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A New Species of Lizard Endemic to Sierra de Fiambalá, Northwestern Argentina (Iguania: Liolaemidae: *Phymaturus*). Integrated Taxonomy Using Morphology and DNA Sequences: Reporting Variation Within the *antofagastensis* Lineage

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The northernmost distributed group of lizards belonging to *Phymaturus* occurs in rocky outcrops of the Puna region between 3600–4200 m in Argentina. In a recent phylogenetic study based on morphological and genetic information, the monophyly of this small lineage was corroborated. This group is formed by *Phymaturus antofagastensis*, *P. laurenti*, *P. denotatus*, *P. mallimaccii* and a population of uncertain taxonomic status until the present study. After obtaining new samples and observations, we described a new species belonging to this lineage that is known only from Sierra de Fiambalá, being the species of *Phymaturus* living at the highest elevation ever recorded (4500 m). Males have a homogeneous yellow dorsum and lack melanic coloration over their heads, a phenomenon found in males of most species of the *palluma* group. We provide a detailed diagnosis, including characters from the squamation, coloration and significant differences found among continuous characters (ANOVA). Furthermore, we present genetic distances among members of the *mallimaccii* subclade based on sequences of the cyt*b* marker. We provide color photos showing pattern variation of males and females. We reanalyze the phylogenetic relationships within the entire *palluma* group and update info on all members of the *antofagastensis* lineage based on new samples and make a better supported hypothesis. We also evaluate the phylogenetic position of the new taxon.

Key words: *Phymaturus fiambala* sp. nov., Taxonomy, Squamata, Liolaemidae, Argentina.

BACKGROUND

The genus *Phymaturus* is known for its extremely endemic species, often known only from their type locality, despite extensive sampling done over the years by different herpetologists. This 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*' morphology is highly conserved, being significantly dorso-ventrally flattened in order to make better use of the crevices (González-

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Marín et al. 2018, Troncoso-Palacios et al. 2018). They are also exclusively herbivorous and viviparous, with biennial reproduction. Due to this morphological conservatism, recognizing new species calls for in-depth knowledge of these animals' systematic and diagnostic traits. Furthermore, given the extremely endemic nature of these species, their low population densities, and their biennial form of reproduction (Boretto and Ibargüengoytía 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 is a primary goal for their conservation.

Etheridge (1995) divided the genus *Phymaturus* in two species groups: the *patagonicus* and the *palluma* groups, based on a study of morphological characters. In his study, he proposed apomorphies, but did not present a formal phylogenetic analysis. Lobo and Quinteros (2005) performed an analysis using phylogenetic methods for the first time, confirming Etheridge's division (1995), although the *patagonicus* group was less supported than the *palluma* group. Based mainly on morphological characters, Lobo and Quinteros (2005) recovered a clade within the *palluma* group (Node 12 fig. 8) formed at this time by *P. antofagastensis* Pereyra 1985, *P. mallimaccii* Cei 1980, *P. punae* Cei, Etheridge and Videla 1983, *P*. cf. *punae* and *P*. cf. *antofagastensis.* All members of this clade are distributed in the highland Andean areas of Puna (an expansive region of western South America which is a part of the Central Andes and forms the world's second largest plateau). Puna is a desertic area situated at high elevation (above 3000 m), has a typical dominant vegetation of shrubs (there are no trees) (Martínez Carretero 1995) and its aridity and general landscape has existed at least since the Miocene (Strecker et al. 2007). In an updated analysis of 206 morphological characters (mainly based on squamation, colors and patterns, body proportions and skeletons), Lobo, Abdala and Valdecantos (2012) recovered this Puna clade (Node G, fig. 9) formed by *P. mallimacci*, *P. punae*, *P. antofagastensis*, *P. laurenti* (Lobo, Abdala and Valdecantos 2010), *P. extrilidus* (Lobo, Espinoza, Sanabria and Quiroga 2012b), and other five *P*. spp. (candidate species). At this time, two subclades were recognized within that node (a northern one with species inhabiting mountains of Catamarca and La Rioja provinces, and a southern one formed by species inhabiting La Rioja and San Juan provinces). After that revisionary contribution, three other species of this clade were formally described by Lobo et al. (2012c) from Laguna Blanca, Catamarca: *P. denotatus* (Lobo et al. 2013), and from San Juan province: *P. aguanegra* and *P. williamsi*. Using nuclear and mitochondrial sequences, Morando et al. (2013) recovered the same Puna-endemic clade including *P. punae*, *P. extrilidus*, *P. mallimaccii* and *P. laurenti* subdivided into the same two subclades previously recovered using morphology in Lobo et al. (2012a). Morando et al. (2013) named this clade the *mallimaccii* group.

Recently, Lobo et al. (2016) sequenced fragments of cytochrome *b* (cyt*b*), *12S*, and *ND4* for all terminals; described 45 new morphological characters; and incorporated all DNA sequences available from GenBank. Within the *palluma* group, two sister clades were recovered, the *vociferator* and *bibroni* clades, and two subclades within the latter: the *roigorum* and *mallimaccii* subclades (the latter equivalent to the *mallimaccii* group of Morando et al. 2013). The *mallimaccii* subclade consists of 13 terminal taxa, to which two Chilean species have been added in the last cladistic analyses: *P. bibroni* (Guichenot 1848) and *P. aguedae* Troncoso-Palacios and Esquerré 2014. Lobo et al. (2016) divided the *mallimaccii* subclade into two lineages: the *antofagastensis* lineage (*P. mallimaccii*, *P. antofagastensis*, *P. laurenti*, *P. denotatus,* sp. gua and *P.* sp. fia) and the *punae* lineage (*P. punae*, *P. extrilidus*, *P. williamsi*, *P. aguanegra*, *P. bibroni* and *P*. sp. lar). Grosso et al. (2017) studied the chromosome morphology of six species of the *palluma* group, including in their analysis three species of the *mallimaccii* subclade (*P. laurenti*, *P. denotatus* and *P. williamsi*). In this last study, interesting chromosome variation within the *palluma* group was described, including a multiple sex-chromosome system and several Robertsonian rearrangements. More recently, Troncoso et al. (2018) provided a multilocus phylogenetic analysis of the *vociferator* clade adding other species and previously unsampled populations from Chile to their data set. Troncoso et al. (2018) included most terminals of the *mallimaccii* subclade, recovering the two main lineages with a third one endemic to Chile. The present study refines the description of an unnamed population of *Phymaturus* that had previously been included in phylogenetic analyses. We reanalyze the phylogenetic relationships within the *palluma* group based on an updated data matrix after studying new samples of nine terminal taxa. We present here a description and diagnosis of other members of the lineage.

MATERIALS AND METHODS

We examined 203 specimens belonging to nine species of *Phymaturus*, including the type series of the new ones therein described (see Appendix 1). For this work, we collected sample data from Fiambalá mountains (WGS 27.25583 S 67.20980 W; altitude:

4533 m), Fiambalá Department, Catamarca Province, Argentina. Four adult males, two juvenile males and six females were sampled. We provide an original description of a new taxon of *Phymaturus*, with data on their variation and phylogenetic relationships. Appropriate actions were taken to minimize pain or discomfort of all lizards involved in this study, in accordance with international standards on animal welfare and national regulations of the "Comité Nacional de Ética en la Ciencia y la Tecnología" of Argentina (Expte. 5344/99 Res. 1047). All specimens were collected in the summer of 2017 by noose or by hand, and then fixed using 10% formalin and deposited in 70% ethanol. All herpetological collection data of the new species are recorded in collection databases in the Museo de Ciencias Naturales, Universidad Nacional de Salta (MCN-UNSa) and Instituto de Bio y Geociencias del Noa, Argentina (IBIGEO). Genetic data on all species in the group were extracted from GenBank, and accession numbers are indicated in table S1. GenBank accession numbers for sequences of the new species are KT203836 (12S), KT203831 (cyt*b*), KT203850 (ND4) and KT203819 (Cmos), first published in Lobo et al. (2016).

