

Exploring the morphological diversity of Patagonian clades of *Phymaturus* (Iguania: Liolaemidae). Integrative study and the description of two new species

Fernando Lobo¹, Diego Andrés Barrasso^{2,3}, Soledad Valdecantos¹, Alejandro R. Giraudo⁴, Diego Omar Di Pietro⁵, Néstor G. Basso^{2,3}

¹ IBIGEO. Instituto de Bio y Geociencias del NOA (CONICET-UNSa), Salta, Argentina.

² Instituto de Diversidad y Evolución Austral (IDEAus-CONICET), Puerto Madryn, Chubut, Argentina.

³ Facultad de Ciencias Naturales y Ciencias de la Salud, Universidad Nacional de la Patagonia “San Juan Bosco” (UNPSJB), Puerto Madryn, Chubut, Argentina.

⁴ INALI (Instituto Nacional de Limnología, CONICET-UNL) Santa Fe, Argentina.

⁵ Sección Herpetología, División Zoología Vertebrados, Facultad de Ciencias. Naturales y Museo, Universidad Nacional de La Plata (UNLP), La Plata, Buenos Aires, Argentina.

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Phymaturus maquinchao:

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Phymaturus chenqueniya:

urn:lsid:zoobank.org:act:98154EF2-

E658-4AC2-878D-CA2534AB4599

ABSTRACT

In the present contribution, we revisited the taxonomy and phylogenetic relationships within the *somuncurensis* and *spurcus* clades of *Phymaturus* lizards. Based on 296 morphological characters and DNA sequences, we evaluated the taxonomic species status of each clade and of two populations sampled in a field trip. Based on this evidence, we describe two new taxa for the genus. We also studied the species recently described for Chubut province, we analyzed their phylogenetic relationships, and compared them with other Patagonian species. Here, we provide data of color in life, squamation, and measurements, and compare in detail the new taxa to other members of their respective clades. We found that the *somuncurensis* clade comprises nine species (plus two other candidate ones) distributed mostly peripherally to the Somuncurá plateau, and present on the margins of it in isolated creeks and small mountain chains. Recent molecular studies arrived to different conclusions about the taxonomic validity of closely related species of the *spurcus* clade of *Phymaturus* lizards. We decided to revisit this group and contribute with a more complete analysis for two reasons: none of these studies revisited carefully the overall morphology and type series, and the only article that revisited this complex of species studied only one color pattern character, without providing voucher information (matching color types-collection specimens-DNA samples-sites). We studied the type series of all species, revisited characters taken from squamation and measurements, revised the color pattern of all terminals, and performed statistical analysis. Our results discovered statistically significant characters, which provide enough morphological support to consider all species of the group as valid in congruence to the multilocus analysis that combined mitochondrial and nuclear data published recently. We also provide discrete color pattern characters that help to adequately differentiate these species.

Key words: Diversity; Lizards; Phylogenetics; Taxonomy; South America

RESUMEN

En la presente contribución, revisamos la taxonomía y las relaciones filogenéticas dentro de los clados *somuncurensis* y *spurcus* de las lagartijas del género *Phymaturus*. Con base en 296 caracteres morfológicos y secuencias de ADN, evaluamos el estado taxonómico de las especies de cada clado y de dos poblaciones muestreadas en un viaje de campo. Con base en este cuerpo de evidencia, describimos dos nuevos taxones. También estudiamos las especies recientemente descritas para la provincia de Chubut, analizamos sus relaciones filogenéticas y las comparamos con otras especies patagónicas. Aquí proporcionamos datos de color en vida, escamación y medidas, y comparamos en detalle los nuevos taxones con otros miembros de sus respectivos clados. El clado *somuncurensis* comprende nueve especies descriptas (más otras dos candidatas)

distribuidas principalmente en la periferia de la meseta de Somuncurá, presentes en quebradas aisladas y pequeñas cadenas montañosas. Estudios moleculares recientes llegaron a diferentes conclusiones sobre la validez taxonómica de especies estrechamente relacionadas dentro del clado *spurcus* de *Phymaturus*. Decidimos revisar este grupo y contribuir con un análisis más completo por dos razones: ninguno de estos estudios revisó cuidadosamente la morfología general y las series tipos, y el único artículo que revisó este complejo de especies estudió solo un carácter de patrón de color, sin proporcionar información sobre vouchers (coincidencia de tipos de color-especímenes de recolección-muestras de ADN-lugares). Estudiamos la serie tipo de todas las especies, revisamos los caracteres tomados de la escamación y las medidas, revisamos el patrón de color de todos los terminales y realizamos análisis estadísticos. Nuestros resultados descubrieron caracteres estadísticamente significativos, que brindan suficiente apoyo morfológico para considerar válidas todas las especies en congruencia con el análisis multilocus que combinó datos mitocondriales y nucleares publicado hace poco tiempo. También proporcionamos caracteres de patrones de color discretos que ayudan a diferenciar adecuadamente estas especies.

Palabras claves: Diversidad; Reptiles; Filogenética; Taxonomía; América del Sur.

Introduction

The genus *Phymaturus* is known for its extremely endemic species, and often known only from their type locality, despite extensive sampling done over the years by different herpetologists. This distribution pattern is likely caused by the genus habitat, which consists of rocky outcrops with crevices that these animals use as refuge from predators. Unlike its morphologically diverse sister genus, *Liolaemus*, *Phymaturus* has a highly conserved body shape (González Marín *et al.*, 2018), probably due to its restricted saxicolous life-style. Divergence time estimates of the sister genus *Liolaemus* support an Eocene origin, whereas the radiation of the current diversity of *Phymaturus* dates back to the Miocene (Hibbard *et al.*, 2018; Esquerré *et al.*, 2019a). *Phymaturus* lizards are also exclusively herbivorous and viviparous, with biennial reproduction (Boretto *et al.*, 2007; Boretto and Ibarquengoytía, 2009). Due to this morphological conservatism, recognizing new species requires in-depth knowledge of these animal's systematic and diagnostic traits. Furthermore, given the extremely endemic nature of these species, their low population densities, and their biennial pattern of reproduction (Boretto and Ibarquengoytía, 2006; 2009), all *Phymaturus* were considered vulnerable in their latest categorization (Abdala *et al.*, 2012). Therefore, recording the morphological diversity and delineating species within this clade are primary goals for their conservation.

Etheridge (1995) divided the genus *Phymaturus* into two species groups, the *patagonicus* and the *palluma* groups, based on morphological characters. In his study, the author proposed apomorphies, but did not present a formal phylogenetic analysis. Etheridge's division (1995) was corroborated later using phylogenetic methods with morphology (Lobo and Quinteros, 2005a; Lobo *et al.*, 2012a) and molecular data (Morando *et al.*, 2013). More recently, two total evidence studies were performed, one for each main species group of the genus (Lobo *et al.*, 2016; Lobo *et al.*, 2018). Knowledge about the diversity of this genus increased exponentially in the last 25 years, from Etheridge (1995), with the recognition of 10 species, to the currently 52 recognized species (Lobo and Barrasso, 2021), with several new species having been described in the last two decades (González Marín *et al.*, 2016a; Scolaro *et al.*, 2016; Troncoso-Palacios *et al.*, 2018; Lobo *et al.*, 2018; Hibbard *et al.*, 2019; Lobo *et al.*, 2019; Lobo *et al.*, 2021; Scolaro *et al.*, 2021, among the most recent ones). New published information in the last years contributed to databases of DNA sequences and morphology for the genus *Phymaturus* (like Troncoso-Palacios *et al.*, 2018; Quipildor *et al.*, 2018a, 2018b; Lobo *et al.*, 2019), providing a very interesting challenge for future research programs.

Within the *patagonicus* group, four clades were recovered in successive phylogenetic analyses (Lobo

et al., 2012a; Morando *et al.*, 2013; Lobo *et al.*, 2018): the *indistinctus*, *payunia*, *somuncurensis*, and *spurcus* clades. In a recent contribution, the composition and phylogenetic relationships within the *payunia* clade were analyzed and two new species were described, *Phymaturus niger* and *P. robustus* (Lobo *et al.*, 2021); however, several populations belonging to the *patagonicus* group remain unrevised.

In the present contribution, we study two clades: the *somuncurensis* and the *spurcus* clades. According to the last analysis (Lobo *et al.*, 2018), the *somuncurensis* clade comprises eight species: *P. calcogaster*, *P. camilae*, *P. ceii*, *P. etheridgei*, *P. sinervoi*, *P. somuncurensis*, *P. tenebrosus*, *P. yachanana*, and two candidate species: *P. sp.22a* and *P. sp.22b* (Morando *et al.*, 2013). Curiously, members of the *somuncurensis* clade are distributed along margins and surrounding the Meseta de Somuncurá, an extensive plateau in Argentinian Patagonia. *Phymaturus yachanana*, *P. calcogaster*, and *P. camilae* form a subclade, which is nested within the *somuncurensis* clade not forming an independent lineage (indicated as *calcogaster* group in Morando *et al.*, 2013). On the other hand, the *spurcus* clade is composed by *P. spurcus*, *P. spectabilis*, *P. excelsus*, and *P. manuelae* (Lobo *et al.*, 2018). Lobo *et al.* (2012b) considered *P. agilis* Scolari *et al.* (2008) as a junior synonym of *P. spectabilis* based on the lack of morphometric differences between these species for the same meristic characters studied by their authors. They also described and provided photographs of the dorsal color pattern of two neonates—one with the uniform dorsal pattern of *P. agilis*, the other with the bold pattern of *P. spectabilis*—born from a single female assignable to *P. spectabilis*. Corbalán *et al.* (2016) used the mitochondrial locus cytochrome c oxidase I to test if this molecular marker would reliably distinguish lizard species of the *patagonicus* group of *Phymaturus* (18 described species and two populations of unidentified species included in their study). They calculated intra- and inter-population genetic distances for all species and performed phylogenetic reconstructions. Based on the low genetic distances found, the authors concluded that *P. agilis*, *P. excelsus*, *P. spectabilis*, and *P. spurcus* are a single species with high polymorphism. Becker *et al.* (2018) arrived to a similar conclusion based on analyses of COI, fragments of Cytb, ND1, ND2 and eight transfer RNAs of *P. agilis*, *P. excelsus*, *P. manuelae*, *P. spectabilis*, and *P. spurcus*. Both Corbalán *et al.* (2016) and Becker *et al.* (2018) restricted their

morphological observations to only one character: the presence/ absence of brown morphs. More recently, in a contribution that studied the evolution of body size and shape of the *patagonicus* group, González Marín *et al.* (2018) analyzed multiple loci simultaneously (mitochondrial and nuclear data). They found that their molecular analysis provided support for divergence among the species *P. spectabilis*, *P. spurcus* and *P. excelsus* and considered them valid species. Morando *et al.* (2020) considered that those species formed a single polymorphic species, following Corbalán *et al.* (2016) and Becker *et al.* (2018).

Assignment to a clade of the *patagonicus* group is uncertain in two cases: *P. curivilcun* Scolari *et al.* (2016) and *P. katenke* Scolari *et al.* (2021); both species were described for Chubut province. *Phymaturus curivilcun*, for which no DNA information is available, has never been included in a phylogenetic analysis, whereas *Phymaturus katenke* was included in an analysis using only COI information (sp. 1 in Corbalán *et al.*, 2016).

Taking into account the contradictory conclusions drawn from the last molecular analyses (especially in the case of the *spurcus* clade), we conducted a study to provide new morphological information, expand observations made in previous works and clarify certain interpretations. We carried out an exhaustive analysis of these species, studied the type series, performed statistical analyses, and showed the diagnostic characters that differentiate the species involved. We completed morphological data for *Phymaturus curivilcun*, *P. camilae*, *P. sinervoi*, and *P. katenke*, and two unnamed populations, and added new DNA sequences. With this new evidence, we analyzed the phylogenetic relationships of all species mentioned and describe two new species for the genus *Phymaturus*, one belonging to the *somuncurensis* clade and the other to the *spurcus* clade. One of these two species was considered as candidate species (sp13) by Morando *et al.* (2013).

Materials and methods

We examined 356 specimens belonging to 19 species of *Phymaturus* of the *patagonicus* group, including all members of the *somuncurensis* and *spurcus* clades, and two unnamed populations: 1) on RP N° 23, approx. 10 km N from Maquinchao town (41° 11.300' S, 68° 38.386' W, 876 m), Veinticinco de Mayo department, Río Negro province, Argentina, and 2)

on RN N° 1s40 (former RN° 40), approx. 7 km S of Las Bayas village (41° 29.238' S, 70° 41.557' W, 1139 m), climbing the plateau Meseta Chenquenián from Las Bayas, Ñorquinco department, Río Negro province, Argentina (see Appendix 1). We updated the morphological data matrix of *Phymaturus*, which includes 271 characters (see character lists in Lobo and Quinteros 2005a; Lobo, *et al.* 2012a, 2016, 2018, 2019, 2021). Part of this variation, 42% of those characters, involves informative features within the *patagonicus* group (114); these characters were revisited across the species included in the present study. Continuous characters were coded and scored following the method of Goloboff *et al.* (2006), as in previous studies. Fifty-three characters are continuous, and 218 characters are discrete: 192 of external morphology (characters are of color pattern, scale counts, scale morphology and ornamentation, scale organs, integumentary glands, skin folding), 73 are anatomical (skeleton, muscles, hemipenis, viscera) and 6 are miscellaneous (chromosomes, fecundity, salt excretion). With respect to our contribution of Lobo *et al.* (2018), for this study, we improved our samples for the whole morphology of *P. camilae*, *P. curivilcun*, *P. calcogaster*, *P. yachanana*, *P. somuncurensis*, *P. ceii*, *P. sinervoi*, and *P. katenke*, taking data from MLP (Museo de La Plata, Argentina), MCN-UNSa (Museo de Ciencias Naturales, Universidad Nacional de Salta, Argentina) and IBIGEO (Reptile collection deposited at Instituto de Bio y Geociencias del NOA, Salta, Argentina). The molecular dataset includes sequences of Cytb, COI, 12S, ND4, NTF3, PNN, PRLR, C-mos, and seven anonymous nuclear loci: Phy38, Phy41, Phy60, Phy64, Phy84, Phy87, Phy89, which were recorded by Morando *et al.* (2013), Corbalán *et al.* (2016), Lobo *et al.* (2018; 2021), and this study (see Appendix 2). To improve the molecular dataset, new DNA sequences of five markers (12S, COI, Cytb, ND4, C-mos) were obtained for *P. curivilcun*, *P. katenke*, and for the unnamed population from Maquinchao area. For the unnamed population from Chenquenián plateau, only the ND4 fragment was amplified and combined with available markers labeled as *Phymaturus* sp. 13 uploaded by Morando *et al.* (2013). The genomic DNA was extracted from 96% ethanol-preserved muscle tissue samples using the phenol/chloroform method (Sambrook and Russell, 2001). Molecular markers were amplified following standard polymerase chain reaction (PCR) procedures, using the following primers: G73 (5'-GCGGT AAAGC AG-

GTG AAGAAA-3') and G78 (5'-AGRGT GATRW CAAAN GARTA RATGTC-3') for the nuclear fragment of C-mos (Saint *et al.* 1998); ND4 (5'-CACCT ATGAC TACCA AAAGC TCATG TAGAAGC-3') and Leu (5'-CATT A CTTTT ACTTG GATTT GCACCA-3') for the ND4 fragment (Arévalo *et al.* 1994); 12e (5'-GTRCG CTTAC CWTG TTACG ACT-3') and tPhe (5'-AAAGC ACRGC ACTGA AGATGC-3') for the 12S fragment (Wiens *et al.* 1999); and GLUDGL (5'-TGACT TGAAR AACCA YCGTTG-3') and CB3-3' (5'-GGCAA ATAGG AARTA TCATTC-3') for Cytb (Palumbi, 1996), and T3-AnF1 (5'-AATAA CCCTC ACTAA AGACH AAYCA YAAAG AYATY GG-3') and T7-AnR1 (5'-AATAC GACTC ACTAT AGCCR AARAA TCARA ADARR TGTTG-3') for COI (Lyra *et al.*, 2017). Sequencing reactions were run using Big Dye Terminators 3.1 in an ABI 3130 Genetic Analyzer (Applied Biosystems). All samples were sequenced in both directions and the contigs were made using DNA BASER 3 (HeracleBioSoft, Pitesti, Romania). Sequences were edited with BioEdit (Hall, 1999) and each gene was aligned with Clustal W (Thompson *et al.*, 1994), and later concatenated using Sequence-Matrix 1.7 (Vaidya *et al.*, 2011). In total, 10,799 bp were obtained (Appendix 2).

To find the best-fitting model for each marker, we used Partition Finder v2 (Lanfear *et al.*, 2017) according to the Akaike Information Criterion (AIC) and using a greedy searching scheme (Lanfear *et al.*, 2012). In each protein-coding gene, the codon positions were treated as a separate partition. We performed two independent analyses using default prior values in MrBayes v3.2 (Ronquist *et al.*, 2012), each one with four independent Monte Carlo Markov chains of 20 000 000 generations, sampled every 2000 generations with a burn-in of 25% of trees. We examined the stationarity of parameters using TRACER 1.5 (Rambaut *et al.*, 2018). Both Partition Finder and MrBayes were run on CIPRES Science Gateway website (Miller *et al.*, 2010). Uncorrected *p-distance* was estimated using the software MEGA 7 (Kumar *et al.*, 2016).

We performed a total evidence analysis including all the available morphological and DNA evidence (a data matrix used in a previous study for the *patagonicus* group, Lobo *et al.*, 2018, adding new information and terminal taxa). Our population sample from Meseta de Chenquenián has no morphological differences from samples of Museum of Vertebrate Zoology, California University (MVZ)

collected by R. Sage at Alto del Escorial, located at 3 km in straight line on the same plateau; therefore, we consider that they are the same species. We also consider that the sample mentioned as candidate species by Morando *et al.* (2013) (as *P. sp13*, 41°330' S, 70°400' W), about 6 km south of our finding is the same species. We analyzed our data matrix with TNT v. 1.5 applying strict parsimony (Goloboff *et al.*, 2008). The search for the most parsimonious trees was performed applying equal weights (EW) to all characters. We made a "traditional search" applying tree bisection and reconnection (TBR) with 10.000 replications (saving 20 trees per replication). Including five species of *Liolaemus* (*L. archeforus*, *L. lineomaculatus*, *L. buergeri*, *L. kingii*, *L. petrophilus*), and three spp of the *palluma* group (*P. palluma*, *P. vociferator*, *P. mallimaccii* see Appendix 2) as outgroup taxa. Support for individual nodes was assessed with symmetric resampling (Goloboff *et al.*, 2003) using 1000 replicates and a deletion value of 25%.

