus tree and common apomorphies

In this study there are competing hypothesis that are shown in the four original topologies (Figures 6 and 7). From these four original analysis we built a majority rule consensus tree shown in Figure 8, because a majority rule tree can choose among hypothesis incongruent among the original runs observations on those contradictory relationships are given below.

Phymaturus somuncurensis is sister taxon of *spurcus* – *spectabilis* (Node 5) in the any instance and missing analysis, *somuncurensis* is related to the pair *payunae* – *zapalensis* in the frequency bins run while in the scaled analysis is basal to a group formed by other four species. *Phymaturus cf. patagonicus* (EC) is sister taxon of the group formed by *nevadoi* and the pair formed by *zapalensis* and *tenebrosus* (Node 6) in any instance and scaled runs, *cf. patagonicus* (EC) is sister taxon of *patagonicus* in the frequency bins analysis. *Phymaturus dorsimaculatus* is sister taxon of *cf. palluma* (CH) (Node 3) in scaled and missing runs, in the frequency bins run *dorsimaculatus* is the basal species of the *palluma* group not related to *cf. palluma* (CH). Northern species (Node 12) are present in any instance and missing runs. *Phymaturus mallimacii* is related to *antofagastensis* in the any instance and missing runs (Node 13); *mallimacii* is related to *antofagastensis* and *cf. antofagastensis* (SC) in the scaled analysis and to *cf. palluma* (EP) in the frequency bins run.

The *palluma* group (Node 1) is supported by the following common apomorphies (all runs) characters 5 (number of ventral scales), character 7 (number of gulars), character 11 (number of upper ciliars), character 13 (supralabial upturned), character 18 (preocular scale separation from lorilabial row) and character 26 (superciliary scales shape subcuadrangular not imbricated). The *patagonicus* group (Node 2) is not monophyletic in all runs and had no support as the *palluma* group, in those topologies where it is found monophyletic common apomorphies involves changes in characters 4 (number of dorsal scales in a head-length), 21 (males trunk length/snout vent length ratio), 28 (number of pterigoid teeth) 119 (lorilabials-subocular scale separation) and 149 (number of scleral ossicles). Evidence for the sister taxa relationship between *dorsimaculatus* and *cf. palluma* (CH) (Node 3) are changes on characters 10 (number of superciliaries) and 14 (subocular fragmentation, Figure 9). Character changes supporting Node 4 are related to characters 8 (number of scales in contact to interparietal), 13 (number of supralabial upturned), 16 (scales in contact to mental, Figure 9) and 130 (dorsal pattern of tails, Figure 10). Node 5 includes *somuncurensis*, *spectabilis* and *spurcus*,

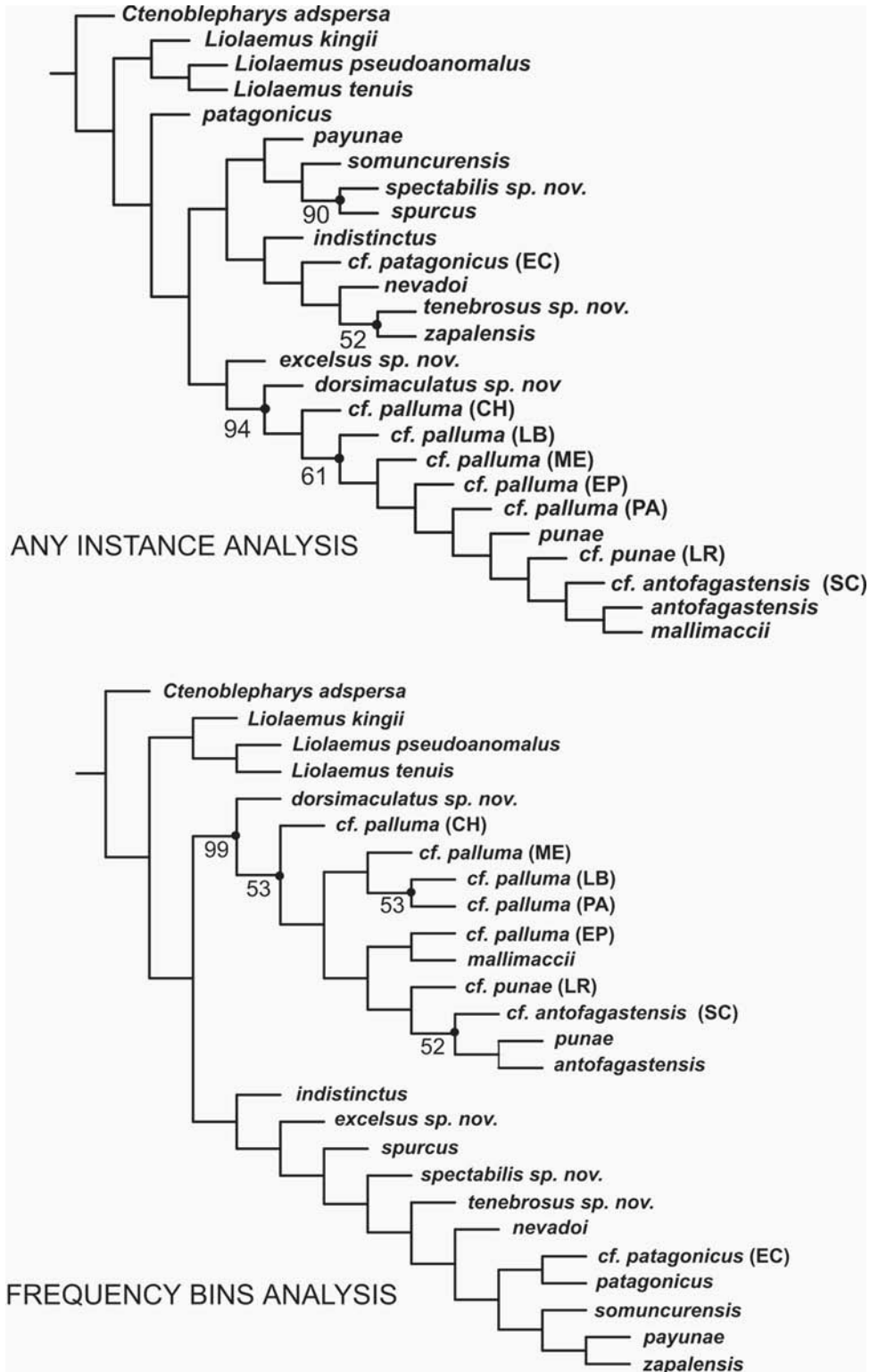


FIGURE 6. Two hypotheses of phylogenetic relationships among species of *Phymaturus* using two different methods for coding binary polymorphisms (any-instance and frequency-bins analysis). Values at some nodes refer to Jackknife support >50% from 1000 replications.

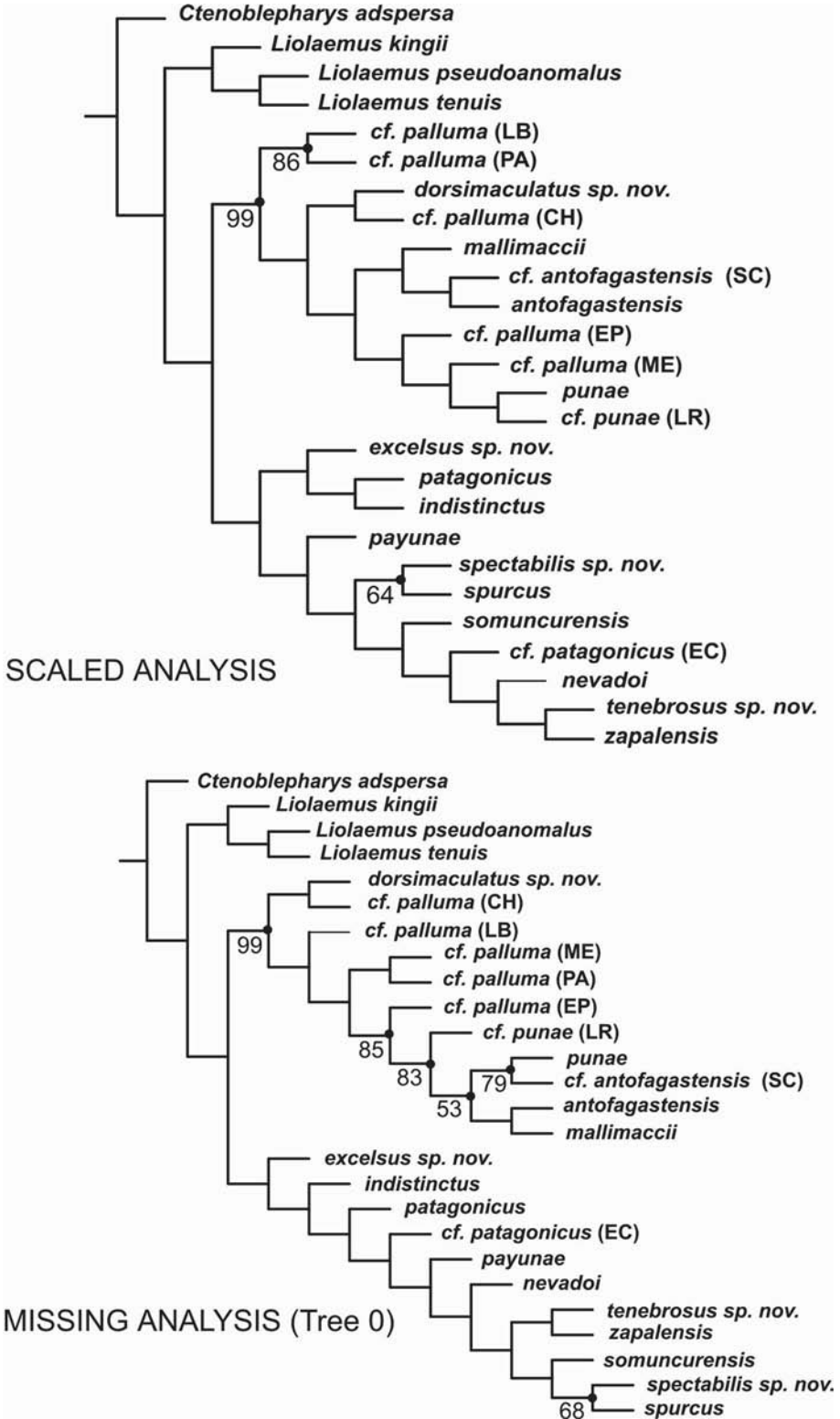


FIGURE 7. Two additional methods for coding binary polymorphic characters (scaled and missing analyses). An additional topology was recovered differing only in the relationships within the *patagonicus* group (see text for details). Values at some nodes refer to Jackknife support >50% from 1000 replications.