The genetic distances for cyt*b* among members of the *mallimaccii* subclade are shown in table 1. 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. Analyses were conducted in MEGA5 (Tamura et al. 2011). Phylogenetic relationships were analyzed updating a data matrix used in previous studies for the *palluma* group (Lobo et al. 2012 2016; Hibbard et al. 2019) and DNA sequences available in GenBank (including those used recently by Troncoso et al. 2018) using TNT, a parsimony software (Goloboff et al. 2008). Accession numbers for sequences from GenBank are reported in a table S1. In previous studies, this new taxon was mentioned as *P*. sp5 in Lobo et al. (2012) and as *P.* sp. fia in Lobo et al. (2016). At the time of those analyses, we had sequences of cyt*b*, 12S and ND4 taken from a female individual (MCN-UNSa 2123) of the new species (see accession numbers above), but morphology data were taken only from two females and a juvenile. In this case we collected all information on males and obtained data from a total of twenty specimens of the new species. Coding procedures were described in detail in the studies above mentioned. We added eighteen new characters (254–267: scale organs; 268–270: color pattern; 271: integumentary glands), which are listed at the end of appendix 1. Also, we improved our samples for the whole morphology of *P. mallimacci*, *P. antofagastensis* and *P. laurenti* taking data from FML, MLP and DC-JMC collections. We updated morphological information on *P. maulense*, *P. vociferator*, *P. damasense*, and *P. timi* (see Appendix 1). Some of the terminals were assigned to species in accordance with the most recent literature. In previous

Table 1. Estimates of divergence among cyt*b* sequences of ten species of the *Phymaturus mallimaccii* subclade (shaded), plus three other representatives of other *palluma* group lineages and two species of the *patagonicus* group. Sequences of *P*. sp. gua, *P*. sp. lar, sensu Lobo et al. (2016) were not available; nor were those of *P. aguanegra*. The number of base differences per site from between sequences are shown. 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. Analyses were conducted in MEGA5 (Tamura et al. 2011)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1) *aguedae*															
2) *antofagastensis*	0.040														
3) *bibroni*	0.037	0.017													
4) *denotatus*	0.043	0.006	0.017												
5) *extrilidus*	0.039	0.015	0.007	0.015											
6) *fiambala*	0.044	0.014	0.018	0.011	0.017										
7) *laurenti*	0.043	0.006	0.017	0.000	0.015	0.011									
8) *mallimaccii*	0.040	0.015	0.018	0.012	0.019	0.017	0.012								
9) *punae*	0.037	0.019	0.010	0.019	0.010	0.019	0.019	0.022							
10) *williamsi*	0.041	0.018	0.012	0.015	0.011	0.017	0.015	0.017	0.014						
11) *dorsimaculatus*	0.061	0.064	0.057	0.066	0.066	0.066	0.066	0.068	0.061	0.064					
12) *palluma*	0.043	0.041	0.032	0.041	0.033	0.041	0.041	0.040	0.033	0.033	0.059				
13) *querque*	0.055	0.052	0.044	0.052	0.048	0.057	0.052	0.055	0.046	0.046	0.054	0.046			
14) *indistinctus*	0.146	0.140	0.137	0.145	0.144	0.148	0.145	0.144	0.146	0.149	0.134	0.149	0.145		
15) *somuncurensis*	0.148	0.151	0.149	0.156	0.153	0.159	0.156	0.152	0.156	0.159	0.138	0.155	0.152	0.065	

studies, we included *Phymaturus* from Termas de Chillán (*P*. cf. *palluma* CH, *P*. sp2 or *P*. sp. chi in Lobo and Quinteros 2005, Lobo et al. 2012 2016); now we assigned this sample to *P. vociferator* following Urra et al. (2017). We assigned other samples from El Planchón (*P*. cf. *palluma* EP, *P*. sp3 or *P*. sp. pla in Lobo and Quinteros 2005, Lobo et al. 2012 2016) to *P. damasense* following Ramírez-Alvarez et al. (2017). We analyzed our data matrix with TNT v. 1.5 applying strict parsimony (Goloboff et al. 2008). Support for individual nodes was assessed with jackknifing resampling (Siddall 1995) using 1000 replicates and a deletion value of 25%. 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. Most characters described in diagnoses and descriptions followed standards published in Smith (1946), Cei (1986 1993), Laurent (1984 1986), Etheridge (1995), Lobo and Quinteros (2005) and Lobo et al. (2010). Additionally, we chose 17 continuous characters of squamation plus snout-vent length (Table 2) to analyze if significant differences exist among species belonging to the *antofagastensis* lineage. These characters were: SVL (snout-vent length), number of scales around midbody, Hellmich's index (scales counted along the mid-line of the head between the occiput and rostrum), number of scales contacting interparietal, number of infralabial scales, number of subocular scales, scales contacting nasal, lorilabial scales, temporal scales, superciliary scales, gular scales and the number of precloacal pores in males (in this lineage there are no pores in females), scales contacting mental, ventral scales, scales projecting over auditory meatus, number of dorsal scales (counted at middle of the trunk in a head-length), scales between frontal-rostral and scale organ on postrostrals. The data met assumptions of normality and homogeneity of variance. We performed an ANOVA (analysis of variance) using a test of multiple comparisons LSD of Fisher running the statistical package INFOSTAT (Di Rienzo et al. 2016).

RESULTS

TAXONOMY

Family Liolaemidae Frost and Etheridge, 1989
Genus *Phymaturus* Gravenhorst, 1838

Phymaturus fiambala sp. nov. Lobo, Hibbard, Quipildor and Valdecantos

(Figs. 1, 3–6)

urn:lsid:zoobank.org:act:04F90EF0-A70A-49C4-A91F-A1FDFCB7466

Table 2. ANOVA results obtained after comparisons across species of the *antofagastensis* lineage of *Phymaturus* for eighteen continuous characters. Different capital letters following mean ± standard error between species indicate a significant difference. Sample size indicated between parentheses

	P. antofagastensis (*n* = 19)		*P. denotatus* (*n* = 15)		*fiambala* (*n* = 18)		*P. laurenti* (*n* = 23)		*P. mallimaccii* (*n* = 16)		Prueba	*p*
SVL	90.02 ± 2.08	B	98.37 ± 2.15	A	97.73 ± 1.96	A	91.43 ± 1.74	B	86.44 ± 2.08	B	F = 6.26	**0.0002**
Scales around midbody	198.11 ± 2.84	B	207.80 ± 3.19	C	193.17 ± 2.91	A B	193.87 ± 2.58	B	185.25 ± 3.09	A	F = 6.93	**0.0001**
Hellmich index	21.63 ± 0.42	B	22.60 ± 0.47	B C	18.78 ± 0.43	A	23.26 ± 0.38	C	21.56 ± 0.46	B	F = 16.70	**< 0.0001**
Contacting interparietal	8.63 ± 0.26	A	8.60 ± 0.29	A	8.28 ± 0.27	A	8.70 ± 0.24	A	9.69 ± 0.28	B	F = 3.67	**0.0083**
Infralabial scales	9.47 ± 0.29		9.80 ± 0.32		9.67 ± 0.29		10.17 ± 0.26		9.56 ± 0.31		F = 1.01	0.4077
Subocular scales	2.16 ± 0.22	B C	2.80 ± 0.24	C D	1.89 ± 0.22	A B	2.91 ± 0.20	D	1.31 ± 0.23	A	F = 8.84	**< 0.0001**
Contacting nasal	9.00 ± 0.21	A B	9.33± 0.24	B	8.39 ± 0.22	A	9.22 ± 0.20	B	8.56 ± 0.23	A	F = 3.37	**0.0130**
Lorilabial scales	11.68 ± 0.28	A	14.33 ± 0.31	C	14.06 ± 0.29	C	12.74 ± 0.25	B	12.19 ± 0.30	A B	F = 15.45	**< 0.0001**
Temporal scales	10.21 ± 0.25	A	11.73 ± 0.28	C	11.44 ± 0.26	B C	10.70 ± 0.23	A	10.75 ± 0.28	A B	F = 5.37	**0.0007**
Superciliary scales	10.16 ± 0.28	A	11.20 ± 0.31	B	11.28 ± 0.28	B	10.35 ± 0.25	A	10.81 ± 0.30	A B	F = 3.18	**0.0173**
Gular scales	83.58 ± 1.70	A B	80.27 ± 1.91	A	89.67 ± 1.7	C	85.78 ± 1.55	B C	83.25 ± 1.85	A B	F = 10.86	**< 0.0001**
Precloacal pores	9.22 ± 0.40	B C	8.00 ± 0.69	A B	10.43 ± 0.45	C	7.40 ± 0.31	A	7.22 ± 0.40	A	F = 3.75	**0.0074**
Contacting mental scales	6.37 ± 0.16	A B	6.80 ± 0.22	B C	6.11 ± 0.08	A	6.04 ± 0.04	A	7.00 ± 0.20	C	H = 18.55	**< 0.0001**
Ventral scales	182.11 ± 2.30		189.93 ± 2.81		183.44 ± 2.28		181.87 ± 1.93		181.13 ± 2.87		F = 1.95	0.1093
Scales projected over auditory meatus	4.05 ± 0.18	C	2.00 ± 0.49	B	4.06 ± 0.39	C	0.83 ± 0.29	A	5.19 ± 0.54	D	F = 23.33	**< 0.0001**
Dorsal scales	34.89 ± 1.23		36.73 ± 1.55		35.67 ± 0.74		35.61 ± 0.90		37.06 ± 0.65		F = 0.68	0.6052
Scales between frontal-rostral Scale	9.05 ± 0.30	B	10.07 ± 0.25	C	8.22 ± 0.27	A	10.39 ± 0.29	C	10.50 ± 0.29	C	F = 11.76	**< 0.0001**
organs on postrostrals	1.33 ± 0.15		1.72 ± 0.18		1.18 ± 0.11		1.43 ± 0.24		1.77 ± 0.19		F = 1.65	0.1698

Synonymy: *Phymaturus* sp5: Lobo et al. 2012: 21. *Phymaturus* sp. fia: Lobo et al. 2016: 650.