To explore the morphological diversity within each clade, we used continuous characters: 18 morphometric measurements and 32 scale counts. The following measurements were taken: abdominal width (AW); fourth toe's claw length (CL); eye length (measured between anterior and posterior commissural angles formed by ciliary scales) (EL); eye-auditory meatus distance (EM); foot length (FL); height head (HH); head length (HL); humerus length (HU); humerus width (Hu); head width (HW); internasal distance (measured between both medial borders of nasal openings) (IN); interorbital distance (IO); auditory meatus height (MH); neck length (NL); snout-vent length (SVL); tibia length (Tb); trunk length (TL) and tail length (TI). All measurements were taken using digital calipers at 0.02 mm of precision. Pictures of live specimens were taken in the field using a digital camera, and most character details were examined under a stereomicroscope. The scale counts included were: scales along lateral neck fold till the antehumeral fold (AF); scales contacting interparietal (CI); scales contacting nasal (CN); scales contacting mental (CM); dorsal scales along the dorsal midline of trunk (counted along a head length distance) (DT); enlarged scales on the anterior margin of the auditory meatus (EM); subdigital plates of fourth finger (FF); scales between frontals and superciliaries (FS); subdigital plates of fourth toe (FT); gular scales taken in ventral view between both auditory openings (GS); number of scales counted along midline over dorsum of head

(Hellmich's index) (He); infralabial scales (IS); internasal scales (Is); lorilabial scales in contact with subocular (LO); lorilabial scales (LS); number of scales counted around midbody (MS); neck scales counted along lateral neck fold (NS); postmental scales (PM); postocular scales (PO); number of preloacal pores in males (PP); postrostral scales (PR); scales between frontals and rostral scale (RF); superciliaries scales (SC); the superciliary scale juxtaposed on both ends can be the fourth, fifth or sixth scale (Sc); average of scale organs counted on postrostral scales (SO); scales separating preocular from lorilabial row (SP); subocular row (SR); supralabial scales (SS); temporal scales (TS); temporal scales counted along a vertical line between labial commissure and the level of superciliaries (TV); upper ciliary scales (UC) and ventral scales (VS). Raw data of all the studied species of *somuncurensis* and *spurcus* clades are provided in S1 and S2 (Supplementaries files). With the only addition of the two measurements of humerus, all these continuous characters (scale counts and measurements) were included in the block of continuous characters in the phylogenetic matrix in previous works and also used for taxonomic comparisons (Lobo *et al.*, 2018, Lobo *et al.*, 2021, among the most recent publications). Principal component analyses (PCAs) were performed separately for scale counts and measurements, and for both the *somuncurensis* and the *spurcus* clades. The variables that most contributed to explain the variability were selected to perform the statistical test. The criterion used to choose the variables was that they contribute 80% or more to each principal component, considering the maximum contribution (100%) that of the character with the highest value. On the other hand, some variables were statistically tested but did not appear in the PCA; this is because some species did not have any data for this variable and to avoid eliminating the entire species from the PCA the variable was better removed. For more details see Supplementary file 3 (S3). The missing variable values were completed with the average obtained from the specimens of the species that did have that data. In the case of the measurements, the same procedure was followed but the sex of each species was considered for the average. We performed Kruskal Wallis tests. All analyses were performed using the statistical package INFOSAT (Di Rienzo *et al.*, 2016). The procedure used to judge the significance of multiple comparisons and postulated contrasts in Kruskal-Wallis analysis is that described

in Conover (1999). Since differences were found in SVL between the analyzed species, the residuals of the regression of each measurement character vs SVL were obtained to remove the possible effects of size across analyses.

Results

Relationships within the *somuncurensis* and *spurcus* clades and phylogenetic position of *Phymaturus katenke* and *P. curivilcun*.

Phylogenetic analyses included the addition of DNA sequences (five markers) for the two new species, as well as for *Phymaturus curivilcun* and *P. katenke*, and new morphological information collected for the two clades. Figure 1A shows the tree obtained in a total evidence analysis that included morphology and molecules (parsimony) and Figure 1B depicts the Bayesian tree built based on all the molecular information available. The phylogenetic analyses found that each of the unnamed populations studied (Maquinchao and Chenqueniye'n) belongs to two different clades. *Phymaturus* sp. nov. from Maquinchao is found nested within the *somuncurensis* clade in the two analyses performed (total evidence and Bayesian). In the analysis of total evidence (Fig. 1A), *Phymaturus tenebrosus* is the sister taxon of all remaining species of the *somuncurensis* clade: then, towards the terminal branches, there are two sister subclades, the *calcogaster* subclade (formed by *P. calcogaster*, *P. yachanana* and *P. camilae*) and the *ceii* subclade (including the remaining species of the clade *somuncurensis*). Within the *calcogaster* subclade, *P. camilae* is the sister taxon of *P. yachanana*, within the *ceii* subclade, *P. ceii* is the sister taxon of *P. somuncurensis* and *P. sp. nov.* from Maquinchao is more closely related to *P. etheridgei* and *P. sinervoi*.

In the Bayesian analysis (Fig. 1B), *Phymaturus tenebrosus* is the sister taxon of the remaining species of the clade *somuncurensis*; then, towards the terminal branches, *P. calcogaster* is more basal (the *calcogaster* subclade is not recovered), *P. yachanana* is the sister taxon of *P. camilae*; within the *ceii* subclade, *P. ceii* is a sister taxon to *P. somuncurensis*, *P. sp. nov.* from Maquinchao is more closely related to *P. etheridgei*, and *P. sinervoi* is the sister taxon of *P. sp.22a*.

Phymaturus sp. nov. from Chenqueniye'n is recovered into the *spurcus* clade. In the total evidence analysis, *P. curivilcun* is the sister taxon of all

remaining species; then *P. sp. nov.* is sister taxon of all remaining species (96% Symmetric Resampling), then towards the terminal branches, *P. spurcus* is related to the pair of species formed by *P. excelsus* and *P. spectabilis* (76% SR). *Phymaturus manuelae* is not included in this clade. There is no strong statistical

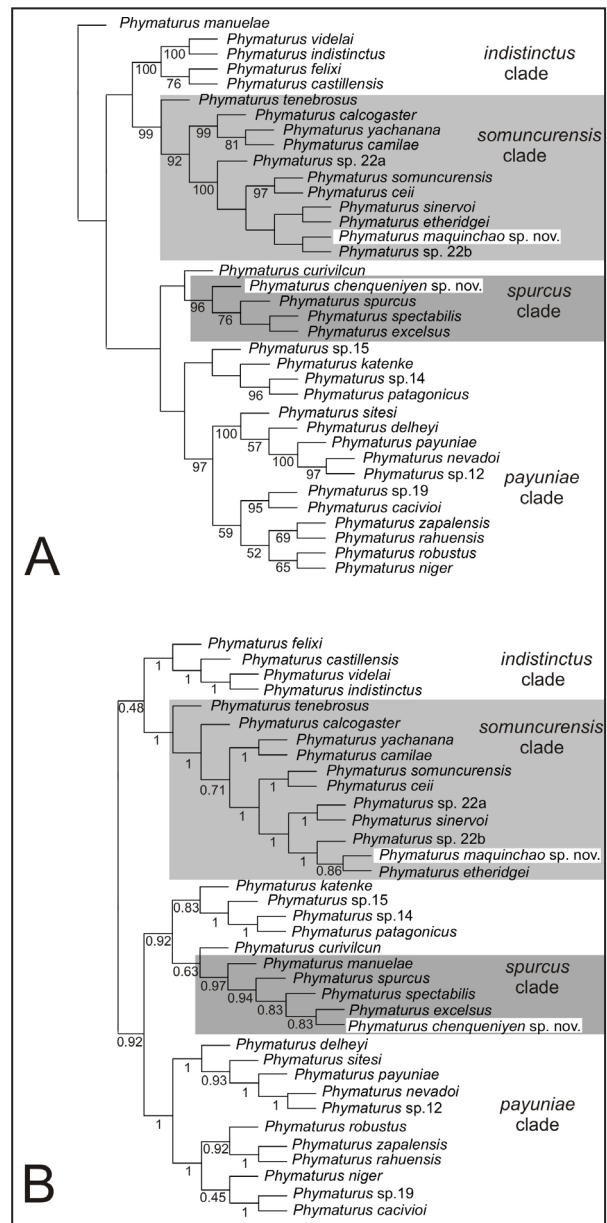


Figure 1. Phylogenetic tree showing phylogenetic relationships within the *patagonicus* after the update of Lobo *et al.* (2018) study including more DNA sequences, morphological data and taxa (*P. curivilcun*, *P. katenke*, *P. chenqueniye'n* sp. nov. and *P. maquinchao* sp. nov.). A- Total evidence analysis of parsimony including all DNA data plus morphological information (running TNT). B- Bayesian tree obtained only for molecules (running MrBayes). The new species described in the present contribution and the *somuncurensis* and *spurcus* clades to which they belong are highlighted. Numbers under branch are support values (A: symmetric resampling, B: posterior probabilities).

support for the position of *P. curivilcun*.

In the Bayesian tree (Fig. 1B), *P. curivilcun* is weakly-supported as sister taxon of all other members of the *spurcus* clade (0.63 pp); then *P. manuelae* is sister taxon of the remaining species (0.97 pp), *P. spurcus* is sister taxon of the other three species (0.94 pp), and *P. spectabilis* is sister taxon (0.83 pp) of the pair of species formed by *P. sp. nov.* (from Chenquenyén) and *P. excelsus* (0.83 pp).

Because we extended the information available for *P. katenke* (only known for COI data in Corbalán *et al.*, 2016) by sequencing Cytb, 12S, ND4, C-mos and revisiting all morphological characters (based on new samples), we checked its phylogenetic position. In the two analyses, *P. katenke* was recovered related to *P. sp15*, *P. sp14* and *P. patagonicus*. The Bayesian tree showed *P. katenke* as the sister taxon of the other three species (0.83 pp); in the total evidence analysis *P. katenke* was recovered as closely related to *P. sp14*-*P. patagonicus* with low support. In the case of *P. curivilcun*, we included DNA information of the species that was unknown until the present study, and we revisited its morphology based on the type series and a new sample. In the two analyses, *P. curivilcun* was recovered as sister of the well-supported *spurcus* clade.

The *somuncurensis* clade: morphological comparisons among its members

Within the *somuncurensis* clade, several characters related to pattern and colors are quite informative for taxonomic purposes and carry phylogenetic information, as proved in previous articles (Lobo *et al.*, 2012a; 2016; 2018). In those phylogenetic articles, 77 characters referred to pattern and colors were described for the entire genus. Here, we highlight only the main and more significant ones for this clade. Species of this clade can exhibit dorsal ocelli but less conspicuous than in the *spurcus* clade (see Lobo *et al.*, 2018: Figure 5A and C), sometimes more often in females than in males. The number of ocelli in this group counted between shoulders and thighs is larger than in the *spurcus* clade (character 130). *Phymaturus somuncurensis*, *P. tenebrosus*, *P. ceii* and *P. sinervoi* share a black coloration along the flank (dark lateral band -character 120-, Lobo and Quinteros, 2005a), which is inconspicuous or absent in the remaining species. This character state also occurs in the species members of the *payunia* clade (*P. payunia*, *P. nevadoi*, *P. sitesi*, *P. delheyi*, *P.*

robustus, *P. rahuensis*, *P. zapalensis*, *P. cacivioi*, *P. ni-ger*). *Phymaturus camilae*, *P. sp.* (from Maquinchao) and *P. calcogaster* show a pattern on dorsum of occipital region of head formed by black transversal bars (“head star pattern”) (character 296), which is shared with species of the *indistinctus* clade and with *P. katenke*. Dark pigmentation of infradigital lamellae concentrated between central keels (remarked as a dark central line) (described in Lobo *et al.*, 2010) is observed only within the clade in *P. ceii*, *P. sp.* (from Maquinchao) and *P. tenebrosus*. This character state is highly homoplastic, occurring in species of all the other clades within the *patagonicus* group. A mixed dorsal pattern consisting of small and medium-sized white spots (character 270) is present in *P. sp.* (from Maquinchao), *P. etheridgei*, the *calcogaster* subclade (*P. calcogaster*, *P. yachanana* and *P. camilae*), and within other clades in *P. patagonicus*, *P. katenke* and the northern subclade of the *payunia* clade. A dorsal tail pattern of males (character 118) is also very informative within the *somuncurensis* clade; the *calcogaster* subclade exhibits ocellated/variegated tails, whereas the tail pattern of the remaining species is markedly ringed or with almost inconspicuous ringing. *Phymaturus tenebrosus*, the sister species of all other members of the clade, lacks a dorsal tail pattern. Variation in the throat pattern was recorded. This pattern can consist of lines densely disposed but disrupted in *P. sinervoi*, *P. etheridgei*, *P. yachanana* and *P. sp.* (from Maquinchao). This throat pattern may be scarce but formed by thick lines interrupted, as in *P. camilae* and *P. calcogaster*, as in *P. camilae* and *P. calcogaster*. In the latter species, the throat pattern can be absent in some individuals, as in *P. tenebrosus*, *P. somuncurensis* and *P. ceii* (see Figures in Lobo *et al.*, 2020). Belly coloration of males is quite informative (character 127). It is yellow in *P. calcogaster* and *P. ceii*, orange in *P. sinervoi*, *P. etheridgei*, *P. yachanana*, and *P. camilae*, and mustard or red in *P. tenebrosus*. In *P. sp.* (from Maquinchao) most males have orange bellies, but an individual with yellow coloration was found. Other characters not referred to color pattern are also useful, i.e. opening of nares with a wide superficial platform inside (character 247); this character state is present in almost all species, except for *P. tenebrosus*, *P. somuncurensis* and *P. sp.* (from Maquinchao). Those miscellaneous characters described above plus all anatomical characters were already included in character lists in Lobo *et al.* (2012a; 2016; 2018).

Several continuous characters exhibit signifi-

cant variation among species. Table 1 shows characters that exhibited significant variation among species of the two clades (in S1 we provide the raw results given by the analyses). Characters that exhibit significant variation among species were 17 of the 32 studied scale counts and 9 of 18 measurements taken. Table 2 shows characters that exhibited significant differences between all pairs of species within the *somuncurensis* clade after our statistical comparisons (scale counts and morphometric characters are indicated below and above the diagonal, respectively). We did not find differences in scale counts between *P. sinervoi* and *P. ceii*. *Phymaturus somuncurensis*, *P. ceii* and *P. sinervoi* differed in only one measurement character (interorbital distance –IO–). Body measurements did not show significant differences among *P. somuncurensis*, *P. ceii*, *P. sinervoi*, *P. sp.* (from Maquinchao), and *P. camilae*, but the latter two differ in scale count characters. *Phymaturus ceii* and *P. somuncurensis* are closely related (Fig. 1), which may explain the lack of greater morphological differentiation. Their morphological discrimination is based on a few characters, mostly of coloration patterns. Of the total pairwise comparisons (scale counts), characters that are discriminant in most comparisons were: scale organs counted on postrostral scales (SO= 15 times), scales along lateral neck fold till the antehumeral fold (AF= 15), neck scales counted along lateral neck fold (NS= 14), and ventral scales (VS= 13). Of the total pairwise comparisons (measurements), characters that were found as more discriminant in most comparisons were: abdominal width (AW= 13), internasal distance (IN= 10), interorbital distance (IO= 11), and humerus length (HU= 9). The PCA allows us to explain the morphological variation in the *somuncurensis* clade based on four components. The S3 file shows the variables with the highest value (of the list of variables used in the analysis, the limit value selected to consider the characters that most contribute was the one calculated up to at least 80% of the maximum value found among the variables). All characters that exhibited significant differences among species are the same as those that exhibit the highest values in the PCA procedure.

Based on the significant amount of evidence provided by our morphological revision (color pattern, scale counts, and morphometry) and the genetic information available (Table 3), we are able to describe the population called *P. sp.* (from Maquinchao) so far in this article as a new species.

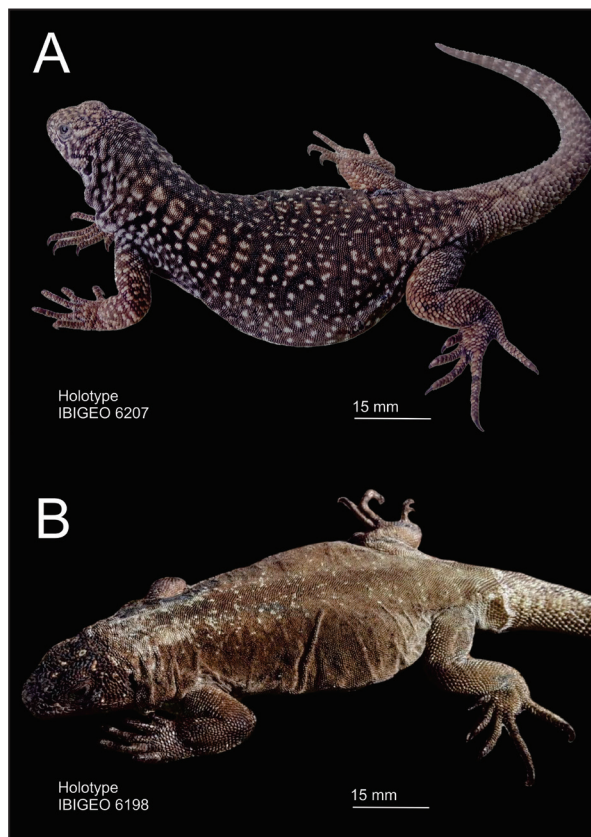


Figure 2. A- Holotype of *Phymaturus maquinchao* sp. nov. showing its typical color pattern. IBIGEO 6207 (male). Snout-vent length: 89.09 mm. B- Holotype of *Phymaturus chenqueniyei* sp. nov. IBIGEO 6198 (male). Snout-vent length: 90.00 mm.

Species description

Phymaturus maquinchao sp. nov.

Holotype.— IBIGEO 6207. Male (Fig. 2A). Deposited at the Reptile collection of the Instituto de Bio y Geociencias del Noa (IBIGEO), Salta, Argentina. Provincial Route (PR) N° 23, approx. 10 km N from Maquinchao (41° 11.300' S, 68° 38.386' W; altitude: 876 m.) Veinticinco de Mayo department, Río Negro province, Argentina.

Paratypes.— IBIGEO 6203, 6205-06, 6208, 6210, 6213, 6215 (4 adult males, 3 juvenile males) and IBIGEO 6209, 6211-12, 6214, 6216 (4 adult females, 1 juvenile female). Deposited at the Reptile collection of the Instituto de Bio y Geociencias del Noa (IBIGEO), Salta, Argentina. Provincial Route (PR) N° 23, approx. 10 km N from Maquinchao (41° 11.300' S, 68° 38.386' W; altitude: 876 m.) Veinticinco de Mayo department, Río Negro province, Argentina. DNA samples: IBIGEO 6211, 6214.

