Redescription of the southernmost snake species, *Bothrops ammodytoides* (Serpentes: Viperidae: Crotalinae)

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Abstract. *Bothrops ammodytoides* is a pitviper species endemic to Argentina that inhabits arid and semiarid areas from sea level to more than 3000 m, reaching the southernmost latitude for snakes. According to previous studies, the species is placed in the *Bothrops alternatus* group. We redescribe *Bothrops ammodytoides* based on examination of 101 specimens and provide new data on lepidosis, hemipenial morphology, cranial osteology, variation in coloration, and distribution. We compare *Bothrops ammodytoides* with representative species of the genus and related genera. Morphological comparisons reveal considerable affinities between *Bothrops ammodytoides*, *Bothrops pictus*, *Bothrops andianus*, and *Bothrocophias microphthalmus*, suggesting that the current taxonomy for *Bothrops ammodytoides* requires to be reassessed.

Keywords: *Bothrops ammodytoides*, cranial osteology, distribution, hemipenis, lepidosis, morphological comparisons.

Introduction

Bothrops ammodytoides, a pitviper species endemic to Argentina, is the snake with the southernmost distribution (Cei, 1993; Greene, 1997; Campbell and Lamar, 2004). The species was described by Leybold (1873), who compared it with *Vipera ammodytes*, a species similar to *Bothrops ammodytoides* in coloration and general aspect, particularly in the elevated snout. This condition is denoted in the local name of *Bothrops ammodytoides*: "yarará ñata".

At present the holotype is lost. The type locality, known as "northern Argentina", was corrected to "Mendoza Province" by Campbell and Lamar (1989) and finally determined by Scrocchi (1997), according to Leybold's "Excursión a las Pampas Argentinas" (1873), as "Estancia Los Aguirre, San Carlos department, Mendoza Province" (33°53′S; 69°05′W). *Bothrops ammodytoides* is distributed in arid regions in the Provinces of Jujuy, Salta, Cata-

marca, La Rioja, Tucumán, San Juan, Mendoza, San Luis, La Pampa, Neuquén, Río Negro, Chubut, Santa Cruz, mountain areas of Córdoba, and coastal areas of Buenos Aires (Cei, 1986, 1993; Giraudo and Scrocchi, 2002; Cabrera, 2004; Campbell and Lamar, 2004; Scolaro, 2005; Scrocchi, Moreta and Kretzschmar, 2006). It is a terrestrial snake that inhabits rocky and sandy areas from sea level to altitudes higher than 3000 m (Moreta, pers. com.). It feeds on saurians and rodents; it is viviparous and the females give birth to 15 to 30 young (Miranda, Couturier and Williams, 1983).

Because of the relatively small size of this species, accidents caused by *Bothrops ammodytoides* were long considered not life-threatening; however, bites by *Bothrops ammodytoides* may cause mild to severe poisoning in domestic animals as well as in humans (De Roodt et al., 2000).

Regarding the systematic position of this species, Vellard (1928, 1946), based on hemipenial morphology, related *Bothrops ammodytoides* to *Bothrops itapetiningae* and *Bothrops erythromelas*, and *Bothrops alternatus* to *Bothrops cotiara* and *Bothrops neuwiedi*. In a revision of the external and internal morphology of crotalines, Burger (1971) proposed three groups: the "*neuwiedi*", the "*alternatus*" and the

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"*ammodytoides*" groups, the latter composed of *Bothrops ammodytoides*, *Bothrops roedingeri*, *Bothrocophias microphthalmus* and *Bothrocophias colombianus*. In a study of the cranial osteology and mandibular musculature of three species of *Bothrops*, Moro (1996) found the relation: (*Bothrops alternatus* (*Bothrops diporus* + *Bothrops ammodytoides*)). In a phylogenetic analysis based on genes of several species of crotalines, Parkinson, Campbell and Chippindale (2002), and Castoe and Parkinson (2006) included *Bothrops ammodytoides*. They hypothesized that the species formed a clade with *Bothrops alternatus* and *Bothrops cotiara*, which was accepted by other authors, such as Martins, Marques and Sazima (2002) and Werman (2005). Recently, Fenwick et al. (2009) included almost all species of *Bothrops* in a phylogenetic analysis using morphological and mithocondrial characters, and they proposed to split the genus into three genera: *Rhinocerophis* for the "*alternatus*" group including "*ammodytoides*", *Bothropoides* for the "*neuwiedi*" and "*jararaca*" groups, and *Bothrops* for the rest of the species, except "*pictus*", "*roedingeri*", "*barnetti*" and "*lojanus*", which remain incertae sedis.

In general, phylogenetic relationships within *Bothrops*, as previously recognized, have been analyzed mostly using molecular evidence (e.g., Salomão et al., 1997, 1999; Wüster et al., 1999; Parkinson, Campbell and Chippindale, 2002; Wüster et al., 2002; Grazziotin and Echeverrigaray, 2005; Castoe and Parkinson, 2006). Werman (1992) and Gutberlet and Harvey (2002) incorporated anatomical features in their analyses, but these studies included several genera of Neotropical pitvipers and only a few species of *Bothrops*. Fenwick et al. (2009) presented an almost complete taxon analysis of this genus, including both morphological and molecular characters, but without examining osteology and hemipenial morphology of several species.

Previous studies made a considerable contribution to the systematics of Neotropical pitvipers. However, morphological characters remain an important source of systematic value (Shultz, 2007; see also Wiens, 2004; Smith and Turner, 2005), and rigorous morphological examinations of *Bothrops* specimens and a deeper understanding of polymorphisms are still needed for a total evidence approach.

After examining a sample of 101 specimens of *Bothrops ammodytoides*, we redescribe the species, including new data on external morphology, color pattern variation, cranial osteology, hemipenial morphology, and distribution. We compare *Bothrops ammodytoides* with species of the genus representing the generally recognized species-groups (*Bothrops alternatus*, *Bothrops cotiara*, *Bothrops jonathani*, *Bothrops diporus*, *Bothrops jararaca*, *Bothrops jararacussu*, *Bothrops atrox*, *Bothrops andianus*, *Bothrops pictus*) and with species of related genera (*Bothrocophias microphthalmus* and *Lachesis muta*). We also address a brief discussion about the reasons for not adopting the taxonomy proposed by Fenwick et al. (2009) in this study.

Material and methods

Because the holotype of *Bothrops ammodytoides* is lost, features for that specimen were made using information available in the original description (Leybold, 1873). Redescription is based on the examination of 101 specimens (see Appendix) from throughout the distributional range, including Mendoza Province, the type locality according to Leybold (1873). For morphological comparisons we examined specimens (see Appendix) of *Bothrops alternatus*, which is partially sympatric with *Bothrops ammodytoides*; *Bothrops cotiara*, a species included in the "*alternatus*" group and that reaches northeastern Argentina (Misiones Province); *Bothrops jonathani*, a species described by Harvey (1994) for the Bolivian Andes, which inhabits geographically similar areas and is probably sympatric or at least parapatric with *Bothrops ammodytoides* in northwestern Argentina (Carrasco, Harvey and Muñoz, 2009); *Bothrops diporus*, which is partially sympatric with *Bothrops ammodytoides* and is considered in this study as representative of the "*neuwiedi*" complex" (Da Silva and Rodrigues, 2008); and *Bothrops andianus* and *Bothrops pictus*, both Andean species. *Bothrops pictus* was recovered in a basal position with respect to *Bothrops* in a few studies (Wüster et al., 2002; Fenwick et al., 2009) and at present the species remains incertae sedis. To represent the rest of the *Bothrops* groups we included *Bothrops jararaca*, *Bothrops jararacussu*, and *Bothrops atrox*. We also compared *Bothrops ammodytoides* with
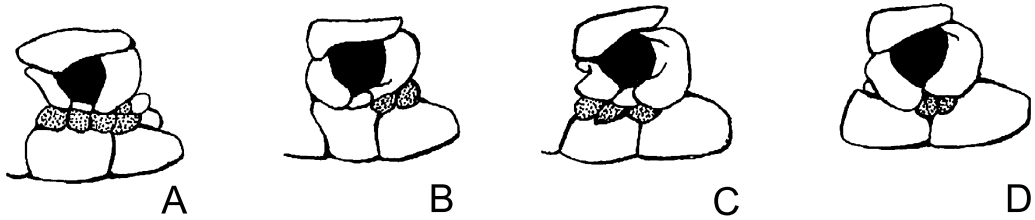
Figure 1. Different disposition of subfoveals. A: Complete row. B-D: Incomplete row.

Bothrocophias microphthalmus and *Lachesis muta*, because these species are considered basal to *Bothrops* (Gutberlet and Campbell, 2001; Gutberlet and Harvey, 2002; Parkinson, Campbell and Chippindale, 2002; Wüster et al., 2002; Castoe and Parkinson, 2006).