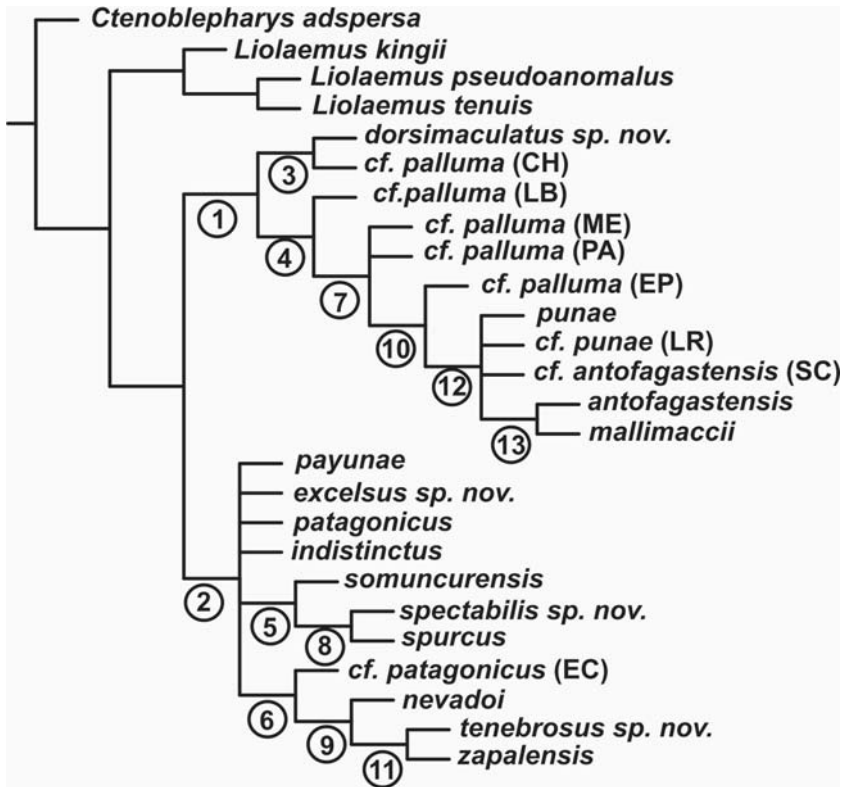


FIGURE 8. Majority-rule consensus tree of the four original runs. Numbered nodes are common to all topologies and their corresponding apomorphies are indicated in the text.

and changes are on characters 7 (number of gulars), 109 (male/female SVL ratio) and 151 (lacrimal foramina opening). Node 6 (within *patagonicus* group) is supported by changes on characters 6 (number of scales on the lateral wall of neck, between earing and shoulder) and 23 (males tibia length (SVL ratio)). Node 7 (within the *palluma* group) is supported by the following changes, characters 9 (number of infralabials), 17 (number of scale organs on posrostrals), 18 (number of scales separating preocular from lorilabial row), 19 (maximum SVL found), 109 (male/female SVL ratio) and 128 (throat of males pattern). Characters supporting the relationship between *spurcus* and *spectabilis* (Node 8) are 14 (subocular fragmentation, Figure 9), 19 (maximum SVL found) and 110 (males trunk length/SVL ratio). Node 9 exhibit changes on characters 10 (number of superciliaries), 13 (number of supralabial upturned), 15 (scales in contact to nasal) and 18 (number of scales separating preocular from the lorilabial row). *Phymaturus* cf. *palluma* (EP) is related to the northern subclade in Node 10: characters 0 (number of dorsal head scales), 7 (number of gulars), 8 (number of scales in contact with interparietal), 17 (number of

scale organs on posrostrals) and 18 (number of scales separating preocular from the lorilabial row). *Phymaturus tenebrosus* is sister taxon of *zapalensis* at Node 11, character 21 (males trunk length/SVL ratio). The northern Argentina subclade is supported by characters 6 (number of scales on the lateral wall of neck, between earing and shoulder) and 12 (number of scales between frontal and rostral). *Phymaturus antifagastensis* and *mallimaccii* are sister taxa at Node 13, characters 19 (maximum SVL found) and 110 (males trunk length/SVL ratio).

Search of additional topologies

Analyzing with the range method of TNT for continuous characters we had an unique shortest tree for three analysis (any instance, frequency bins. and scaled analysis) while running with the missing coding method for binary polymorphic characters we had two topologies. Continuous characters ranges were entered with three decimals, so length measures of trees are given with three decimals, this fact make less expectable reaching more than one topology for the same run. For this reason we wanted to know how many

other topologies are close to the shortest one for each analysis, and look if exist a tree or/and trees repeated among these four different analysis. We made a search looking for suboptimal trees up to one step longer having a total of 383 topologies (any instance-analysis: 57 trees, scaled-analysis: 199, frequency bins-analysis: 29 and missing-analysis: 98). In this analysis we got three topologies repeated in two of the four runs (tree 13 of any instance-analysis = tree 369 of the missing-analysis; tree 50 of any instance-analysis = tree 84 of the scaled-analysis and tree 177 of the scaled-analysis = tree 296 of the missing-analysis) and two trees were recovered in three of the four analysis: tree 18 of any instance-analysis = tree 82 of the scaled-analysis = tree 295 of the missing-analysis; and tree 54 of the any instance-analysis = tree 176 of the scaled-analysis = tree 294 of the missing-analysis. Trees 18 and 54 repeated in three of the four analysis differs between them in the arrangement of the *patagonicus* group. The *palluma* group in these trees show the same topology obtained in the missing-analysis, for the *patagonicus*

group recover the following topologies: (((((((((*tenebrosus zapalensis*) *nevadoi*) ((*spurus spectabilis*) *somuncurensis*)) *payunae*) cf. *patagonicus* EC) *patagonicus*) *indistinctus excelsus*); and the other differing only in the position of *payunae*, here as follows: (((*tenebrosus zapalensis*) *nevadoi*) (((*spectabilis spurcus*) *somuncurensis*) *payunae*)). Terminal arrangements of the *patagonicus* group are the same recovered in the majority rule consensus tree and in other topologies see Figures 6 to 8.

3) Observations on the ontogenetic shift of morphological characters

A sample of 15 juvenile *Phymaturus* cf. *palluma* (PA), presumably in their first range from 65.6-83.0 mm SVL allowed us to make observations on their dimorphic differentiation. Dissection of these specimens were dissected to determine sex for all but two individuals. SVL X = 75.2 (SD = 4.8; range = 69.3-80.5) for males, and X = 75.0 (SD = 4.8; range = 67.3-83.1) for females. All specimens have the same dorsal pattern as adults, three of five males have their abdomi-

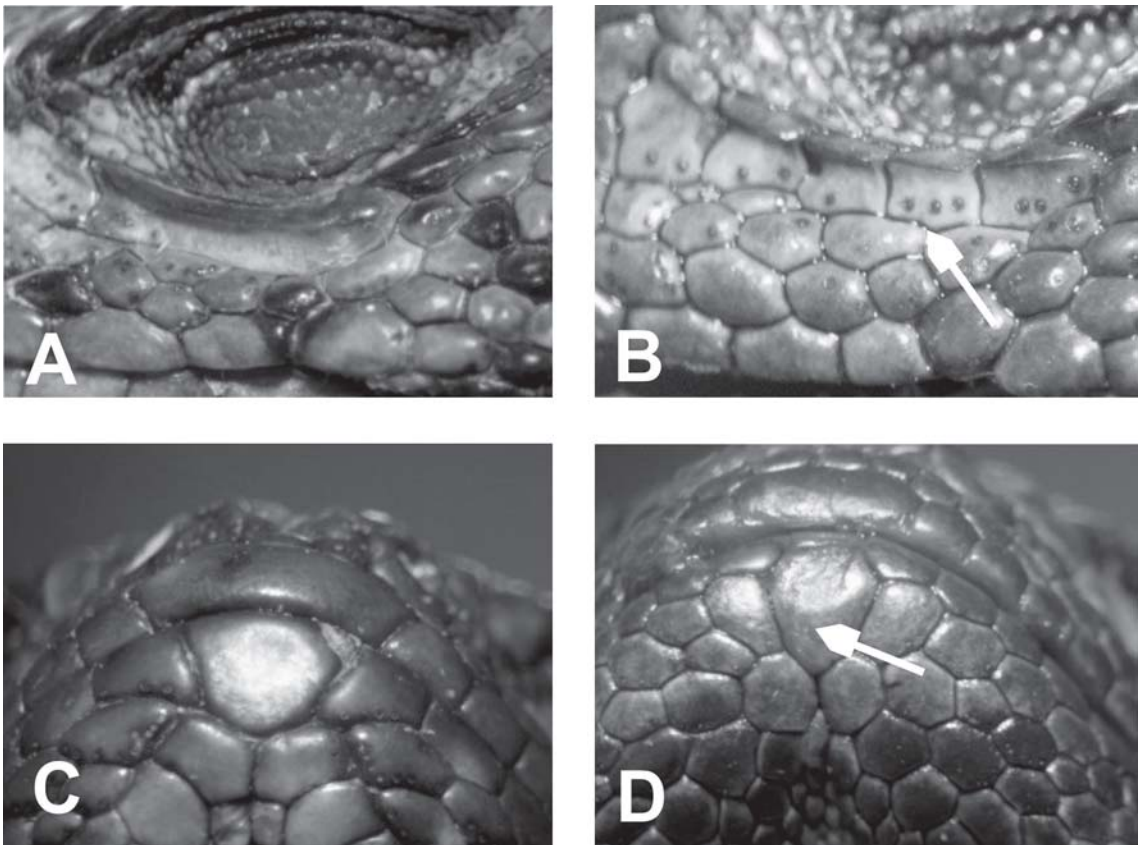


FIGURE 9. Character 60: (A) Subocular complete, not divided (*Phymaturus zapalensis*, MCN 1600); (B) Subocular fragmented, in this case into four scales (*Phymaturus spurcus*, MCN 1241); Character 62: (C) Mental in contact with four scales (*Phymaturus tenebrosus*, MCN 1271); (D) Mental in contact with six scales (*Phymaturus* cf. *palluma* ME, IBA 760-3). Images are at different scales.