Diagnosis (Figs. 2, 3 & 4. Table 2, S1).— *Phymaturus maquinchao* sp. nov. belongs to the *patagonicus* group of *Phymaturus* because it exhibits flat and

imbricated superciliary scales, smooth tail scales, and a set of enlarged scales projected onto the auditory meatus (Etheridge, 1995; Lobo and Quinteros, 1995). Within the *patagonicus* group, *Phymaturus maquinchao* sp. nov. belongs to the *somuncurensis* clade, supported by four morphological and 62 molecular sinapomorphies. The *somuncurensis* clade comprises nine species: *P. calcogaster*, *P. camilae*, *P. ceii*, *P. etheridgei*, *P. maquinchao* sp. nov., *P. sinervoi*, *P. somuncurensis*, *P. tenebrosus* and *P. yachanana*, and was found as a monophyletic group (Fig. 1; see also Lobo *et al.*, 2018 Figure 1).

Phymaturus maquinchao sp. nov. is discriminated from the most closely related members of the *somuncurensis* clade (Fig. 1), *P. ceii*, *P. somuncurensis*, *P. sinervoi* and *P. etheridgei*, as follows: *Phymaturus ceii* shows more conspicuous black coloration along its flank; males are ventrally yellow (most males of *P. maquinchao* sp. nov. are orange); there are completely melanistic individuals (no melanism in *P. maquinchao* sp. nov.). The throat pattern in *P. ceii* is absent or inconspicuous (thin conspicuous pattern in males and females of *P. maquinchao* sp.

nov.). *Phymaturus maquinchao* sp. nov. also shows statistically significant differences (with overlapping ranges) from *P. ceii* in the following characters: it has fewer scales along lateral neck fold counted up to the antehumeral fold (AF), more enlarged scales in the anterior margin of the auditory meatus (EM) and shorter forelimbs (HU). *Phymaturus somuncurensis* exhibits a quite homogenous dorsal pattern; no ocelli are evident, as in *P. maquinchao* sp. nov. *Phymaturus somuncurensis* shows black coloration along its flank more conspicuous than in *P. maquinchao* sp. nov. (inconspicuous or absent). *Phymaturus somuncurensis* lacks throat reticulation, which is conspicuous in *P. maquinchao* sp. nov. Males and females of *P. somuncurensis* show pink ventral coloration, but in males of *P. maquinchao* sp. nov. it is orange or yellow (Fig. 3). *Phymaturus maquinchao* sp. nov. exhibits significant differences from *P. somuncurensis* in two squamation characters: more scales contacting mental scale (CM) and enlarged scales on the anterior margin of the auditory meatus (EM), and in two morphometric characters: smaller eyes (EL) and shorter head (HL). No differences in scale counts were found between these species (Table 2). *Phymaturus sinervoi* lacks sexual dimorphism in its color pattern; it also lacks dorsal ocelli, which are present in all females of *P. maquinchao* sp. nov., and even in males, but are not so evident. *Phymaturus sinervoi* shows more conspicuous black coloration along its flank than *P. maquinchao* sp. nov., in which it is inconspicuous or absent. The anterior gular fold is almost conspicuous in *P. sinervoi* (absent in *P. maquinchao* sp. nov.). Enlarged scales on the anterior margin of auditory meatus are directed backwardly in *P. sinervoi*, but they are perpendicular to temporals in *P. maquinchao* sp. nov. There are two differences in scale counts: *P. maquinchao* sp. nov. exhibits more scales contacting mental scale (CM) and more enlarged scales on the anterior margin of the auditory meatus (EM); there are no differences in morphometry between these species (Table 2). Males of *P. sinervoi* and *P. maquinchao* sp. nov. can exhibit orange or yellow ventral color; in *P. etheridgei*, ventral coloration is orange, and it can exhibit yellow mustard only in ventral surfaces of thighs. Contrary to *P. maquinchao* sp. nov., *P. etheridgei* has a dorsal black to dark brown coloration with very small white spots, contrasting the light brown coloration of tails; no dorsal ocelli are present in this species. Ventral coloration of *P. etheridgei* males is orange, turning to bright mustard/yellowish on ventral surfaces of

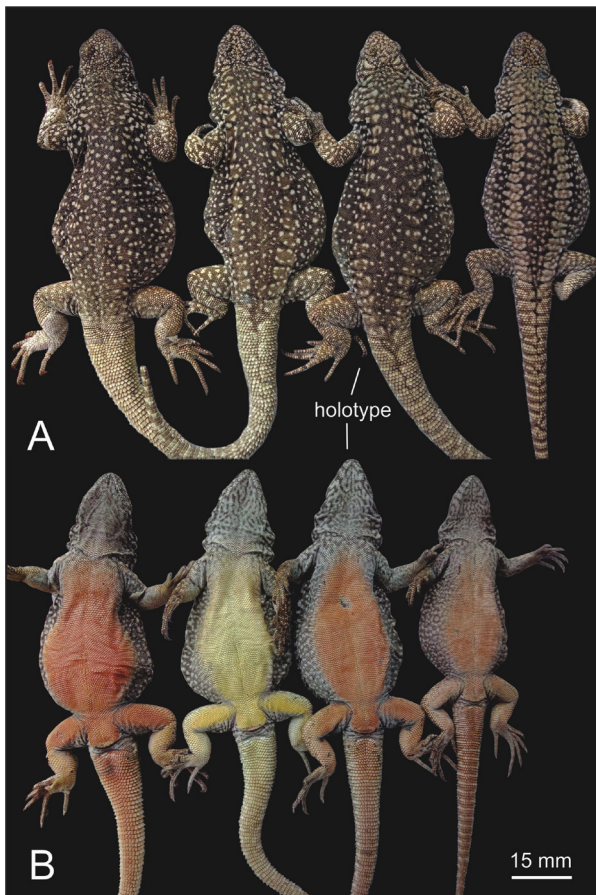


Figure 3. A- Male individuals of the type series of *Phymaturus maquinchao* sp. nov. Dorsal and ventral views.

thighs and cloaca; in females, ventral coloration is pink, whereas in *P. maquinchao* sp. nov., both males and females exhibit orange ventral coloration (brighter in males), and some males have yellow coloration (Fig. 3). *Phymaturus etheridgei* presents the white dorsal spotting in two sizes: small to very small spots irregularly scattered and densely covering their backs; this condition of fore and hind limbs found in *P. etheridgei* is shared with *P. yachanana*. *P. maquinchao* sp. nov. shows a similar condition of white spotting but scarcely distributed and not extended onto the limbs. *Phymaturus maquinchao* sp. nov. also differs from *P. etheridgei* in six scale count characters: it has more postrostral scales (PR), scales contacting nasal (CN), scales contacting mental scale (CM), scales in the subocular row (SR) and fewer scales along lateral neck fold up to the antehumeral fold (AF), and ventral scales (VS). They also differ in four morphometric characters: *P. maquinchao* sp. nov. has smaller eyes (EL), shorter head (HL), lower internasal distance (IN), and greater abdominal width (AW).

Phymaturus maquinchao sp. nov. is discriminated from all other members of the *somuncurensis* clade as follows: *Phymaturus maquinchao* sp. nov. exhibits a quite different color pattern from that of *P. tenebrosus*; the latter species exhibits brown or red morphs, or even black individuals (Cerro Alto) with thin and homogeneously distributed white spotting. Brown morphs of *P. tenebrosus* can exhibit black coloration in flanks, as *P. ceii*, *P. sinervoii* and *P. somuncurensis*. *Phymaturus tenebrosus* never exhibits dorsal ocelli. *Phymaturus maquinchao* sp. nov. also differs from *P. tenebrosus* in having a higher number of: scales contacting nasal (CN), scales contacting mental (CM), dorsal scales along the dorsal midline of trunk (counted along a head length distance) (DT), enlarged scales on the anterior margin of the auditory meatus (EM), more scales counted along midline over dorsum of head (Hellmich's index) (He), internasal scales (Is), lorilabial scales (LS), neck scales (NS), postrostral scales (PR), the superciliary scale juxtaposed on both ends tends to be the sixth rather than the fifth (Sc), and ventral scales (VS), and fewer scale organs on postrostral scales (SO). *P. maquinchao* shows a longer neck (NL), greater forelimb width (Hu) and abdominal width (AW). Dorsal white spots of *P. calcogaster* are large (formed by 9 to 16 scales, see fig. 2 in Lobo *et al.*, 2018), contrary to *P. maquinchao* sp. nov. (no more than six or seven scales). The throat pattern consists of a dark thick



Figure 4. Female paratypes of *Phymaturus maquinchao* sp. nov. Dorsal and ventral views.

reticulation (especially in males) in *P. calcogaster* (thin reticulation in *P. maquinchao* sp. nov.), dorsal pattern of head reticulated in *P. calcogaster*, inconspicuous in *P. maquinchao* sp. nov. Males have yellow chests and abdomen in *P. calcogaster* (orange in 3 of 4 individuals in *P. maquinchao* sp. nov.). Dorsal ocelli are absent in *P. calcogaster*. In *P. calcogaster*, transversal rows of white spots are evident (absent in *P. maquinchao* sp. nov.). *Phymaturus maquinchao* sp. nov. also differs from *P. calcogaster* in four scale count characters: more postrostral scales (PR) and scales contacting nasal (CN), fewer scales organs in postrostrals (SO), and fewer scales along lateral neck fold up to the antehumeral fold (AF). No morphometric characters exhibiting significant differences between these species were found. Dark brown to black dorsal pattern of trunk and limbs in *P. camilae*, differs from brown to light brown in *P. maquinchao* sp. nov. Dorsal pattern of head marked in *P. camilae* (light and almost inconspicuous in *P. maquinchao* sp. nov.), white scales on dorsum of tail contrasting from the brown background coloration in *P. camilae*

Table 1. Characters of squamation (scale counts) and measurements that exhibit significant differences among members of the *somuncurensis* and *spurcus* clades after performing Kruskal Wallis tests. We provide the raw data for all species studied in Supplementary files 1 and 2. Abbreviations of scale counts are as follow: Scales along lateral neck fold up to the antehumeral fold (AF); contacting nasal (CN); contacting mental (CM); dorsal scales along the dorsal midline of trunk (counted along a head length distance) (DT); enlarged scales at the anterior margin of the auditory meatus (EM); subdigital plates of fourth finger (FF); gular scales, between both auditory openings (GS); number of scales counted along midline over dorsum of head (Hellmich's index) (He); infralabial scales (IS); internasal scales (Is); lorilabial scales in contact with subocular (LO); lorilabial scales (LS); number of scales counted around midbody (MS); neck scales counted along lateral neck fold (NS); postmental scales (PM); postocular scales (PO); postrostral scales (PR); scales between frontals and rostral scale (RF); superciliary scale juxtaposed to the others in both endings (Sc); average of scale organs counted on postrostral scales (SO); subocular row (SR); supralabial scales (SS); temporal scales counted in a vertical line between labial commissure and the superciliaries level (TV); upper ciliary scales (UC); ventral scales (VS). Measurements: abdominal width (AW); fourth toe's claw length (CL); eye length (EL measured between anterior and posterior commissural angles formed by ciliary scales); height head (HH); head length (HL); humerus length (HU); humerus diameter (Hu); head width (HW); internasal distance (IN measured between both medial borders of nasal openings); interorbital distance (IO); auditory meatus height (MH); neck length (NL); trunk length (TL) and tail length (TI).

Character	<i>somuncurensis</i> clade		<i>spurcus</i> clade	
	H	P	F	P
AF	H=51.89	<0.0001	H=40.31	<0.0001
CM	H=34.86	<0.0001		
CN	H=21.21	0.0027	H=13.07	0.0052
DT	H=30.35	0.0002		
EM	H=22.98	0.0023		
FF	H=17.20	0.0208	H=16.81	0.0017
GS			H=15.55	0.0036
He	H=38.80	<0.0001	H=27.98	<0.0001
IS	H=23.58	0.0006		
Is	H=23.74	<0.0001	H=10.75	0.0043
LO			H=20.63	0.0001
LS	H=34.21	<0.0001	H=13.22	0.0075
MS			H=16.20	0.0027
NS	H=46.86	<0.0001	H=29.01	<0.0001
PM	H=17.32	0.0160	H=14.77	0.0015
PO			H=15.46	0.0002
PR	H=48.88	<0.0001	H=19.24	0.0001
RF			H=21.43	0.0001
Sc	H=11.52	0.0370		
SO	H=68.92	<0.0001	H=26.45	<0.0001
SR	H=27.25	<0.0001		
SS			H=16.12	0.0006
TV			H=14.51	0.0040
UC			H=16.38	0.0018
VS	H=49.03	<0.0001		
AW	H=44.74	<0.0001	H=15.87	0.0032
CL			H=13.50	0.0091
EL	H=22.41	0.0042	H=24.58	0.0001
HH	H=18.50	0.0178		
HL	H=26.79	0.0008		
HU	H=31.98	0.0001		
Hu			H=24.41	0.0001

HW			H=9.76	0.0448
IN	H=39.92	<0.0001		
IO	H=25.21	0.0014		
MH			H=14.32	0.0063
NL	H=23.68	0.0006	H=11.41	0.0223
TL	H=15.81	0.0451		
TI			H=32.84	<0.0001

(inconspicuous in *P. maquinchao* sp. nov.). *Phymaturus maquinchao* sp. nov. also differs from *P. camilae* in seven scale count characters: it has more scales contacting mental scale (CM), scales contacting nasal (CN), enlarged scales on the anterior margin of the auditory meatus (EM), postmental scales (PM) and postrostral scales (PR), fewer scales along lateral neck fold up to the antehumeral fold (AF) and scale organs on postrostral scales (SO). No morphometric characters exhibiting significant differences between these species were found. *Phymaturus maquinchao* sp. nov. has no reddish/clay coloration on dorsum, which is commonly found in *P. calcogaster* and *P. yachanana*. In *P. yachanana* dorsum of females has black transversal bars forming a longitudinal paired series, no ocelli are evident (they can be present in some females of *P. maquinchao* sp. nov. but as margins of light ocelli). Chest and abdomen of most individuals with light gray spotting in *P. yachanana* (immaculate in *P. maquinchao* sp. nov.). *Phymaturus maquinchao* sp. nov. also differs from *P. yachanana* in one scale count character: it has more neck scales (NS), ventral scales (VS) and the superciliary scale juxtaposed on both ends tends to be the sixth rather than the fifth (Sc). They differ in two morphometric characters: *P. maquinchao* sp. nov. smaller eye (EL) and greater head height (HH).

Description of holotype (Fig. 2A).— Male. SVL 89.09 mm. Head length: 15.42 mm. Head width: 14.98 mm. Head height (at parietal): 8.15 mm. Axilla-groin length: 47.93 mm (53.80 % of SVL). Tail length (complete, not regenerated): 97.88 mm. Body moderately wide, trunk width: 37.74 mm (42.4 % of SVL). Twenty-two smooth dorsal head scales. Three scale organs in each of the four postrostrals. Nasal bordered by nine scales, not in contact with rostral. Canthal separated from nasal by two scales. Loreal region flat. Eight enlarged supralabial scales, none contacting subocular. Eight enlarged infralabials. Auditory meatus oval (height: 4.2 mm; width: 2.4 mm) with six enlarged, flat and smooth perpendicu-

lar scales projecting on the anterior margin. Auricular scale absent. Ten convex, juxtaposed temporals. Auditory meatus - ciliary scales distance: 5.2 mm. Rostral undivided. Mental scale sub-pentagonal, in contact with six scales. Interparietal scale bordered by eight scales, larger than postparietals. Frontal region without an azygous scale. Supraorbital semi-circles inconspicuous. No distinctly enlarged supraoculars. Nine juxtaposed superciliaries, 15 upper ciliaries and 11 lower ciliaries. Subocular unique (not fragmented). Eleven lorilabials, the 11th contacting subocular. Preocular smaller than canthal, these two scales separated by another one. Preocular separated from lorilabial row by two scales. Scales of throat round, small, and juxtaposed. Seventy-nine gulars between auditory meata. Lateral nuchal folds well developed, with granular scales on longitudinal fold. Antehumeral pocket well developed. Seventy-seven scales between auditory meatus and shoulder. Sixty scales between antehumeral fold and shoulder. In ventral view, anterior gular fold absent, posterior gular fold present with its anterior margins with two enlarged scales on their borders. Dorsal scales round, smooth and juxtaposed. Thirty-eight dorsal scales along midline of the trunk in a length equivalent to head length. Scales around midbody: 209. Ventral scales larger than dorsal scales. Ventral scales between mental and preloacal pores: 185. Seven preloacal pores in an undivided row without supernumerary pores. Four moderately enlarged postloacal scales. Brachial and antebrachial scales smooth, with round posterior margins. Supracarpals laminar, round and smooth. Subdigital lamellae of fingers have three keels. Subdigital lamellae of finger (left manus) IV: 22. Supradigital lamellae convex, imbricate. Infracarpals and infratarsals have round margins and 2–3 keels. Supracarpals and supratarsals smooth, with rounded posterior margins. Subdigital lamellae of toe (left pes) IV: 27. Claws moderately long (fourth toe's claw: 1.9 mm).

Coloration (in life).—The holotype exhibits a

Table 2. Continuous characters that exhibit significant variation between all pairs of species within the *somuncurensis* clade (17 of 32 scale counts studied and 9 of 18 measurements studied). Below the diagonal are scale counts characters, and above measurement characters. Same abbreviations of Table 1.