Deposition of types: Holotype: IBIGEO 5756. Male (Fig. 1). Paratypes: IBIGEO 5757–59, 5765, 5774 (4 adult males); 5769–70 (2 juvenile males). 5760–61, 63–64, 5766, 68 (6 females) deposited at the Reptiles collection of the Instituto de Bio y Geociencias del Noa (IBIGEO), Salta, Argentina. Site: 27.25583 S 67.20980 W; altitude: 4533 m. Locality: Cerca del Puesto de la lagunilla, Fiambalá Department, Catamarca Province, Argentina. Dates: 6 December 2017. Collectors: Thomas Hibbard and Matías Quipildor. MACN 51034-035 (ex IBIGEO 5762, 5767). Same data, deposited at the Herpetological collection of the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina. MCN-UNSa 2122, 2123 (2 females, MCN-UNSa 2123 is voucher of DNA sequences), deposited at Museo de Ciencias Naturales, Universidad Nacional de Salta, Salta, Argentina. Locality: Puesto la Lagunita, 35–38 km NE of Medanitos, climbing from Medanitos, Fiambalá Department, Catamarca Province, Argentina. Dates: 23 March 2006. Collectors: Sebastián Barrionuevo, Juan Manuel Díaz Gómez and Sebastián Quinteros. MCN-UNSa 2125 juvenile. Same data, deposited at Museo de Ciencias Naturales, Universidad Nacional de Salta, Salta, Argentina.

Diagnosis: *Phymaturus fiambala* sp. nov. Doral pattern with very thin spray, throats and chests light

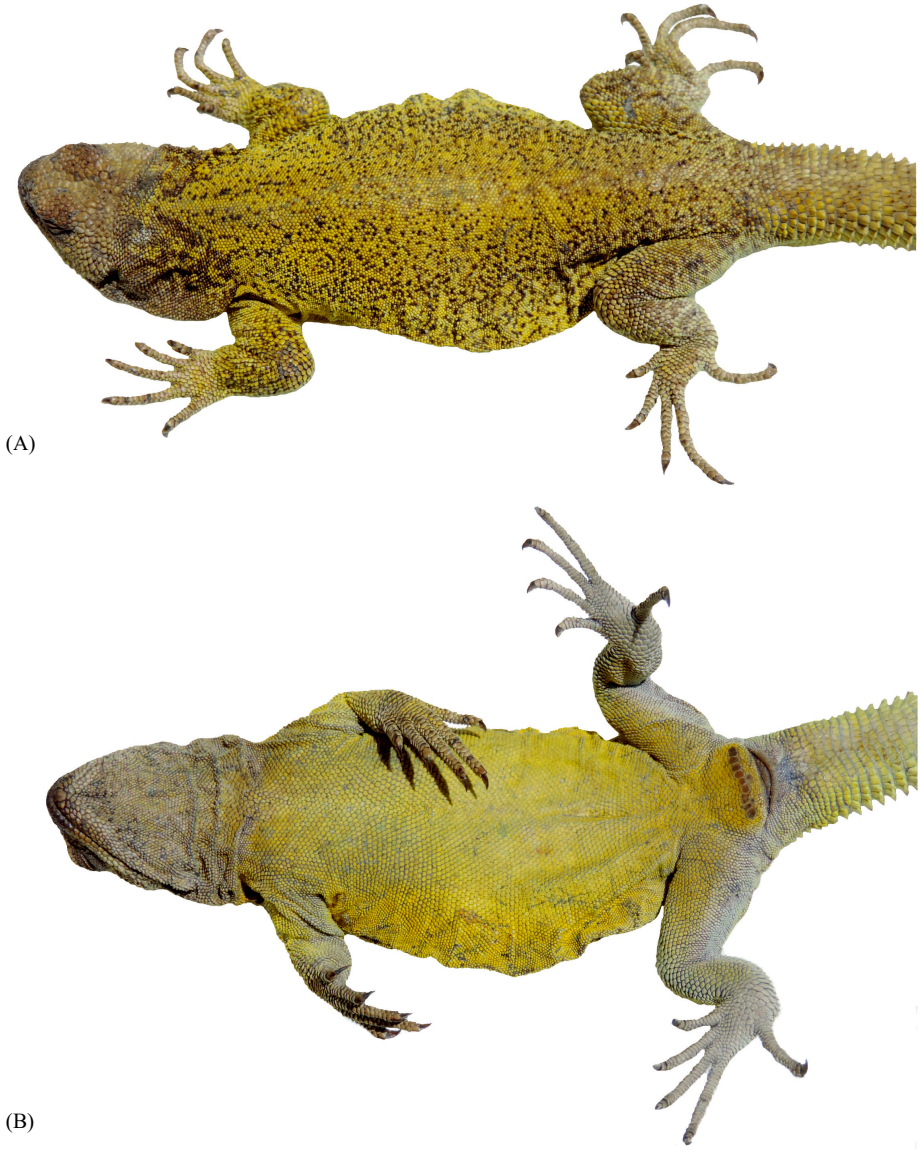


Fig. 1. (A) Dorsal view of the holotype of *Phymaturus fiambala* sp. nov. IBIGEO 5756. (B) Ventral view of the same specimen (Photos: M. Quipildor).

gray, rostral scales always undivided. Males with enlarged postcloacal scales, females with slender white transversal lines over trunk, enlarged scales on posterior gular fold, a patch of enlarged scales between gular folds evident, vertebral stripe absent.

Deposition of types: Holotype: IBIGEO 5756. Male (Fig. 1). Paratypes: IBIGEO 5757–59, 5765, 5774 (4 adult males); 5769–70 (2 juvenile males). 5760–61, 63–64, 5766, 68 (6 females) deposited at the Reptiles collection of the Instituto de Bio y Geociencias del Noa (IBIGEO), Salta, Argentina. Site: 27.25583 S 67.20980 W; altitude: 4533 m. Locality: Cerca del Puesto de la lagunilla, Fiambalá Department, Catamarca Province, Argentina. Dates: 6 December 2017. Collectors: Thomas Hibbard and Matías Quipildor. MACN 51034–035 (ex IBIGEO 5762, 5767). Same data, deposited at the Herpetological collection of the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina. MCN-UNSa 2122, 2123 (2 females), deposited at Museo de Ciencias Naturales, Universidad Nacional de Salta, Salta, Argentina. Locality: Puesto la Lagunita, 35–38 km NE of Medanitos, climbing from Medanitos, Fiambalá Department, Catamarca Province, Argentina. Dates: 23 March 2006. Collectors: Sebastián Barrionuevo, Juan Manuel Díaz Gómez and Sebastián Quinteros. MCN-UNSa 2125 juvenile. Same data, deposited at Museo de Ciencias Naturales, Universidad Nacional de Salta, Salta, Argentina.

Description of holotype (Fig. 1): Male. SVL 98.4 mm. Head length: 18.1 mm. Head width: 18.7 mm. Head height (at parietal): 8.2 mm. Axilla-groin length: 50.1 mm (50.9% of SVL). Tail length (complete, not regenerated): 71.3 mm to the point of regeneration. Body moderately wide, trunk width: 36.5 mm (37.1% of SVL). Twenty smooth dorsal head scales. Three scale organs in three postrostrals. Nasal bordered by ten scales, not in contact with rostral. Canthal separated from nasal by two scales. Loreal region flat. Twelve enlarged supralabial scales, none contacting subocular. Ten enlarged infralabials. Auditory meatus oval shaped (height: 3.9 mm; width: 2.1 mm) with four enlarged, flat and keeled backwardly projecting scales on the anterior margin. Auricular scale absent. Twelve convex, juxtaposed temporals. Auditory meatus-ciliary scales posterior commissure distance: 6.3 mm. Rostral undivided. Mental scale sub-pentagonal, in contact with six scales. Interparietal scale bordered by eight scales, being of larger size than postparietals. Frontal region without an azygous scale. Supraorbital semicircles inconspicuous. No distinctly enlarged supraoculars. Eleven juxtaposed superciliaries, seventeen upper ciliaries and sixteen lower ciliaries. Subocular fragmented in two scales. Fifteen lorilabials, without contacting subocular. Preocular larger than canthal, separated by one scale. Preocular separated from lorilabial row by three scales. Scales of throat round, small, and juxtaposed. Eighty-eight gulars between auditory meata. Lateral nuchal folds well developed, with granular scales over longitudinal fold. Antehumeral pocket well developed. Sixty-four scales between auditory meatus and shoulder. Forty-one scales between antehumeral fold and shoulder. In ventral view, anterior and posterior gular folds present, their anterior margins with two to three enlarged scales on their borders. Dorsal scales round, smooth and juxtaposed. Thirty-six dorsal scales along midline of the trunk in a length equivalent to head length. Scales around midbody: 178. Ventral scales larger than dorsals. Ventral scales between mental and precloacal pores: 187. Ten precloacal pores in an undivided row with two supernumerary pores. Two slightly enlarged postcloacal 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: 21. Claws moderately long (fourth toe's claw: 2.6 mm). 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: 25.