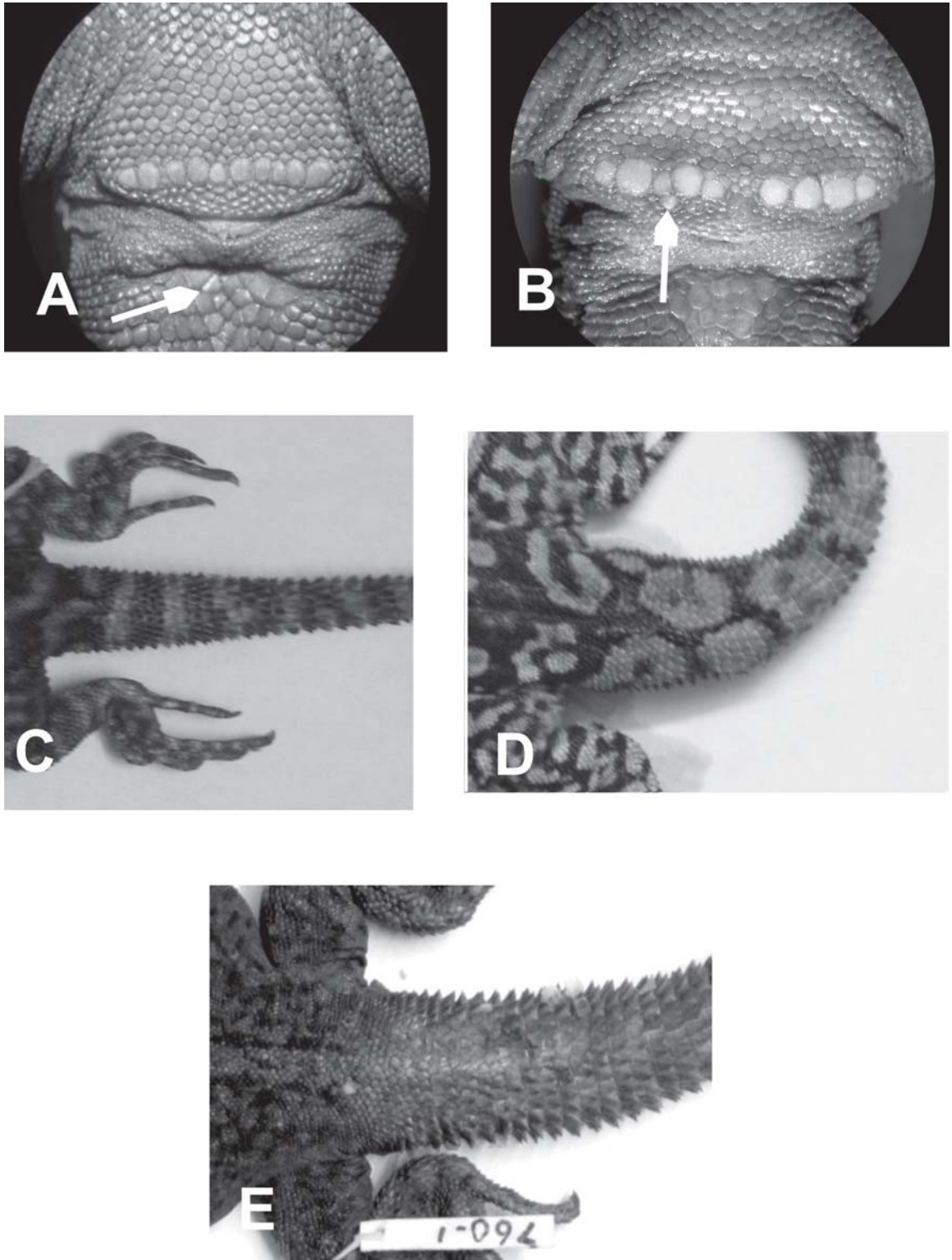


FIGURE 10. Characters 84 and 85: (A) Unique row of preloacal pores, supernumerary preloacal pores absent (*Phymaturus* cf. *palluma* ME, IBA 760-1), the arrow indicates enlarged scales in tail base typically present in males; (B) Divided row of preloacal pores, supernumerary pores present (one supernumerary indicated by an arrow) (*Phymaturus* cf. *palluma* EP, MNHN 2461); Character 90: dorsal tail patterns: (C) ringed (*Phymaturus dorsimaculatus*, MCN 1568); (D) variegated (*Phymaturus excelsus*, MCN 1582) and (E) absence of tail pattern (*Phymaturus* cf. *palluma* ME, IBA 760-1). Images are at different scales.

nal region variegated as do two of eight females. All male juveniles lack precloacal pores, but four of them (4/5) have a row of slightly modified scales suggesting the development of precloacal pores. All male juveniles have 2-3 enlarged scales on the base of the tail adjacent to the posterior margin of the cloacal aperture as can be seen in most adult males of the *palluma* group. This character is more obvious than the presence or absence of precloacal pores and be used to sex very early stages of neonate and new-born specimens without the need for dissections. Two individuals of undetermined sex were among the smallest examined: 66.1 and 65.6 mm SVL (SDSU 1955 and 1961, respectively), both lack enlarged scales on the base of the tail and no traces of precloacal pores.

Four embryos taken from two gravid dissected females of *P. dorsimaculatus* exhibit the following differences in comparison to adults of their species: more, smaller scales on the dorsum and flanks, counting dorsal scales in a head length (moving with the caliper a head length on the middle of the back) in these embryos are 46-60 (36-44 in adults), fewer scale organs on the postrostrals 2-3 in two embryos but not formed in the other two ($X = 2.20$; $SD = 0.45$) than in adults ($X = 3.4$; $SD = 1.27$); temporals are flat and forming a pavement in embryos, whereas in adults these become more prominent and, in some specimens, conical; dorsal scales of the tail are smooth, whereas in adults these are rugose (as for members of the *palluma* group). All other characters of squamation and those referred to dorsal, ventral, and tail pattern are the same as the adults. Almost the same differences were observed between juvenile and adult *P. cf. palluma* (CH): more, smaller scales in the dorsum of body (39-42 in juvenile versus 32 in both adult females), temporals flat in juveniles vs. conical to spiny in adults, and dorsal scales of the tail are smooth in juveniles, whereas these are conspicuously rugose in adults. There was no distinction in the number of scale organs on the postrostrals as was detected between embryos and adults of *P. dorsimaculatus*. Later conditions of characters (exhibited by adults) described here having change from embryo-juvenile-adult specimens like the number of dorsal body scales (in a head length), shape of the temporals, and dorsal tail rugosity are present only in species belonging to the *palluma* group. In species of the "patagonicus" group, those earlier stages (greater number of dorsal scales, temporals flat, tail scales smooth) for all *Phymaturus* species are present also in adults, and because this condition is the same in adults of *Ctenoblepharys* and *Liolaemus*, we assume that terminal additions on the

ontogeny of those characters happened in the common ancestor of the *palluma* group.

4) Biogeography of *Phymaturus*

Taking into account endemism areas described for this southern region of South America (Flores & Roig-Juñent, 2001; Roig-Juñent & Flores, 2001; Roig-Juñent *et al.*, 2002) terminals of our analysis are distributed as it follows: *patagonicus*, *somuncurensis* and cf. *patagonicus* (EC) in Monte Austral (MAUS); *indistinctus*, *spectabilis*, *spurcus* and *excelsus* in Patagonia Central (PCEN); *tenebrosus* in two areas Patagonia Central y Patagonia Occidental (POCC); cf. *palluma* (LB) cf. *palluma* (PA), *nevadoi*, *payunae* and *zapalensis* in Payunia (PAY); cf. *palluma* (ME), cf. *palluma* (EP) and cf. *palluma* (CH) in Cordillera Andina and Valle Central (CAVC); *dorsimaculatus* in Patagonia Occidental; *punae*, *mallimacchii*, cf. *punae* (LR), *antofagastensis* and cf. *antofagastensis* (SC) should be assigned to areas called Prepuna (PREP) and Puna (PUNA) for the last two species. Curiously this subclade of northern populations of *Phymaturus* is distributed exclusively in the transitional Puna subdistrict delimited by Martínez Carretero (1995) that occupies western region of Catamarca, La Rioja and northwestern San Juan. Splitting this group in two areas in any further biogeographic analysis (like Fitch optimization, DIVA, etc.) can carry to make extra assumptions of historical events (vicariance, extinctions or/and dispersals). Delimitation of areas among members of the northern subclade of the *palluma* group between Prepuna and Puna it is not enough explicit and assigning one or other area to these taxa becomes problematic. In cladistic biogeography comparing original cladograms of taxa with general area cladograms is a way to assess how our historical hypothesis are congruent with that history of the geography they occupies as it was recovered from the phylogenies of other taxa (plants or animals). Our four hypothesis for *Phymaturus* are incongruent among them in many nodes of the tree, but some part of the relationships recovered are congruent to the general area cladogram published by Flores & Roig-Juñent (2001), Roig-Juñent & Flores (2001) and Roig-Juñent *et al.*, (2002), the relationship between Monte Austral and Patagonia Central is suggested in three of the four trees: ((*somuncurensis* (*spectabilis spurcus*))) in two runs, the any instance and missing analysis, and the relationship between *patagonicus* and *indistinctus* in the scaled analysis. The relationship between Payunia and Patagonia Occidental is suggested here by *tenebrosus* and *zapalensis* in three runs, any instance, scaled and missing analysis. The relationship between Cordillera Andina Valle Central as basal of