	<i>P. maquinchao</i>	<i>P. calcogaster</i>	<i>P. camilae</i>	<i>P. ceii</i>	<i>P. etheridgei</i>	<i>P. sinervoii</i>	<i>P. somuncurensis</i>	<i>P. tenebrosus</i>	<i>P. yachanana</i>
<i>P. maquinchao</i>		–	–	HU	AW EL HL IN	–	EL HL	AW NL	EL HH
<i>P. calcogaster</i>	AF CN PR SO		IO NL	–	AW EL HL IN IO	IO	HL HU	AW HU	HH
<i>P. camilae</i>	AF CM CN EM PM PR SO	EM PM		IO HU	AW EL IN	–	–	AW IO NL	AW HH IO
<i>P. ceii</i>	AF EM	EM IS PR SO	Is PM PR SO		AW EL IO	IO	HU	AW HU TL	HU IN TL
<i>P. etheridgei</i>	AF CM CN PR SR VS	He IS SR	PM VS	PR SR VS		AW EL HL IN	IN TL	EL HU Is IO NL TL	AW HH HL IN IO TL
<i>P. sinervoii</i>	CM EM	EM SO	SO	–	SO SR		–	AW HU NL IO	HH IN IO
<i>P. somuncurensis</i>	CM EM	EM	VS	FF	FF He SR	–	–	–	HH HL IN
<i>P. tenebrosus</i>	CM CN DT EM He Is LS NS PR Sc SO VS	AF CM DT EM He IS Is LS NS PR SO VS	AF DT He NS PM	AF CM DT FF He Is LS NS PR SO VS	AF DT FF He Is LS NS PR SO SR VS	AF DT He Is LS NS PR SO VS	DT He Is IS LS NS PR SO VS		AW HH IN NL
<i>P. yachanana</i>	NS Sc VS	AF He NS VS	AF CN CM DT NS PM	AF FF NS	AF CM FF NS SR VS	AF CM NS PM SO VS	AF CM He NS PM VS	CM CN He Is LS PR SO	

brown color as dorsal background, with a pair of longitudinal rows of ocelli (14 between shoulders and thighs). On the anterior ocelli (anterior half of trunk) transversal rows of white scales are conspicuous. Upper half of flanks darker, almost black, with irregularly scattered white spots. The dorsal body pattern consists of white spots of two sizes is more evident on the vertebral band between the rows of ocelli (also commonly found in other species of the clade). The “star pattern” is conspicuous on the back of neck and nuchal region. Tail and limbs exhibit a light brown coloration. There is no evident pattern on the tail. In ventral view, throat, anterior half of chest and forearms are light gray. The throat exhibits thin reticulation. Posterior half of chest, abdomen, cloacal region, hind limbs and tail orange.

Variation.— Squamation based on 13 specimens (8 males and 5 females), including four juvenile individuals (3 males and 1 female); mea-

surements only based on adult individuals. SVL 78.9–95.3 mm (mean = 88.09; SD = 5.8). Head length 16.3–18.2% (mean = 17.4%; SD = 0.1) of SVL. Tail length 1.04–1.26 (mean = 1.15; SD = 0.08) times SVL. Scales around midbody 204–231 (mean = 216.6; SD = 9.11). Dorsal head scales (Hellmich’s index) 19–26 (mean = 22.6; SD = 1.7). Ventral scales 161–188 (mean = 176.2; SD = 8.6). Scales surrounding interparietal 6–8 (mean = 7.2; SD = 0.7). Scales surrounding nasal 7–10 (mean = 8.9; SD = 0.8). Number of scale organs on postrostrals 2–5 (mean = 3.3; SD = 0.8). Superciliaries 7–11 (mean = 9.6; SD = 1.2). Subocular never fragmented (a single scale in all individuals). Mental scale in contact with six scales in all the samples. Number of chinshields 6–8 (mean = 6.7; SD = 0.7). Enlarged scales on the border of the posterior gular fold: 2–5 (mean = 3.3; SD = 1.0). Lorilabials 11–14 (mean = 11.8; SD = 1.1). Enlarged scales on the anterior border of the audi-

Table 3. Estimates of Evolutionary Divergence between Sequences. The number of base differences per site from between sequences are shown. The analysis involved 9 nucleotide sequences. All positions with less than 95% site coverage were eliminated. That is, fewer than 5% alignment gaps, missing data, and ambiguous bases were allowed at any position. There were a total of 838 positions in the final dataset. Evolutionary analyses were conducted in MEGA7. Above: Cytb pairwise comparisons; below: 12S.

somuncurensis clade									
	<i>P. calcogaster</i>	<i>P. camilae</i>	<i>P. ceii</i>	<i>P. etheridgei</i>	<i>P. maquinchao</i>	<i>P. sinervoi</i>	<i>P. somuncurensis</i>	<i>P. tenebrosus</i>	<i>P. yachanana</i>
<i>P. calcogaster</i>		1.45	2.17	2.90	3.26	2.65	2.90	3.38	2.29
<i>P. camilae</i>	0.36		1.93	2.65	2.53	2.05	2.65	2.90	2.17
<i>P. ceii</i>	1.43	1.55		2.90	3.02	2.17	1.21	2.90	2.29
<i>P. etheridgei</i>	1.07	1.07	1.07		1.57	2.41	3.14	3.38	3.02
<i>P. maquinchao</i>	1.07	1.07	1.07	0.24		2.29	3.26	3.74	3.14
<i>P. sinervoi</i>	1.31	1.31	1.07	0.48	0.48		2.65	3.14	2.53
<i>P. somuncurensis</i>	1.31	1.31	0.36	0.72	0.72	0.72		3.14	2.53
<i>P. tenebrosus</i>	1.19	1.19	1.91	1.31	1.07	1.55	1.55		2.77
<i>P. yachanana</i>	0.95	1.07	1.91	1.55	1.55	1.79	1.79	1.67	
spurcus clade									
	<i>P. chenqueni-yen</i>	<i>P. curvilcun</i>	<i>P. excelsus</i>	<i>P. manuelae</i>	<i>P. spectabilis</i>	<i>P. spurcus</i>			
<i>P. chenqueni-yen</i>		1.22	2.32	1.46	1.46				
<i>P. curvilcun</i>	1.56		1.83	2.20	1.83	1.83			
<i>P. excelsus</i>	1.08	1.20		1.59	0.24	0.24			
<i>P. manuelae</i>	0.96	1.32	0.84		1.83	1.83			
<i>P. spectabilis</i>	0.96	1.08	0.36	0.72		0.24			
<i>P. spurcus</i>	0.96	1.08	0.36	0.72	0.00				

tory meatus 4–9 (mean = 6.8; SD = 1.7). Scales of neck along longitudinal fold from posterior border of auditory meatus to shoulder 74–88 (mean = 80.2; SD = 4.9). Gulars 68–89 (mean = 77.3; SD = 6.0). Scales between rostral and frontal 9–11 (mean = 9.7; SD = 0.8). Subdigital lamellae on fourth finger 21–26 (mean = 23.2; SD = 1.6). Subdigital lamellae on fourth toe 26–31 (mean = 28.1; SD = 1.6). Males with 7–9 preloacal pores (mean = 8.0; SD = 1.0). One female shows preloacal pores (3). Measurements: Eye length 3.4–3.7 (3.5; SD = 0.1). Head length 14.3–15.8 (mean = 15.3; SD = 0.5). Neck length 10.9–14.8 (mean = 13.4; SD = 1.3). Head width 12.8–15.5 (mean = 14.6; SD = 0.9). Head height 7.6–9.3 (mean = 8.5; SD = 0.6). Internares distance 2.4–2.8 (mean = 2.6; SD = 0.1). Interorbita distance 6.2–7.9 (mean = 7.1; SD = 0.5). Trunk length 37.5–50.6 (mean = 44.9;

SD = 4.2). Humerus length 12.5–15.5 (mean = 13.9; SD = 1.0). Humerus width 5.2–7.5 (mean = 6.5; SD = 0.7). Tibia length 14.9–17.5 (mean = 16.3; SD = 1.1). Foot length 22.8–24.8 (mean = 24.1; SD = 0.7). Tail length 93.9–114.0 (mean = 99.9; SD = 6.6). Eye -auditory meatus distance 4.4–5.3 (mean = 5.0; SD = 0.3). Auditory meatus height 3.3–4.2 (mean = 3.8; SD = 0.3). Fourth toe's claw length 1.7–2.1 (mean = 1.9; SD = 1.1). Abdominal width 31.0–43.6 (mean = 37.2; SD = 3.9).

Males exhibit a brown background coloration (Fig. 3); small to medium-sized white spots are widespread all over their backs, dorsum of neck, fore and hind limbs, but fading towards the tail. All males except one show a pair of longitudinal rows of dorsal ocelli that are different from the background coloration because of their lighter

coloration. Poorly conspicuous black transversal lines separate ocelli, and sometimes white small spots form a transversal line inside ocelli. Half of the males exhibit a conspicuous “star head pattern”, forming a reticulum in the posparietal area. There is no evident pattern on limbs, except for the white regular spotting. No pattern is evident on the tail, except for one specimen (ringed pattern). The throat is light gray, with slender black lines forming a reticulum; one specimen has no pattern. Three males have homogeneously orange chest and bellies; one male has yellow ventral coloration. All males exhibit small orange preloacal pores. Posloacal enlarged scales are more or less conspicuous. Orange or yellow coloration of their ventral surfaces is extended on the cloacal region, tail and thighs. Dorsal pattern of females is similar to that of males (Fig. 4), but ocelli rows are more conspicuous; the upper half of flanks is darker (lateral black band usually present in *P. somuncurensis*, *P. ceii*, *P. sinervoi* and *P. tenebrosus* and in the *payuniaie* clade), the white spotting is continuous on tails, and half of the females exhibit ringed tails. Ventral surfaces are of similar pattern and coloration to those of males.

Etymology.— Maquinchao refers to the locality where this species was found; it is an ancient native language word that means “site of wintering”.

Distribution (Fig. 5).—This species inhabits the northwestern margin of Meseta de Somuncurá and is only known for the type locality. Morando *et al.* (2013) sampled individuals from two sites 35 km south to this place (candidate species *P. sp22a* and *P. sp22b*); further studies are needed to evaluate the identity of these populations. The Somuncurá plateau covers a vast territory of about 25,000 km² in Argentine Patagonia. This geological structure is located more than 1000 meters above sea level; it is a formation with several canyons generated by different water streams that drain in the lowlands. It is a basaltic plateau, with reliefs of volcanic cones, mountain ranges, hills that are almost 1900 meters above sea level, interspersed with temporary and clay lagoons. Figure 5 shows how this diversified clade of lizards (*somuncurensis* clade outlined in orange) inhabits mainly inside this plateau and all around its margins.

The *spurcus* clade: morphological comparisons among its members

Analysis of continuous characters taken from squa-

mation and measurements. — Continuous characters exhibit significant variation among species. Table 1 shows characters that exhibited significant variation among species of both clades; scale counts characters are displayed below the diagonal and the morphometric ones, above this diagonal (we provide the raw results of the analyses in S2). The characters that exhibit significant variation among species were 18 of the 32 scale counts studied and 8 of the 18 measurements taken. Table 4 shows characters that exhibited significant differences between all pairs of species within the *spurcus* clade. We did not find differences in measurements between *P. sp* (Chenqueniyeén) and *P. spectabilis* (but they differ in 12 scale counts). Of all the pairwise comparisons (scale counts), the characters that are most discriminant and present in most comparisons were: scales between frontals and rostral scale (RF= 6 times), number of scales counted around midbody (MS= 6); scales along lateral neck fold up to the antehumeral fold (AF= 6); lorilabial scales in contact with subocular (LO= 4), and number of scale organs in postrostral scales (SO= 6). Of all the pairwise comparisons (measurements), the characters that were found as most discriminant and present in most comparisons were: tail length (TL= 7), fourth toe’s claw length (CL= 6), abdominal width (AW= 5), auditory meatus height (MH= 5) and humerus width (Hu= 4). The PCA allows us to explain the morphological variation in the *spurcus* clade based on three components that account for 100%. The S3 file shows the variables with the highest value. All characters that showed significant differences among species are the same as those that exhibit higher values in the PCA. Figure 6 shows one of the PCA graphics obtained (squamation); in this case, PC1xPC2, PC2 discriminates *P. spurcus*, *P. spectabilis* and *P. excelsus* from each other, whereas PC1 discriminates *P. manuelae* and *P. chenqueniyeen* from the other three. Tables with individual values of characters and for each component and accumulated percentages are included in S3.

Identification of brown morphs in the *spurcus* clade (Fig. 7).— Since coloration pattern was an essential topic in a recent publication about this group of *Phymaturus*, we considered it important to revisit it and make the necessary remarks and observations to avoid confusion. In Lobo and Quinteros (2005a) we described *P. excelsus* and *P. spectabilis* from a restricted area of Río Negro province in Argentina. At that time, we considered certain brown morphs as a variation within *P. spectabilis* species. In the

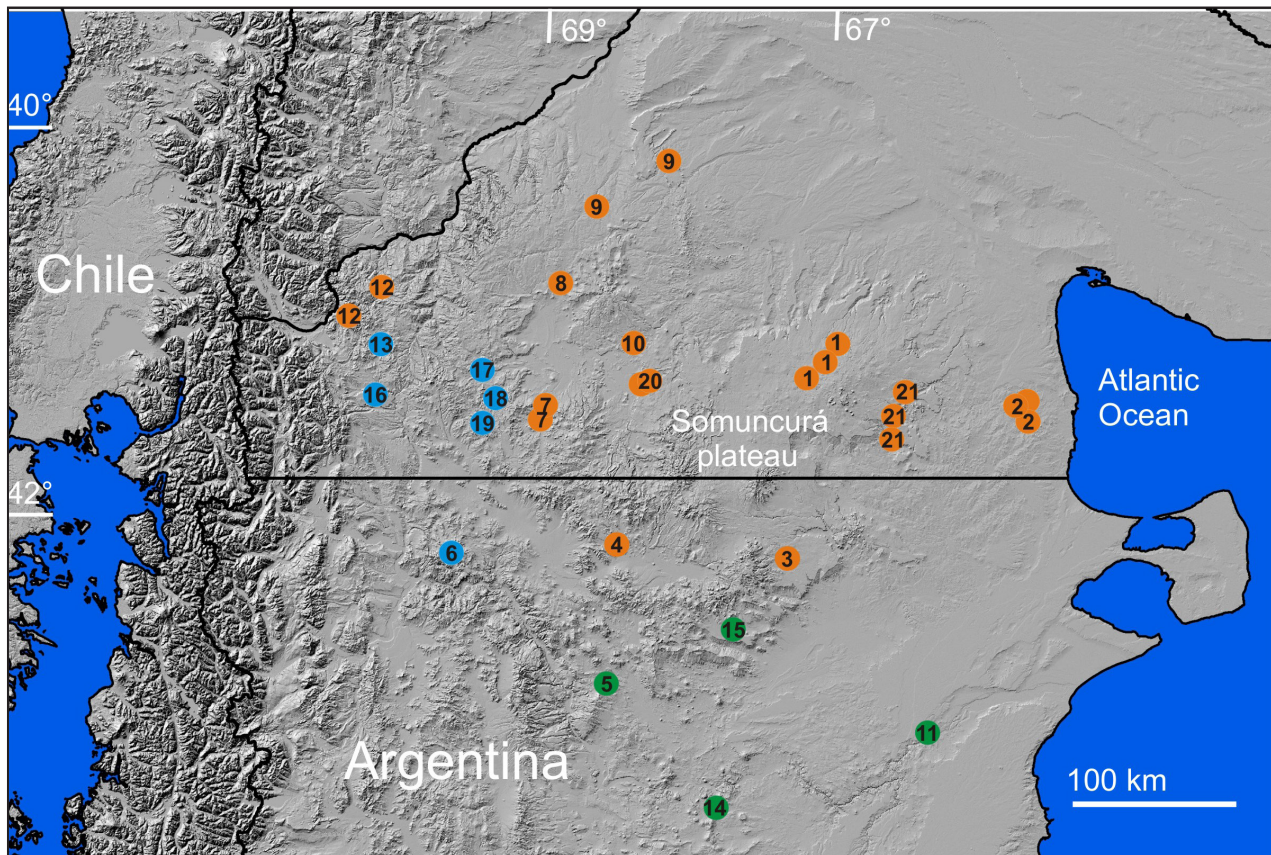


Figure 5. Map of distribution of the *somuncurensis* (orange), *spurcus* (light blue), and *P. katenke* and related species (green) in Rio Negro and Chubut provinces of Argentina (Somuncura plateau is indicated, one of the most massive geomorphological formations in Patagonia). Numbers indicate: 1- *P. somuncurensis*, 2- *P. yachanana*, 3- *P. calcogaster*, 4- *P. camilae*, 5- *P. katenke*, 6- *P. curvilcun*, 7- *P. etheridgei*, 8- *P. sinervoi*, 9- *P. ceii*, 10- *P. maquinchao* sp. nov., 11- *P. patagonicus*, 12- *P. tenebrosus*, 13- *P. manuelae*, 14- *P. sp14*, 15- *P. sp15*, 16- *P. chenqueniyei* sp. nov., 17- *P. spurcus*, 18- *P. spectabilis*, 19- *P. excelsus*, 20- *P. sp22a* and *P. sp22b*. “*P. sp.*” are Morando *et al.* (2013) candidate species.

case of *P. excelsus*, we found only three individuals in Ojo de Agua (its type locality) exhibiting brown morphs; since these brown morphs in particular resemble *P. spurcus* (Huanualuan), a species we resurrected in another article (Lobo and Quinteros, 2005b), we assumed that *P. spurcus* could be syntopic to *P. excelsus*. Later, after the description of *P. agilis* provided by Scolari *et al.* (2008), we analyzed (Lobo *et al.*, 2012b) this new species statistically for different continuous characters and because we found a female giving birth both patterns “*agilis*” (brown morph) and “*spectabilis*” (ocellated morph), we concluded that these two species are synonymous. At that time, we also considered the brown morphs of *P. excelsus* as being part of that species, rejecting the idea of *P. spurcus* being syntopic with *P. excelsus*. We discriminated brown morphs of *P. spectabilis* from *P. excelsus* (shown in Lobo *et al.*, 2012b Fig. 2). At that time, we considered the brown morphs of the species to be different from each other and

very constant for each species. Figure 7A shows an individual of *P. excelsus* from the MCN collection, and an individual of “*agilis*” deposited at the MLP collection (Fig. 7B). As can be seen, the brown pattern of *P. spectabilis* (= *agilis*) shows constancy in dorsal pattern, which is difficult to confuse with the *P. spurcus* one; this “*agilis* pattern” is a brown dorsal pattern with darker coloration on both sides of the back, named in Lobo *et al.* (2018) as a kind of “*elongatus* pattern” because it resembles the pattern found in members of the *Liolaemus elongatus* group. This color pattern is not present in any other *Phymaturus* species (*P. spurcus*, *P. excelsus* or *P. sp. nov.* from Chenqueniyei described in the present article). All specimens of the type series of *P. agilis* deposited at MLP, several other individuals deposited at the same museum, and all *P. spectabilis* specimens with brown pattern deposited at FML collection exhibit the same pattern. Pictures published in the description of *P. agilis* by Scolari *et al.* (2008) are quite illustrative of