Coloration of holotype: the holotype exhibits a homogeneous yellow dorsal background, with small light brown scales scattered irregularly over all its body. Dorsum of tail of the same yellow coloration as trunk (no ringed or variegated pattern). Head uniformly light brown, with this coloration extended over the lateral neck folds. Throat immaculate light gray with no variegation. It has almost inconspicuous, very small and disperse spots, slightly darker than the background. Immaculate chest and belly entirely yellow from the anterior gular fold to the cloacal opening, extended over fore and hindlimbs and ventral surfaces of thighs and tail. Ventral surface of tail does not have any pattern.

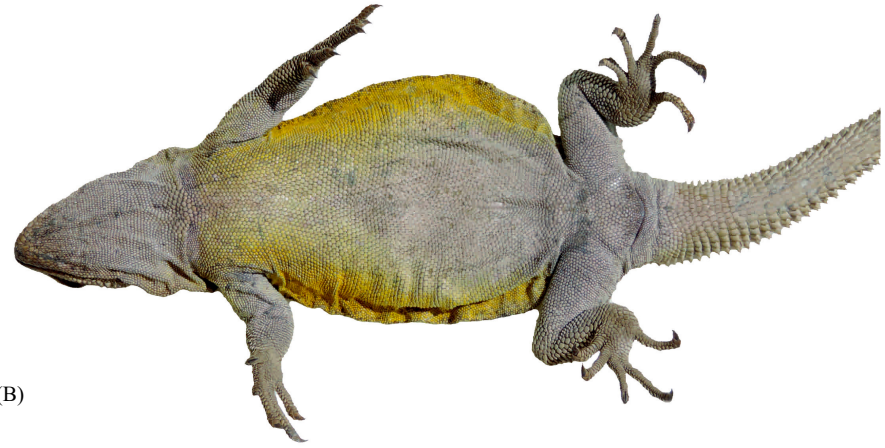
Color of a female (Fig. 2): background dorsal coloration light brown all over head, trunk, tail and limbs. Light brown coloration speckled with darker brown scales, which become confluent on the sides of neck and shoulders. Scapular spot conspicuous. Flanks with yellow coloration that extends to the belly as symmetrical patches. Most of ventral surfaces immaculate, light gray to white. Dorsal pattern of tail ringed. Ventral surface of tail lacks any kind of pattern.

Etymology: The species inhabits Sierra de Fiambalá (Fiambalá mountains). The toponym Fiambalá comes from an ancient language (Cacán) of natives who lived in northwestern Argentina before Quechua (Inca) and Spanish became dominant. "Cacán" voice:

fiambalao (fiambal = wind; ao = house, place), meaning "house of winds".

Variation: based on 16 adult specimens (7 males and 9 females). SVL 90.2–102.3 mm (x = 97.5; SD = 3.2) (two juveniles not included to avoid including ontogenetic variation). Head length 16.7–18.9% (x = 17.7%; SD = 0.7) of SVL. Tail length 0.80–1.08 (x = 0.96; SD = 0.08) times SVL. Scales around midbody 178–212 (x = 192.4; SD = 9.6). Dorsal head scales 15–22 (x = 18.6; SD = 1.9). Ventral scales 168–203 (x = 184.4; SD = 8.3). Scales surrounding interparietal 7–10 (x = 8.3; SD = 0.9). Scales surrounding nasal 7–10 (x = 8.4; SD = 0.9). Number of scale organs on postrostrals 1–3 (x = 1.1; SD = 0.5). Superciliaries 10–13 (x = 11.2; SD = 0.9). Subocular fragmented in half of the sample (ten specimens). Mental scale in contact with 6–7 (x = 6.1; SD = 0.3). Number of chinshields 2–7 (x = 4.5; SD = 1.8). All specimens exhibit enlarged scales on the border of the posterior gular fold (varying in number). Lorilabials 12–16 (x = 13.9; SD = 1.1). Enlarged scales on the anterior border of the auditory meatus 3–7 (x = 4.5; SD = 1.3) (Fig. 3A). Scales of neck along longitudinal fold from posterior border of auditory meatus to shoulder 60–76 (x = 68.4; SD = 4.6). Gulars 77–100 (x = 89.2; SD = 6.2). Scales between rostral and frontal 6–10 (x= 8.2; SD = 1.2). Subdigital lamellae on fourth finger 18–21 (x = 19.4; SD = 1.1). Subdigital lamellae on fourth toe 22–28 (x = 24.1; SD = 1.6). Males with 9–12 precloacal pores (x = 10.3; SD = 1.0). No females show precloacal pores. A small, newborn-sized individual was collected with 52.1 mm SVL (IBIGEO 5770). It shows two conspicuous enlarged postcloacal scales and a row of differentiated scales that will house later (at its maturity) precloacal pores (Fig. 3B). A juvenile male (IBIGEO 5769) with 78.2 mm SVL shows a row of differentiated scales but without pit or any signal of secretion. It has slightly conspicuous enlarged postcloacal scales and it exhibits a

(A)



(B)

Fig. 2. (A) Dorsal view of a female of *Phymaturus fiambala* sp. nov. IBIGEO 5763. (B) Ventral view of the same specimen (Photos: M. Quipildor).

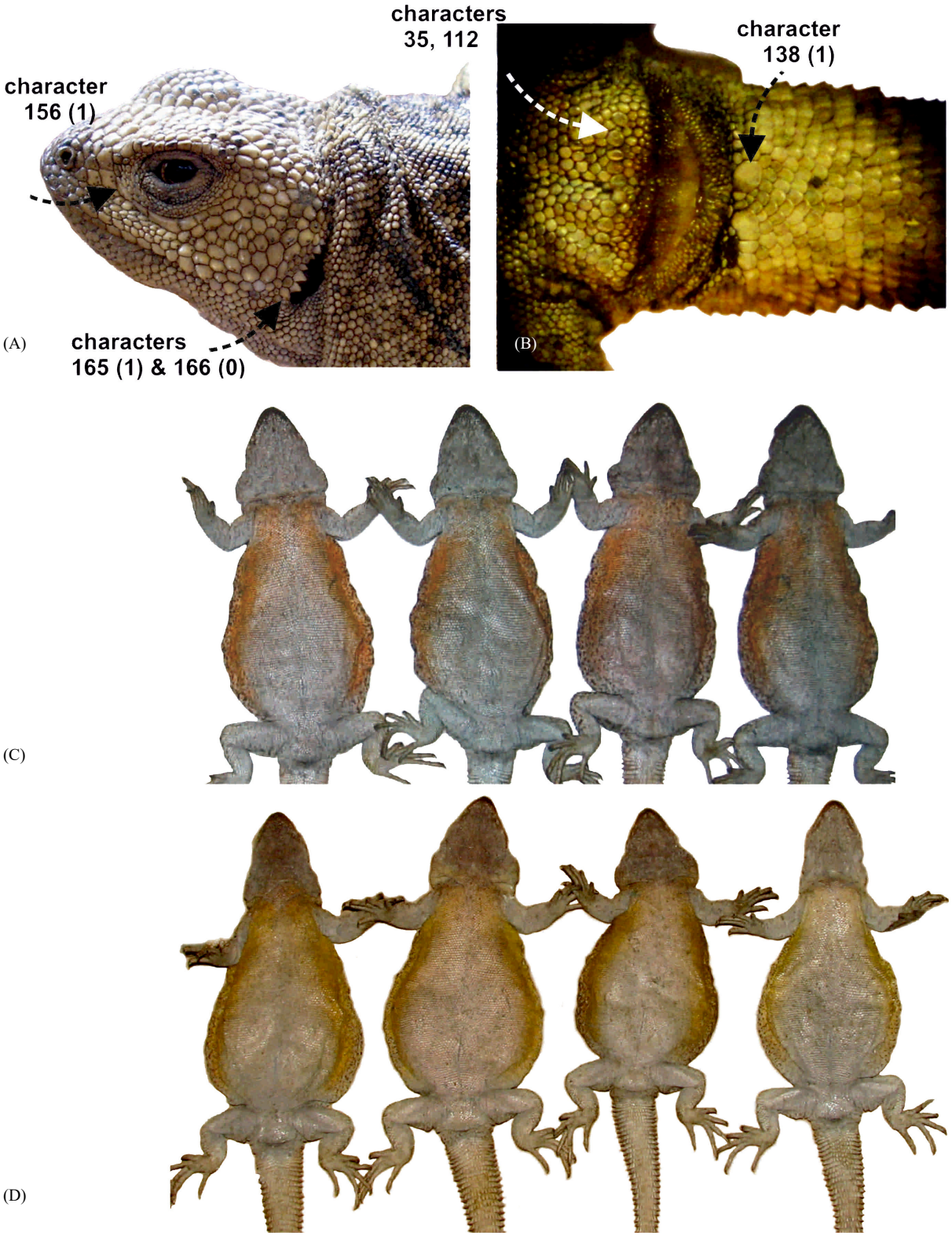


Fig. 3. (A) Details of the head in a female of *Phymaturus fiambala* sp. nov. (MCN-UNSa 2123); (B) newborn *P. fiambala* sp. nov. (IBIGEO 5770); (C) ventral view of females of *P. laurenti*; (D) females of *P. denotatus*. Character 35 (number of precloacal pores in males) 112 (row of precloacal pores); character 138 (1) presence of enlarged postcloacal scales in males; character 156 (1) preocular scale small separated from canthal by another scale; character 165 (1) three to seven enlarged scales on the anterior border of the auditory meatus; character 166 (0) enlarged scales on the anterior border of auditory meatus projected posteriorly over the ear opening (Photos: M. Quipildor).