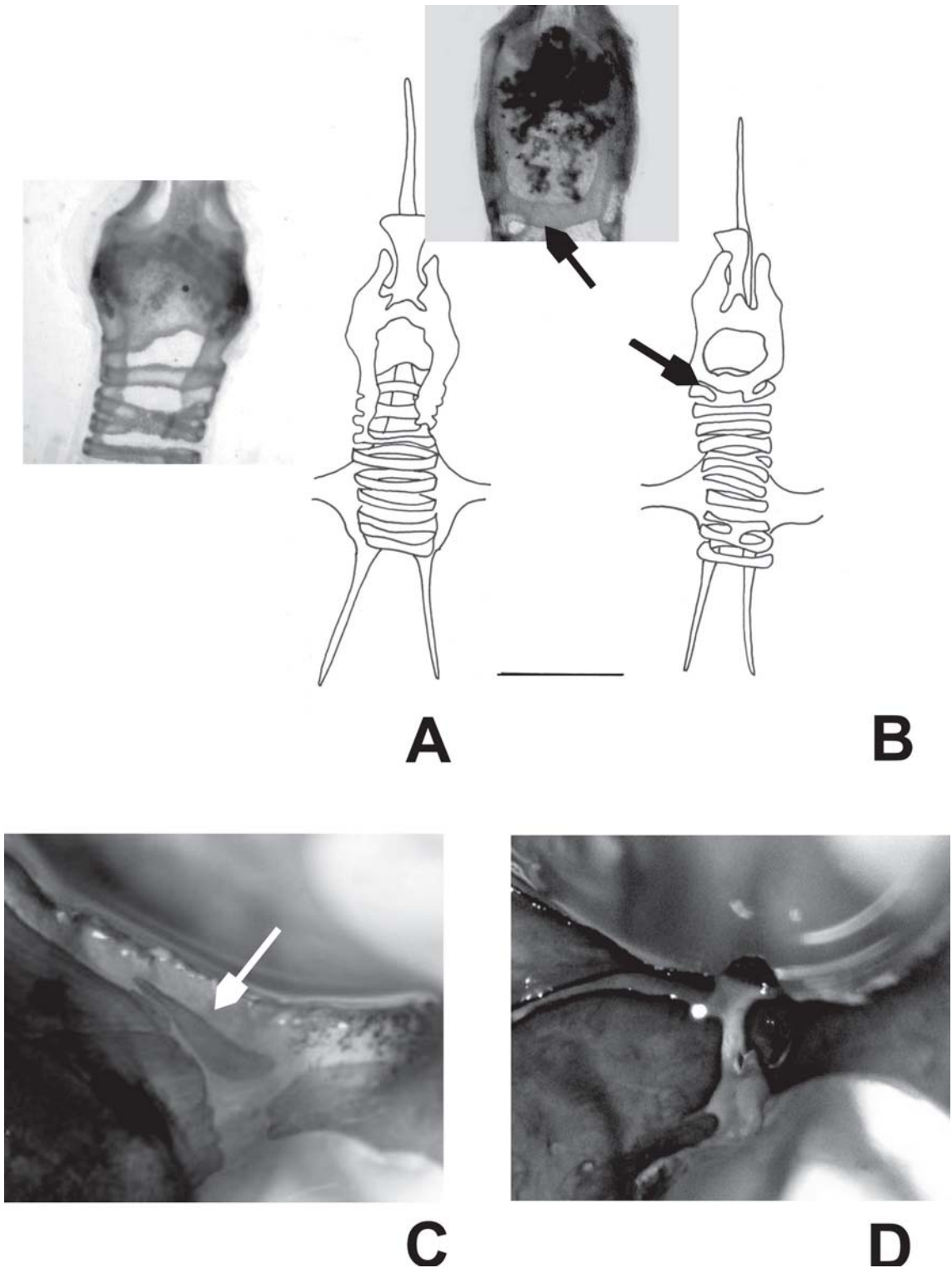


FIGURE 11. Character 115: (A) Arytenoid fenestra open with no posterior enclosure (*Phymaturus dorsimaculatus*, MCN 921); (B) Arytenoid fenestra closed (indicated by arrow) (*Phymaturus* cf. *patagonicus* EC, MCN 908). Scale = 2 mm. Character 124: postfrontal: (C) postfrontal bone present (*Phymaturus excelsus*, MCN 922); (D) postfrontal absent (*Phymaturus* cf. *antofagastensis* SC, MCN 326). Postfrontal length in C = 1.2 mm.

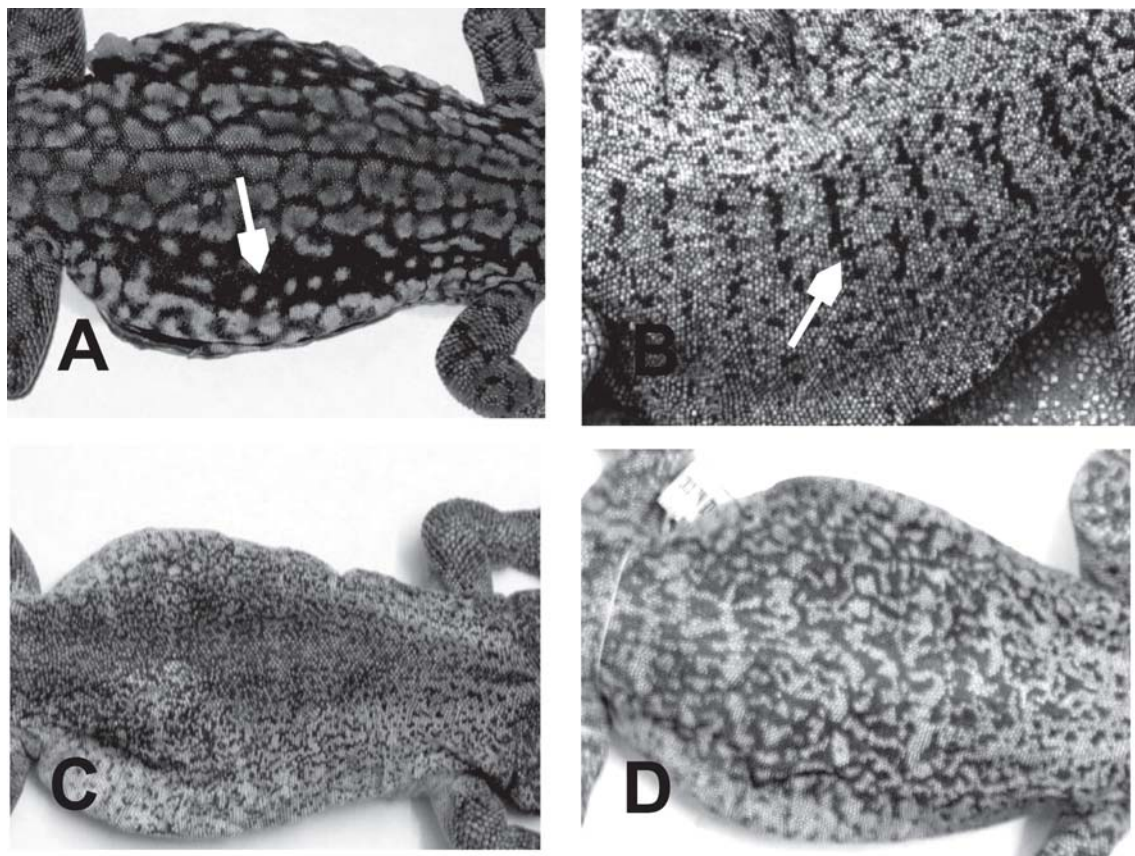


FIGURE 12. Character 91: (A) Lateral black band on the sides of trunk (*Phymaturus zapalensis*, MCN 1600). Character 132: (B) Transverse fine stripes on the back (*Phymaturus indistinctus*, MCN 1274). Character 128: (C) Dense homogeneous “spray” pattern (*Phymaturus antofagastensis* SC, MCN 313); (D) Aggregate pattern (*Phymaturus antofagastensis*, MCN 1432). Images are at different scales.

these two pairs of areas is not seen here in *Phymaturus* cladograms, in the four analysis species distributed in that area are close related to the norther subclade (Transitional Puna). Area relationships suggested by the frequency bins analysis is not congruent with the other three analysis of *Phymaturus* and with general area cladograms known. In this hypothesis (Figure 6) a repeated vicariant hypothesis is suggested within both groups of species: there exist a pair of sister taxa linking the Payunia plateau (Mendoza) with Laguna Blanca (Neuquén), cf. *palluma* (PA) with cf. *palluma* (LB) in the *palluma* group and other couple of species in the *patagonicus* group, *payunae* and *zapalensis*.

In Figure 8 a majority rule consensus tree of the four original analysis show species of Prepuna and Puna areas of the *palluma* group forming a monophyletic group with cf. *palluma* (EP) inhabiting Valle Central and Cordillera Andina as the sister taxon. *Phymaturus dorsimaculatus* found in Patagonia Occidental is sister taxon of cf. *palluma* (CH) a Chilean species distributed

not far from this locality. *Phymaturus* cf. *palluma* (LB) distributed at southern latitude as *dorsimaculatus* and cf. *palluma* (CH) is the subsequent basal species. Western central Argentina species as cf. *palluma* (ME) and cf. *palluma* (PA) are more related to the cf. *palluma* (EP) and the northern clade than any other. In the *patagonicus* group there exist a repeated pattern where Monte Austral was related to the patagonian areas, at Node 5 *somuncurensis* basal species of this clade, and cf. *patagonicus* (EC) basal to the other clade.

DISCUSION

Taxonomic remarks

The taxonomic use of *palluma* or *flagellifer* for designating the oldest known species of the genus should be resolved soon by the International Commission of Zoological Nomenclature (ICZN). There are two com-

peting positions: Cei & Lescure (1985) and Lescure & Cei (1991) proposed the use of *flagellifer* instead of *palluma* Molina, 1782, owing to confusion involving the type specimen, which was an individual of the Chilean teiid *Callopiastes maculatus*. Recently, Etheridge & Savage (2003) proposed conserving the usage of the name *palluma* by designation of a neotype for *Lacerta palluma* Molina, 1782, because its wide use in the literature for the last 150 years. Both requests are reasonable and will be considered by the ICZN in 2005.

The name *Phymaturus adrianae*, proposed by Pereyra (1992b) for a new species in an meeting abstract is a nomen nudum (ICZN, Art. 9, 1999). However, Cei & Videla (2003) used the name and provided a photograph and some characteristics to diagnose the species, and thus may be considered the authors of the name *Phymaturus adrianae*. But because there was no type material indicated in this publication, we do not consider this name valid. Considering that at this time we do not know certainly the identity of the true *palluma* (if it is assignable to populations of Mendoza in Argentina or to populations of Chile, as noted by Cei & Videla, 2003) exist the risk that *adrianae* (populations of Argentine side of the Andes) could be a synonym of *palluma*. The aim of this study was extracting phylogenetic information from morphological characters and the description of new taxa, the resolution of those taxonomic problems requires others kind of information.

In this study we reexamined materials from Baños del Campanario (Talca), Puesto Militar San Pedro, Cuesta Vergara (Curicó), El Planchón (Curicó) at MNHN and Paso de los Cóndores, Laguna del Maule (Talca) (deposited at MVZ). We considered those populations to be conspecific because we could not find obvious morphological differences. Similar conclusions can be addressed following the cytogenetic studies done on these populations. Lamborot & Navarro Suárez (1984) studied materials from Cordillera de Curicó close to El Planchón & Pereyra (1992a) examined *Phymaturus flagellifer* from the same region: Termas del Flaco (Curicó), Mina la Disputada (La Colina), Laguna del Maule (Talca). Both cytogenetic studies provided the same results.

Recently Scolaro & Cei (2003) described a new species of *Phymaturus* based on a single specimen collected in the area of Esquel (Chubut, Argentina). Characters provided in this description make it difficult to assign this new taxon to either species group, but some comments are warranted. According to their description, the specimen has imbricate superciliaries (pg. 109) and a spiny tail, but not as spiny as that seen among

members of the *palluma* group (pg. 111). These characters suggest this new species is allied outside of the *palluma* group, but the authors also describe the new taxon as possessing four suboculars separated from the supralabials by two rows of lorilabials – a character that is shared by all members of the *palluma* group. However, fragmentation of the subocular was also described for *P. spurcus* (Lobo & Quinteros, in press). The dorsal pattern of this lizard resembles specimens of *P. tenebrosus* and some *P. zapalensis*, as well as other species of the “patagonicus” group: *P. excelsus*, *P. spectabilis*, *P. tenebrosus*, and *P. spurcus*, which exhibit orange-red coloration on their abdominal region. Given this evidence, it seems unlikely that this new taxon is nested within the *palluma* group. A more careful examination of the material and the collection of additional specimens should help to resolve this question.

The new species described in this investigation have distinctive color patterns, and all (except *P. excelsus*) are allopatric. *Phymaturus tenebrosus* and *P. spectabilis* exhibit an interesting polymorphism in pattern, but they do not resemble other species of the genus. Some specimens of *P. tenebrosus* have a brown background coloration with irregular black spots, which becomes increasingly melanistic in intermediate specimens reaching the completely black pattern. A few specimens of *P. spectabilis* have a brown background coloration (without typical white ocellation) with irregularly located small markings on the dorsolateral region of the trunk. The only species living syntopically are *P. excelsus* and *P. spurcus*, yet no intermediate individuals were found at Ojo de Agua. Rocky formations in western Argentina and Patagonia are disjunct, forming small patches (of a few kilometers of area) that isolates these populations of lizards, which are very restricted in their microhabitat preferences (restricted to rocky outcrops). Other terminals included in this study (as “cf.”) are the subjects of current studies associated with determining their taxonomic status.