Bothrops ammodytoides specimens and comparative material examined are deposited in Museums from Argentina: Centro de Zoología Aplicada, Córdoba (CZA), Fundación Miguel Lillo, San Miguel de Tucumán, Tucumán (FML), Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (MACN), Museo de Ciencias Naturales de La Plata, La Plata, Buenos Aires, (MLP-JW, MLP-R), Cátedra de Anatomía Comparada, Universidad Nacional de Córdoba, Córdoba (AC); Perú: Museo de Historia Natural Javier Prado, Lima (MHNJP); and Bolivia: Museo de Historia Natural Noel Kempff Mercado, Santa Cruz (MNKR), Centro de Biodiversidad y Genética, Cochabamba (CBGR), Museo de Historia Natural Alcides D'Orbigny, Cochabamba (MHNC-R), and Colección Boliviana de Fauna, La Paz (CBF). Hemipenial morphology for *Bothrops cotiara* was examined in the Instituto Butantan, São Paulo, Brazil (IB), and cranial osteology data for this species were provided by Martão (pers. com.) and also follows Zanella and De Lema (1999).

Specimens were examined using a stereomicroscope. Most structures were measured with dial calipers. Snout-vent length (SVL) and tail length (TL) were measured with measuring tape. Specimens having a SVL < 300 mm were considered juveniles. For lepidosis description we followed Klauber (1972), Gutberlet and Campbell (2001), and Harvey, Aparicio and Gonzales (2005). Scales around supraoculars were counted excluding superior pre- and postoculars. Interrictals were counted in a straight line between last supralabials and including them. A divided sublacunal was recognized when more than one scale contacted the inferior margin of the loreal pit (besides the prelacunal). When this condition was present, anterior and posterior portions were recognized, in agreement with Werman (1992), Gutberlet (1998), and Gutberlet and Harvey (2002). We observed the different conditions of the prelacunal with respect to the supralabials: prelacunal separated from second supralabial (subfoveals present); prelacunal in contact with second supralabial (subfoveals present or absent); prelacunal partially or totally fused with second supralabial forming a "lacunolabial" scale (subfoveals generally absent). The prelacunal condition was previously recognized as a character of systematic relevance by some authors (Burger, 1971; Pesantes, 1989; Werman, 1992; Salomão et al., 1997) who noted a basal dichotomy between the "*alternatus*" and "*neuwiedi*" groups (lacunolabial absent = prelacunal discrete) and the "*atrox*" and "*jararacussu*" groups (lacunolabial present = prelacunal fused with second supralabial). Harvey, Aparicio and Gonzalez (2005) also considered that the presence of subfoveals would have diagnostic value in *Bothrops*. We considered subfoveals as being those scales below lacunals, between the posterior margin of the sublacunal and the anterior margin of the prelacunal. Subfoveals may form a complete row (fig. 1), with both sublacunal and prelacunal separated from supralabials; or they may form an incomplete row, in which case any of three conditions are possible: prelacunal in contact and sublacunal separated from supralabials, prelacunal separated and sublacunal in contact with supralabials, or prelacunal and sublacunal in contact with supralabials. We considered postfoveals those scales between the posterior margin of the sublacunal and the anterior margin of the orbit. The first ventral scale was considered as the first scale wider than long. We followed Klauber (1972), Moro (1996), and Zanella and De Lema (1999) for terminology of cranial osteology; and Dowling and Savage (1960) and Pesantes (1989) for describing hemipenial morphology. Dried and disarticulated skulls were examined. Hemipenes were everted using the technique proposed by Pesantes (1994) and Zaher (1999), and examined ex situ. Cranial and hemipenial preparations are detailed in the Appendix. In the description, a back slash (/) separates counts from opposite sides of the same specimen and a dash (–) separates ranges; polymorphic characters are followed by percentages of specimens presenting the alternative state.

Results

Redescription

Bothrops ammodytoides Leybold, 1873

Bothrops ammodytoides Leybold, 1873. Excursión a las Pampas Argentinas: 80. Type locality: Estancia Los Aguirre, Departamento San Carlos, Mendoza, Argentina. (See Scrocchi, 1997.)

Rhinocerophis nasus Garman, 1881. Bull. Mus. Comp. Zool. 8: 85.

Bothrops nasus Berg, 1884. Acta Acad. Nac. Cienc. Córdoba 5: 96.

Bothrops patagonicus Müller, 1885. Verh. Nat. Ges. Basel 7(3): 697.

Bothrops burmeisteri Koslowsky, 1895. Rev. Mus. La Plata 6: 369.

Lachesis ammodytoides Boulenger, 1896. Cat. Snakes British Mus. 3: 543.

Bothrops ammodytoides Amaral, 1930. Mem. Inst. Butantan 4: 233.

Rhinocerophis ammodytoides Fenwick, Gutberlet, Evans and Parkinson, 2009. Zool. J. Linn. Soc. 156: 630.

Diagnosis – *Bothrops ammodytoides* may be distinguished from other species of the genus by the presence of a subtriangular rostral, upturned snout and internasals that give the species the "elevated snout" aspect, and by the following combination of characters: discrete prelacunal contacting second supralabial; subfoveals, when present, 1/1; canthals 2/2 and occasionally 3/3; rectangular or elongated loreal contacting second canthal; one row of scales between suboculars and supralabials (= three interoculabials) (fig. 2).

External morphology – Snout-vent length 360-640 mm in females and 340-570 mm in males. Tail length 46-72 mm in females and 53-80 mm in males. 21-23 dorsal scales on the anterior part of the body, 22-24 on the midbody, and 15-19 on the posterior portion of the body. 149-170 ventrals and 25-37 subcaudals in females; 144-163 ventrals and 29-41 subcaudals in males. Caudal appendix, 3-7 mm, with

slightly curved apex and lateral grooves. Internasals elevated anteriorly, contact each other (except in MLP-JW 951 and MACN 22061, where internasals are separated by one and three scales, respectively). Internasals followed by 2/2 canthals (3/3 in 20%), the posterior one generally greater and depressed. 5-8 keeled intercanthals. Supraoculars oval and surrounded by 8-9 scales. Two or three postoculars and three suboculars (when two, at least one of them elongated). 7-11 intersupraoculars. Preoculars contact the orbit, except the inferior one. Superior, larger preocular contributes to the canthus, discrete or divided in two portions (32%). Medial preocular discrete or fused with supralacunal (27%). Inferior preocular partially fused with the sublacunal or discrete (20%). Sublacunal contacts third supralabial; discrete or divided in two portions (25%) (more than two in FML 7322). Discrete prelacunal contacts the second supralabial in all specimens (we do not observe any case of the prelacunal contacting the third supralabial or other variation in this character that, according to Campbell and Lamar, 2004, was unclear). Rectangular or elongated loreal contacts second canthal. 2-6 prefoveals and 1/1 postfoveals. Subfoveals 1/1 (60%), 1/0 (20%), or totally absent. Nasal partially fused with postnasal, ending sharply upwards. 9-11 supralabials (third and fourth larger), 11-14 infralabials, 26-32 interrictals, and 5-7 gulars in 5-6 rows. Suboculars and supralabials separated by single row of scales (= three interoculabials); at level of fifth supralabial, additional scale
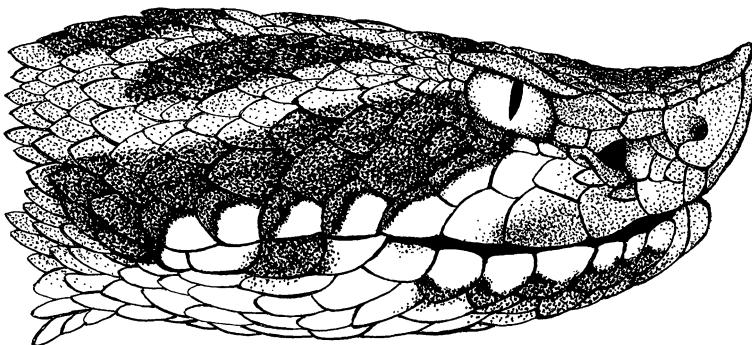

Figure 2. *Bothrops ammodytoides*. Facial pattern and lepidosis (MLP-JW 20; head length: 32 mm).

may appear in this single row. Rostral uplifted and subtriangular, sharper and more elevated in some specimens, particularly in juveniles, probably due to allometry. Presence of depression in the region between loreal pit and nasal, involving pre-sublacunal and prefoveals, is characteristic of the species.

Coloration – All specimens of *Bothrops ammodytoides* examined have a pale tan ground coloration. Dorsally, rectangular blotches alternate or juxtapose (fig. 3); these blotches are brown, darker towards the borders and are edged by a fine white or whitish line. On the flanks, smaller, rounded and dark tan blotches are distributed in two rows. We observed pale or cream-yellow tail tips in juveniles. Dorsally in the head, a subtriangular dark tan blotch is present in the intercanthal area; dark tan blotches are symmetrically distributed in the intersupraocular area (generally two blotches that sometimes cover part of the supraocular), in the parietal area (generally two pairs), and in the occipital area (a pair). In the lateral surface of the head, a postocular dark stripe is 2.5-3 scales wide, and extends from the inferior margin of the orbit to the neck, surrounding the rictus and giving dark corners to the posterior supralabials.

Anterior supralabials are diffusely pigmented, and some specimens have darker dots in the third and fourth supralabials. Infralabials 9-11 have a dark blotch, 6-8 are slightly dotted and 1-5 have dark borders, which are extensions of a pair of dark blotches in the gular area.