typical ringed tail as the smallest juvenile. Males (Fig. 4) exhibit a yellow coloration all around their trunks. This color can be extended over tails, and in lesser degree over fore and hindlimbs. Dorsum and flanks speckled of dark brown/black scales that become more densely distributed in the neck and shoulders. Dorsal melanism of neck incomplete over the mid vertebral line (character 172). All males show a scapular yellow spot (character 139). Chest and abdomen immaculate yellow. Heads light brown, not a single specimen exhibits melanization common in the *palluma* group (character 124). Females (Fig. 5) homogeneous brown (head, body, limbs and tail), their trunks speckled with black to dark brown scales. Lateral sides of neck, in several cases melanic, can be extended over the shoulders and the axilla. Scapular spot conspicuous in most females (character 140). Most females exhibit white slender transverse stripes across their backs (character 180). Ventral surfaces light gray almost white with a pair of yellow patches on the sides extended over flanks (character 183). Tails patterned (irregularly distributed darker spots) like in males but more conspicuous.

Distribution: At present, only known from its type locality.

Detailed comparisons to other members of the *antofagastensis* lineage

Phymaturus fiambala sp. nov. belongs to the *antofagastensis* lineage because it shares synapomorphies with all other members of the lineage: four discrete and three continuous characters (presence of flank color in females, loss of scale organ in mental, dark sides of neck speckled with small white spots among them) plus eight DNA changes (see below "Phylogenetic relationships"). Because of this, comparisons are restricted to all members of the lineage. *Phymaturus fiambala* sp. nov. males exhibit yellow tails continuing the same color of trunks, different from all other members of the *mallimaccii* subclade with males that exhibit brown tails (yellow tails are found in the *vociferator* clade, and the *roigorum* subclade).

Phymaturus fiambala sp. nov. differs from *P. antofagastensis* in that has a pattern of very thin spray, while *P. antofagastensis* exhibits a typical aggregated pattern (Lobo and Quinteros 2005, fig. 12D) formed by larger brown spots irregularly distributed over its body. Males exhibit a yellow coloration covering head, trunk, limbs and tail (Fig. 1) while in *P. antofagastensis*, yellow is more restricted to flanks, shoulders and neck, never shown in tails (Fig. 6). Throats and chests in *P. fiambala* sp. nov. are light gray, being dark, almost completely melanic in *P. antofagastensis*. In *P. fiambala* sp. nov., granular scales among dorsal tibial scales are absent, while they are present in *P. antofagastensis*. In *P. fiambala* sp. nov. the rostral scale is always undivided, while 63% of studied individuals of *P. antofagastensis* show a divided rostral scale. In *P. fiambala* sp. nov., all males exhibit enlarged poscloacal scales (like in *P. laurenti* see Lobo et al. 2012c, fig. 3D) while only 37.5% of males of *P. antofagastensis* do. White transversal stripes are quite evident and wide in females of *P. antofagastensis*, but slender and almost inconspicuous in *P. fiambala* sp. nov. Also, *P. fiambala* sp. nov. shows significant differences in other five continuous characters (Table 2): *P. fiambala* sp. nov. shows a larger SVL than *P. antofagastensis*, more lorilabials, superciliaries and gular scales, fewer scales between rostral and frontal, and fewer scales along mid-line of head (Hellmich's index).

Phymaturus fiambala sp. nov. differs from *P. mallimaccii* in that males of the second species exhibit melanic throats, and several a very dark pattern formed by a dense distribution of small dark spots over dorsum. Also, in *P. mallimaccii*, a vertebral stripe is conspicuous, *i.e.*, a vertebral stripe of a lighter coloration similar to the one shown by species of the *punae* lineage but absent in *P. fiambala* sp. nov. In *P. mallimaccii*, lateral neck folding is dark and speckled with small white spots even in males (Fig. 6D) but in certain individuals it is not so evident while in *P. fiambala* sp. nov. this character is absent. In *P. fiambala* sp. nov., enlarged scales on posterior gular fold and a patch of enlarged scales between gular folds are evident, while in *P. mallimaccii* they are inconspicuous or absent. Flank coloration in females of *P. fiambala* sp. nov. is yellow but orange in females of *P. mallimaccii*. According to statistical tests, *P. fiambala* sp. nov. have significantly larger SVL than *P. mallimaccii*, lower Hellmich's index, fewer scales contacting interparietal, scales contacting mental (Lobo and Quinteros 2005, fig. 9C & D), scales projecting on the anterior margin of the auditory meatus (Fig. 3A), scales between rostral and frontal but more lorilabial scales, gular scales and precloacal pores.

Phymaturus fiambala sp. nov. is different from *P. laurenti* in that the scapular spot is absent in *P. laurenti*, present in *P. fiambala* sp. nov. Flank coloration of females is orange in *P. laurenti* (Fig. 3C) but yellow in *P. fiambala* sp. nov. Tarsal scales in *P. fiambala* sp. nov. are strongly keeled but slightly keeled in *P. laurenti.* Enlarged poscloacal scales in males are larger in *P. laurenti*. *Phymaturus fiambala* sp. nov. lacks granular scales among dorsal tibial scales that are present in *P. laurenti* (see this character in Lobo et al. 2016, fig. 8F). Also, there are eight continuous characters that exhibit significant differences: *P. fiambala* sp. nov. has a larger SVL, lower Hellmich's index, fewer subocular scales (Lobo and Quinteros 2005, fig. 9A & B), scales