Phylogenetic conclusions

Using different coding methods for analyzing polymorphisms can affect results and can yield to different topologies. Systematists analyzing morphological information should not avoid using polymorphic or/and continuous characters and should pay more attention in methods they apply (not just one as we can see in most of published analysis). Studying congruence between our results and others constructed from different (independent) evidence (e.g., DNA)

could provide tests of the accuracy and performance of these different approaches to understanding morphological variation. Another way of evaluating these competing hypothesis would be applying reconciled trees (Page, 1994; Page & Charleston, 1998) or other alternative methods for studying the biogeographic history of a group of organisms, those hypothesis that implies fewer hypothesis of events (dispersals, extinction, etc.) would be the preferred ones.

The palluma and patagonicus groups – The *palluma* group is strongly supported in this analysis (always over 90% of jackknife values), so there is no doubt about its monophyly. Characters supporting the *palluma* group are not seen in the other two genera of Liolaemidae. There are three additional characters that could be considered apomorphies for this group (that should be revisited in future studies): all members of the group exhibit a longitudinal central band in the dorsum of slightly enlarged scales that are larger than those along the flanks. This character is not exhibited by species of the *patagonicus* group. Scales of the tail are spinier than those of the *patagonicus* group and have surface rugosities, which are absent in members of the *patagonicus* group. Scales of the tail of *Phymaturus patagonicus* are not more spinose than many species of *Liolaemus*, a closer observation of scale shape and arrangements reveals that the difference between the genera is not the size of spines but their shape (subquadrangular/rectangular in *Phymaturus*, round to lanceolate in *Liolaemus*) and their disposition, forming more conspicuous rings around the tail perimeter in *Phymaturus*. Characters states given by Etheridge (1995) for the *patagonicus* group are shared with *Liolaemus* or exhibit variation within that genus, so it is not surprising to find that this group lacks support in our analysis or was even found to be paraphyletic in some analyses (see Figures 4 and 5).

Relationships within the palluma group – In all analysis performed northern species of the *palluma* group (*P. punae*, *P. cf. punae* LR, *P. antofagastensis*, *P. cf. antofagastensis* SC, and *P. mallimacii*) formed a monophyletic group, and in all topologies *P. cf. palluma* (EP) is nested within the group or as the sister taxon of the group. *Phymaturus dorsimaculatus* is the basal species of the group. Cei & Videla (2003) described a pattern of transverse black bars over the dorsum of specimens of *P. verdugo*, we were not able to examine those specimens, but this character suggests a relationship with *P. dorsimaculatus*. In some analysis *Phymaturus cf. palluma* (CH) falls as sister taxon to *P. dorsimaculatus* or occupied a basal position in the *palluma* group. Both species have ringed tails and their distribution are proxi-

mate. However, larger samples of *P. cf. palluma* (CH) are needed for study. The position of *P. cf. palluma* (ME), *P. cf. palluma* (PA), and *P. cf. palluma* (LB) are uncertain, in some analysis they form a monophyletic group, yet in others they are not closely related and represent subsequent diverging branches in the evolution of the group previous to the origin of the northern subclade.

Relationships within the “patagonicus” group – Within this “group” relationships are problematic. Few of the internal nodes were well supported and the competing hypothesis indicate that much additional work is needed. Relationships between *P. spurcus* and *P. spectabilis*, like those found between *P. tenebrosus* and *P. zapalensis*, were paired in several analyses, but not in every case (see frequency bins analysis, Figure 6). Even without specific analysis of levels of polymorphism and degree of overlap of continuous characters across the genus, preliminary observations suggest that the *patagonicus* group is more evident and that fact can affect more the morphological analysis than in the *palluma* group. Perhaps in the *patagonicus* complex radiation of independent lineages was fast and more recent, not giving sufficient time for the accumulation of morphological differentiation. Overall, we found more divergent patterns of morphological variation within the *patagonicus* group than in the *palluma* group (see Figures 3 and 4), yet we found less differentiation in other types of characters (squamation, skeleton, etc.).

Sampling limitations – This first morphological approach to recovering the phylogeny of *Phymaturus* is based on a heterogeneous assemblage of evidence. First, it is obvious that the alpha-taxonomy of the genus is less studied and known than in many groups of *Liolaemus*, so it seems likely that many more terminal taxa should be included in future analyses (including the recently described species *P. verdugo* and *P. calcogaster*). Second, we had incomplete information from allozymes (only for 27% of terminals) and skeletons (only 59% of terminals). In some cases we had only a small number of specimens (i.e., *P. cf. palluma* LB, *P. cf. palluma* CH; *P. nevadoi*, only known from three specimens), which can affect results of the phylogenetic analysis (Hillis, 1998). One of our goals for future studies will be increase these samples both in characters and taxa.

Comparisons to a previous revision of the genus – The main goals of this investigation were proposing hypothesis about the history and phylogenetic relationships within the genus *Phymaturus* based on derived shared characters. The most extensive recent study on *Phymaturus* was conducted by Pereyra (1992a), he

studied 35 meristic, 52 morphometric, 19 enzymatic, and 4 chromosomal characters for six species including in his clustering analysis five of them. Because Pereyra's (1992a) study was conducted using phenetic criteria it is difficult to compare his results with ours, yet some observations are warranted. Even when a phenetic analysis only show degree of similarity without discriminating similarities originated by common ancestry from homoplasy or plesiomorphy, Pereyra (1992a) made phylogenetic conclusions including a proposed common ancestry for *P. antofagastensis*, *P. mallimacii*, and *P. payunae* (pg. 99), saying that conclusion is consistent with phenograms obtained. He adds to his conclusions that the rest of "flagellifer group" species as derived from close ancestor to the *P. antofagastensis*-*P. mallimacii* node which is contradictory with the previous sentence. His separated phenetic analysis of meristic, morphometric, chromosomal and biochemical data show incongruent results among them. The meristic analysis of Pereyra (1992a) found *payunae* as the most distant phenetic species (((*P. antofagastensis*-*P. punae*) (*P. cf. palluma* ME *P. cf. palluma* CH)) *P. mallimacii*) *P. payunae*) (fig. 15, pg. 36) while its morphometric data-based phenogram shows (((*antofagastensis* cf. *palluma* ME) *P. mallimacii*) *P. punae*) *P. payunae*) cf. *palluma* CH) with *P. palluma* from Chile as the most distant phenetic species (fig. 24, pg. 47). Pereyra's chromosomal analysis found the node *P. payunae*-*P. cf. palluma* CH (fig. 38, pg. 61) linked to ((*P. antofagastensis*-*P. mallimacii*) *P. cf. palluma* ME) and his analysis of enzymes found *P. payunae*-*P. cf. palluma* ME (fig. 39, pg. 64) linked to ((*P. antofagastensis*-*P. mallimacii*) *P. cf. palluma* CH). Thus, his own results as was shown above do not allow conclusions as those proposed. Beyond systematic or/and phylogenetic conclusions that circumstantially we can agree or disagree, Pereyra's (1992a) study brings valuable information that we already re-analyzed in the context of our cladistic analysis (see methods section).

Biogeographic Implications

Morrone (1994, 1996) analyzed relationships among provinces of the Andean subregion (corresponding to southern South America below 30° South latitude) based mainly on arthropod fauna. He found subantarctic and central Chilean provinces as sister taxa and more closely related to Puna province. In our analysis, *P. cf. palluma* (EP) inhabiting Cordillera andina and Valle Central (circa Santiago latitude) is related to spe-

cies of Prepuna and Puna, whereas *P. cf. palluma* (CH) (southern populations) and *P. cf. palluma* (ME) distributed in the Argentine province of Mendoza (eastern Andean mountains) are related to other "palluma" of Payún and central Neuquén. Recent analysis of the *chiliensis* group of *Liolaemus* (Lobo, in press) found species groups living mainly at Valle Central (*L. gravenhorsti* and *L. robertmertensi*) more related to the *alticolor* group (Puna) than to any other group.

An obvious conclusion of this study is that more taxonomic and phylogenetic studies of *Phymaturus* are needed. We are confronted with a group that is substantially more species rich than originally thought and because their distribution and peculiar natural and life history (saxicolous, herbivorous, and viviparous) offers a very interesting and tempting challenge to herpetologists, both systematic and ecological.

RESUMO

Estudaram-se as relações dentro do gênero *Phymaturus* da família *Liolaemidae*, usando análise de parsimônia de uma matriz formada principalmente por dados morfológicos. A matriz inclui 133 caracteres: 28 descritos na literatura como apomorfias dos três gêneros de *Liolaemidae* (*Ctenoblepharys*, *Liolaemus* e *Phymaturus*), 21 caracteres de alozimas e carilogia, 53 caracteres de morfologia externa e 31 do esqueleto, de todos os terminais de *Phymaturus*. A matriz inclui representantes de dez das doze espécies reconhecidas na literatura, e outros 12 terminais que neste estudo se consideram linhagens independentes e identificadas como *P. patagonicus* ou *P. palluma* na literatura prévia e nas coleções. Quatro destes terminais são descritos neste trabalho como espécies novas, uma pertencente ao grupo de *P. palluma* e outras três ao grupo de *P. patagonicus*. Realizaram-se quatro análises usando quatro métodos diferentes para codificar binariamente caracteres polimórficos, e um novo método para codificar os caracteres contínuos. A divisão tradicional do gênero em dois grupos não é apoiada pelo presente estudo, o grupo de *P. patagonicus* é parafilético em parte da análise. O grupo de *P. palluma* é monofilético e se sustenta por vários caracteres, as árvores de consenso por maioria, de todas as análises, mostraram com exceção de um par de politomias, uma topologia do grupo bem resolvida. Dentro do grupo de *P. palluma*, encontra-se um subclado formado por espécies distribuídas no norte da Argentina desde o norte da província de San Juan (ao norte dos 30° de latitude). Nesta análise, o *P. palluma* de El Planchón (Chile), relaciona-se mais com este subclado do norte que com qualquer outra forma de "P. palluma".

PALAVRAS-CHAVE: *Liolaemidae*; *Phymaturus*; novas espécies; morfologia; análise filogenética.

ACKNOWLEDGMENTS

We thank R. Espinoza for making valuable comments on an earlier draft of the MS and his help with its translation. We would like to thank the following individuals (and museums) for allowing us to study specimens under their care: E. Pereyra (Instituto de Biología Animal, Universidad Nacional de Cuyo, Mendoza), F. Videla (IADIZA, Mendoza), E. Lavilla and S. Kretzschmar (Instituto de Herpetología, Fundación Miguel Lillo, Tucumán), H. Núñez (Museo Nacional de Historia Natural, Santiago), R. Etheridge and T. Reeder (San Diego State University), J. Hanken and J. Rosado (Museum of Comparative Zoology, Harvard), J. Wiens (Carnegie Museum of Natural History, Pittsburgh), J. McGuire (Museum of Vertebrate Zoology, Berkeley). We thank F. Cruz, N. Ibarguengoytía, J.C. Acosta, J. Wiens, R. Espinoza, L. Avila, M. Morando, I. Martínez Oliver, C. Abdala, and J.M. Díaz Gómez for helping us in the field, in the lab, or discussing ideas related to this study. We thank S. Kretzschmar for helping us with the translation of our abstract to Portuguese. We acknowledge the Provincial Departments of Fauna of Argentina for providing authorization for collecting and field work. The senior autor thanks C. Hitchcock, Andrea and José Rosado, Carlos and Monica Calvo, and Richard Etheridge for their hospitality and kindness during a study trip in the United States. This study was supported by a grant (FL) from Agencia Nacional de Promoción Científica y Tecnológica (PICT 98-4867) and from a National Geographic Society grant to R. Espinoza and J. Wiens.