We did not observe sexual dimorphism in coloration, but variations in the intensity of melanism in the body and in the cephalic dorsal pattern were noted. In both cases, we identified a wide spectrum of variation that includes several combinations. In general, less pigmented specimens have an immaculate or sparsely dotted venter, with dorsal blotches of relatively well defined margins, and the space separating them is of equal size or slightly smaller than the blotches. In individuals of dark coloration the abdomen is heavily dotted; in some cases dotting forms a dark stripe on the anterior portion, extending to the gular region. Dorsal blotches are larger than the space between them and have diffuse contours. This more intense pigmentation is also observed in the cephalic region, where supra and infralabial spots are more intense, gular spots are wider, and the postocular stripe is longer and usually begins at the first rather than the second subocular. The cepha-

Figure 3. *Bothrops ammodytoides* from Sierras Grandes, Córdoba, Argentina (CZA live collection).

lic pattern varies in the arrangement of occipital blotches (fig. 4). While in some individuals these blotches are divided by a transversal whitish stripe, resulting in a cross pattern, in other individuals these blotches are not divided and extend posteriorly. Both patterns, with their intermediate variations, are observed in individuals with slight and strong pigmentation. How-
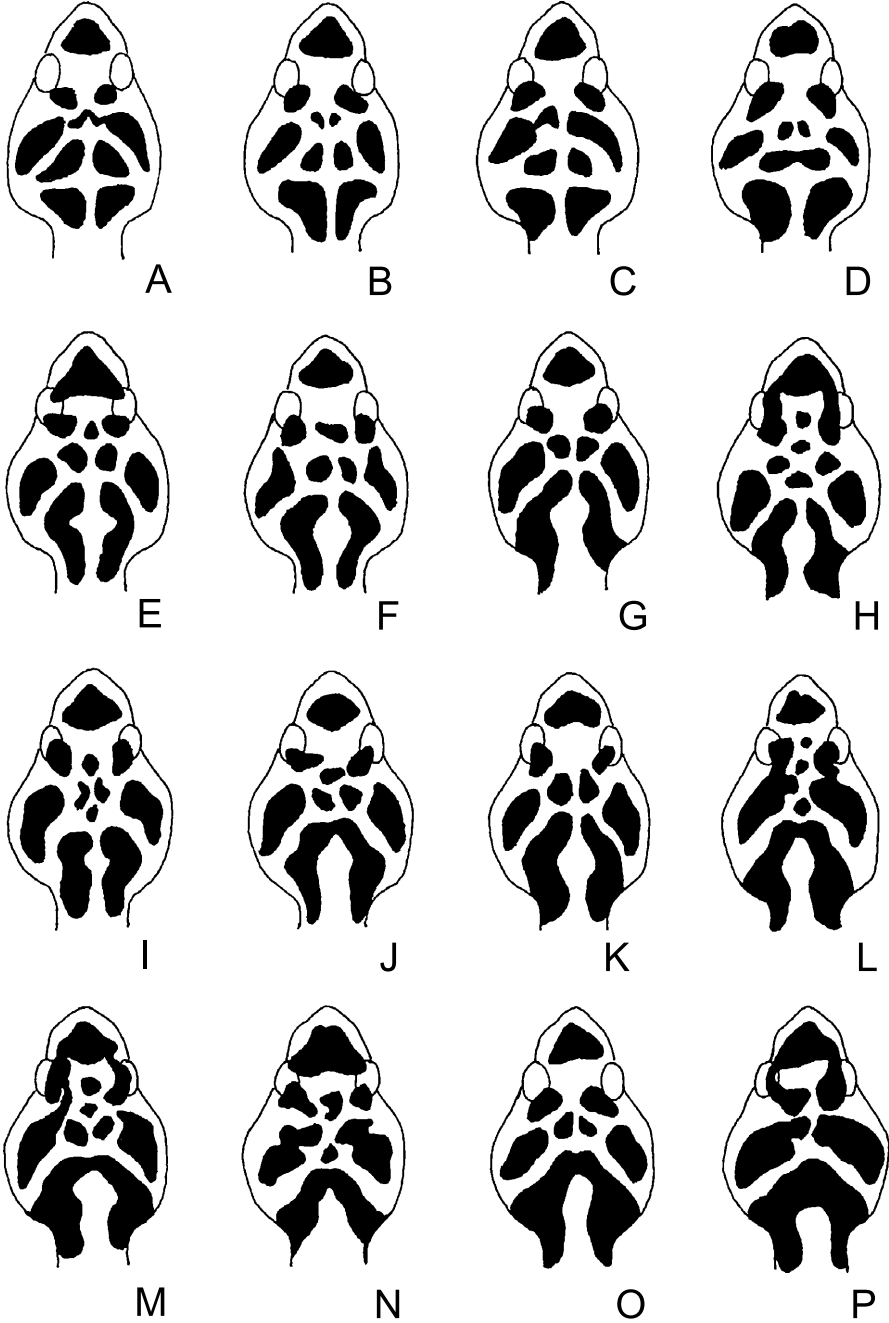

Figure 4. Variation in cephalic color pattern. A: FML 1405, B: FML 1953, C: CZA 125, D: FML 1592, E: MACN 1620, F: FML 7326, G: CZA 126, H: MACN 22061, I: MLP-JW 951, J: MACN 39066, K: FML 7324, L: MLP-JW 20, M: MACN 1803, N: FML 9602, O: FML 7699, P: MACN 39070.

ever, a predominance of non-divided occipital blotches is observed in the latter case. The color variation observed does not reveal a geographic pattern. Specimens with both extreme and intermediate pigmentation and with different arrangement of the cephalic blotches are found at various localities within the distribution range of the species. However, we observe a dominance of strongly pigmented specimens in Córdoba and Buenos Aires Provinces.

Hemipenial morphology – Hemipenis bilobed (fig. 5), 13.6-20 mm long (27-30% of TL). Lobes subcylindrical and parallel with each other. In some specimens we observe a papilla (FML 7699 and MACN 32893) or indication of a papilla in the lobe apex (MACN 35351, MACN 39071). Hemipenial body 35-40% of total hemipenial length. Capitulum extends half or more (56-77%) of lobe length on both ventral (sulcate) and dorsal (asulcate) sur-

face. Micro-ornamentation of capitulum varies: CZA 43, MACN 32888, and MACN 39066 have microspines in all calyces except in the apex; FML 7699, MACN 39068, MACN 39071, and MACN 39073 have microspines in the proximal half of the capitulum; FML 1592 and MACN 32893 have microspines only in basal calyces. 39-55 hook-shaped spines distribute homogeneously in the lobes and body. Smaller and undifferentiated spines are distributed in the intralobular area. Microspines in body surface and sulcus spermaticus margins. Microspines in intrasulcar area present or absent (50%). Lateral surface of the body bears a small depression and dorsal one bears a small protuberance or swollen area. Variation observed among specimens does not reveal a geographical pattern.

Cranial osteology – Cranial features of *Bothrops ammodytoides* (fig. 6) were described by Moro (1996) and our observations are consistent with that description, except in a few features. In all specimens examined we found a higher number of ectopterygoid teeth (11-10 vs. 6-8), poorly developed (vs. developed) supraoccipital crests, and superior portion of the angular-splenial present (vs. absent).

Distribution

Bothrops ammodytoides is sympatric with *Bothrops diporus* over most of its range. However, the latter species extends to Neuquén Province (Cei, 1986, 1993), whereas *Bothrops ammodytoides* reaches locations farther to the south in the Río Deseado Basin, Santa Cruz Province (Cei, 1986, 1993; Scolaro, 2005; Scolaro, pers. com.). In this study, the southernmost specimens examined are from Península de Valdés, Chubut Province (fig. 7) and Avila (pers. com.) informed us about one specimen collected in Telsen, Chubut Province, and deposited in the Centro Nacional Patagónico, Chubut (LJAMM-CNP 3280). The maximum elevation known for *Bothrops ammodytoides* was reported to be at least 2000 m (Campbell and Lamar, 2004) and actually extends to more than 3000 m, since the species was observed in the local-
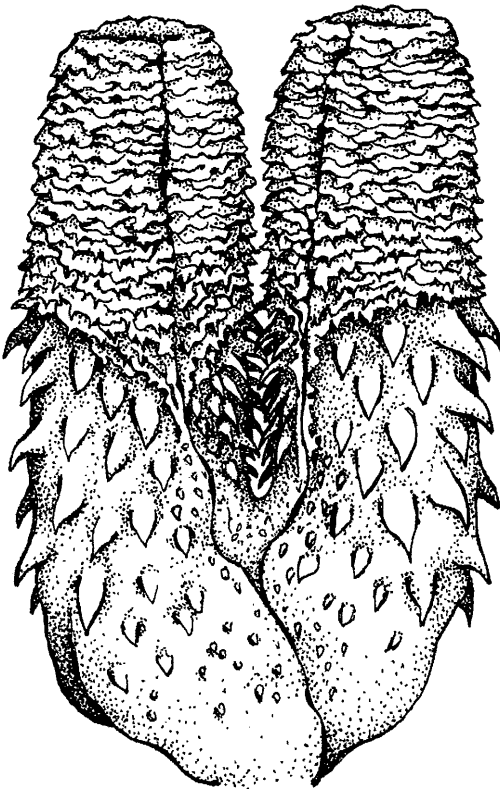