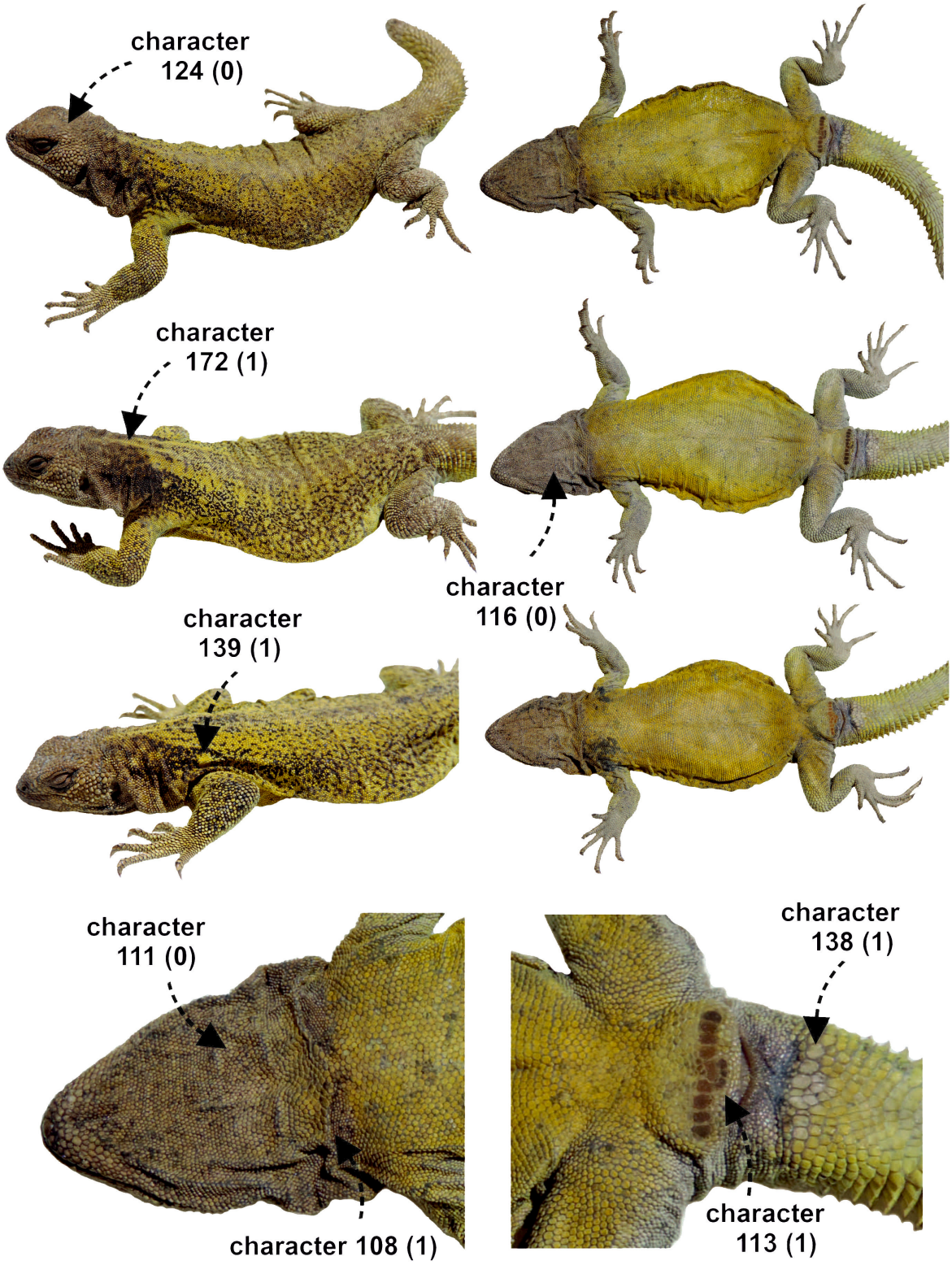


Fig. 4. Homogeneous pattern and color of males of *Phymaturus fiambala* sp. nov. Character 124 (0): sides and dorsum of head melanism of mature males absent; character 111 (0): anterior gular fold absent; character 108 (1): presence of enlarged scales on posterior gular fold; character 113 (1): presence of supernumerary precloacal pores; character 139 (1): presence of a scapular yellow to grey spot in males; character 172 (1): dorsal melanism of neck incomplete over the mid vertebral line (Photos: M. Quipildor); character 116 (0): Throat of males immaculate; character 138 (1): Presence of enlarged postcloacal scales in males.

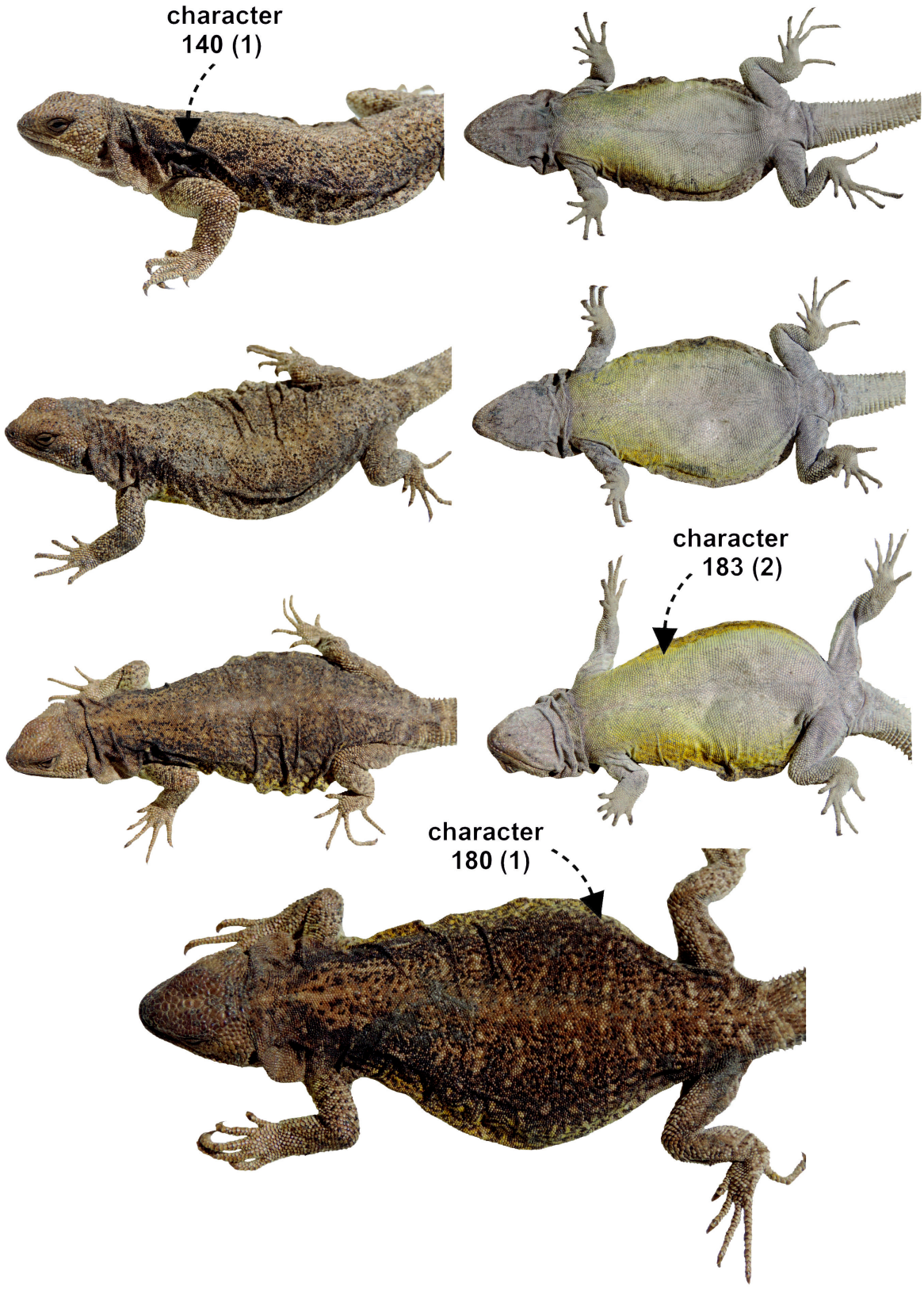


Fig. 5. Female variation of *Phymaturus fiambala* sp. nov. Character 140 (1): presence of a scapular yellow to grey spot (females); character 180 (1): females or/and juvenile with transversal lighter stripes (whitish) over their backs; character 183 (2): flank color in females yellow (Photos: M. Quipildor).

contacting nasal, scales between frontal-rostral and more lorilabial scales, temporal scales and superciliaries scales, scales projecting over the auditory meatus and precloacal pores.

Phymaturus fiambala sp. nov. is different from *P. denotatus* in that this last species lacks enlarged postcloacal scales in males; it lacks a patch of enlarged scales in the center of chest between posterior gular folds (present in *P. fiambala* sp. nov.); throats of males are dark or completely melanic in *P. denotatus* males (light gray in *P. fiambala* sp. nov.); females of *P. denotatus* exhibit a well-differentiated pattern of dark neck folds speckled with small white spots (Lobo et al. 2012c, fig. 2), almost absent in *P. fiambala* sp. nov. *Phymaturus fiambala* sp. nov. lacks granular scales among dorsal tibial scales that are present in *P. denotatus* (Lobo et al. 2016, fig. 8F). Pattern of trunks in *P. denotatus* is formed by irregularly distributed small brown markings that are almost absent in *P. fiambala* sp. nov. (see figs. 1 and 2 of Lobo et al. 2012c) rostral scale can be divided in *P. denotatus* (36%) while this never happens in *P. fiambala* sp. nov., and also there are six continuous characters that exhibit significant differences: *P. fiambala* sp. nov. has fewer scales around midbody, subocular scales, scales contacting nasal, scales contacting mental, scales between frontal-rostral and a lower Hellmich's index, but more gular scales, scales projected over auditory meatus and precloacal pores.