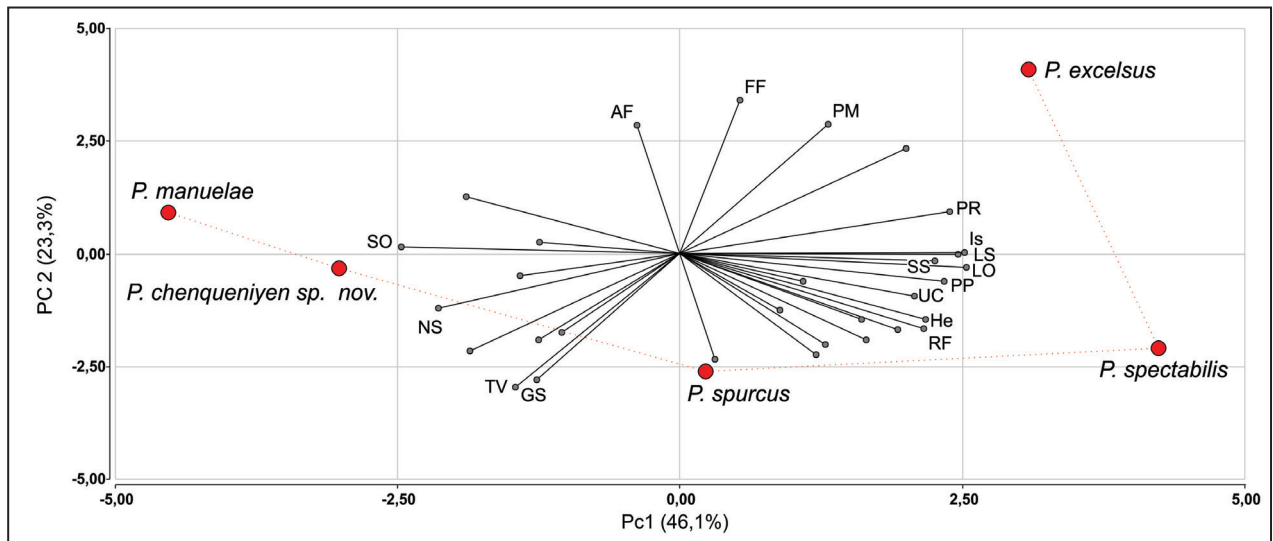


Figure 6. PC1 versus PC2 of squamation characters. *Phymaturus excelsus* discriminated from *P. spectabilis* (PC2) and *P. chenqueniyei* sp. nov. from the three *P. spurus*, *P. spectabilis*, and *P. excelsus* (PC1). Tables with individual values of characters and for each component and accumulated percentages are shown in S3.

this pattern. Therefore, because this design of brown patterns is different among *P. spurus*, *P. excelsus* and *P. spectabilis*, it is a mistake to call all of them simply “*spurus*” morphotype based only on the color without considering the design, as in Becker *et al.* (2018). The most similar brown morphs are the ones of *P. excelsus* with *P. spurus*. For this reason, the brown *excelsus* found at that time was assigned to *P. spurus* (Lobo and Quinteros, 2005a). But later, another case of intraspecific polymorphism was considered (Lobo *et al.*, 2012b). All the examined individuals (MCN-UNSA and FML collections) of brown morphs of *P. excelsus* exhibit a fading ocellated pattern in a lighter brown shade than the darker background color similar to that of individuals of *P. sp. nov.* from Chenqueniyei; in *P. spurus* this fading ocellated pattern is absent or inconspicuous, but present in most newborns and small juveniles. This pattern of fading ocelli in brown morphs is completely absent in *P. spectabilis* brown morphs. Interparietal scale is white in both morphs of *P. excelsus*, in ocellated individuals of *P. spectabilis* and in a few individuals of *P. sp. nov.* from Chenqueniyei, but never in *P. spurus* or in brown morphs of *P. spectabilis*. The throats do not exhibit a pattern in most individuals of *P. excelsus* or *P. spurus*; when there is a pattern, in *P. excelsus* it is a vanished reticulation (light brown almost inconspicuous) but in *P. spurus* it consists of small light brown dots. In addition, the abdominal region is yellow in *P. spurus* males versus orange in those of *P. excelsus* and *P. spectabilis*.

How to distinguish the ocellated patterns of *P. spectabilis* and *P. excelsus* (Figs. 7C-D).—The occurrence of specific brown morphs is not the only feature of color patterns that discriminates *P. spectabilis* from *P. excelsus*. Ocelli on dorsum of *P. spectabilis* and *P. excelsus* are constant in number. Lobo *et al.* (2012a, Fig. 6A) used this information for phylogenetic analysis (character 130) and described the variation found within the *patagonicus* group. Species belonging to the *somuncurensis* clade, *payunia* clade and *P. manuelae* (Lobo *et al.*, 2018) showed more ocelli along their backs (9-11) counted between hips and shoulders, whereas *P. spectabilis* and *P. excelsus* had fewer ocelli, between 6-8 (Lobo *et al.*, 2012a). Fading pattern of ocelli (almost inconspicuous) on brown morphs of *P. excelsus*, *P. spurus* and in *P. sp. nov.* (from Chenqueniyei) are 6-8, the same numbers of ocellated morphs of *P. spectabilis* and *P. excelsus*. The presence of this character in all species, except for *P. manuelae* (higher number of ocelli) or *P. curivilcun* (melanic), is an apomorphy of the subclade of the *spurus* clade (with the addition of the occurrence of brown morphs, fixed in all population in *P. spurus* and *P. sp. nov.* (Chenqueniyei), and in part of the population in *P. spectabilis* and *P. excelsus*). Even though the number of ocelli on the backs of these two species is similar, they are different in size and coloration. In most *P. spectabilis* individuals, ocelli are larger, formed by more cream to white scales (Fig. 7D) than those of *P. excelsus*. There are more white scales irregularly

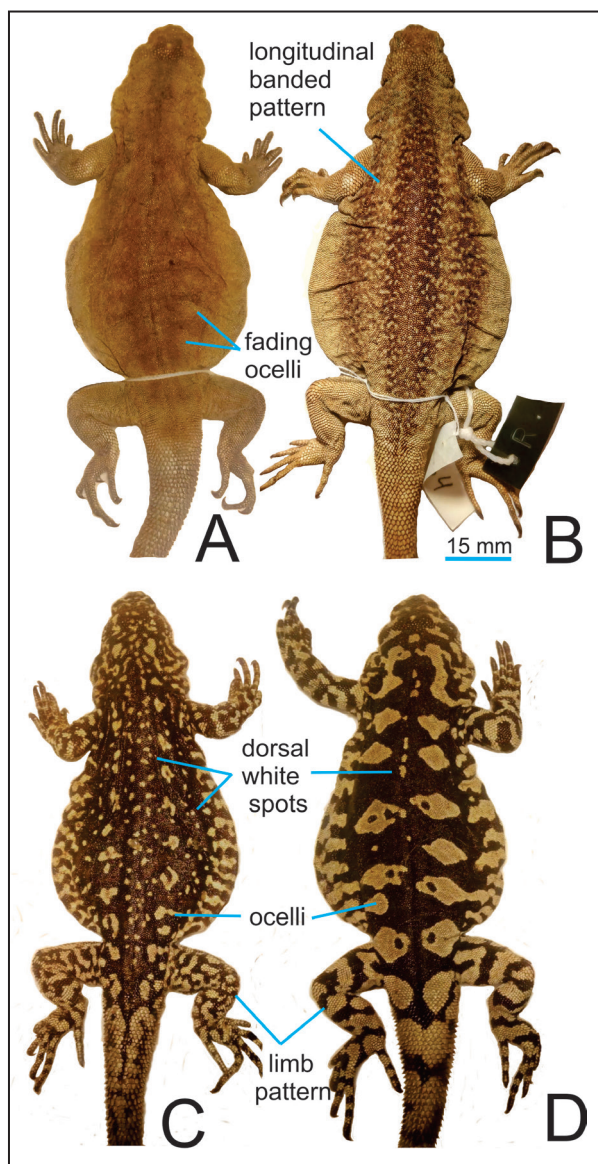


Figure 7. Typical color pattern of A- *Phymaturus excelsus* (MCN-UNSa 1385). B- Brown morph of *Phymaturus spectabilis* (MLP 5346). C and D ocellated morphs of C- *Phymaturus excelsus* (MCN-UNSa 1336) and D- *Phymaturus spectabilis* (MCN-UNSa 1205). Typical banded pattern is present in all samples of brown morphs of *P. spectabilis*, absent in *P. spurcus* and *P. excelsus*. Ocelli are usually larger in *P. spectabilis*, limb pattern consisting of thicker lines, and small white spots more concentrated on the vertebral area.

scattered on the background black coloration of the back in *P. excelsus* (Fig. 7C) while in *P. spectabilis* these white scales are much fewer and concentrated along the vertebral midline. The rostral scale is cream or almost white in *P. excelsus*, but dark brown to black in *P. spectabilis*. Chinshields (posmental row) are white and differentiated in color from the rest of the throat in *P. excelsus*, but not differentiated in *P. spectabilis*. Fore and hind limbs with a reticulated

pattern of black slender bands is typical of *P. excelsus*, being formed by thick bands and on a wider/extended cream background in *P. spectabilis*. Based on the study of a population sampled from Meseta de Chenqueniye'n and samples deposited at MVZ collection (considered in previous articles as *P. spurcus*), as well as on morphological (see Table 4) and genetic differences (Table 3) found in our comparisons, we conclude that these lizards represent an independent lineage (see phylogenetic tree in Figure 1) that deserves a formal description.

Species description

Phymaturus chenqueniye'n sp. nov.

(Figs. 2B and 8).

Phymaturus spurcus: Lobo and Quinteros (2005a), in part; Lobo *et al.* (2012a) in part; Lobo *et al.* (2018), in part.

Phymaturus sp. 13: Morando *et al.* (2013).

Holotype.— IBIGEO 6198. Male (Fig. 2B). Between Las Bayas village and Las Bayas hill (also named as Alto del Escorial), at the edge of the Chenqueniye'n plateau (41° 29.238' S, 70° 41.557' W; 1139 m) Ñorquinco department, Río Negro province, Argentina. Date 16 January 2020. Deposited at the Reptile collection of the Instituto de Bio y Geociencias del Noa (IBIGEO), Salta, Argentina.

Paratypes.— IBIGEO 6184, 6186, 6200; MVZ 188904-05, 247102-03, 247105 (6 adult males, 2 juvenile males); IBIGEO 6185, 6196-97, 6199; MVZ 247101, 247104, 247106, 188906-07 (6 adult females, 3 juvenile females). Deposited at the Reptile collection of the Instituto de Bio y Geociencias del Noa (IBIGEO), Salta, Argentina, and Museum of Vertebrate Zoology (Berkeley, California, USA). IBIGEO samples collected from Meseta Chenqueniye'n, same site of Holotype between Las Bayas and Alto el Escorial or Cerro Las Bayas (41° 29.238' S, 70° 41.557' W; 1139 m). Ñorquinco department, Río Negro province, Argentina. Date 16 January 2020. MVZ samples: MVZ 188904-07. Ñorquinco department, along rimrock, 4 km S and 1 km E Alto del Escorial, elevation: 1100 m. Río Negro province, Argentina. 25 February 1982. MVZ 247101-07. Ñorquinco department, along rimrock, 4 km S and 1 km E Alto del Escorial, elevation: 1100 m. Río Negro province, Argentina. 23 November 1986. DNA samples: IBIGEO 6197, 6199.

Diagnosis (Fig. 2B and 8; Table 4; S2).— *Phymaturus chenqueniyei* sp. nov. belongs to the *patagonicus* group of *Phymaturus* because it exhibits flat and imbricated superciliary scales, smooth tail scales, and a set of enlarged scales projected onto the auditory meatus (Etheridge, 1995; Lobo and Quinteros, 1995). Within the *patagonicus* group, *Phymaturus chenqueniyei* sp. nov. belongs to the *spurcus* clade because it shares the following morphological apomorphies (according to the total evidence analysis, excluding *P. manuelae*): females exhibit ocellated (not ringed) tails, presence of two longitudinal rows of ocelli in both sexes, and scale organs in rostral scale (six changes in DNA positions also support this clade). Since *P. manuelae* is included in the group (with high support value) in the Bayesian analysis, we also include this species in our comparisons. *Phymaturus chenqueniyei* sp. nov. has dark brown coloration all over its head, body and limbs; half of the males studied exhibit irregularly distributed light brown markings (mostly on shoulders or neck); belly and chests of *P. chenqueniyei* sp. nov. are dark brown (light gray to white immaculate in all the other members of the *spurcus* group). It is the only species within the *spurcus* clade with melanic individuals, but at a low frequency (3/17, 17%). This melanism was reported in *P. cacivioi*, *P. ceii*, *P. curivilcun*, *P. niger* and *P. tenebrosus* (Lobo et al., 2021). *Phymaturus curivilcun* is sister to the other taxa of the group but without support. *Phymaturus chenqueniyei* sp. nov. differs from *P. manuelae* because it lacks any kind of dorsal pattern, its coloration is dark brown with almost inconspicuous light brown ocelli (*P. manuelae* exhibits white small scattered spots, ir-

regularly distributed or forming transversal rows, as well as conspicuous white dorsal ocelli along the paravertebral region between thighs and shoulder). The interparietal scale is white in *P. chenqueniyei* sp. nov. but brown and inconspicuous in *P. manuelae*. *Phymaturus chenqueniyei* sp. nov. has spinier tail scales than *P. manuelae* (in this species, tail scales are not different from those of the *somuncurensis* or *payunia* clades). Most of specimens of *P. chenqueniyei* sp. nov. have enlarged (3-5) scales on the posterior gular fold margin (absent in *P. manuelae*), *Phymaturus chenqueniyei* sp. nov. has conspicuous anterior gular fold, whereas it is absent in *P. manuelae*; *P. chenqueniyei* sp. nov. has more scales contacting nasal (CN), postocular scales (PO), scales between frontals and rostral scale (RF), and fewer scales counted around midbody (MS). *Phymaturus chenqueniyei* sp. nov. differs from *P. manuelae* in five body measurements: slender trunk (AW), lower auditory meatus height (MH), shorter fourth's toe claw (CL), neck (NL), and tail (TL). *Phymaturus chenqueniyei* sp. nov. differs from *P. spurcus* in that it exhibits a darker brown dorsal coloration; belly and chests are dark brown in *P. chenqueniyei* sp. nov. and light gray/white immaculate in *P. spurcus*. The collected males or females of *P. chenqueniyei* sp. nov. did not exhibit any abdominal coloration typical of the *patagonicus* group (males and some females of *P. spurcus* have yellow abdomen). The interparietal scale is white in *P. chenqueniyei* sp. nov. but brown and inconspicuous in *P. spurcus*. Enlarged scales at the anterior border of the auditory meatus are perpendicular but in *P. spurcus* they extend backward, covering part of the auditory opening;

Table 4. Continuous characters that exhibit significant variation between all pairs of species within the *spurcus* clade (18 of 32 scale counts studied and 8 of 18 measurements studied). Below the diagonal are scale counts significant characters, and above measurement significant characters. Same abbreviations of Table 1.

	<i>P. chenqueniyei</i>	<i>P. excelsus</i>	<i>P. manuelae</i>	<i>P. spectabilis</i>	<i>P. spurcus</i>
<i>P. chenqueniyei</i>		CL EL Hu HW	AW CL MH NL TI	—	AW TI
<i>P. excelsus</i>	GS NS PM PR SO SS TV		AW EL Hu HW MH NL TI	CL EL Hu HW MH	AW CL EL TI
<i>P. manuelae</i>	CN MS PO RF	AF FF GS LO MS PM PR SO TV		CL MH NL TI	CL Hu MH TI
<i>P. spectabilis</i>	AF He Is LO LS NS PO PR RF SO SS UC	AF FF GS He PM RF TV UC	AF CN He Is Ls LO MS NS PR RF SO UC		AW TI
<i>P. spurcus</i>	FF MS PO PR SO SS	AF FF GS MS NS PM TV	RF SO	AF He LO LS MS NS RF UC	



Figure 8. Colors in life of *Phymaturus chenqueniyei* sp. nov. (individuals photographed on rocks of their typical environment). A- Dorsal view of a male (IBIGEO 6200); B- ventral view of the same individual; C- Dorsal view of a female (IBIGEO 6185); D- ventral view of the same individual; E- Dorsal view of a melanic female (IBIGEO 6196); F- ventral view of the same individual.

most of *P. chenqueniyei* sp. nov. individuals have a dorsal fading tail pattern (absent in *P. spurcus*); 8/17 individuals exhibit a fading ocellated pattern in a lighter brown tone with respect to the darker color of background (absent or inconspicuous in adult *P. spurcus*, but present in most newborns and small juveniles); dorsal scales of tail more spiny and ending in dark brown spine (less spiny and with less developed light brown spine in *P. spurcus*); all ven-

tral surface of fingers and toes dark brown to black (in *P. spurcus* a central longitudinal row is darker than the rest of finger or toes, see Lobo *et al.* (2010, Fig. 8D)). *Phymaturus chenqueniyei* sp. nov. shows significant differences from *P. spurcus* in the following continuous characters (eight characters): fewer scales counted around midbody (MS), supralabial scales (SS), postrostral scales (PR) and more scale organs over postrostral scales (SO), postocular scales

(PO), and subdigital plates of fourth finger (FF) and morphometric: slender trunk (AW) and longer tail (TL). *Phymaturus chenqueniyei* sp. nov. differs from *P. spectabilis* in that all *P. chenqueniyei* sp. nov. are dark brown; they may exhibit some lighter coloration on the shoulders or neck and a fading (almost inconspicuous) pattern of ocelli, whereas the brown morphs of *P. spectabilis* show a brown dorsal pattern, speckled with lighter brown or some almost white scales scattered irregularly, sometimes concentrated on sides of dorsum of the trunk (Fig. 6B). Belly and chests are dark brown in *P. chenqueniyei* sp. nov., and light gray/white immaculate in *P. spectabilis*. Ocellated morphs of *P. spectabilis* have black background coloration of the back, with large cream almost white ocelli. The interparietal scale is white in *P. chenqueniyei* sp. nov. but brown in brown morphs of *P. spectabilis*. *Phymaturus chenqueniyei* sp. nov. did not exhibit any abdominal coloration that is typical in the *patagonicus* group (males and females of *P. spectabilis* show abdominal orange color). *Phymaturus chenqueniyei* sp. nov. shows significant differences from *P. spectabilis* in the following continuous characters (12 characters): fewer scales on dorsum of head (He), postrostral scales (PR), supralabials (SS), upper ciliary scales (UC), scales between rostral and frontal (RF), lorilabial scales in contact with subocular (LO), lorilabial scales (LS) internasal scales (Is) more scales along lateral neck fold till the antehumeral fold (AF), neck scales (NS), postocular scales (PO) and scale organs counted on postrostral scales (SO). No morphometric differences between these two species were found. *Phymaturus chenqueniyei* sp. nov. differs from *P. excelsus* in the homogeneous dark brown coloration on the head, body and limbs, sometimes with lighter coloration on shoulders and neck, whereas *P. excelsus* brown morphs have lighter background coloration; the interparietal scale is white in *P. chenqueniyei* sp. nov. but brown and inconspicuous in brown morphs of *P. excelsus*. Belly and chests are dark brown in *P. chenqueniyei* sp. nov. and light gray/white immaculate in *P. excelsus*; the collected males and females of *P. chenqueniyei* sp. nov. did not exhibit any abdominal coloration (males and females of *P. excelsus* show abdominal orange color). *Phymaturus chenqueniyei* sp. nov. shows significant differences from *P. excelsus* in the following continuous characters (11 characters): fewer neck scales (NS), postrostral scales (PR), supralabial scales (SS), postmental scales (PM), more scale organs in postrostrals (SO), gulars (GS), and temporal scales

counted in a vertical line between labial commissure and the superciliaries level (TV). Morphometric: shorter fourth toe claw (CL), smaller eyes (EL), wider head (HW), and wider forelimbs (Hu).