Figure 5. Hemipenis of *Bothrops ammodytoides* (MACN 32893; 13.6 mm long).
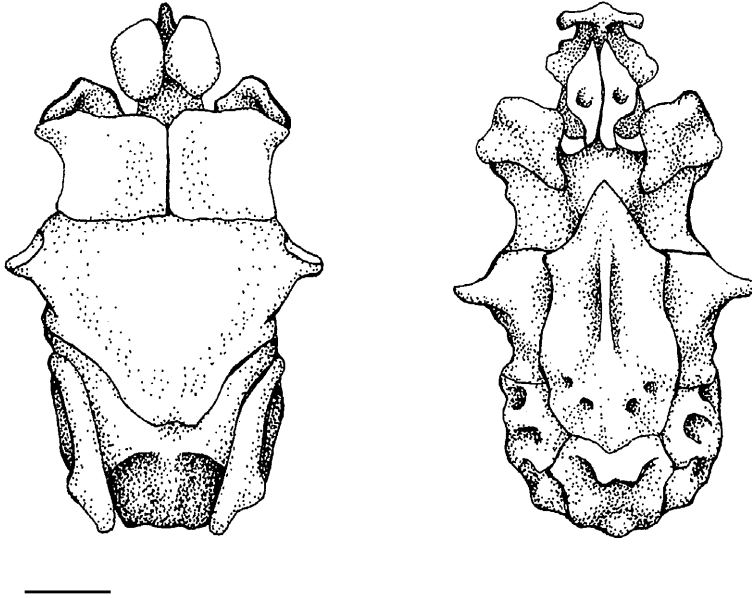
Figure 6. Cranium of *Bothrops ammodytoides* (MACN 39068; left: dorsal view; right: ventral view; scale bar: 4 mm).

ity of Tres Cruces, Jujuy Province, at 3700 m (Moreta, pers. com.). Thus, together with *Bothrops jonathani* (3220 m) and *Bothrops lojanus* (2300 m) (Harvey, 1994; Campbell and Lamar, 2004) *Bothrops ammodytoides* is one of the few species of the genus that inhabits xeric areas in the Andes at such high elevations.

Morphological comparisons

Bothrops ammodytoides, *B. alternatus*, *B. cotiara*, *B. jonathani*, and *B. diporus* are similar in having a discrete prelacunal and subfoveals. However, while in *B. ammodytoides*, *B. cotiara*, and *B. diporus* the prelacunal contacts the second supralabial and the number of subfoveals is low, in *B. jonathani* the prelacunal is separated from supralabials, in *B. alternatus* the condition is variable, and the latter two species have a higher number of subfoveals (table 1). On the other hand, *B. ammodytoides* differs from the other four species mentioned above by the presence of an elevated rostral different in shape (subtriangular vs. trapezoidal) (fig. 8) and in having no more than three interoculabials. *B. jararaca*, *B. jararacussu*, *B. atrox*, *B. pictus* and *B. andianus* also have three interoc-

ulabials, but these species lack subfoveals and bear a lacunolabial scale (prelacunal fused with second supralabial); however, the latter character is variable in *B. andianus* since we observed that 88% of the specimens present a partially divided lacunolabial (prelacunal incompletely fused). The character prelacunal is also variable in *B. pictus* and *Lachesis muta*: these species present both conditions (prelacunal discrete or totally fused) in similar proportion.

The elongated loreal is a condition shared by *B. ammodytoides*, *B. andianus*, *B. microphthalmus*, some specimens of *B. jonathani* and some of *B. pictus*. In the remaining species, the loreal scale is not elongated but as high as wide. *B. ammodytoides* and *B. microphthalmus* share an elevated rostral (but different in shape: subtriangular vs. rectangular), a discrete prelacunal contacting second supralabial, three interoculabials, and low number of subfoveals. *B. microphthalmus* differs in the presence of smooth or slightly keeled intersupraoculars, and in the characteristic canthorostrals and tuberculate keels in dorsoposterior scales (Gutberlet and Campbell, 2001). *B. andianus* also bears slightly keeled intersupraoculars and some specimens (MNKR
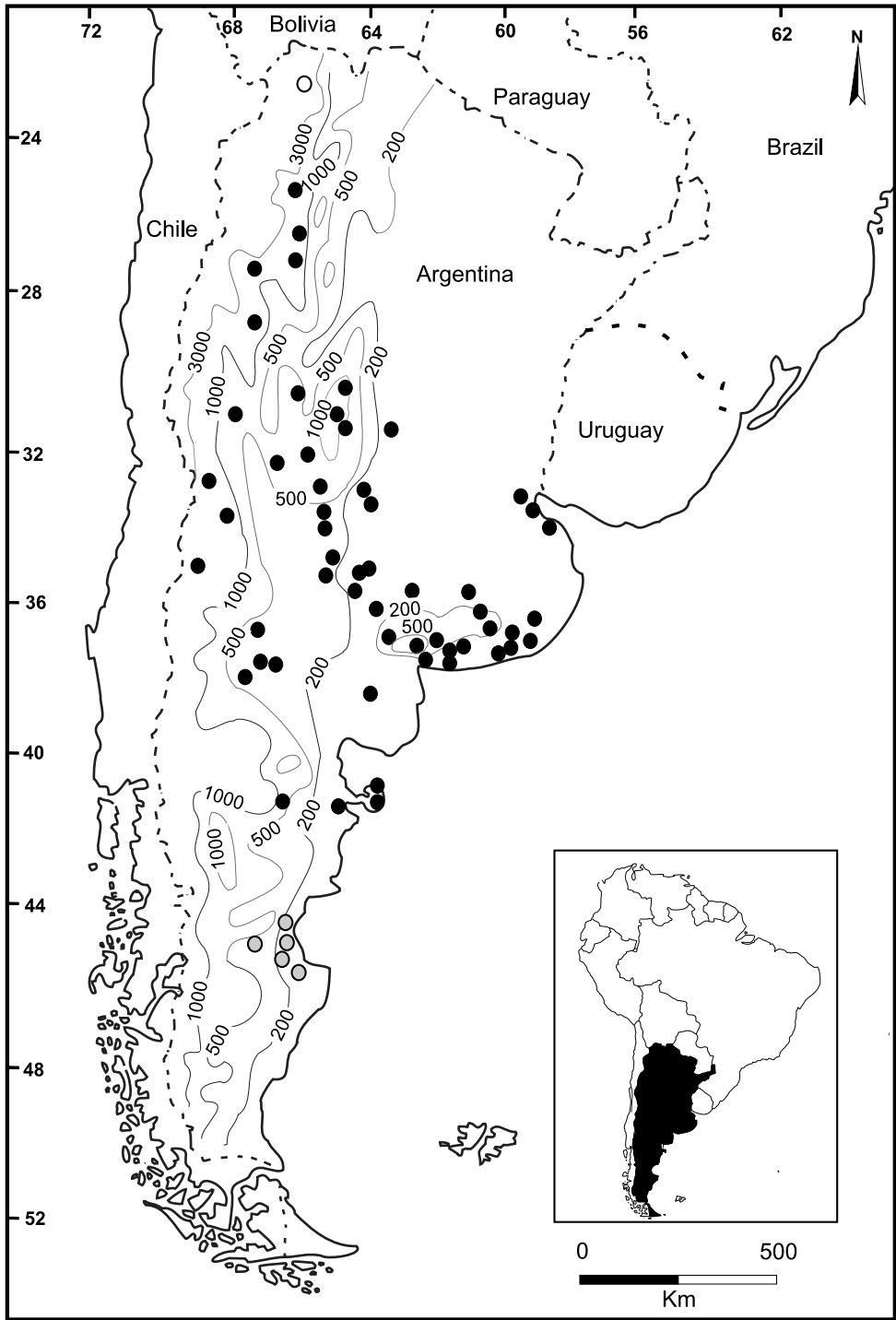
Figure 7. Distribution of *Bothrops ammodytoides* in Argentina. White dot: locality where the species was observed by Moreta at 3700 m (Tres Cruces, Jujuy Province); black dots: localities of the specimens of *B. ammodytoides* examined in this study; grey dots: southernmost localities of the species according to Scolaro (pers. com.).
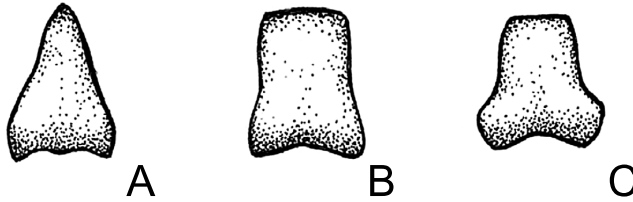
Table 1. Comparison of selected characters among the species examined in this study.