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Recebido em: 10.01.2005

Aceito em: 29.08.2005

APPENDIX I

Skeletonized specimens are indicated by CS (claired and stained skeletons) and with DS (dry skeletons).

Phymaturus antofagastensis: SDSU 1991. Argentina: Prov. Catamarca: Dpto Antofagasta: Agua de los Pocitos. E. Teran & O. Pagaburo cols. 28.XI.81. MCN 309-310. Camino a Paso San Francisco, Abdala, C.; R. Espinoza, F. Lobo & M.I. Martínez Oliver. MCN 1429-1436. A 130 km de Fiambalá sobre ruta a Paso San Francisco. Dpto. Antofagasta, Prov. de Catamarca, Argentina. J.C. Acosta col. *Phymaturus* cf. *antofagastensis* (SC): MCN 323-27, 306-308. Argentina, Cuesta de Calalaste, Dpto. Antofagasta de la Sierra, Prov. Catamarca. Abdala, C.; R. Espinoza, F. Lobo & M.I. Martínez Oliver. 20/01/01. MCN 313-322. Argentina, Cuesta de Randolpho, Prov. Catamarca. Abdala, C.; R. Espinoza, F. Lobo & M.I. Martínez Oliver. 18/01/01.

Phymaturus dorsimaculatus (additional materials not considered as paratypes). MVZ 232503. Depto. Ñorquin, Barda W Termas de Copahue; elevation 2050 m. Prov. Neuquén, Argentina, M.I. Christie. 29/12/94. MCN 1566-67 and MCN 1487-88 (CS) Copahue, Dpto. Ñorquin, Neuquén, Argentina. D. Pérez col. 01/99. *Phymaturus indistinctus*: IBA 666-1 (holotype), IBA-2, IBA-3. 2 km O de Las Pulgas (lago Munsters), prov. del Chubut, Argentina. 700-800 m. J.M. Cei & L. Cei cols. 23/1/70. MCN 1274-77. Las Pulgas (cerro frente a Gruta de la Virgen). Dpto. Sarmiento, Prov. de Chubut, Argentina. Abdala, C.; F. Lobo; I. Martinez; S. Quinteros cols. MCN 810 (CS) Las Pulgas, 50 km al SO de Lago Munster. L. Avila col. Ruta Prov. 20, Sierra de San Bernardo, 19 km W Los Manantiales, 669 m. 45°27'41"S; 69°42'52"W. Dpto. Rio Senguier, Prov. de Chubut, Argentina. L. Avila & M. Morando cols. MCN 1482 (CS) Ruta Prov. 20, 4 km N de intersección ruta prov. 22, 502 m. 45°25'54"S; 69°50'25"W. Dpto. Rio Senguier, Prov. de Chubut, Argentina. L. Avila & M. Morando cols. *Phymaturus mallimacii*: REE-CSUN 183, 489-491. Cueva de Perez, Sierra de Famatina, Prov. de La Rioja. Argentina. R. Espinoza & F. Cruz cols. MCN 920 and MCN 1483-84 (CS). Camino a la Mejicana, 3430 m. 28°54'43"S; 67°42'47"W. Dpto. Famatina. Prov. de La Rioja. Morando, M.; L. Avila y L. Bolver cols. 7/12/99. *Phymaturus nevadoi*: IBA 999 (3 specimens) (type series). Agua de la India Muerta, 1750 m, Macizo Nevado, SE Mendoza. XII/73. J.M. Cei, J. Williams, Stassi, Castro cols. *Phymaturus* cf. *palluma* (ME): SDSU 1969-1970. Argentina: Prov. Mendoza: Dpto Las Heras: 20 km NE Uspallata, 2500 m. R. Etheridge. 26.I.83. SDSU 3387. Argentina: Prov. Mendoza: Dpto La Heras: 27 km NE Uspallata. 32°28'52.2"S-69°09'59.2"W. 2768 m. R. Etheridge, R. Espinoza, S. Torres, E. Pereyra. 10.II.95. SDSU 3388. Argentina: Prov. Mendoza: Dpto La Heras: 27 km NE Uspallata. 32°28'52.2"S-69°09'59.2"W. 2768 m. R. Etheridge, R. Espinoza, S. Torres. MVZ 126991. Dpto Malargüe, Valle Hermoso, Prov. De Mendoza, Argentina. R. Sage col. 5/1/69. 35°20'S; 70°15'W. MVZ 126992-94. Lago de la Niña Encantada. 6 km E de los Molles, elevation 2000 m. Prov. De Mendoza, Argentina. R. Sage. 9/1/69. 33°18'S; 69°83'W. MVZ 126995. Dpto Malargüe, en el extremo norte del Valle Hermoso. Prov. De Mendoza, Argentina. R. Sage. 12/1/69. 35°11'S; 70°10'W. MVZ 126996-126999. Depto. Tupungato, Quebrada de Chupasangral, 4 km NW Cerro Chupasangral; elevation 2800 m. Prov. Mendoza, Argentina R. Sage. 28/1/69. 33°21'S; 69°51'W. MVZ 127023. Depto. Las Heras, 2 km E Los Hornillos, Prov. Mendoza, Argentina. R. Sage col. 13/2/70. 32°51'S; 68°99'W. MVZ 127025-27. Depto. Malargüe, 2 km E Agua Botada Prov. Mendoza, Argentina R. Sage col. 24/3/70. 35°62' S; 69°95' W. MVZ 145146. Depto. Las Heras, Pampa de Canota, 20 km E, 8 km S Estancia Uspallata; elevation 3000 m. Prov. Mendoza, Argentina. R. Sage col. 12/11/68. 32°65'S; 69°27'W. MVZ 180771-74. Depto. San Carlos, Quebrada Cruz de Piedra. Prov. Mendoza, Argentina. R. Sage. 28/12/75. 34°26'S; 68°90'W. MVZ 92902, 04, 08. (DS) Dpto. Las Heras, Mendoza, Argentina. 16/XII/67. R. Sage col. REE-SDSU 2306-07, 2312-13, 2315 (DS). 20 km NE Uspallata, 2500 m. R. Etheridge col. 26/1/83. IADIZA-CH. S/N (2 specimens) Paramillos, Prov. de Mendoza, Argentina. IBA 760 (4 specimens). Paramillos, Mendoza. 2000 m. Argentina. 1/71. L. G. Castro col. *Phymaturus* cf. *palluma* (Maule, Chile) MVZ 232506-07. On the road to Laguna del Maule (Los Condores Pass), Talca Prov.; elevation 1800 m. Region VII (= Region del Maule), Chile. R. Sage col. 18/4/87. *Phymaturus* cf. *palluma* (PA): SDSU 1948-51, 56, 62 64-65. Argentina: Prov. Mendoza: Dpto Malargüe: 3 km NW of base of Volcán Payún. R. Etheridge. 4.II.83. SDSU 1972, 1974-75. Argentina: Prov. Mendoza: Dpto Malargüe: 10 km south of base of Volcán Payún. R. Etheridge. 4.II.83. REE-SDSU 2323-27 (DS). 4 km W Base Volcán Payún, 200 m, Dpto. Malargüe, Prov. de Mendoza, Argentina. R. Etheridge col. 4/II/83. IADIZA-CH 00091. Base del Volcán Payún. 1800-2000 m., Prov. de Mendoza, Argentina, J.M. Cei 7 F. Videla cols. 31/1/82. IBA 733 (5 specimens). Base Campamento. Lado SW del Payún. Mendoza. Argentina. 06/01/71. L.P. Castro col. *Phymaturus*

cf. *palluma* (CH). MVZ 199435-38 & 230992. Hotel Termas de Chillán. Region VIII (= Region del Bío Bío), Chile. J. H. Carothers col. 1/12/1985. MCZ 165456. Cordillera de Chillán. Chile. G. Moreno col. 25/02/78. MCZ 169935. Chile. Philippi col. *Phymaturus* cf. *palluma* (LB): IBA 793 (4 specimens). Laguna Blanca. Neuquén, Argentina. J.M. Ceí, L. Ceí & R. Ferreira cols. 6/01/72. MVZ 232504-05. Puesto Control, 3.5 km N Co. de 1 Laguna PN Laguna Blanca. 23°80'S; 56°83'W. Dpto. Zapala, prov. de Neuquén, Argentina. 1800 m. 18/03/94. M.I. Christie col. SDSU 1971. Argentina: Prov. Neuquén: Dpto Zapala: south shore of Laguna Blanca. R.E. Etheridge col. 22/02/83.