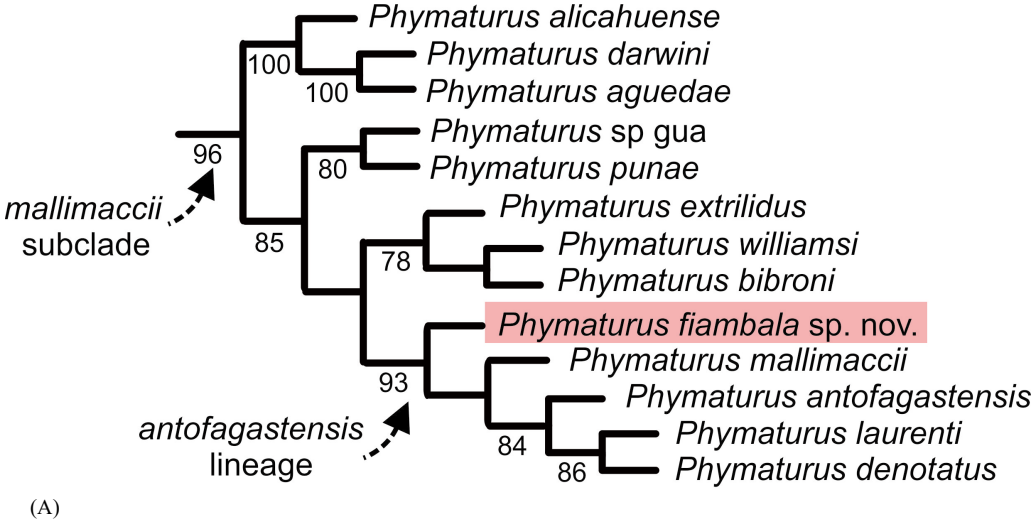
Phylogenetic relationships

The molecular analysis (all evidence available in GenBank, see supplementary file) with TNT recovered one most parsimonious tree of 2816 steps for the entire *palluma* group. The *mallimaccii* subclade is strongly supported (96% of jackknife). *Phymaturus fiambala* sp. nov. (sequences of the paratype MCN-UNSa 2123) is found as sister to all other members of the *antofagastensis* lineage (Fig. 7A), *P. mallimaccii* is sister to the group formed by *P. antofagastensis*, *P. laurenti* and *P. denotatus*. Most of the nodes are well supported, with the exception of the one linking *P. mallimaccii* to the other species, the relationship

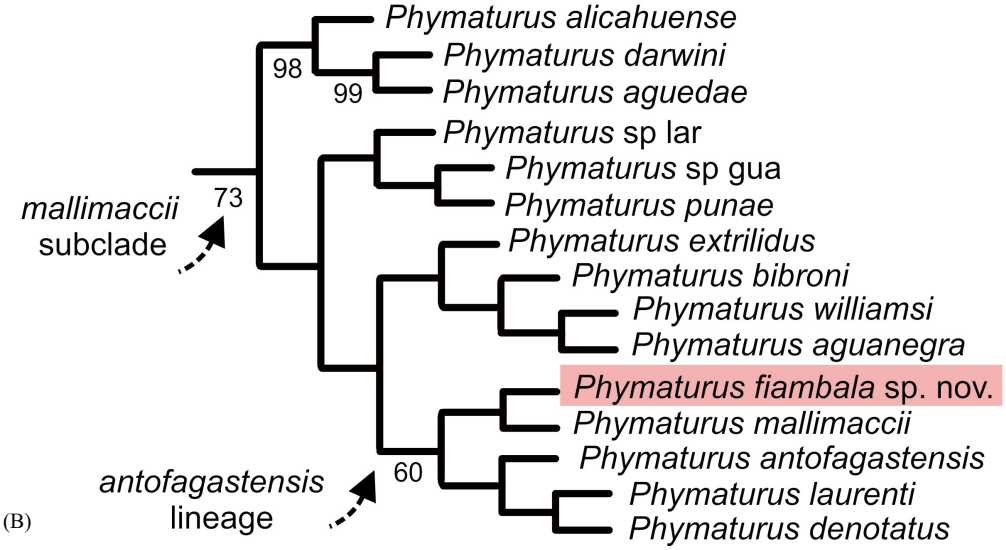
Fig. 6. Color in life of species of the *Phymaturus antofagastensis* lineage (males). (A) *Phymaturus antofagastensis* (Photo: S. Nenda); (B) *Phymaturus laurenti* (Photo: F. Lobo); (C) *Phymaturus denotatus* (Photo: D. Slodki); (D) *Phymaturus mallimaccii* (Photo: C. Abdala).

between *P. williamsi* and *P. bibroni* and a basal node to these species plus *P. williamsi*, *P. extrilidus* and *P. bibroni*.

The reanalysis of the original matrix updated from Lobo et al. (2016), combining all DNA sequences available at GenBank and morphology, recovered four optimal trees of 3830,516 steps for the entire *palluma* group (Fig. 7B). In the present analysis, *Phymaturus fiambala* sp. nov. is recovered nested within the *mallimaccii* subclade, within the *antofagastensis* lineage, being sister to *P. mallimaccii*, basal to the node formed by *P. antofagastensis* and the sister species *P. laurenti* and *P. denotatus*. The *antofagastensis* lineage is supported (60% of jackknife) by three discrete characters: flank color in females (character 182 0→1), acquisition of yellow flank color in females (character 183 0→2), dark sides of neck speckled with small white spots (character 268 0→1) (secondary loss in *P. laurenti* and *P. antofagastensis*). Four continuous characters: decrease in the number of scales counted around midbody (character 3), decrease of the number of lateral scales on neck (character 5), increase of the



(A)



(B)

Fig. 7. Phylogenetic relationships recovered for the *mallimaccii* subclade of the *Phymaturus palluma* group. (A) based on all available DNA sequences of the genbank (*P. aguanegra* and *P.* sp. lar not included because the lack of data). (B) based on a combined data set of DNA sequences and morphology. We updated morphological information on the new species and other nine species and added 15 new characters to Lobo et al. (2016) and Hibbard et al. (2019) original data sets. Values under branches are Jackknife support calculated TNT v1.5. Running the analysis with only DNA sequences *P. fiambala* sp. nov. is basal to the remaining species of the *antofagastensis* lineage.

number of scales in contact to interparietal (character 7), the supralabial scale upturned situated more posteriorly in the row (character 12), plus six nucleotide changes.

Phymaturus fiambala sp. nov. and *P. mallimaccii* as sister taxa are supported by four morphological discrete characters: rostral scale undivided (character 106 1→0), scapular yellow to grey spot in males (character 139 0→1), anterior projection of dorsal fascia melanism reaching the level over nuchal musculature (character 217 0→1), dorsal tibial scales larger than anterior ones (character 221 0→2). Four continuous characters: decrease in the number of scales counted around midbody (character 3), decrease in the number of scales contacting mental (character 14), decrease in the interorbit distance/head length ratio in females (character 26) decrease of the abdominal width/snout-vent length ratio (character 30). No DNA apomorphies.

Phymaturus antofagastensis is related to *P. laurenti* and *P. denotatus* supported by two discrete characters: lorilabial-subocular contact lost (character107 1→2), 3-7 scales enlarged scales on the anterior border of the auditory meatus (character 165 1→2), one continuous character: increase lateral rami / medial rami of interclavicle ratio (character 42). Five nucleotide changes.

Phymaturus laurenti and *P. denotatus* are closely related because they share nine synapomorphies: three discrete morphological characters, presence of enlarged scales on posterior gular fold (character 108 1→2), sexual presence of sexual dimorphism in dorsal pattern (character 125 0→1), parietal eye without opaque coloration conspicuous under corneal surface (character 175 1→0). Three continuous characters, increase of subocular scales (character 13), increase of scales in contact to mental (character 14), increase number of scales separating the preocular from lorilabial row (character 17). Three nucleotide changes.

Genetic distances

Divergence among cyt*b* sequences are shown in table 1 among members of the *mallimaccii* subclade, three species of other *palluma* group species and *P. indistinctus* and *P. somuncurensis* (*patagonicus* group). *Phymaturus fiambala* sp. nov. shows 1.4% distance from *P. antofagastensis*, 1.1% from *P. denotatus* (the shortest distances recorded). The shortest distance within the *mallimaccii* subclade is 0.6% between *P. denotatus* and *P. antofagastensis*, and 0.7% between *P. extrilidus* and *P. bibroni*. We found between *P. denotatus* and *P. laurenti* 0.0% of distance. Sequence used for *P. laurenti* is the one used by Morando et al. (2013), which belongs to a specimen collected at Cuesta de Randolfo that was considered *P. laurenti* in Lobo et al. (2010) before the discovery of *P. denotatus* (Lobo et al. 2012). This population deserves to be re-evaluated, as it probably corresponds to *P. denotatus*. In a future contribution we will provide sequences from the type locality of *P. laurenti*. The average distance among members of the *mallimaccii* subclade is 1.9%, while that for the *antofagastensis* lineage is 1.1%. Average distance of *P. dorsimaculatus* and *P. palluma* from members of the *mallimaccii* subclade is 5.1%.

DISCUSSION

Morphological, chromosome and genetic divergence within the group

Although there are characters of color patterns that exhibit variation within this lineage, like throat pattern (light gray versus melanic), lateral neck folds melanic speckled with small white markings (presence or absence), a vertebral lighter coloration along the trunk (presence or absence), flank coloration in females (yellow versus orange), scapular spot conspicuous (yes or no), white slender transversal stripes over the trunk in females (presence versus absence), tail color in males (brown versus yellow), melanism over dorsum and lateral sides of heads (presence versus absence), in general they are quite constant and permit a practical and direct diagnosis. For example, in the holotype of *P. mallimaccii*, a male individual photographed by J.M. Cei (fig. 2, Cei 1980) is almost identical to the specimen collected and photographed by C. Abdala almost 30 years later, FML 21117 (see Fig. 2D of the present study). Other males examined by the senior author show exactly the same pattern (DC-JMC, FML, MCN-UNSa, CSUN-REE).