	Bothrops ammodytoides	*Bothrops pictus*	*Bothrops andianus*	*Bothrops alternatus*	*Bothrops jonathani*	*Bothrops cotiara*	*Bothrops diporus*	*Bothrops jararaca*	*Bothrops jararacussu*	*Bothrops atrox*	*Bothrocophias microphthalmus*	*Lachesis muta*
Rostral	Subtriangular	Trapezoidal	Rectangular	Trapezoidal	Trapezoidal	Trapezoidal	Trapezoidal	Trapezoidal	Trapezoidal	Trapezoidal	Rectangular	Subtriangular
Internasals	In contact, eventually separated	In contact	Separated, eventually in contact	In contact	In contact	In contact or separated	In contact	In contact	In contact	In contact	Separated	Separated
Canthals	2-3	1-2		1	1-2	1	1	1	1	1	1	2-3
Supralabials	9-11	9-11	7-8	9-11	9-12	8	8-9	8	8-9	7-8	7	8-10
Infralabials	11-13	11-13	8-10	12-15	12-15	10-12	10-12	9-11	10	9-11	8-10	13-15
Supraocular	Oval	Oval	Oval	Elongated	Moderately elongated	Elongated	Oval	Oval	Oval	Oval	Oval	Moderately elongated
Interoculabials	3-4	3	3	4-5	4-6	4	4	3	3	3	3	5
Prelacunal/2° supralabial	In contact	In contact or fused	Partially fused or fused	Separated or in contact	Separated	In contact	In contact	Fused	Fused	Fused	In contact	In contact or fused
Loreal	Elongated	Not elongated or elongated	Elongated	Not elongated	Not elongated or elongated	Not elongated	Not elongated	Not elongated	Not elongated	Not elongated	Elongated	Not elongated
Subfoveals	0-1	0	0	1-6	1-6	1-4	1-2	0	0	0	0-3	0-2
Middorsals	22-24	23-25	21-23	26-31	25-30	23-27	23-25	23-27	22-25	23-25	20-23	28-34
Supraoccipital crests	Separated from parietal	Close to parietal	Close to parietal	Close to parietal	Separated	Close to parietal	Separated from parietal	Separated	Separated	Close to parietal	Separated	Close to parietal
Mandibular crest	Asymmetric	Asymmetric	Asymmetric	Symmetric	Symmetric	Asymmetric	Asymmetric	Symmetric	Symmetric	Symmetric	Asymmetric	Symmetric
Palatine dorsal process	Medial	Medial	Medial	Anterior	Anterior	Medial	Medial	Medial or posterior	Posterior	Posterior	Medial	Anterior
N° of palatine teeth	3	4-5	5	2	2-3	3	3-4	4-5	4-5	4-5	5-6	3
Hemipenial lobes orientation	Parallel	Parallel, U-shaped	Parallel	Parallel	Parallel	Parallel	Divergent	Divergent	Divergent	Slightly divergent	Parallel, U-shaped	Parallel
Hemipenial spines distribution	Symmetric	Symmetric	Symmetric	Asymmetric	Asymmetric	Asymmetric	Asymmetric	Symmetric	Symmetric	Symmetric	Symmetric	Symmetric
Hemipenial spines shape	Hook	Slender and curve	Hook	Hook	Hook	Hook	Hook	Hook	Slender and curve	Slender and curve	Slender and curve	Hook
Lateral depression	Poorly developed or absent	Absent	Absent	Developed	Developed	Developed	Absent	Absent	Absent	Absent	Absent	Developed
Dorsal protuberance	Poorly developed	Absent	Poorly developed	Developed	Developed	Developed	Absent	Absent	Absent	Absent	Absent	Developed

Figure 8. Rostral scale of *Bothrops ammodytoides* (A), *Bothrocophias microphthalmus* and *Bothrops andianus* (B), and of the rest of the *Bothrops* species examined (C).

3327, MNKR 4542, MNKR 3722, MNKR un-catalogued) present tuberculate keels in dorsoposterior scales; apparently, *B. andianus* is polymorphic for this character.

The hemipenes of *B. ammodytoides*, *B. jonathani*, *B. alternatus* and *B. cotiara* have subcylindrical and parallel lobes, and hooked spines. Well developed lateral depression and a protuberance or swollen area in the dorsal surface of the body are present in *B. alternatus*, *B. cotiara* (Pesantes, 1989), *B. jonathani* (Carrasco, Harvey and Muñoz, 2009) and *Lachesis muta*; the latter structure is present but poorly developed in *B. ammodytoides* and *B. andianus*. On the other hand, *B. ammodytoides* and *B. andianus* differ from *B. alternatus*, *B. cotiara* and *B. jonathani* in the distribution of spines (symmetric vs. asymmetric) and in the proportion of body length with respect to lobe length (smaller in *B. ammodytoides* and *B. andianus*). Hooked spines are also present in *B. diporus*, *B. jararaca* and *Lachesis muta*; but hemipenes in these species are fusiform and in *B. diporus* the organ has divergent lobes and the spines are asymmetrically distributed. Spines in *B. jararacussu*, *B. atrox*, *B. pictus* and *B. microphthalmus* are not hooked but slender and curve. *B. microphthalmus* and *B. pictus* have U-shaped hemipenis (the lobes are well separated from each other), which differentiates them from the rest of the species included in this study. Except for *B. ammodytoides*, all other species examined lack a papilla in the hemipenis apex.

Cranial features in *B. ammodytoides*, as reported by Moro (1996), are similar to those of *B. diporus*. Both species have moderately developed postfrontals, supraoccipital crests separated from parietal, well developed lateral expansions of basisphenoid and medial palatine dorsal process (fig. 9). The latter condition is also observed in *B. pictus*, *B. andianus* and *B. microphthalmus*, while in *B. alternatus*, *B. jonathani* and *Lachesis muta*, the palatine dorsal process is positioned anteriorly, in *B. cotiara* the process is slightly anterior, in *B. jararaca* and *B. jararacussu* it is slightly posterior, and posterior in *B. atrox*. We also find additional similarities between *B. ammodytoides*, *B. pictus*, *B. andianus*, and *B. microphthalmus*: little development of basioccipital crests, asymmetric mandibular crest, and poorly developed basisphenoid crest and uniformly elevated along its extension. The latter condition is not observed in the remaining species, where the basisphenoid crest bears a rounded differentiated elevation in the middle. *B. andianus* and *B. microphthalmus* have subtriangular parietals, whereas in *B. ammodytoides* and *B. pictus* the parietal is quadrangular.

Discussion

Morphologically, *Bothrops ammodytoides* is relatively conservative compared with other species that show high levels of polymorphism (e.g., facial squamation), such as *B. alternatus*, *B. jonathani*, and *Lachesis muta*. Most of the variation observed in *Bothrops ammodytoides* involves body pigmentation and cephalic pattern. Because the species is widely distributed in Argentina, variation in coloration could be the effect of a recent differentiation process. In addition, differences in the intensity of melanism may be related to thermoregula-
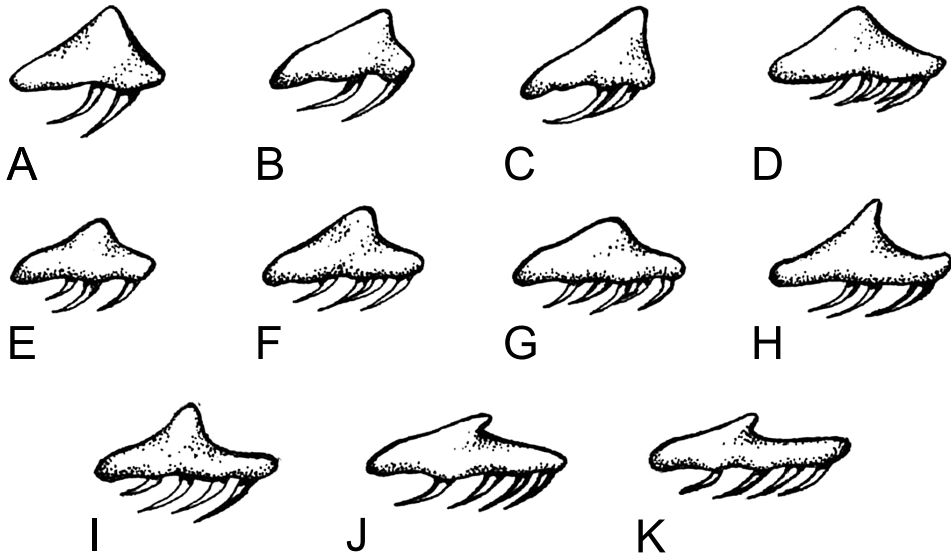
Figure 9. Palatine features in *Lachesis muta* (A), *Bothrops alternatus* (B), *Bothrops jonathani* (C), *Bothrocophias microphthalmus* (D), *Bothrops ammodytoides* (E), *Bothrops pictus* (F), *Bothrops andianus* (G), *Bothrops diporus* (H), *Bothrops jararaca* (I), *Bothrops jararacussu* (J) and *Bothrops atrox* (K).

tory functions (Allsteadt et al., 2006) or cryptic behavior (Stuart-Fox et al., 2004) and these items are probably related to habitat characteristics, such as elevation and/or vegetation. Pale tail tips in juveniles probably involve a "caudal luring" behavior (Greene and Campbell, 1972; Strimple, 1995; Greene, 1997; Martins, Marques and Sazima, 2002); although this may also be a sexually dimorphic character in this species (Campbell, pers. com.). It has been reported that the species exceptionally reaches 900-1000 mm in total length (Cabrera, 2004; Campbell and Lamar, 2004; Scrocchi pers. obs.), but none of the specimens examined in the present study reached such values.