Description of holotype (Fig. 2B).— Male. SVL 89.09 mm. Head length: 16.88 mm. Head width: 16.07 mm. Head height at parietal level 8.46 mm. Axilla-groin length 45.01 mm (44.4 % of SVL). Tail length (complete, not regenerated) 100.22 mm. Body moderately wide, trunk width 34.17 mm (38.3 % of SVL). Nineteen smooth dorsal head scales. Five, two and three scale organs in three postrostrals. Nasal bordered by seven scales, not in contact with rostral. Canthal separated from nasal by two scales. Loreal region flat. Nine enlarged supralabial scales, none contacting subocular. Eight enlarged infralabials. Auditory meatus oval (height 3.8 mm; width 2.7 mm) with six enlarged, flat and smooth perpendicular projecting scales on the anterior margin. Auricular scale absent. Nine convex, juxtaposed temporals. Auditory meatus - ciliary scale distance: 5.5 mm. Rostral scale undivided. Mental scale sub-pentagonal, in contact with four scales. Interparietal scale bordered by eight scales, larger than postparietals. Frontal region without an azygous scale. Supraorbital semicircles inconspicuous. No distinctly enlarged supraoculars. Six juxtaposed superciliaries, 14 upper ciliaries, and 12 lower ciliaries. Subocular fragmented in two scales. Ten lorilabials, ninth to tenth contacting subocular. Preocular of the same size as that of canthal, in contact. Preocular contacting lorilabial row. Scales of throat round, small and juxtaposed. Eighty-three gulars between auditory meata. Lateral nuchal folds well developed, with granular scales on longitudinal fold. Antehumeral pocket well developed. Ninety-three scales between auditory meatus and shoulder. Seventy-four scales between antehumeral fold and shoulder. In ventral view, anterior gular fold absent, posterior gular fold present with its anterior margins with three enlarged scales on their borders. Dorsal scales round, smooth and juxtaposed. Forty dorsal scales along midline of the trunk in a length equivalent to head length. Scales around midbody: 218. Ventral scales larger than dorsal scales. Ventral scales between mental and preloacal pores: 174. Nine preloacal pores in an undivided row without supernumerary pores. Two enlarged postloacal scales. Brachial and antibrachial scales smooth, with round posterior margins. Supracarpals laminar, round and smooth. Subdigital lamellae of fingers have three keels.

Subdigital lamellae of finger (left manus) IV: 22. Supradigital lamellae convex, imbricate. Infracarpals and infratarsals have round margins and 2–3 keels. Supracarpals and supratarsals smooth, with rounded posterior margins. Subdigital lamellae of toe (left pes) IV: 28. Claws moderately long (fourth toe's claw: 2.4 mm).

Coloration in life (Fig. 2B).— The holotype exhibits a homogeneous brown dorsal background, with light brown cream colored scales on dorsum of neck and shoulders. Toward the trunk, these cream scales become more scattered and irregularly distributed, and are almost absent towards the posterior half of trunk. Dorsum of tail of the same creamy coloration (no obvious ringed or variegated pattern). Head uniformly dark brown, with this coloration extended on the lateral neck folds. Interparietal scale white. Two large melanic spots are conspicuous on the right side, one anterior to the forearm and the other on the shoulder. Flank, fore and hind limbs brown, as the rest of body. Throat immaculate light gray with no variegation. Chest, abdomen, ventral surface of limbs, and tail light gray. Ventral surface of tail does not have any pattern.

Variation.— Squamation based on thirteen adult specimens (7 males and 6 females) and five juvenile individuals (2 males and 3 females); measurements only based on adult individuals. SVL 75.1–99.4 mm (mean = 91.4; SD = 6.8). Head length 16.4–19.9% (mean = 17.7%; SD = 0.9) of SVL. Tail length 0.95–1.12 (mean = 1.05; SD = 0.05) times SVL. Scales around midbody 185–234 (mean = 207.4; SD = 11.9). Dorsal head scales (Hellmich's index) 17–21 (mean = 19.1; SD = 1.2). Ventral scales 155–182 (mean = 167.2; SD = 6.5). Scales contacting interparietal 7–9 (mean = 7.7; SD = 0.6). Scales surrounding nasal 7–11 (mean = 8.6; SD = 1.1). Number of scale organs on postrostrals 3–8 (mean = 4.8; SD = 1.2). Superciliaries 6–9 (mean = 7.6; SD = 0.8). Subocular fragmented in 1–4 scales (mean = 2.6; SD = 0.9). Mental scale in contact with 4–5 (mean = 4.1; SD = 0.3). Number of chinshields 4–7 (mean = 5.9; SD = 0.9). Twelve of 18 specimens exhibit enlarged scales on the border of the posterior gular fold: 0–5 (mean = 2.4; SD = 1.7). Lorilabials 8–13 (mean = 10.1; SD = 1.4). Enlarged scales on the anterior border of the auditory meatus 4–8 (mean = 6.8; SD = 1.3). Scales of neck along longitudinal fold from posterior border of auditory meatus to shoulder 77–97 (mean = 87.4; SD = 5.8). Gulars 71–96 (mean = 78.7; SD = 6.3). Scales between rostral

and frontal 7–10 (mean = 8.5; SD = 0.9). Subdigital lamellae on fourth finger 19–27 (mean = 22.9; SD = 2.2). Subdigital lamellae on fourth toe 23–31 (mean = 27.4; SD = 1.9). Males with 8–11 precloacal pores (mean = 9.0; SD = 1.1). No females show precloacal pores. Eye length 3–4.1 (mean = 3.4; SD = 0.4). Head length 13.4–17.3 (mean = 15.9; SD = 1.0). Neck length 10.7–16.4 (x = 13.3; SD = 1.2). Head width 13.2–16.9 (mean = 15.5; SD = 1.1). Head height 7.0–9.9 (mean = 8.5; SD = 0.8). Internares distance 2.3–3.3 (mean = 2.9; SD = 0.3). Interorbital distance 5.9–7.6 (mean = 7.1; SD = 0.5). Trunk length 35.6–54.5 (mean = 46.9; SD = 4.9). Humerus length 12.2–16.4 (mean = 13.8; SD = 1.0). Humerus width 4.7–6.7 (mean = 5.9; SD = 0.7). Tibia length 13.5–18.8 (mean = 16.9; SD = 1.4). Foot length 19.9–25.6 (mean = 24.2; SD = 1.5). Tail length 85.2–104.7 (mean = 96.8; SD = 5.8). Eye -auditory meatus distance 4.3–5.9 (mean = 5.3; SD = 0.4). Auditory meatus height 3.1–4.2 (mean = 3.8; SD = 0.3). Fourth toe's claw length 2.3–0.3 (mean = 2.3; SD = 0.3). Abdominal width 28.9–44.3 (mean = 35.7; SD = 4.3). Individuals of *Phymaturus chenqueniye* sp. nov. (Fig. 8) exhibit a brown coloration all around their trunks. This color is extended on the tail and fore and hind limbs. Four males (of a total of nine) also exhibit an irregular spotting of a lighter coloration (cream) on neck and shoulders. Eight of 18 individuals (independent of sexes) show a vanishing pattern of lighter brown ocelli than the dark brown background coloration. In addition, three individuals are completely melanic (Fig. 8E and F). Only six specimens have a white interparietal. Five individuals show few scattered black scales on throats. Tails of half of the sample of individuals exhibit reticulated pattern (not very conspicuous), with irregular light brown cream spots scattered on the darker brown coloration. Females with dorsal background coloration brown all over head, trunk, tail and limbs. Interparietal brown, inconspicuous. Light brown coloration speckled on flank and on the mid-dorsal line. Most of the ventral surfaces immaculate, brown to light brown. Darker coloration on ventral surfaces of jaws than in the middle of throat. Tail light-brown creamy, no pattern is evident.

Etymology.—Its name refers to the Patagonian plateau called Chenqueniye.

Distribution (Fig. 5).— The species occurs in Meseta de Chenqueniye, a flat elevated plateau area

of about 260 square kilometers. Known from three close sites along National Road 1s40 (ex 40), with less than 6-km distance between the two extreme sites.

Discussion

Relationships within the *somuncurensis* and *spurcus* clades

Relationships among clades of the *patagonicus* group remain uncertain, with none of the hypothesis obtained in the last years having support to be accepted with confidence. Our inclusion of two new taxa, more sequences (five DNA markers of four species) and additional morphological data for several species has not modified this situation.

Our results about the *somuncurensis* clade agree with those obtained by Lobo *et al.* (2018). *Phymaturus tenebrosus* is the sister taxon of the other members of the *somuncurensis* clade and the subclade *calcogaster* (*P. calcogaster*, *P. camilae*, and *P. yachanana*) is sister to the remaining species. The relationships found among most terminal taxa differ from those reported by Lobo *et al.* (2018). *Phymaturus etheridgei* is sister taxon of *P. sp. 22b* and *P. sinervoi* of *P. sp. 22a* in Lobo *et al.* (2018) but it is sister taxon of *P. sinervoi* in the present total evidence analysis and of *P. maquinchao* sp. nov. in the Bayesian tree (Fig 1B). The inclusion of *P. maquinchao* sp. nov. with additional sequences and morphology changes this position (Fig. 1). Our Bayesian analysis breaks the monophyly of the *calcogaster* subclade recovered in Lobo *et al.* (2018); the remaining relationships are the same, i.e. *P. maquinchao* sp. nov. is sister taxon of *P. sp. 22b*. The inclusion of new data (taxa, morphology, and DNA sequences) can affect the results of the analyses and, consequently, the topologies; however, we consider that such effect is not very drastic. The completion of our knowledge of morphologies and DNA markers in candidate species, and the more careful exploration of this clade will probably provide a more complete picture of the *somuncurensis* clade, its composition and evolutionary relationships.

The inclusion of *Phymaturus curivilcun* and *P. chenqueniyei* sp. nov. did not affect the main topology; in the total evidence analysis, *P. manuelae* is not related to *somuncurensis* clade, and *P. curivilcun* –a species that was not previously evaluated– is recovered as sister of the remaining species of the *spurcus* clade but with weak statistical support. Then,

P. chenqueniyei sp. nov. (*P. sp. 13* in Morando *et al.*, 2013) is the sister taxon of the remaining species (in Lobo *et al.*, 2018, sister taxon of *P. excelsus*), and *P. spurcus* is the sister taxon of the clade formed by *P. excelsus* and *P. spectabilis*. In comparison to Lobo *et al.* (2018), with the inclusion of *P. curivilcun* and *P. chenqueniyei* sp. nov., the Bayesian topology only changed in the position of *P. spurcus*, now placed as sister taxon of *P. spectabilis* plus the clade formed by *P. excelsus* and *P. chenqueniyei* sp. nov. In contrast to findings reported by González Marín *et al.* (2018), we do not consider *P. calcogaster* as an independent clade because 1) *P. yachanana*, *P. camilae* and *P. calcogaster* (forming or not a monophyletic grouping) are nested within the *somuncurensis* clade, and 2) the authors include *P. patagonicus* within their *calcogaster* clade, and our previous phylogenetic analysis does not support this relationship (*P. patagonicus* is outside the *somuncurensis* clade and more related to *P. katenke*, and *P. sp14* and *P. sp15*.) (Lobo *et al.*, 2018; Morando *et al.*, 2020). In addition, we considered *P. tenebrosus* as member of the *somuncurensis* clade (recovered in both the total evidence analysis and the Bayesian tree), González Marín *et al.* (2018) included this species in the *spurcus* clade.

More information on morphology is available for the study of *Phymaturus*

Morphological data can be used for many purposes, sometimes for studying the evolution and the effect of selection in certain systems of characters (e.g. Tulli *et al.*, 2011; Reaney *et al.*, 2018; Valdecantos *et al.*, 2019; among others), for resolving taxonomic problems or the description of the diversity of a group (e.g. Avila *et al.*, 2011; Scolaro *et al.*, 2012; Avila *et al.*, 2014; Scolaro *et al.*, 2016; González Marín *et al.*, 2016a; 2016b; among others), or for providing phylogenetic information (Lobo and Quinteros, 2005a; Lobo *et al.*, 2012a; 2016; 2018). Morphology is not restricted to the revision of a limited set of characters, as is done in certain publications, but involves much more diverse data. Therefore, authors' conclusions in those examples often suggest the power of morphology in this group as highly conservative and not very informative. Their conclusions sometimes are based on the study of a subset of characters or systems of characters, which should not be taken as a general morphological rule, but which were obviously useful just for meeting the objectives that they set. In fact, in a recent study, González Marín *et al.* (2018)

analyzed the body shape morphology (based on 11 linear measurements and the geometric analysis of heads in species of the *patagonicus* group). “*In this study we quantify levels of morphological divergence (size and shape) among the multiple species relative to interspecific molecular divergence, and show that most species have not diverged significantly in size and/or shape to permit unambiguous species diagnosis with morphological data alone*”. It is a type of generalization that we do not agree with the authors’ conclusion indicates that morphological data are insufficient to make species diagnosis, since diagnoses are usually built based on squamation and color pattern characters. They studied a reduced dataset with respect to the 271 characters described in the literature (see character lists in Lobo and Quinteros 2005; Lobo *et al.*, 2012a; 2016; 2018; 2019; 2021) for the genus *Phymaturus*; of those characters, 114 were found informative for the *patagonicus* group. The need for such claims is unclear, since, to our knowledge, there is no description of *Phymaturus* based solely on body size or body shape characters. Similarly, if we study only a couple of DNA markers and state that genomes of these species are invariant or constant, probably we may be arbitrary in our conclusions. After 15 years of morphological, taxonomic and phylogenetic studies, we have incorporated new characters that we can be used to address new questions. Over this period, we have gathered a body of more than 300 characters that can be used (see character lists in Lobo *et al.*, 2012a; 2019; 2021). Anyway, our results show that most morphometric (linear) characters have ranges of values that overlap among species and are not useful to elaborate a diagnosis of a species, but they are very informative to determine the taxonomic status of different populations (when added to other sources of evidence) see Tables 1-2 and 4. In the present contribution, we have added this information to qualitative characters derived from scalation, bones, hemipenis, precloacal glands, colors, and color patterns (see Lobo *et al.*, 2021). Curiously, González Marín *et al.* (2018, Table 2) found significant differences in measurements among most of the species of the *patagonicus* group, even though these characters alone cannot be used to make a taxonomic diagnosis. How does evolution occur through the different character systems? Do integumentary traits, like scale numbers or ornamentation features, exhibit the same evolutionary degree of change as that of color and patterns, or morphometric traits?. In Lobo *et al.* (2021) we

measured those sets of characters separately for the entire *patagonicus* group. In the phylogenetic trees inferred for the *patagonicus* group, we estimated the evolutionary lability index (ELI) for the whole morphological data set *sensu* Poe and Wake (2004), who proposed this method for ontogenetic changes in evolution. We calculated the index for each character as follows: (number of changes – number of stases) / (number of changes + number of stases). A stasis is a branch of the tree that does not exhibit a change in the character. For example: character 120 (presence/absence of dark lateral band) changed three times on the tree, whereas the number of branches in stasis is 67, so the lability index is $(3 - 67) / (3 + 67) = -0.914$. Values range between -1 and 1. Continuous characters were divided into two subsets: morphometric (20 characters) and scale counts (21). We found the first subset to be more conservative, given that the average ELI of all morphometric characters was -0.885 versus -0.764 for the scale counts. The discrete characters were divided into scalation (33 characters) versus pattern and color (43 characters). The scalation characters were slightly less conservative than pattern and color characters (scalation = -0.801; pattern and colors = -0.852).

According to these results, when reviewing the literature of species descriptions of *Phymaturus* and phylogenetic studies, we found that scale characters (scale counts and discrete characters), the most widely used were those that exhibited most of the changes during the evolution of the group (after calculating ELI), followed by the characters referring to pattern designs and colors. However, our analyses in Lobo *et al.* (2021) are preliminary. Have we addressed only a part of the general morphology of these animals, and what would happen if we also analyzed the anatomical features, like skeletal, muscular, or genital characters? Regarding the taxonomy objectives of this article, we demonstrate that overall morphology is more informative than can be expected, even in clades and subclades of closely related species like in *Phymaturus* (see Tables 1-2 and 4). This amount of information, along with other qualitative characters, like scale ornamentation and color patterns, is useful for analyzing the taxonomic status of the described species, even when mtDNA distances can be small in some complexes.

The truly integrative taxonomy

Corbalán *et al.* (2016) remarked the low genetic

distance among *P. ceii*, *P. somuncurensis*, and *P. sinervoi*, as for species of the *spurcus* clade (*P. spurcus*, *P. excelsus*, and *P. spectabilis*), but they made an asymmetric decision, since they proposed only the synonymy for all species of the latter clade. Contrary to DNA information, our morphological analyses of continuous characters including scale counts and morphometry (see Tables 1, 2 and 4) show more morphological divergence among species of the *spurcus* clade than that detected among the three species of the *somuncurensis* clade. In fact, within the *somuncurensis* clade we found: *P. camilae*-*P. calcogaster* (scalation: 0 character; morphometry: 1); *P. camilae*-*P. sinervoi* (1/0); *P. sinervoi*-*P. ceii* (0/1), *P. camilae*-*P. somuncurensis* (0/0); *P. somuncurensis*-*P. maquinchao* sp. nov. (0/2); *P. somuncurensis*-*P. calcogaster* (0/4); *P. sinervoi*-*P. somuncurensis* (1/0), *P. ceii*-*P. somuncurensis* (2/1).

Within the *spurcus* clade we found: *P. excelsus*-*P. spectabilis* (8/5), *P. excelsus*-*P. spurcus* (6/3) and *P. spectabilis*-*P. spurcus* (8/2). We consider here all taxa (of the two clades) as valid, taking into account that, beyond the comparisons we made on continuous characters, there are also characters of color and patterns that discriminate all these species.