Phymaturus cf. *palluma* (EP): MNHN 2352, 2460-61. Baños del Campanario (1500 m), Talca, San Clemente. 2-3/2/1992. J.C. Torres-Mura. MNHN 3505-09. Curicó Puesto Militar San Pedro, Pichuante, Cuesta Vergara. Chile. 35°10'S; 70°36'W. H. Núñez & A. Labra cols. 27/02/84. MNHN 1632-33, 1638, 1643. El Planchón (Int. Curicó). 26/II/1984. M.A. Labra and H. Núñez cols. *Phymaturus patagonicus*: MLP 778, 777 (sintypes). Territorio del Chubut (Patagonia). SDSU 1980. Argentina: Prov. Chubut: Dpto Gaiman: 40 km WSW Dolavon. Retheridge col. 25.II.83. IADIZA-CH 00080. 40 km W Dolavon, 350 m. Prov. del Chubut, Argentina. J.M. Ceí & J. Williams cols. 3/3/83. IBA 789 (7 specimens). Argentina: Prov. Chubut: Dpto Gaiman: 40 km W Dolavon. Ceí J.M.; L. Ceí & L. Ferreyra cols. 16/01/72. MCN 1284-1286. A 40 km al Oeste Dolavon. Dpto Gaiman, Prov. de Chubut, Argentina. Abdala, C.; F. Lobo; I. Martínez; S. Quinteros cols. 10/2003. IBA 783 (5 specimens). 20 km. W Sombrero. Prov. del Chubut, Argentina. 15/1/72. J.M. Ceí, L. Ceí & R. Ferreira cols. FML 10077-85. 1 km W Interseccion Ruta Prov. 53 y 90. 2,2 km SW Meseta El Sombrero. Pto. Paso de Los Indios, Prov. del Chubut. C. Abdala, R. Espinoza & J. Wiens cols. 16/2/01. MCN 1250-58, 1261. Cerro frente a El Sombrero. Dpto. Paso de Indios. Prov. de Chubut. Argentina. Abdala, C.; F. Lobo; I. Martínez; S. Quinteros cols. 10/03. *Phymaturus* cf. *patagonicus* (EC): MCN 910-918. Argentina, Prov. de Río Negro, Dpto. 25 de Mayo, Ruta Prov. 8, 17 km S de San Antonio del Cuy. L. Avila; M. Morando & D. Pérez cols. 11/03/99. MCN 908-909 (CS). Ruta Provincial 8. A 17 kms S de San Antonio del Cuy. Prov. Río Negro, Argentina. 40°17'13"S; 68°27'32"W. L. Avila col. *Phymaturus payunae*: IBA 769 2,4-8, 10, 12, 17, 20, 24, 26. (specimens of type series). Payún Plateau, 5 km from the Volcán Payún, 2000 m, Mendoza, Argentina. Ceí, J. M., L.P. Castro and T. Ferreyra cols. XII/1971. IADIZA-CH 00087-8, 00087-9. 20 km SE Volcan Payún. 1800 m. Ceí & Videla cols. 31/01/82. SDSU 1981-1984. Argentina: Prov. Mendoza: Dpto Malargüe: 10 km SW base of Volcán Payún. R.E. Etheridge col. 4.II.83. MCZ 152079-81. Basaltic rocks of the Payún plateau, Mendoza, Argentina. L.P. Castro col. 01/72. REE-SDSU 2330-32, 2339, 2360 (DS). 10 km S base Volcan Payun, Dpto. Malargüe, Prov. de Mendoza. *Phymaturus punae*: MCZ 19217 (Holotype). 7 km SE refuge de la Reserva Provincial, cerca del Río San Guillermo, 3500 m. Prov. de San Juan, Argentina, R. Etheridge, J.M. Ceí & F. Videla cols. 9/02/83. MCZ 163982,84,86-88. (paratypes). Same data of holotype. SDSU 1978-79. Argentina: Prov. San Juan: Dpto Iglesia: Llano de los Hoyos, Reserva Prov. San Guillermo. R.E. Etheridge col. 9.II.83. REE-SDSU 2356-57 (DS). Caserones, 4 km SW refuge, Res. Prov. San Guillermo. 3500 m. Dpto. Iglesia, prov. de San Juan, Argentina. 10/II/83. R. Etheridge col., 2383-84 (DS). Llano de Los Hoyos, 10 km SE refuge, res. Prov. San Guillermo, 3400 m. 9/II83. R. Etheridge col. *Phymaturus cf. punae* (LR): REE-CSUN 270-271, 504-508. Agua Quemada, Puesto Leoncito. Reserva Laguna Brava, Prov. de La Rioja. R. Espinoza & F. Cruz cols. FML 2925-2, 4, 8-11,13. Puerta Quebrada del Leoncito, camino a Laguna Brava, 57 km de Alto Jagüel, Dpto. Sarmiento, Prov. de La Rioja. 14-15/11/91. FML 2926.1-3. Agua Quemada, camino a Laguna Brava, Alto Jagüel, Dpto. Sarmiento, Prov. de La Rioja. O. Pagaburo & Bracamonte cols. 01/93.

Phymaturus somuncurensis: IBA 470 (2 specimens). (Types). Laguna Raimunda, Meseta de Somuncurá, Prov. de Río Negro. Argentina. Ceí. & Tuzi cols. 10/4/68. IBA 507 (4 specimens). Cerca Laguna Raimunda, Meseta de Somuncurá, Prov. de Río Negro. Argentina. Ceí, Castro & Tuzi cols. 17/11/68. IADIZA 212. Cerro Corona, Meseta de Somuncurá. Prov. de Río Negro. Argentina. J. Scolaro col. 16/12/85. SDSU 1780-1783. Argentina: Prov. Río Negro: Dpto 9 de Julio: 2 km N Laguna Raimundo, Meseta Somuncurá, R.E. Etheridge col. 19.II.92. REE-SDSU 2433-2435, 2439 (DS). N Laguna Raimundo, Meseta de Somuncura, Dpto. Valcheta, Prov. de Río Negro, Argentina. R. Etheridge col. 19/II/83. IADIZA-CH 00212. Co. Corona. Meseta de Somuncura. Prov. de Río Negro, Argentina. J.A. Scolaro col. FML 8435. 43 km al N de Moligüe. Dpto. 25 de Mayo, Río Negro. 41°35'S; 69°22'W. F. Cruz col. 15/03/99. 16/XII/85. FML 1038. Meseta de Somuncurá, Laguna Raimundo (1400 m). Prov. de Río Negro. Argentina. J.M. Ceí col. 19/02/83. MCZ 156909, 170443-44. Laguna Raimunda, Meseta de Somuncurá, Prov. de Río Negro. Argentina. Ceí. & Tuzi cols. 10/4/68. *Phymaturus spurcus*: MCZ 14791

(holotype). Huanuluan, Prov. de Río Negro, Argentina. J.L. Peters col. 1920. MCZ 14914-15 (paratypes) same data of holotype. MCN 1238-40, 1244-49. Cerro frente Estancia Huanuluan. Ruta 23 a 22 km al Oeste de Jacobacci Abdala, C.; F. Lobo; I. Martínez; S. Quinteros cols. 10/2003. MVZ 188904-07. Depto. Ñorquinco, along Rimrock, 4 km S and 1 km E Alto del Escorial; elevation 1100 m. Prov. Río Negro, Argentina. R. Sage col. 25/2/82. MCN 1385, 1387. Ojo de Agua. Ruta 6. Dpto. Ñorquinco, Prov. de Río Negro, Argentina. Abdala, C.; F. Lobo; I. Martínez Oliver; S. Quinteros cols. MCN 1590. Ruta prov. 6, 1 km NW de Ojo de Agua, 1141 m. Dpto. Ñorquinco, Prov. de Río Negro, Argentina. L. Avila & M. Morando cols. 41°32'30"S; 69°51'33"W. *Phymaturus tenebrosus* (additional materials not considered paratypes): MCN 1591-1595, 1597-1599. Entre Bariloche y Pilcaniyeu, Prov. de Río Negro, Argentina. N. Ibarquengoytia col. MCN 189-92 (CS) Entre Bariloche y Pilcaniyeu. Prov. de Río Negro, Argentina. N. Ibarquengoytia col. *Phymaturus zapalensis*: IBA 792 (type series, 4 specimens). Laguna Tern (L. Blanca). Prov. de Neuquén, Argentina. 6/1/72. J.M. Cei, L. Cei & R. Ferreira cols. IBA 866-1 & 998-3 (2 specimens. 55 km S Piedra del Aguila, Neuquén, Argentina. 21/1/73. SDSU 1985-1988. Argentina: Prov. Neuquén: Dpto Zapala: S. shore Laguna Blanca. R.E. Etheridge. 22.II.83. MCN 1600-02 and MCN 1485-86 (CS). 1 km al S del Salitral, Ruta nac. 40. Dpto. Catán Lil, Neuquén. 39°40.600' S; 70°36.925' W; 994 m. C. Abdala, R.E. Espinoza, & J. J. Wiens cols. 10/02/01. SDSU 1989-90. Argentina: Prov. Neuquén: Dpto Zapala: S shore Laguna Blanca, 1275 m. W. E. Duellman. 18.XII.74. MVZ 232508-12. R. Prov. 46, 1580 m. 9.5 km S, 5 km Co Chachil, Dpto. Catan Lil, Prov. de Neuquen, Argentina. M.I.Christie col. 22/01/96. MVZ 232514. Puesto de Control, 3.5 km N. de Co. de 1 laguna. PN Laguna Blanca (23°80', 56°83'). Dpto. Zapala, Prov. de Neuquen. Argentina. 1300 m. M.I. Christie col. 18/03/94. MVZ 232515-16. Ruta provincial 46, Dpto. Zapala, Prov. de Neuquen, Argentina. M.I. Christie col. 16/03/94. MVZ 232513. 1/2 km W Primeros Pinos, 1600 m. Dpto. Pirunches. Prov. de Neuquen. Argentina. M.I. Christie col. 20/01/96. REE-SDSU 2451-2453 (DS). Margen sur de Laguna Blanca, Dpto. Zapala, Prov. de Neuquen. R. Etheridge col. 22/II/83. MVZ 188908-10. Depto. Huiliches, rocks along Río Malleo, 8 km N and 4 km E Junin de los Andes; elevation 800 m. Prov. Neuquén, Argentina R. Sage col. 23/11/82. 39857104. *Ctenoblepharys adspersa*: SDSU 3781. FML 0368, 0464. Ciudad de Dios Perú. Weyrauch col. 1/56. REE-SDSU 2513 (DS). Playa Ventanilla cerca de Lima. 11/XII/50. Peru. LACM 49147 (DS). Dpto. Ica. Museo Peracas. 30.2 km SW Pisco, 7.2 km SW Peracas. *Liolaemus kingii*: SDSU 1670-71, 3378. MCZ 150291. Golfo de San José, Pen. Valdéz, Chubut, Argentina. MCZ 11837, 39-40. Patagonia. Hatcher col. MCZ 18948-49. Ultra Cautín, Prov. Cautín Chile. C. Reed col. MCN 1545-50. Río Seco, Ruta Nac. 3 entre San Julián y Tres Cerros, S 48°31.817'; O 67°44.081'. C. Abdala, P. Cacivio, L. Federico & Lobo cols. MCN 1551-52. Tres Cerros, S48°07.160'; O67°38.384'. C. Abdala, P. Cacivio, L. Federico & Lobo cols. MCN 1324. Las Pulgas (Cerro frente a Gruta de la virgen) Dpto. Sarmiento, Prov. Chubut, Argentina. Abdala, C.; F. Lobo; I. Martínez Oliver; S. Quinteros col. MCN 565-568 (CS). Sin datos. *Liolaemus tenuis*. MACN 36558. Costa Sur, lago Ñorquinco. 1050 m. PN Lanín, Neuquén. Argentina. I. Belke col. MACN 36559. 1-2 km al El Lago Pillhué, 1075 m. PN Lanín, Neuquén. Argentina. MACN 36560. Extremo SW Lago Ruca Choroi, 1250 m, PN Lanín, Neuquen. Argentina. MCN 531 (CS). 1190 m. Ruta Provincial N°11, 2 km O. de Arroyo Remecó, 39°02'59"S; 71°21'32"O. Dpto. Aluminé, Prov. de Neuquén, Argentina. MCN 532-533 y 518 (CS). Ruta Prov. 23, 8 km. N. Pilolil, orillas Río Aluminé. 39°32'29"S; 70°57'21"W, Dpto. Catán Lil, Prov. de Neuquén, Argentina. *Liolaemus pseudoanomalus*. MCN 526-527 (CS). 6 km. E de Anillaco (28°47'S; 66°52'O), Dpto. Castro Barros, Prov. de La Rioja, Argentina. MCN 529 (CS). Mismos datos. MCN 528 (CS). 4 km. E de Anillaco (28°47'S; 66°52'O), Dpto. Castro Barros, Prov. de La Rioja, Argentina. MCN 530 (CS). 6 km. E de Anillaco (28°47'S; 66°52'O), Dpto. Castro Barros, Prov. de La Rioja, Argentina. MCN 1603. Sin datos. MCN 1636-1637. 4 km. E de Anillaco (28°47'S; 66°52'O), Dpto. Castro Barros, Prov. de La Rioja, Argentina.