Morphological features that characterize *Bothrops ammodytoides* are rare within the genus. No other species of *Bothrops* has an elevated snout; this feature also characterizes most species of *Bothrocophias* and *Porthidium* (Campbell and Lamar, 2004). A rectangular or elongated loreal is a condition reported by Harvey, Aparicio and Gonzales (2005) as a relatively unusual state among South American crotalines. Another rare condition within *Bothrops* is the presence of more than one pair

of canthals. Interestingly, some specimens of *Bothrops pictus* examined in this study present that condition together with an elongated loreal. Campbell and Lamar (2004) suggested that resemblance in color patterns of *Bothrops ammodytoides* and *Bothrops pictus* may be due to convergence because of their similar habitat. However, the present study reveals that there are more shared character states between these species.

These observations suggest that western *Bothrops-Bothrocophias* species may be a group with a common biogeographical history. In that context, Werman (2005) presented a hypothesis for South American crotalines, proposing that *Bothrops ammodytoides* and other species distributed in the southern portion of the continent (e.g., *Bothrops alternatus*) differentiated by vicariance from a northeastern group. Alternatively, this author suggested that these species might share affinities with Andean species, whose presence or that of their common ancestor could predate the uplift of the Andes; we consider the latter possibility more probable. This possible biogeographical history was also mentioned in other taxa: Reig (1986) and

Lanzone, Ojeda and Gallardo (2006) proposed that the genus *Eligmodontia* (Rodentia: Criceti- dae), distributed in the arid Monte of Argentina, could have differentiated from an Andean an- cestral stock to the desert low areas 11.6 my ago, these lowlands being a secondary diversi- fication center.

With regards to the systematics of *Both- rops ammodytoides*, we have some reasons to question the classification proposed by Fen- wick et al. (2009). These authors diagnosed *Rhinocerophis* with 27 mitochondrial characters and 1-2 palatine teeth as a unique morpholo- gical synapomorphy; however, they did not ex- amine cranial osteology of *Bothrops ammody- toides*, which is the type species of the genus. Carrasco, Harvey and Muñoz (2009) noticed that the number of palatine teeth varies among species of *Rhinocerophis*, that the position of palatine dorsal process in *Bothrops ammody- toides* differs from that of *Bothrops alternatus* and *Bothrops jonathani*, and that palatine fea- tures overlap among genera. Furthermore, Fen- wick et al. (2009) did not examine skulls of *Bothrops andianus* or *Bothrops pictus*; hence, they might not have realized that these species share character states of cranial osteology with *Bothrops ammodytoides* and *Bothrocophias mi- crophthalmus*. This is consistent with previ- ous observations made by Burger (1971). On the basis of lepidosis and hemipenial charac- ters only, Fenwick et al. (2009) recovered *Both- rops andianus* in a basal position with respect to the *Bothrops-Bothriopsis* clade. Probably due to the sampling method employed, they did not find the species having tuberculate keels in dorsoposterior scales (a synapomorphy reported by Gutberlet and Campbell, 2001, for *Bothro- cophias*) and predominance of partially divided lacunolabial. The presence of these features in *Bothrops andianus* emphasizes the basal posi- tion obtained by Fenwick et al. (2009) for this taxon, so its placement within *Bothrops*, accord- ing to them, results in this genus being para- phyletic.

The adoption of taxonomic rearrangements of medically important species would have to be considered carefully. Possible confusion and misunderstanding among clinicians, toxinolo- gists, herpetological curators and researchers working on human ophidism, are concerns that justify special attention. For practical aims, recognizing the existence of groups of closely related species could be as useful as assign- ing these groups the genus category. However; recognizing these groups as genera cannot be an arbitrary decision since it requires that mono- phyly of the clades be well supported in all cases (see Pauly, Hillis and Cannatella, 2009). We recommend reevaluating the classification proposed by Fenwick et al. (2009) with all the evidence available.

References

Allsteadt, J., Savitzky, A.H., Petersen, C.E., Naik, D.N. (2006): Geographic variation in the morphology of *Cro- talus horridus* (Serpentes: Viperidae). Herpetol. Monog. **20**: 1-63.

Burger, W.L. (1971): Genera of pitvipers. Unpubl. Ph.D. Dissertation, University of Kansas, Kansas, Lawrence.

Cabrera, M. (2004): Las serpientes de Argentina Central. Publicaciones de la Universidad Nacional de Córdoba, Córdoba, Argentina, Ed.

Campbell, J.A., Lamar, W.W. (1989): Venomous Reptiles of the Western Hemisphere. Cornell University Press, Ithaca, New York.

Campbell, J.A., Lamar, W.W. (2004): Venomous Reptiles of Latin America. Cornell University Press, Ithaca, New York.

Carrasco, P.A., Harvey, M.B., Muñoz Saravia, A. (2009): The rare Andean pitviper *Rhinocerophis jonathani* (Serpentes: Viperidae: Crotalinae): redescription with comments on its systematics and biogeography. Zootaxa **2283**: 1-15.

Castoe, T.A., Parkinson, C.L. (2006): Bayesian mixed models and the phylogeny of pitvipers (Viperidae: Serpentes). Mol. Phylogenet. Evol. **39**: 91-110.

Cei, J.M. (1986): Reptiles del Centro, Centro-oeste y Sur de la Argentina. Herpetofauna de las zonas áridas y semiáridas. Mus. Reg. Sc. Nat. Torino **14**: 1-527.

Cei, J.M. (1993): Reptiles del nordeste y este de Argentina. Herpetofauna de las selvas subtropicales, Puna y pampas. Mus. Reg. Sc. Nat. Torino **14**: 1-949.

Da Silva, V.X., Rodrigues, M.T. (2008): Taxonomic revision of the *Bothrops neuwiedi* complex (Serpentes, Viperidae) with description of a new species. Phyllomedusa **7**: 45-90.

De Roodt, A.R., Dolab, J.A., Hajos, S.E., Gould, E., Dinapoli, H., Troiano, J.C., Gould, J., Dokmetjian, J.C., Carfagnini, J.C., Fernandez, T., Amoroso, M., Segre, L., Vidal, J.C. (2000): Some toxic and enzymatic activities of *Bothrops ammodytoides* (yarará ñata) venom. Toxicon **38**: 49-61.

Dowling, H.G., Savage, J.M. (1960): A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. Zoologica **45**: 17-31.

Fenwick, A.M., Gutberlet, R.L., Evans, J.A., Parkinson, C.L. (2009): Morphological and molecular evidence for phylogeny and classification of South American pitvipers, genera *Bothrops*, *Bothriopsis*, and *Bothrocophias* (Serpentes: Viperidae). Zool. J. Linn. Soc. **156**: 617-640.

Giraudo, A.R., Scrocchi, G.J. (2002): Argentinian snakes: an annotated checklist. Smithson. Herpetol. Inform. Serv. **132**: 1-53.

Grazziotin, F., Echeverrigaray, S. (2005): Genetic relationships among species of the genus *Bothrops* based on RAPD markers. Braz. Arch. Biol. Techn. **48**: 359-365.

Greene, H.W. (1997): Snakes: The Evolution of Mystery in Nature. University of California Press, Berkeley and Los Angeles.

Greene, H.W., Campbell, J.A. (1972): Notes on the use of caudal lures in arboreal green pitvipers. Herpetologica **28**: 32-34.

Gutberlet, R.L. (1998): Phylogenetic relationships of New World pitvipers (Squamata: Crotalinae) as inferred from gross anatomy, epidermal microstructure, and mitochondrial DNA. Ph.D. Thesis, University of Texas, Arlington.

Gutberlet, R.L., Campbell, J.A. (2001): Generic recognition for a neglected lineage of South American pitvipers (Squamata: Viperidae: Crotalinae), with the description of a new species form the Colombian Chocó. Amer. Mus. Novitates **3316**: 1-15.

Gutberlet, R.L., Harvey, M.B. (2002): Phylogenetic relationships of New World pitvipers as inferred from anatomical evidence. In: Biology of the Vipers, p. 51-68. Schuett, G.W., Höggren, M., Douglas, M.E., Greene, H.W., Eds, Eagle Mountain Publishing, Eagle Mountain, Utah.

Harvey, M.B. (1994): A new species of montane pitviper (Serpentes: Viperidae: *Bothrops*) from Cochabamba, Bolivia. Proc. Biol. Soc. Wash. **107**: 60-66.

Harvey, M.B., Aparicio, J., Gonzales, L. (2005): Revision of the venomous snakes of Bolivia: Part II. The pitvipers (Serpentes: Viperidae). Ann. Carnegie Mus. **74**: 1-37.

Klauber, L.M. (1972): Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind, 2nd Edition. University of California Press, California, Berkeley.