Brown morphs of *Phymaturus spectabilis*, always show the striped type, unlike those of *P. spurcus* and *P. excelsus*, which exhibit the homogeneous brown, not striped type (Fig. 7). That was probably one of reasons why Scolaro *et al.* (2008) described *Phymaturus agilis*. In Becker's (2018) contribution, the authors advocated, even in the title, for the integrative taxonomy as the preferred tool to discriminate and/or delimit species, but in this pursue they just made some remarks on what they call the "*spurcus*" morph. They restricted their analysis of integrative taxonomy to a single morphological character (presence or absence of a "*spurcus* morphotype"). Here we analyzed 49 continuous characters of squamation and measurements plus four color pattern characters, and revised the brown morphs of all species, the only morphological character studied by Becker *et al.* (2018). Confusion arose and led authors to wrong conclusions because they assigned the same character state to all members of the group, *P. spurcus*, *P. excelsus* and *P. spectabilis*, since all of them exhibited the same "*spurcus* morphotype". Their observations on the offspring recorded from *P. agilis* and *P. spectabilis* confirmed our observations (Lobo *et al.* 2012b). Their observations on brown morph giving birth to an *excelsus* in Ojo de Agua is

also not surprising, since we pointed out that it is the polymorphism of that species. Unfortunately, Becker *et al.* (2018) did not show pictures of patterns of the female and the newborn. Becker *et al.* (2018) were not able to discriminate that brown morph (*spurcus*) from the *spectabilis* one. What we never found until today is a single *P. spurcus* individual from its type locality (Estancia Huanuluan) showing the ocellated pattern. Noticeably, some brown morphs of other species of the *patagonicus* group are more similar to *spurcus* than to *spectabilis* or *excelsus* ones (see Fig. 5 in Lobo *et al.*, 2018). Here, based on different collection samples, we demonstrate that each of the above mentioned species have its particular brown morph (see Fig. 7). In addition, we provide morphometric and squamation characters that show statistically significant differences among species (Tables 1, 2 and 4), and five characters of color pattern: abdominal life color (yellow in *P. spurcus* but orange in *P. spectabilis* and *P. excelsus*), brown morphs, limb pattern, size and shape of dorsal ocelli, and dorsal white spots distribution (Fig. 7). Morphology can provide more information than that used so far; regarding this aspect, Becker *et al.* (2018) indicate in the discussion section: "*The P. spurcus populations studied here might be useful in identifying similar processes of incipient speciation, given that their dorsal pattern polymorphisms are also associated with ventral color polymorphisms (Fernández JB, Boretto JM, Ibargüengoytia NR, and Sinervo B, unpublished observations).*"

No shared haplotypes among species supported by morphology

In both analyses, Corbalán *et al.* (2016) and Becker *et al.* (2018), built their tree using COI, and recovered the monophyly of *P. spurcus* and *P. excelsus*, but not of *P. spectabilis* and/or *P. agilis*. Because this complex of species does not match their BIN definition (barcoding index), they concluded that *P. spurcus*, *P. spectabilis*, *P. agilis* and *P. excelsus* are the same species. Corbalán *et al.* (2016) after their comparisons considered *P. ceii*-*P. somuncurensis*-*P. sinervoi*; *P. indistinctus*-*P. videlai*; and *P. payuniaie*-*P. nevadoi* as valid species despite having a very short genetic distance (such as the genetic distance found between *P. spurcus*-*P. excelsus*-*P. spectabilis*). Their interpretation was different for both clades only based on the fact that the species of the *somuncurensis* clade are geographically separated by greater distances. We consider that geographic/spatial isolation can occur

between populations and cause speciation at a much smaller geographic scale than the one exhibited by for example between *P. ceii* and *P. somuncurensis*. In their final considerations, Corbalán *et al.* (2016) indicate that “species delimitation ideally requires data from many different sources such as morphology, behavior, and multiple molecular markers (Funk and Omland, 2003; Hajibabaei *et al.*, 2007)” and: “Therefore, DNA barcoding can fail to identify species when introgression, incomplete lineage sorting, or complex species are involved (Vences *et al.*, 2005a, b; Smith *et al.*, 2008). In such cases, nuclear loci are necessary to reliably identify species (Hebert *et al.*, 2003a; Murphy *et al.*, 2013).” In their Discussion section, Becker *et al.* (2018) remark: “Despite their relatively narrow distribution, gene flow seems to be restricted among *P. spurcus* populations as revealed by genetic structure, except between the North and South Yuquiche Hill, whose haplotypes were found in common. Thus, *P. spurcus* appears to be a single highly structured species whose populations seem to be experiencing a process of divergence in morphometric and meristic characteristics and dorsal color patterns from a common, ancestral population. The star-shaped haplotype network agrees with this hypothesis, and the small genetic pairwise distances among haplotypes are in accordance with a recent diversification.”

Becker *et al.* (2018) found no shared haplotypes among *spurcus* type locality, *excelsus* and *spectabilis* / *agilis*, but they only found shared haplotypes between south and north of Yuquiche Hill (individuals identified as *spectabilis* and *agilis*), in agreement with Lobo *et al.* (2012b), who showed that *P. spectabilis* and *P. agilis* are synonyms, based on the lack of statistical differences in measurements or squamation, and on the evidence of a mother giving birth individuals with both patterns. Divergence in morphometric and meristic characteristics as well as color patterns suggests that these lizards may be distinguishable species; in such a case, we agree that it must be a recent process of isolation. Anyway introgression and the existence of shared haplotypes have been detected among different closely related vertebrate species (i.e. Méndez Rodríguez *et al.*, 2021 in bats, Chen *et al.*, 2009 in frogs, etc.); therefore, this fact cannot be a sufficient argument to synonymize the described species. We agree that the genetic distance is quite low for mitochondrial DNA among *P. spurcus*, *P. excelsus* and *P. spectabilis* (Table 3).

González Marín *et al.* (2018) performed a combined analysis of mitochondrial and nuclear mark-

ers, and indicated that the limitation of these two studies (Corbalán *et al.*, 2016; and Becker *et al.*, 2018) to detect the independence of lineages in the case of the *spurcus* clade is that they are almost exclusively based on mtDNA. In fact, our morphological results agree with findings of González Marín *et al.* (2018, Fig.2), who provided molecular support for divergence for the species *P. spectabilis*, *P. spurcus*, and *P. excelsus*. In a recent contribution to the taxonomy of a *Liolaemus* complex of species (*leopardinus* group) made by Esquerré *et al.* (2019b), they found strong conflicting signals between phylogenetic analyses of the nuclear and mtDNA data, but they discovered a consistent match between nuclear and morphological data. The authors stressed the importance of using multiple lines of evidence to resolve evolutionary histories, and the potential misleading results from relying solely on mtDNA. Our results are similar to previous findings in other groups of vertebrates, such as those reported by Pedraza Marrón *et al.* (2019). The authors combined different molecular sources of evidence and discriminated two species of fishes that were previously lumped after only mtDNA analyses. The conclusions of Pedraza Marrón *et al.* (2019) are in agreement with the old morphology-based taxonomy of the group that discriminated these two species just based on two morphological traits.

Conclusion

Phymaturus katenke is related to *P. patagonicus* and other two candidate species (*P. sp.* 14 and *P. sp.* 15), one of them close to the locality of El Sombrero. Lobo and Quinteros (2005b) collected a sample of specimens from that locality and at that time assigned it to *P. patagonicus*, indicating some differences with the type locality population (Dolavon, Chubut province), such as the presence of two rows of dorsal ocelli. Further studies are needed to revise those two candidate species. This natural group might be recognized as the *katenke* clade (Fig. 1 and Fig. 5 green circles), but its relationships with other clades is uncertain and not well supported. *Phymaturus curivilcun* is recovered in both analyses as sister to all members of the *spurcus* clade, but without support; indeed, because of the extreme melanism of this species, it was not possible to record color characters and patterns that are so informative in the systematics of this group. Its phylogenetic position continues to be a subject pending investigation. The *somuncurensis* clade still needs more studies. *P.*

sinervoi, *P. ceii*, and *P. somuncurensis* exhibit quite low morphological differentiation among them; DNA markers studied to date also show restricted to null distance among them (Corbalán *et al.*, 2016). A similar situation is observed within the *spurcus* clade, but in the latter case more morphological differentiation is evident (see Tables 2 and 4). *Phymaturus maquinchao* sp. nov. is closely related to *P. etheridgei* and *P. sp. 22b*; the morphology of *P. sp. 22a* and *P. sp. 22b* is lacking and should be analyzed. It would also be very useful to add ND4 sequences because they were proved to be very informative for recovering phylogenetic relationships (see Lobo *et al.*, 2018: Table 2). Although the title of Becker *et al.* (2018) claims "An integrative approach to elucidate the taxonomic status...", the work analyzed a single morphological character (presence/absence of "*spurcus* morphotype. This "*spurcus* morphotype" was wrongly interpreted as being the same for all taxa, and, what is more controversial, the authors arrived to that conclusions without studying the type series of the involved species. Furthermore, they did not show vouchers of individuals that allow the scrutiny of other researchers about the identity of specimens, and the correspondence between phenotypes, haplotypes and localities. They indicate: "*Species assignment was based on external morphology. Most lizards (N = 130) were released at their exact site of capture within 48 h after tissue sampling from the tip of the tail, and only seven individuals were euthanized and tissue samples taken from liver.*" Their Appendix 2 shows the number of DNA extracts deposited at the MACN barcoding laboratory, but no vouchers of specimens are mentioned. The lack of vouchered samples does not allow other authors to corroborate their interpretations and the proper taxonomic identification. Because results shown in the present study (statistical analysis of continuous characters and the revision of color pattern variation) and results obtained by Becker *et al.* (2018) that did not find shared haplotypes among species (only within *spectabilis-agilis* samples), we consider that the taxonomic status of *P. spurcus* Barbour 1921, *P. excelsus* Lobo and Quinteros 2005, *P. spectabilis* Lobo and Quinteros 2005 should be maintained. Our results indicate several morphological traits showing significant differences among species/populations within the *spurcus* clade. If these entities are not species, is it possible to have such levels of morphological differentiation? If these cannot be considered full species, then can we say that we are

able to discriminate populations within *Phymaturus* based on morphological characters? In terms of conservation, recent diversification processes should be considered, reported and classified. From the point of view of conservation, in the case of *P. spurcus*, *P. excelsus* and *P. spectabilis*, if we consider them only a single species distributed in a vast extension, this would require less concern and conservation priorities than if we valued them as they really are: independent entities that carry their own particular phenotypic diversity. There are no sufficient arguments to change the taxonomy of the *spurcus* clade as it is known up to now (Lobo and Quinteros, 2005a; Lobo *et al.*, 2012a; Morando *et al.*, 2013; González Marín *et al.*, 2018; Lobo *et al.*, 2018).

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- SUPPLEMENTARY FILES**
- Supplementary materials cited in this article are available upon request from FL
- Supplementary 1.** All character information (average, standard deviation, and sample size) taken for comparisons among species of the *somuncurensis* clade and outgroup species.
- Supplementary 2.** All character information (average, standard deviation, and sample size) taken for comparisons among species of the *spurcus* clade and outgroup species.
- Supplementary 3.** PCA tables resuming information of analyses.
- APPENDIX 1**
- Specimens included in the present study (type series data of *Phymaturus chenqueniyei* sp. nov. and *Phymaturus maquinchao* sp. nov. are provided in their respective descriptions).
- Phymaturus calcogaster* (n = 16)
MACN 39990-91 (paratypes), JAS-DC 799, 803, 1096-97: Laguna de las Vacas, Telsen Dept, Chubut Province, Argentina; JAS-DC 1154-55, Bajo Amarillo, Telsen Dept, Chubut Province, Argentina. MCN-UNSa 4295-98, 4301-04, Laguna de las Vacas, southwestern end of the lake (42°29'05.60"S, 67°21'00.03"O, 651 m), Telsen Dept, Chubut Province, Argentina.
- Phymaturus camilae* (n = 4)
MLP5786 (holotype), MLP 5787-89 (paratypes). In volcanic rocky outcrops (1100 m) of Sacanana stream bridge, adjacent to Provincial Road 4, (42°27'55.4"S, 68°43'33.3"W), Chubut Province, Argentina.
- Phymaturus ceii* (n = 21)
MCN-UNSa 910-18, RP No. 8, 17 km S of San Antonio del Cuy, 25 de Mayo Dept, Río Negro Province, Argentina. MACN 44738 (ex MCN-UNSa 3914), MACN 44739 (ex MCN-UNSa 3918), MACN 44740 (ex MCN-UNSa 3921), MACN 44741 (ex MCN-UNSa 3923), MACN 44742 (ex MCN-UNSa 3928), MACN 44743 (ex MCN-UNSa 3941), MCN-UNSa 3913, 3916, 3920, 3939-40, 3942, on RP No. 6 (40°20'047.1"S, 68°58'050.3"W, 1,194 m), El Cuy Dept, Río Negro Province, Argentina.
- Phymaturus curivilcun* (n = 8)
MLP 6339 (holotype). 6340-41, 6342 (three individuals), 6343. Paraje El Mirador (42° 27' S; 70° 03' W; 1100 m, datum = WGS84), Provincial road N° 4, approximately 80 km NW of Gastre, Cushamen Department, Chubut Province, Argentina. IBIGEO 6180. Paraje El Mirador 42° 26.980' S 70° 02.154' W. 1178m. Provincial road N° 4, approximately 80 km NW of Gastre, Cushamen Department, Chubut Province, Argentina.
- Phymaturus etheridgei* (n = 17)
FML 23495 (holotype) FML 23496-501 (paratypes), MCN-UNSa 4305, 07-08, 10, on RP No. 76, between Ingeniero Jacobacci and Moligüe (41°34'047.2"S, 69°23'033.0"W, 818 m), 25 de Mayo Dept, Río Negro Province, Argentina. FML 8435, MCN-UNSa 3109-13, 43 km N of Moligüe (41°35.8800S, 69°22.6280W), 25 de Mayo Dept, Río Negro Province, Argentina.
- Phymaturus excelsus* (n = 13)
MCN-UNSa 1582 (holotype), MCN-UNSa 1582-89, RP No. 6, 1 km NW from Ojo de Agua (41°32'030"S, 69°51'033"W, 1,141 m), Ñorquinco Dept, Río Negro Province, Argentina. MCN-UNSa 1590. RP No. 6, 1 km NW from Ojo de Agua (41°32'030"S, 69°51'033"W, 1,141 m), Ñorquinco Dept, Río Negro Province, Argentina. MCN-UNSa 1386,88. from Ojo de Agua, Ñorquinco Dept, Río Negro Province, Argentina. MCN-UNSa 1385,87. from Ojo de Agua, Ñorquinco Dept, Río Negro Province, Argentina.
- Phymaturus indistinctus* (n = 24)
IBA 666-1, (Holotype), IBA 666-2-3, 2 km W Lago Munsters, Las Pulgas (700-800 m), Sarmiento Dept., Chubut Province, Argentina. MCN-UNSa 1274-77, Las Pulgas, Sarmiento Dept, Chubut Province, Argentina. MCN-UNSa 3943-55. RP No. 20, 19 km W to Los Manantiales (45°27'0S, 69°42'0W, 669 m).
- Phymaturus katenke* (n = 8) IBIGEO 6165-72. Los Adobes, Paso de Indios, Chubut Province. Argentina. (43°15'37.59"S; 68°53'16.83"W 839m).

Phymaturus manuelae (n = 7)

UNCo-PH 201-02 (paratypes), JAS-DC 1251, 26 km W Comallo, adjacent to RN No. 23, Pilcaniyeu Dept, Río Negro Province, Argentina. MCN-UNSa 3929-30, 3932-33, between Pilcaniyeu and Las Bayas on RN1S40 (ex- RN No. 40; 41°12011.1"S, 70°41030.9"W, 1,014 m), Pilcaniyeu Dept, Río Negro Province, Argentina.

Phymaturus patagonicus (n = 37)

MLP 778 (lectotype), MLP 777 (paralectotype), Chubut Province, Patagonia, Argentina. FML 10079-85, 1 km W from junction of RP 53 and RP 90, 2.2 km SW Meseta El Sombrero, Paso de Los Indios Dept, Chubut Province, Argentina. IADIZA 80, 40 km W Dolavon, 350 m, Gaiman Dept, Chubut Province, Argentina. IBA 783(4), IBA 785, 20 km W from Sombrero, Paso de Los Indios Dept, Chubut Province, Argentina. IBA 787, IBA 789 (7), MCN-UNSa 1284-86, 40 km W Dolavon, Gaiman Dept, Chubut Province, Argentina. MCN-UNSa 1250-58, 1261, hills in front of El Sombrero, Paso de Los Indios Dept, Chubut Province, Argentina. SDSU 1980, 40 km WSW Dolavon, Gaiman Dept, Chubut Province, Argentina.

Phymaturus payuniiae (n = 45)

IBA 769-2, 769-4-8, 769-10, 76912, 769-17, 769-20, 769-24, 769-26 (type series), Payún Plateau (2,000 m), 5 km from Volcán Payún Malargüe Dept, Mendoza Province, Argentina. IADIZA 87-8-9, 20 km SE Volcán Payún (1,800 m) Malargüe Dept, Mendoza Province,

Argentina. MCZ 152079-81, basaltic rocks of the Payún Plateau, Malargüe Dept, Mendoza Province, Argentina. REE-SDSU 2330-32, 2339, SDSU 1981-84, 10 km SW base of Volcán Payún, Mendoza Province, Malargüe Dept, Argentina. MCN-UNSa 3648-51, 3665-79, on RP No. 183, 16 km S to Payún vulcano (36°40020.8"S, 69°16010.9"W, 1,737 m).

Phymaturus sinervoi (n=9)

MLP 5660 (holotype); MLP 5664; 5920-22; 5929 (paratypes). In rocky outcrops (1000 m) of Cari Laufquen basaltic Tableland in Abi-Saad farm (41°02'12"S, 70°24'30.6"W), adjacent to Provincial Road 6, 61 km north of Ingeniero Jacobacci town, Río Negro Province, Argentina.