APPENDIX II

List of Characters

The following characters are listed according to their position in the analyzed data matrix: characters 0-25 are apomorphies described by Etheridge (1995) for *Liolaemus* (0-7), *Ctenoblepharys* (8-19), and *Phymaturus* (20-25). Characters 26 and 27 diagnose the *palluma* and *patagonicus* groups of *Phymaturus* (Etheridge, 1995). One character cited by Etheridge (1995) as an apomorphy of *Phymaturus* was eliminated from the list (lateral nuchal sacs filled with fat) because this character is also present in some species of *Liolaemus* (i.e., basal species in the *chiliensis* group, Lobo, 2001). Another character (number of sternal ribs) was included in the skeletal characters because of variation (3-4 ribs). We selected only two chromosomal characters because the number of meta- and submetacentric chromosomes and the number of telo- and subtelocentric as proposed by Pereyra (1992a) may result from the same evolutionary phenomena (i.e., they can be redundant characters), and because there is no banding studies at hand (as were suggested by Borowik, 1995), homology for these characters should be assumed with caution.

The numbers of characters follow the order in the matrix and are separated according to the different sources of data. Apomorphies of genera were coded as binary characters. Abbreviations are as follows: BP (binary polymorphic), BIN (binary non-polymorphic), CON (continuous), MUL (multistate), and MR (majority rule).

I – CHARACTERS LIST:

APOMORPHIES FOR LIOLAEMID GENERA (Etheridge, 1995)

- 0 – Frontals separating prefrontals from orbitonasal fenestra.
- 1 – Supratemporal hidden in a groove of the supratemporal process of parietal.
- 2 – Dentary extended backward to the level of the apex of coronoid.
- 3 – Lingual process of angular short or absent.
- 4 – Secondary coracoid fenestra present.
- 5 – Pygal region of males larger than in females.
- 6 – Scales of pygal region larger in males.
- 7 – Retractor muscle of hemipenis located anteriorly and hypertrophied.
- 8 – Head short and wide.
- 9 – Superciliaries short.
- 10 – Outer ciliaries projected.
- 11 – Orbit large (0.43-0.47/skull length).
- 12 – Snout short (0.29/skull length).
- 13 – Temporal fenestra wide (1.5-1.6/length/wide).
- 14 – Prefrontals wider than long.
- 15 – Ectopterygoides short.
- 16 – Maxillary process of ectopterygoid truncated distally.
- 17 – Retroarticular process in lower jaw shorter than angular process.
- 18 – Parapophysis of atlas flat and directed backward.
- 19 – Neural arcs of trunk vertebrae broad.
- 20 – Head and body flat.
- 21 – Body wide.
- 22 – Tail spiny.
- 23 – Interclavicle short.
- 24 – Suprascapular curved medially.
- 25 – Maxillary teeth expanded (including at least some premaxillary teeth) with three conspicuous cusps (sometimes four).

POTENTIAL APOMORPHIES FOR *PHYMATURUS* SPECIES GROUPS (Etheridge, 1995)

- 26 – Superciliary shape (elongate and imbricate versus short and juxtaposed).
- 27 – Splenial size (short versus long).

ALLOZYMES

Characters 28 to 46 are the allozyme described by Pereyra (1992a).

CHROMOSOMES (Pereyra, 1992a)

- 47 – Number of chromosomes. (0 = 28 chromosomes; 1 = 30; 2 = 32; 3 = 34; 4 = 36; 5 = 38; 6 = 40; 7 = 42).
- 48 – Number of microchromosomes in females. (0 = 16 microchromosomes; 1 = 18).

EXTERNAL MORPHOLOGY

- 49 – Dorsal head scales counted from the occiput at the level of the anterior margin of earing along midline of head till rostral scale (CON).
- 50 – Number of temporals (vertical count across the temporal region between the mouth-commisura level to the level of superciliaries) (CON).
- 51 – Number of lorilabials (first row of scales in contact to supralabials to the level of the posterior of the subocular scale) (CON).
- 52 – Number of midbody scales (CON).
- 53 – Number of dorsal scales in head length (CON).
- 54 – Number of ventrals (CON).
- 55 – Number of lateral scales on neck (counted following postauricular, longitudinal folds, and across the antehumeral pocket to the base of humeri) (CON).
- 56 – Number of gulars (CON).
- 57 – Number of scales in contact with interparietal (CON).
- 58 – Number of infralabials (CON).
- 59 – Number of superciliaries (CON).
- 60 – Number of upper ciliaries (CON).
- 61 – Number of scales between frontal and rostral (CON).
- 62 – Supralabial upturned (CON).
- 63 – Subocular fragmentation (number of subocular scales) (CON). Figure 9.
- 64 – Scales in contact to nasal (CON).
- 65 – Scales in contact to mental (CON). Figure 9.
- 66 – Number of scale organs on postrostrals (CON).
- 67 – Number of scales separating the preocular from lorilabial row (CON).
- 68 – Maximum snout-vent length (CON).
- 69 – Snout-vent length largest male/largest female ratio (CON).
- 70 – Males trunk length/snout-vent length (CON).
- 71 – Abdominal width/snout-vent length (CON).
- 72 – Males tibia length/snout-vent length (CON).
- 73 – Tail length/snout-vent length (CON).
- 74 – Number of preloacal pores (CON).
- 75 – Surface of dorsal head scales. 0 = smooth; 1 = rugose (BP).
- 76 – Surface of temporal scales. 0 = smooth; 1 = rugose (BP).
- 77 – Nasal-rostral contact. 0 = no contact; 1 = contact (BP).
- 78 – Rostral scale. 0 = undivided; 1 = divided (BP).
- 79 – Lorilabials-subocular contact. 0 = contact; 1 = no contact (BP).
- 80 – Enlarged scales on posterior gular fold. 0 = absent; 1 = present (BP).

- 81 – Dorsal white spots. 0 = absent; 1 = present (BP).
 82 – Abdominal region. 0 = immaculate; 1 = spotted (BP).
 83 – Anterior gular fold. 0 = absent; 1 = present; (BP).
 84 – Row of precloacal pores. 0 = unique; 1 = divided. (BP). Figure 10.
 85 – Supernumerary precloacal pores. 0 = absent; 1 = present (BP). Figure 10.
 86 – Precloacal pores in females. 0 = absent; 1 = present (BP).
 87 – Temporals shape (0 = mosaic, 1 = cone, 2 = spiny) MUL-MR.
 88 – Throat of males (0 = immaculate; 1 = spotted; 2 = melanic) MUL-MR.
 89 – Throat of females (0 = immaculate; 1 = spotted; 2 = melanic) MUL-MR.
 90 – Dorsal pattern of tails (0 = none; 1 = ringed; 2 = variegated) MUL-MR. Figure 10.
 91 – Dark lateral band (0 = ausente; 1 = presente) BIN. Figure 12.
 92 – Spotted chest (0 = ausente; 1 = presente) BIN.
 93 – Interparietal color (0 = absent; 1 = present) BIN.
 94 – Enlarged scales in the center of chest. (0 = absent; 1 = present) BIN.
 126 – Head and neck melanism (0 = absent; 1 = present) BIN.
 127 – Sexual dimorphism in dorsal pattern (0 = absent; 1 = present) BIN.
 128 – Dense homogeneous “spray” pattern (0 = absent, 1 = present in females only, 2 = both sexes) MUL. Figure 12.
 129 – Pink-orange belly (0 = absent; 1 = present) BIN.
 130 – Dorsal pattern black or dark brown with two rows of ocelli. (0 = absent; 1 = present in females; 2 = present in both sexes) BIN.
 131 – Brown morphs. 0 = absent; 1 = present. BIN.
 132 – Transverse fine stripes on the back. 0 = absent; 1 = present. BIN. Figure 12.

SKELETAL CHARACTERS

- 95 – Number of tracheal rings (CON).
 96 – Percentage of incomplete tracheal rings. Number of incomplete posterior rings/total number of tracheal rings (CON).
 97 – Number of pterygoid teeth (CON).
 98 – Number of maxillary teeth (CON).
 99 – Number of modified maxillary teeth (heterodonty). Anterior maxillary teeth become unicusped in many taxa (CON).
 100 – Number of elongated postxiphysternal ribs (CON).
 101 – Skull height/skull length (CON).
 102 – Skull width/skull length (CON).
 103 – Lateral rami/medial rami of interclavicle (CON).
 104 – Hypoischial length/skull length (CON).
 105 – Xiphysternal length/skull length. Length of the xiphysternal unique rod carrying two ribs (CON).
 106 – Clavicle length/skull length (CON).
 107 – Medial width of clavicle/skull length. Taken at the point of its flexure (CON).
 108 – Sternal width/sternal length (CON).
 109 – Number of scleral ossicles (0 = 13 ossicles; 1 = 14; 2 = 15) (MUL-POL).
 110 – Anterior edge of palatines (0 = Contact between palatines anteriorly to the posterior borders of vomers; 1 = posteriorly to this level) (BP).
 111 – Lacrimal foramina opening (0 = vertical diameter of lacrimal foramen larger than its distance to palatine; 1 = equal to this distance; 2 = smaller) (MUL-MR).
 112 – Ceratohyal process (0 = slender; 1 = widens gradually; 2 = widens abruptly) (MUL).
 113 – Free ending of ceratobranchial II (0 = slender not expanded; 1 = expanded) (BP).
 114 – Anterior process of aritenoid cartilage (0 = at the level of the anterior process of cricoid cartilage; 1 = behind this level) (BP).
 115 – Arytenoid fenestrae (0 = opened; 1 = closed) (BP). Figure 11.

- 116 – Arytenoid posterior process (0 = present; 1 = absent) (BIN).
- 117 – Premaxillary teeth (0 = unicusped; 1 = tricusped) (BP).
- 118 – Meckel' groove (0 = bones enclosing the cartilage form a suture; 1 = bones are fused, no suture is visible) (BIN).
- 119 – Cervical rib III (0 = present; 1 = absent) (BP).
- 120 – Cartilaginous tip of rib IV (0 = bifurcated; 1 = not bifurcated) (BP).
- 121 – Number of sternal ribs (0 = three sternal ribs; 1 = four) (BP).
- 122 – Hypoischial fenestra (0 = absent; 1 = present) (BP).
- 123 – Posterior ending of hypoischial cartilage (0 = expanded; 1 = not expanded) (BP).
- 124 – Postfrontal (0 = present; 1 = absent) (BP). Figure 11.
- 125 – Intercalary incomplete tracheal rings (0 = absent; 1 = present) (BIN).