Lanzone, C., Ojeda, R.A., Gallardo, M.H. (2006): Integrative taxonomy, systematics and distribution of the genus Eligmodontia (Rodentia, Cricetidae, Sigmodontinae) in the temperate Monte Desert of Argentina. Mamm. Biol. **72**: 299-312.

Leybold, F. (1873): Excursión a las Pampas Argentinas. Hojas de mi diario. Imprenta Nacional, Santiago de Chile.

Martins, M., Marques, O., Sazima, I. (2002): Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers of the genus *Bothrops*. In: Biology of the Vipers, p. 307-328. Schuett, G.W., Höggren, M., Douglas, M.E., Greene, H., Eds, Eagle Mountain Publishing, Eagle Mountain, Utah.

Miranda, E.M., Couturier, G.A., Williams, J.D. (1983): Guía de los Ofidios Bonaerenses, 2nd Edition. Asociación Cooperadora del Jardín Zoológico de La Plata, La Plata, Argentina.

Moro, S. (1996): Osteología craneal y musculatura mandibular de tres especies de *Bothrops* (Serpentes: Crotalidae). Acta Zool. Lilloana **43**: 293-316.

Parkinson, C.L., Campbell, J.A., Chippindale, P.T. (2002): Multigene phylogenetic analysis of pitvipers, with comments on their biogeography. In: Biology of the Vipers, p. 93-110. Schuett, G.W., Höggren, M., Douglas, M.E., Greene, H., Eds, Eagle Mountain Publishing, Utah.

Pauly, G.B., Hillis, D.M., Cannatella, D.C. (2009): Taxonomic freedom and the role of official lists of species names. Herpetologica **65** (2): 115-128.

Pesantes, O.S. (1989): Relacões entre algunas espécies do genero *Bothrops* pela eletroforese do plasma e morfologia do hemipenis (Serpentes: Viperidae). Unpubl. M.Sc. Dissertation, Universidade Estadual Paulista Julio de Mesquita Filho, Rio Claro, São Paulo, Brasil.

Pesantes, O.S. (1994): A method for preparing the hemipenis of preserved snakes. J. Herpetol. **28**: 93-95.

Reig, O.A. (1986): Diversity patterns and differentiation of high Andean rodents. In: High Altitude Tropical Biogeography, p. 404-438. Vuilleumier, F., Monasterio, M., Eds, Oxford University Press, Oxford.

Salomão, M.G., Wüster, W., Thorpe, R.S., BBBSP (1997): DNA evolution of South American pitvipers of the genus *Bothrops*. In: Venomous Snakes: Ecology, Evolution, and Snakebite, p. 89-98. Thorpe, R.S., Wüster, W., Malhotra, A., Eds, Clarendon Press, Oxford.

Salomão, M.G., Wüster, W., Thorpe, R.S., BBBSP (1999): MtDNA phylogeny of Neotropical pitvipers of the genus *Bothrops* (Squamata: Serpentes: Viperidae). Kaupia **8**: 127-134.

Scolaro, A. (2005): Reptiles Patagónicos Sur: Una guía de campo. Ed. Universidad Nacional de La Patagonia, Trelew, Argentina.

Scrocchi, G.J. (1997): Acerca de la localidad tipo de *Bothrops ammodytoides* Leybold (Serpentes: Viperidae) y *Pseudotomodon trigonatus* Leybold (Serpentes: Colubridae). Cuad. Herpetol. **11**: 69-70.

Scrocchi, G.J., Moreta, J.C., Kretzschmar, S. (2006): Serpientes del Noroeste Argentino. Ed. Fundación Miguel Lillo, Tucumán, Argentina.

Shultz, J.W. (2007): A phylogenetic analysis of the arachnid orders based on morphological characters. Zool. J. Linn. Soc. **150**: 221-265.

Smith, N.D., Turner, A.H. (2005): Morphology's role in phylogeny reconstruction: perspectives from paleontology. Syst. Biol. **54** (1): 166-173.

Strimple, P. (1995): Comments on caudal luring in snakes with observations on this behaviour in two subspecies of cantils, *Agkistrodon bilineatus* spp. Litt. Serp. **15**: 74-77.

Stuart-Fox, D.M., Moussalli, A., Johnston, G.R., Owens, I.P. (2004): Evolution of color variation in dragon lizards: quantitative tests of the role of crypsis and local adaptation. Evolution **58**: 1549-1559.

Vellard, J. (1928): O hemipenis dos ophidios. Importância de seus caracteres para a classificação das serpentes. Bol. Inst. Vital Brasil **6**: 1-19.

Vellard, J. (1946): Morfología del hemipenis y evolución de los ofidios. Acta Zool. Lilloana **3**: 263-288.

Werman, S.D. (1992): Phylogenetic relationships of Central and South American pitvipers of the genus *Bothrops* (sensu lato): cladistic analysis of biochemical and anatomical characters. In: Biology of the Pitvipers, p. 21-40. Campbell, J.A., Brodie Jr., E.D., Eds, Tyler, Texas, Selva.

Werman, S.D. (2005): Hypotheses on the historical biogeography of Bothropoid pitvipers and related genera of the Neotropics. In: Ecology and Evolution in the Tropics: a Herpetological Perspective, p. 306-365. Donnelly, M.A., Crother, B.I., Guyer, C., Wake, M.H., White, M.E., Eds, University of Chicago Press, Chicago.

Wiens, J.J. (2004): The role of morphological data in phylogeny reconstruction. Syst. Boil. **53** (4): 653-661.

Wüster, W., Salomão, M.G., Duckett, G.J., Thorpe, R.S., BBBSP (1999): Mitochondrial DNA phylogeny of the *Bothrops atrox* species complex (Squamata: Serpentes: Viperidae). Kaupia **8**: 135-144.

Wüster, W., Salomão, M.G., Quijada-Mascareñas, J.A., Thorpe, R.S., BBBSP (2002): Origins and evolution of the South American pitvipers fauna: evidence from mitochondrial DNA sequence analysis. In: Biology of the Vipers, p. 111-129. Schuett, G.W., Höggren, M., Douglas, M.E., Greene, H., Eds, Eagle Mountain Publishing, Eagle Mountain, Utah.

Zaher, H. (1999): Hemipenial morphology of the South American Xenodontinae, with a proposal for a monophyletic Xenodontinae and a reappraisal of Colubroid hemipenes. Bull. Am. Mus. Nat. Hist. **240**: 1-168.

Zanella, N., De Lema, T. (1999): Osteologia craniana de *Bothrops alternatus* Duméril, Bibron and Duméril, 1854, e a comparação com espécies de *Bothrops* Wagler, 1824, ocorrentes no sul do Brasil (Serpentes: Viperidae: Crotalinae). Cuad. Herpetol. **13**: 47-68.

Appendix

Specimens examined

Bothrops ammodytoides: <u>ARGENTINA</u>. SALTA. Cafayate: FML 01802. CATAMARCA. Andalgalá: FML 01405; Tinogasta: FML 01953. LA RIOJA. Castro Barros: FML 07804; Chilecito: MACN (ex-CENAI) 1803, MLP-JW 1968, MLP-JW 594, MLP-JW 1968. TUCUMAN. Tafí del Valle: FML 01592. SAN JUAN. El Leoncito: MACN 35643. CORDOBA. Calamuchita: CZA 29, MACN (ex-CENAI) 1632; Cruz Grande: MACN 21450; General San Martín: MACN 2486; La Cumbrecita: CZA 126; Los Reartes: MACN 24797; Mattaldi: MACN (ex-CENAI) 1819; Modestino Pizarro: MACN 39066; unknown locality: MLP-JW 264. SAN LUIS. Buena Esperanza: MACN 2329, MACN 39073; Chacabuco: FML 09602; unknown locality: MLP-R 5206; Unión: MACN (ex-CENAI) 1620, MACN (ex-CENAI) 2112, MACN 7364, MACN 39067; Villa Mercedes: CZA 76, MLP-R 5309, MACN 39074; Ruta Nacional 148 (between Arizona and Anchorena): MLP-R 5281; unknown locality: MACN 5751. LA PAMPA. Bernasconi: MLP-JW 789; Cochico: MACN 22061; Hucal: FML 0297; Potrillo Oscuro: MACN 28313-14; Santa Rosa: MACN 30006; 25 de Mayo: MACN (ex-CENAI) 3603. Telen: MACN 39075. BUENOS AIRES. Bahía Blanca: MLP-JW 787, MLP-JW 791; Balcarce: MLP-JW 1640, MLP-JW 1642; San Antonio de Areco: MPL-JW 951; Bordenave: MACN 34371; Claraz: MACN 39065, MACN 39071; Coronel Dorrego: MACN 39070, MACN 39072, MACN uncatalogued; Chasicó: MLP-JW 792; Chaves: MACN 9407; unknown locality: MACN (ex-CENAI) 1505; Juarez: MACN 34649; La Plata: MLP-JW 1819; Laguna Brava: MACN 3426; Loberías: MACN 39069, MACN uncatalogued; Miramar: MLP-JW 249, MACN 2841; Monte Hermoso: MACN (ex-CENAI) 1427, MLP-JW 020; Necochea: MACN (ex-CENAI) 3475, MACN 4958; Olavarría: MLP-JW 1639; Quequen: MACN 6577; Sauce Grande: MACN 31394, MACN 36353; San Germán: MLP-JW 595; Tres Arroyos: MACN (ex-CENAI) 3631, MACN 32791; Tornquist: MACN (ex-CENAI) 1598, MACN 39068; unknown locality: MACN 1394. MENDOZA. Cerro Los Leones: MACN 29051; Malargüe: FML 07699; Tupungato: CZA 43; unknown locality MACN (ex-CENAI) 3392. NEUQUEN. Unknown locality: MLP-JW 21. RIO NEGRO. Allen: MACN 3638-39; General Roca: FML 073322-26; Río Colorado: MLP-JW 28. CHUBUT. Península de Valdés: MLP-JW 563, MACN 29101, MACN 32887-93, MACN 35351; Puerto Madryn: MLP-JW 562; Puerto Pirámides: MLP-JW 636; unknown locality: MACN 32293.