Phymaturus spectabilis (n = 38)

MCN-UNSa 1203 (holotype), MCN-UNSa 1204-11, 1214 (paratypes), on RP No. 6, 28 km S Ingeniero Jacobacci, 25 de Mayo Dept, Río Negro Province, Argentina. MCN-UNSa (agilis) 1212-13, 1215. on RP No. 6, 28 km S Ingeniero Jacobacci, 25 de Mayo Dept, Río Negro Province, Argentina. MLP (agilis) 5343 (Holotype), 5344-46, collected in rocky tableland (41° 25' 40" S; 69° 45' 07" W; 1030 m), close to Provincial road 6 south of Ingeniero Jacobacci, Río Negro Province, Argentina. 10 March 2006. MLP (agilis) 5880-83. 41,4342 S; 69,7534 W. 25 de Mayo Dept, Río Negro Province, Argentina. 5/2/2011. MLP 5877-79. 41,4342 S; 69,7534 W. 25 de Mayo Dept, Río Negro Province, Argentina 5/2/2011. FML 23502-15. On provincial road 6, approximately 27 km S of intersection with provincial road 23, Río Negro, Argentina (41°25'43.25"S, 69°45'24"W; 924 m). FML (agilis) 23503-23505, 23508-09. On Ruta Prov. 6, approximately 27 km S of intersection with Ruta Prov. 23, Río Negro, Argentina (41°25'43.25"S, 69°45'24"W; 924 m).

Phymaturus spurcus (n = 17)

MCZ 14791 (Holotype), MCZ 14915 (paratype) Huanuluan,

Pilcaniyeu Dept, Río Negro Province, Argentina. MCN-UNSa 1237-44, 1246-49, hills opposite of Estancia Huanuluan, RN No. 23, 22 km W from Ingeniero Jacobacci, 25 de Mayo Dept, Río Negro Province, Argentina. MVZ 6177. Huanuluan, Pilcaniyeu Dept, Río Negro Province, Argentina.

Phymaturus somuncurensis (n = 29)

IBA 470, IBA 472 (type series), MACN 37436-40, MCZ 156909, 170443-44, Laguna Raimunda, Meseta de Somuncurá, 9 de Julio Dept, Río Negro Province, Argentina. FML 1038, Laguna Raimunda, Meseta de Somuncurá (1400 m) 9 de Julio Dept., Río Negro Province Argentina. IADIZA 212, Meseta de Somuncurá, Cerro Corona, 9 de Julio Dept., Río Negro Province, Argentina. IBA 507, 4, Laguna Raimunda, Meseta de Somuncurá, Río Negro Province, 9 de Julio Dept., Argentina. MACN 37431-35, 2 km N Casco Cecchi, Meseta de Somuncurá, 9 de Julio Dept, Río Negro Province Argentina. REE-SDSU 2433-35, N from Laguna Raimunda, Meseta de Somuncurá. 9 de Julio Dept, Río Negro Province, Argentina. SDSU 1780-83, 2 km N Laguna Raimunda, Meseta Somuncurá, 9 de Julio Dept, Río Negro Province, Argentina. MCN-UNSa 4550 (SJ 25) (41°12013.95"S, 66°53031.94"W, 1060 m), Meseta Somuncurá. 9 de Julio Dept, Río Negro Province, Argentina.

Phymaturus tenebrosus (n = 18)

MCN-UNSa 1271 (Holotype), MCN-UNSa 1264-70, 1272-73 (paratypes), RN No. 40, 20 km S Cerro Alto; Pilcaniyeu Dept, Río Negro Province, Argentina. MCN-UNSa 1591-95, 1597-99, RN No. 23 between San Carlos de Bariloche and Pilcaniyeu, Pilcaniyeu Dept, Río Negro Province, Argentina.

Phymaturus yachanana (n = 14)

MLP 2636 (holotype). 1.74 km South of the Sierra Grande town, east of National Road 3 (41°37'S, 65°20'W, 270 m, datum = WGS 84), San Antonio department, Río Negro province, Argentina. MCN-UNSa 1334-35. Eight kilometer north from junction of RP No. 8 and RP No. 4, Sierra Colorada, Telsen Dept, Chubut Province, Argentina. MCN-UNSa 3281, MCN-UNSa 4314, 4319-20, 8 km north of junction between RP No. 8 and RP No. 4 (on RP No. 8-42°41040.9"S, 65°49017.7"W), Telsen Dept, Chubut Province, Argentina. MCN-UNSa 3272,3274, 3276-78, 3280. Provincial road 8, 80 km NW from intersection of provincial road 4. 42° 11' 20.8" S; 66° 23' 6.7"W. IBIGEO 6228. A 64 km de Pto Madryn cerca del cruce rutas 4 y 8, sobre ruta 8.

Outgroups (DNA sequences)

L. archeforus LJAMM-CNP 9240; *L. buergeri* LJAMM-CNP 2744; *L. kingii* LJAMM-CNP 326/LJAMM3040; *L. lineomaculatus* LJAMM-CNP 7471/SDSU4268; *L. petrophilus* LJAMM-CNP 11121/BYU47098. *P. palluma* MCN 3627. *P. vociferator* LJAMM-CNP 3432. *P. mallimaccii* LJAMM-CNP 2035/MCN1741.

Morphology data:

Liolaemus kingii: SDSU 1670-71, 3378. MCZ 150291. Golfo de San José, Pen. Valdéz, Chubut, Argentina. MCZ 11837, 39-40. Patagonia. MCZ 18948-49. Ultra Cautín, Prov. Cautín Chile. MCN 1545-50. Río Seco, Ruta Nac. 3 entre San Julián y Tres Cerros, S 48°31.817'; O 67°44.081'. MCN 1551-52. Tres Cerros, S48°07.160'; O67°38.384'. MCN 1324. Las

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Pulgas (Cerro frente a Gruta de la virgen) Dpto. Sarmiento, Prov. Chubut, Argentina.

Phymaturus mallimaccii (N = 17): FML 21114. Camino entre Famatina y Mina la Mejicana, 3460 m a.s.l. 28°58'45,9"; S67°42'58,1"W. FML 21117. Camino entre Alto Carrizal y Cueva de Pérez, pasando Famatina 8 kms al sur. 3460 m a.s.l. 28°58'45,9"S; 67°42'58,1"W. FML 1721. (6 ejemplares) Nevado de Famatina, Cueva de Pérez. 3800-4000 m a.s.l. MCN-UNSa 920 (LA 2779) on the road to La Mejicana (28°54'43'S, 67°42'47"W, 3430 m a.s.l.), Sierra de Famatina, Famatina Department, La Rioja Province, Argentina. MCN-UNSa 1483-84 (LA 2035 2002). Camino a la Mejicana, 3430 m a.s.l. 28°54'43"S; 67°42'47"W. Dpto. Famatina. Prov. de La Rioja (CS). MCN-UNSa 1741, Cueva de Pérez, Famatina Department, La Rioja Province, Argentina. MCN-UNSa 3567 (LA 2196). Camino a Mina La Mejicana, 3420 m a.s.l. 28°54'43''S; 67°42'47''W. Famatina Department, Prov. La Rioja. MLP 5360. Quebrada de Ampallados, Cerro de la Cueva de Pérez. S 28 99798; W 67 73719. REE-CSUN 183, 489-491, Sierra de Famatina, Cueva de Pérez, Famatina Department, La Rioja Province, Argentina.

Phymaturus palluma (= *Phymaturus gynechlomus*; N = 32). MCN 3130-3131, Portillo Argentino (Cordón del Portillo, 33°36'53.8"S, 69°29'16.7"W), Mendoza Province,

Argentina. MCN 3612-13, 3619-22, Portillo Argentino, Arroyo Guardia Vieja (33°36'53.8"S, 69°29'16.7"W), Mendoza Province, Argentina. MVZ 126991, Valle Hermoso (35°20'S, 70°15'W), Malargüe Department, Mendoza Province, Argentina. MVZ 126992-126894, Lago de la Niña Encantada (33°18'S, 69°83'W, 2000 m a.s.l.), 6 km east of Molles, Mendoza Province, Argentina. MVZ 126995, at the north end of Valle Hermoso (35°11'S, 70°10'W), Malargüe Department, Mendoza Province, Argentina. MVZ 126996-126999, 4 km NW from Cerro Chupasangral (33°21'S, 69°51'W, 2800 m a.s.l.), Quebrada de Chupasangral, Tupungato Department, Mendoza Province, Argentina. MVZ 127025-127027, 2 km east from Agua Botada (35°62'S, 69°95'W), Malargüe Department, Mendoza Province, Argentina. MVZ 180771-180774, Quebrada Cruz de Piedra (34°26'S, 68°90'W), San Carlos Department, Mendoza Province, Argentina. MCN 3627-30, 3635-43, 3645, Road to Laguna Diamante (34°14'33.6"S, 69°24'00.0"W), San Carlos Department, Mendoza Province, Argentina.

Phymaturus vociferator (N= 7) (*P. cf. palluma* CH, *P. sp. chi* in Lobo and Quinteros, 2005; Lobo *et al.* 2012; Lobo *et al.* 2016). MVZ 199435-38 & 230992. Hotel Termas de Chillán. Región VIII (= Región del Bío Bío), Chile. MCZ 165456. Cordillera de Chillán. Chile. MCZ 169935. Chile.

APPENDIX 2. List of all the species, voucher numbers and Genbank accession numbers of the sequences employed in this study, new sequences obtained in this study are marked in bold. Observations: *P. sp. 11* of Morando *et al.* (2013) here is named as *P. camiliae* (Scolaro *et al.*, 2013); *P. sp. 16* of Morando *et al.* (2013) is named here as *P. rahuensis* (González Martín *et al.*, 2016); *P. sp. 17* of Morando *et al.* (2013) here is named as *P. robustus* (Lobo *et al.*, 2021); *P. sp. 18* of Morando *et al.* (2013) is named here as *P. caciui* (Lobo & Nenda, 2015); *P. sp. 20* of Morando *et al.* (2013) is named here as *P. sinerovi* (Scolaro *et al.*, 2012); *P. sp. 21* of Morando *et al.* (2013) is named here as *P. yachanana* (Avila *et al.*, 2014); *P. felixi_b* of Morando *et al.* (2013) is named here as *P. felixi*. * Asterisks mark species with fragments belonging to different vouchers specimens. The accession numbers AY173912, KF967760, KF967803, KF967809, KF967837, JF272897, JF272908, KF967611 and KF967641 could be aligned only when reverse complement transformation was used.

Species	Vouchers	COI	12S	Cytb	ND4	Cmos	NTF3	PLRL	PNN	Phy38	Phy41	Phy60	Phy64	Phy84	Phy87	Phy89
<i>L. archeiformis</i>	LJAMM- CNP 9240		KF969004	KF968826		KF968633		JF272897	KF967760							
<i>L. buergeri</i>	LJAMM- CNP 2744		AY173912	AY173843	AY367868	AY367896										
<i>L. kingii</i> *	LJAMM- CNP 326/ LJAMM3040		KF969053	JN614929	DQ237465	KF968680		JF272908	KF967803							
<i>L. lineomaculatus</i> *	LJAMM- CNP 7471/ SDSU4268		JX522193	JX522338	AY367875	KF968687		KF967611	KF967809							
<i>L. petrophilus</i> *	LJAMM- CNP 11121/ BYU47098		KF969091	JN847092	AY367849	KF968714		KF967641	KF967837							
<i>P. palluma</i>	MCN 3627		KT203839	KT203834	KT203854	KT203821										JX969274
<i>P. vociferator</i>	LJAMM- CNP 3432		JX969067	JX969016		JX969524		JX969602	JX969425	JX969130	JX969322	JX969177	JX969117	JX969223		JX969269
<i>P. mallinacii</i> *	LJAMM- CNP 2035/ MCN1741		JX969062	JX969011	KT203847	JX969519		JX969499	JX969422		JX969317	JX969173	JX969112	JX969218		JX969269
<i>P. caciui</i> *	LJAMM- CNP 5549/ MCN3938		JX969106	JX969055	MG888420	JX969559		JX969492	JX969461	JX969166	JX969360	JX969211	JX969385	JX969262	JX969415	JX969310
<i>P. calcogaster</i> *	CHIVC472/ LJAMM- CNP 6856/ MCN4301		KU565043	JX969030	MG888406	JX969535		JX969467	JX969438	JX969144	JX969336	JX969187	JX969366	JX969237	JX969391	JX969287
<i>P. camiliae</i>	LJAMM- CNP 3408		JX969110	JX969059		JX969563		JX969496	JX969465	JX969170	JX969364	JX969215	JX969389		JX969419	JX969314
<i>P. castillensis</i> *	CHIVC345/ MCN3976		KU565051	MG888428	MG888407	MG888430										
<i>P. ceii</i> *	CHIVC444/ LJAMM- CNP 1584/ MCN3940		JX969082	JX969031	MG888408	JX969536		JX969566	JX969468	JX969145	JX969337		JX969367	JX969238	JX969392	JX969288
<i>P. chenquienyi</i> *	LJAMM- CNP 3507/ IBIGE0197		OP422205	JX969101	OP433649	JX969554		JX969585	JX969487	JX969161	JX969355	JX969206	JX969380	JX969257	JX969411	JX969306
<i>P. curviflucan</i>	IBIGE06180		OP422206	OP453556	OP425723	OP425726										

<i>P. delheyi</i> *	L J A M M – CNP 5221/ MCN4970	JX969098	JX969047	MG888409	JX969551	JX969582	JX969484	JX969455	JX969158	JX969352	JX969203	JX969379	JX969254	JX969408	JX969303
<i>P. etheridgei</i> *	KU565058	JX969080	JX969029	MG888410	JX969534	JX969564	JX969466	JX969437	JX969143	JX969335	JX969186	JX969365	JX969236	JX969390	JX969286
<i>P. excelsus</i> *	KU565061	JX969083	JX969032	MG888411	JX969537	JX969567	JX969469	JX969440	JX969146	JX969338	JX969188	JX969368	JX969239	JX969393	JX969289
<i>P. felixi</i> *	KU565064	JX969095	JX969044	MG888412	JX969549	JX969579	JX969481	JX969452	JX969156	JX969349	JX969200	JX969377	JX969251	JX969405	JX969300
<i>P. indistinctus</i> *	KU565066	JX969084	JX969033	MG888413	JX969538	JX969568	JX969470	JX969441	JX969147	JX969339	JX969189	JX969369	JX969240	JX969394	JX969290
<i>P. katenke</i>	OP422207	OP453357	OP425724	OP425727	OP425730										
<i>P. maquinchao</i>	OP422208	OP453358	OP425725	OP425728	OP425731										
<i>P. manuelae</i> *	JX969085	JX969085	JX969034	MG888414	JX969539	JX969569	JX969471	JX969442	JX969190	JX969370	JX969241	JX969395	JX969241	JX969395	JX969291
<i>P. nevadoti</i> *	KU565080	JX969086	JX969035	MG888415	JX969540	JX969570	JX969472	JX969443	JX969148	JX969340	JX969191	JX969242	JX969396	JX969292	
<i>P. niger</i>	MCN 5565	MW310691	MW310692	MW310694											
<i>P. patagonicus</i> *	KU565083	JX969087	JX969036	MG888416	JX969541	JX969571	JX969473	JX969444	JX969149	JX969341	JX969192	JX969371	JX969243	JX969397	JX969293
<i>P. payuninae</i> *	KU565110	JX969088	JX969037	MG888417	JX969542	JX969572	JX969474	JX969445	JX969150	JX969342	JX969193	JX969372	JX969244	JX969398	JX969294
<i>P. rahuensis</i>	JX969104	JX969104	JX969053		JX969557	JX969588	JX969490	JX969459	JX969164	JX969358	JX969209	JX969383	JX969260	JX969413	JX969308
<i>P. robustus</i> *	JX969105	JX969105	JX969054	MW310693	JX969558	JX969589	JX969491	JX969460	JX969165	JX969359	JX969210	JX969384	JX969261	JX969414	JX969309
<i>P. silesi</i> *	JX969100	JX969100	JX969049	MG888418	JX969553	JX969584	JX969486	JX969456	JX969160	JX969354	JX969205	JX969256	JX969410	JX969305	

<i>P. sinerwei</i>	LJAMM- CNP 6543	JX969108	JX969057	JX969561	JX969592	JX969494	JX969463	JX969168	JX969362	JX969213	JX969387	JX969264	JX969417	JX969312
	CHIVC494/													
<i>P. somuncurensis</i> *	LJAMM- CNP 4453/ MCN4550	JX969089	JX969038	MG888419	JX969543	JX969475	JX969446	JX969151	JX969343	JX969194	JX969373	JX969245	JX969399	JX969295
<i>P. sp. 12</i>	LJAMM- CNP 7975	JX969099	JX969048	JX969552	JX969583	JX969485	JX969488	JX969159	JX969353	JX969204	JX969255	JX969409	JX969304	
<i>P. sp. 14</i>	LJAMM- CNP 3459	JX969102	JX969051	JX969555	JX969586	JX969488	JX969488	JX969162	JX969356	JX969207	JX969381	JX969258	JX969412	JX969307
<i>P. sp. 15</i>	LJAMM- CNP 8190	JX969103	JX969052	JX969556	JX969587	JX969489	JX969458	JX969163	JX969357	JX969208	JX969382	JX969259		
<i>P. sp. 19</i>	LJAMM- CNP 5541	JX969107	JX969056	JX969560	JX969591	JX969493	JX969462	JX969167	JX969361	JX969212	JX969386	JX969263	JX969416	JX969311
<i>P. sp. 22a</i> *	LJAMM- CNP 6538-6256	JX969096	JX969045	JX969580	JX969580	JX969482	JX969453	JX969157	JX969350	JX969201	JX969378	JX969252	JX969406	JX969301
<i>P. sp. 22b</i>	LJAMM- CNP 6257	JX969097	JX969046	JX969550	JX969581	JX969483	JX969454		JX969351	JX969202	JX969253	JX969407	JX969302	
<i>P. spectabilis</i> *	CHIVC449/ LJAMM- CNP 3600/ MCN1215	KU565120	JX969039	MG888421	JX969544	JX969476	JX969447		JX969344	JX969195	JX969246	JX969400	JX969296	
<i>P. spurcus</i> *	CHIVC450/ LJAMM- CNP 3586/ MCN1248	KU565124	JX969040	MG888422	JX969545	JX969575	JX969448	JX969152	JX969345	JX969196	JX969247	JX969401	JX969297	
<i>P. tenebrosus</i> *	CHIVC440/ LJAMM- CNP 5426/ MCN1272	KU565128	JX969092	JX969041	JX969546	JX969478	JX969449	JX969153	JX969346	JX969197	JX969374	JX969248	JX969402	JX969298
<i>P. vidalari</i> *	CHIVC359/ MCN4203	KU565131	MG888426	MG888429	MG888424	MG888431								
<i>P. yachanana</i>	LJAMM- CNP 3234	JX969109	JX969058	JX969562	JX969593	JX969495	JX969464	JX969169	JX969363	JX969214	JX969388	JX969418	JX969313	
<i>P. zapalensis</i> *	LJAMM- CNP 8067/ MCN3850	JX969093	JX969042	MG888425	JX969547	JX969479	JX969450	JX969154	JX969347	JX969198	JX969375	JX969249	JX969403	