As can be seen in table 2, continuous characters taken from squamation exhibit similar values in all species of the *antofagastensis* lineage, with overlapping ranges, but anyway are all useful in cladistic analyses and in taxonomic diagnoses. From eighteen characters evaluated, fourteen exhibited significant differences among species. Seven of those characters showed significant differences at p values < 0.0001 (Hellmich index, number of subocular scales, number of lorilabial scales, number of gular scales, scales contacting mental, scales projected over the auditory meatus and number of scales between frontal-rostral). The number of infralabial scales, ventral scales, dorsal scales (counted at middle of the trunk in a head-length) and the number of scale organs on postrostrals did not present differences among species (Table 2). Results obtained in the present study from the *antofagastensis* lineage show that, even in terminal lineages with very closely related

species, morphology provides valuable information. Information on chromosome morphology available for species of the *palluma* group shows no variation within the *antofagastensis* lineage (Grosso et al. 2017). Species belonging to the *antofagastensis* lineage share an identical 2n, 27 (females) and 28 (males), which is a plesiomorphic condition (also present in the *roigorum* subclade), being apomorphic 2n = 29/30 for members of the *punae* lineage (Grosso et al. 2017). Other characters analyzed by Grosso et al. (2017) show differences between *P. williamsi* (a *punae* lineage representative: pairs 4, 6, 7, 8, and 9) and the sister taxa *P. laurenti*-*P. denotatus*, which show identical chromosome morphology. Unfortunately, no chromosome data exist of *P. fiambala* sp. nov. in literature. Significant variation exists within clades of *Phymaturus* regarding internal cyt*b* distances. For example, among species of the *payuniae* clade (*patagonicus* group), distances range between 1.5–6.2% (x = 3.74 DS = 1.29), while within the *mallimaccii* subclade (*palluma* group), they range between 0.60–4.4% (x = 1.9 DS = 1.17). Comparatively, pairwise distances for *P. fiambala* sp. nov. are within the expected range for the genus, the lowest being 1.1% within the *antofagastensis* lineage (Table 1). *Phymaturus aguedae* was recovered as a member of a monophyletic group of species of Chilean distribution (Troncoso et al. 2018), which is basal to the *antofagastensis* and *punae* lineages. Cyt*b* distances calculated in the present work between this species and other species of the *mallimaccii* subclade are consistent with its more distant phylogenetic position. Pairwise distances of cyt*b* are sometimes incongruent with cladistics and patristic distances. For example, *P. extrilidus* (*punae* lineage) inhabits the Sierra de la Invernada, an isolated chain of mountains far east from the Andean massif, where another species lives. Yet, it shows quite low cyt*b* distance (0.7%) with *P. bibroni*, which is found on the western slopes of the Andes and is more closely related to *P. punae*, *P. aguanegra* and *P. williamsi* (eastern slopes of the andean mountains). *Phymaturus antofagastensis*, which shows very low distance (0.6%) with *P. denotatus* (whose closest relative is *P. laurenti*, Fig. 7), lives isolated and quite far from the other species in high elevations of Las Grutas and Paso San Francisco (western Andean Catamarca).

Phylogenetic relationships

The phylogenetic hypothesis shown in this work is not fully congruent with the one published in Lobo et al. (2016). Due to the fact that we added morphological information to three terminals of the *vociferator* clade, and new sequences (from Troncoso et al. 2018), we obtained a different hypothesis to that of Lobo et al. (2016). Our analysis was also not identical to that of Troncoso et al. (2018), probably due to different optimal criteria used in both studies, *i.e.*, strict parsimony here versus Bayesian analysis of Troncoso et al. (2018). *Phymaturus maulense*, *P. damasense* and *P*. sp5 are related in the same way but the other species are not. Relationships within the *roigorum* subclade are the same, except for the position of *P*. sp9 (undetermined in Lobo et al. 2016). In the present study, *P. timi* is sister taxon of *P. roigorum*, a relationship previously recovered by Hibbard et al. (2018). In Lobo et al. (2016), *P*. sp8 is related to the *verdugo* lineage, but in the present analysis it is related to the pair formed by *P. timi* and *P. roigorum*.

In the *mallimaccii* subclade, *P. aguedae* is basal, as in the 2016 analysis, but there are some changes. Among these, four lineages have been recovered (Fig. 7B), a basal one formed by *P. alicahuense*, *P. darwini* and *P. aguedae* (identical to Troncoso et al. 2018). Basal to the rest of the group is the lineage formed by *P*. sp. lar, *P*. sp. gua and *P. punae*. A couple of sister lineages, one formed by *P. extrilidus*, *P. bibroni*, *P. aguanegra* and *P. williamsi*, and the other by *P. mallimaccii* and *P. fiambala* sp. nov. sister taxa of a group formed by *P. antofagastensis*, *P. laurenti* and *P. denotatus*. This hypothesis is different from Troncoso et al. (2018) in that it recovers three lineages instead of four, but in their study they lack some terminal taxa. In Lobo et al. (2016) we recovered two lineages rendering *P. aguedae* as basal to them, here the "*punae*" lineage is not recovered because *P. punae* is more related to other species (Fig. 7). The relationship of *P*. sp. lar (Laguna Brava population) and of *P*. sp. gua (El Peñón, Gualcamayo) closely related to *P. punae* is different from Lobo et al. (2016) analysis, where both candidate species were recovered as members of different lineages.

In sum, the present analysis has changed the composition and relationships among the different lineages within the *mallimaccii* subclade, and better supported their monophyly. On the other hand, there still exists weak support for most internal relationships among and within lineages in the combined analysis (Fig. 7B). This fact can be explained by the fragmentary information we have about some species in the group, since we lack sequences of *P*. sp. lar, *P. aguanegra* and cyt*b* for *P*. sp. gua. Also, morphological data for *P. aguedae* is in great part incomplete, and samples of *P*. sp. lar and *P*. sp. gua are small. The parsimony and Bayesian analyses ran exclusively with the DNA partition in Lobo et al. (2016) for the entire *palluma* group recovered a very good support for the *antofagastensis* lineage and their internal nodes with the exception of the position of *P. fiambala* sp. nov. and *P. mallimaccii* (uncertainty about which one

is the most basal taxon). In the combined analysis of Lobo et al. (2016, fig. 2), we recovered the same topology recovered here, with the exception of *P*. sp. gua, which now is not included in the lineage. In the present analysis with only the molecular information, we found with parsimony *P. fiambala* sp. nov. as the most basal species of the *antofagastensis* lineage but lack of support for *P. mallimaccii* as sister taxon of the rest of members of that lineage (Fig. 7A). Although the molecular analysis was made for comparison, we believe that total evidence analysis is more accurate, as information given by the more than 260 morphological characters has been exhaustively researched for the last 10 years. The position of *P. mallimaccii* as sister to *P. fiambala* sp. nov. is therefore preferred. In any case, we find that independent lines of evidence both indicate that *P. fiambala* sp. nov. is indeed a member of the *P. antofagastensis* clade with good support, which indicates that at least the composition of this previously named group undoubtedly stays firm. Finally, it should be mentioned that a character that was recovered as an apomorphy of the *antofagastensis* lineage in Lobo et al. (2016)—brown-pigmented dorsal fascia of longissimus dorsi and transverso spinalis without pigmentation (character 216)—is not recovered now. The present study it is recovered it as an apomorphy that links both terminal lineages, with a secondary loss in the group formed by *P. aguanegra* and *P. williamsi.*

Species of the *mallimaccii* subclade exhibit phenotypic characters that allow for a clear differentiation among them, but low cyt*b* distances in comparison to other clades. Species of the *antofagastensis* lineage are an example of this phenomenon. This highlights the importance of including phenotypic characters in phylogenetic analyses.

CONCLUSIONS

Phymaturus fiambala sp. nov. belongs to the *antofagastensis* lineage because it shares synapomorphies with all other members of the lineage: four discrete and three continuous characters (presence of flank color in females, loss of scale organ in mental, dark sides of neck speckled with small white spots among them) plus eight DNA changes. *Phymaturus fiambala* sp. nov. males exhibit yellow tails continuing the same color of trunks, different from all other members of the *mallimaccii* subclade, which is composed of males that exhibit brown tails (yellow tails are found in the *vociferator* clade, and the *roigorum* subclade). Furthermore, we found morphological and molecular evidence that allows us to differentiate *P. fiambala* sp. nov. from other species within *antofagastensis* lineage. Our present phylogenetic analysis provides a new hypothesis of relationships within the *mallimaccii* subclade that allow for more confident studies on evolutionary comparisons and the biogeography of these Andean lizards in the future.

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Supplementary materials

Appendix 1. List of individuals studied for each species and list of morphological characters added to the matrix. (download)

Table S1. List of all the species, voucher numbers and Genbank accession numbers of the sequences employed in this study. (download)