Bothrops alternatus: <u>ARGENTINA</u>. FORMOSA. Reserva Ecológica El Bagual: FML 11410, FML 1434, FML 11442, FML 15920. CHACO. 25 km S from Santa Silvina: MACN uncatalogued. TUCUMAN. San Javier: FML 1616; Leales: FML 157. MISIONES. El Bonito: FML 673; Loreto: MACN n/n. CORRIENTES. Yacyretá: FML 2565, MLP-JW 911; Caá Catí: FML 7396; Sauce: MACN (ex-CENAI) 284; Mercedes: MACN uncatalogued. ENTRE RÍOS. Salto Grande: MLP-JW 265; Colón: MACN 34582. SANTA FE. Campo Garay: MACN (ex-CENAI) 285; Monje: MACN n/n. SANTIAGO DEL ESTERO. Quimili: FML 2007. CORDOBA. Las Rabonas: CZA 138; unknown locality: MLP-JW 784. BUENOS AIRES. Punta Lara: MLP-JW 286; Chasicó: MLP-JW 505; Sierra la Ventana: MLP-JW 749, MLP-JW 781, MACN uncatalogued; Zárate: MLP-JW 774; Tornquist: MLP-JW 783; Balcarce: MLP-JW 869, Punta Indio: MLP-JW 1579.

Bothrops andianus: <u>BOLIVIA</u>. COCHABAMBA. Chapare: MNKR 3722; unknown locality CBG-R 23, CBG-R 29. SANTA CRUZ. Florida: MNKR 2715, MNKR 2955, MNKR 3327, MNKR 4319, MNKR 4542, MNKR 4543, MNKR uncatalogued. LA PAZ. El Piñalito: CBF 221; Irupana: CBF 467. <u>PERU</u>. CUSCO. Machu picchu: FML 01197, MHNJP 2324, MHNJP 2680, MHNJP 3093; Río Mantalo: MHNJP 26492.

Bothrops atrox: <u>BOLIVIA</u>. LA PAZ. Madidi: CBF 2347. PANDO. San Silvestre: MNKR 2269. Unknown locality: MHNC-R (AMS) 1484. <u>PERU</u>. PASCO. Ciudad Constitución: MHNJP 20070. LORETO. Loreto: MHNJP 22293.

Bothrops cotiara: <u>ARGENTINA</u>. MISIONES. 2 de Mayo: MLP-JW 882; unknown locality: MACN 12712. <u>BRASIL</u>. PARANA. Curitiba: MACN 31386; unknown locality: FML 1710; unknown locality: MACN 3558.

Bothrops diporus: <u>ARGENTINA</u>. SALTA. Los Colorados: CZA-GL 38, CZA-GL 67. FORMOSA. Palmar Largo: MLP-R 5002. CHACO. Antequera. FML 6607; Resistencia: MLP-R 5006. TUCUMAN. Estancia La Argentina: FML 1185; Atahona: FML 1726; Agua Dulce: 1847; Cruz Alta: FML 13664. SANTIAGO DEL ESTERO. Guardia Escolta: MLP-JW 1573. CORDOBA. Punilla: CZA 127. MENDOZA. Doctor Gassul: MLP-JW 881. NEUQUEN. Fortín de la Piedra: MLP-JW 1797.

Bothrops jonathani: <u>ARGENTINA</u>. JUJUY. Santa Bárbara: FML 1050. SALTA. La Caldera: FML 570; Santa Victoria: FML 1480. <u>BOLIVIA</u>. SANTA CRUZ. San Juan del Potrero: MNKR 1618, MNKR 2036; Valle Grande: MNKR 718. COCHABAMBA. Quillacollo: CBF 2673; unknown locality: CBGR 65. TARIJA. Curqui: CBF 2318-20; Quebrada Loray: MHNC-R 206, MHNC-R 207.

Bothrops jararaca: <u>ARGENTINA</u>. MISIONES. Bernardo de Irigoyen: MACN 33030; Puerto Esperanza: MACN 38731; Montecarlo: MLP-JW 1571; Aristóbulo del Valle: MLP-JW 1812. <u>BRASIL</u>. PARANA. Morretes: FML 2110.

Bothrops jararacussu: <u>ARGENTINA</u>. MISIONES. San Pedro: FML 976; Libertad: MACN 35346; El Alcázar: MACN 38663; unknown locality: MLP-JW 853.

Bothrops pictus: <u>PERU</u>. LIMA. Lima: MHNJP 2827, MHNJP 2954; Cieneguilla: MHNJP 2125; Jicamarca: MHNJP 2433, MHNJP 2365, MHNJP 2536; Hacienda Santiaguillo: MHNJP 2139; Tornamesa: MHNJP 25395; Lachay: MHNJP 2705; La Molina: MHNJP 27292. ICA. Nazca: MHNJP 24749. ANCASH. Huarmey: MHNJP 25396; Recuay: MHNJP 25397.

Bothrocophias microphthalmus: <u>BOLIVIA</u>. COCHABAMBA. Parque Nacional Carrasco: CBF 1899; Rio Leche: MHNC-R 103-104. LA PAZ. Reserva de la Biósfera Pilon Lajas: MNKR 1801, MNKR 1814. BENI. Rurenabaque: MNKR 493. <u>PERU</u>. CUSCO. Timpia: MHNJ 25673, MHNJP 26443; La Convención: MHNJP 26093. SAN MARTIN. Tarapoto: MHNJP 3066. JUNIN. Tarma: MHNJP 2035. HUANUCO. Sira: MHNJP 8605.

Crotalus durissus: <u>ARGENTINA</u>. CORDOBA. Cañada de Luque: CZA uncatalogued. MISIONES. San Vicente: MACN 36869. <u>BOLIVIA</u>. CHUQUISACA: CBF 02462. SANTA CRUZ. Mataral: MNKR 2150.

Lachesis muta: <u>BOLIVIA</u>. LA PAZ: Iturralde: CBF 740. <u>PERU</u>. CUSCO. Tambopata: MHNJP 7376, MHNJP 7377.

Osteological preparations

Bothrops ammodytoides: FML 1953, CZA 29, CZA 126, CZA 43, MACN 39068, MACN 39071, MACN 32888. *Bothrops alternatus*: FML 673, CZA 138, MLP-JW 279. *Bothrops andianus*: MNKR 4319, CBGR 29, MHNJP 2680. *Bothrops atrox*: MHNJP 20070. *Bothrops jonathani*: FML 1408, CBF 2319, MNKR 1618, CBGR 65. *Bothrops cotiara*: IB 2580, IB 33218. *Bothrops diporus*: CZA-GL 38, CZA-GL 67, FML 1185, FML 1726, FML 1847. *Bothrops jararaca*: MLP-JW 1571, MACN 38731. *Bothrops jararacussu*: MLP-JW 853, MACN 38669. *Bothrops pictus*: MHNJP 24749, MHNJP 27292, MHNJP 2705. *Bothrocophias microphthalmus*: MNKR 1801, MHNC-R 104, MHNJP 3066. *Crotalus durissus*: CZA uncatalogued, CBF 02462, MNKR 2150. *Lachesis muta*: CBF 740.

Hemipenis preparations

Bothrops ammodytoides: CZA 43, FML 7699, FML 1592; MACN 29051, MACN 32888, MACN 32893, MACN 35351, MACN 39066, MACN 39068, MACN 39071, MACN 39073. *Bothrops alternatus*: FML 2565, FML 7396, MACN 39203, MACN 39208-09. *Bothrops jonathani*: FML 1050, CBF 2320, MNKR 718, CBGR 65, MHNC-R 206. *Bothrops cotiara*: IB 16080, IB 50079, IB 57598. *Bothrops diporus*: CZA-GL 67, CZA-GL 38, FML 6607, FML 136664. *Bothrops andianus*: MNKR 4319, CBGR 29. *Bothrops jararaca*: FML 2110, FML 2691. *Bothrops jararacussu*: FML 2692. *Bothrops atrox*: CBF 2347. *Bothrocophias microphthalmus*: MNKR 1801, MHNC-R 104. *Crotalus durissus*: AC 913, AC 215, CBF 2462.