

Phyllomedusa 9(1):69-73, 2010 © 2010 Departamento de Ciências Biológicas - ESALQ - USP ISSN 1519-1397

SHORT COMMUNICATION

Hemipenes of the long-tailed rattlesnakes (Serpentes: Viperidae) from Mexico

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Keywords: Serpentes, Crotalinae, Crotalus, hemipenis, morphology.

Palavras-chave: Serpentes, Crotalinae, Crotalus, hemipênis, morfologia.

Endemic to the foothills of western México, long-tailed rattlesnakes are a group of three poorly known species: the Sinaloan Long-tailed Rattlesnake, Crotalus stejnegeri Dunn, 1919; the Manantlán Long-tailed Rattlesnake, C. lannomi Tanner, 1966; and the Guerreran Long-tailed Rattlesnake, C. ericsmithi Campbell and Flores-Villela, 2008. They received their common name from their unique tail length, about 9.7–15.9% of the total length (Campbell and Flores-Villela 2008, Reyes-Velasco et al. 2010). All three species inhabit mid-elevation (500–1200 m), tropical deciduous, oak, and pine forests in the states of Durango and Sinaloa (C. stejnegeri), Jalisco and Colima (C. lannomi) and Guerrero (C. ericsmithi) (Campbell and Lamar 2004, Campbell and Flores-Villela 2008, Reyes-Velasco et al. 2010). Until recently, approximately 15 specimens of long-tailed rattlesnakes had been deposited in museum collections (Campbell and Lamar 2004, Campbell and Flores-Villela 2008).

Received 28 August 2009. Accepted 9 June 2010. Distributed July 2010.

Because of the paucity of specimens and their unique morphology, evolutionary relationships between the long-tailed rattlesnakes and other groups have been difficult to establish. Historically, the relationships of long-tailed rattlesnakes have been considered "uncertain" or incertae sedis (Gloyd 1940, Meik and Pires-da-Silva 2009), tentatively associated with C. polystictus (Brattstrom 1964), or assigned to the C. triseriatus Group (Klauber 1972). The snakes share a number of morphological similarities-most notably a long, slender tail; a tiny rattle; a rostral scale that is wider than long; and a relatively high number of ventrals compared to other small, montane rattlesnakes. These resemblances led Campbell and Flores-Villela (2008) to conclude that the three species form a clade. However, Meik and Pires-da-Silva (2009) argued that a long tail might be a primitive character state in rattlesnakes thereby casting doubt on the monophyly of long-tailed rattlesnakes. Unfortunately, no molecular analyses have been undertaken to investigate their relationships.

Hemipenial characters are particularly useful in evolutionary studies because they are closely

associated with species differentiation and reproductive behaviors (e.g., King et al. 2009, Jadin et al. 2010). Several hemipenial features within the rattlesnakes are known exclusively from the Mexican Lancehead Rattlesnake, Crotalus polystictus, and C. stejnegeri. These include possession of: more than 100 spines on each lobe; small and numerous mesial spines; spines that grade into calyces; and basal spines that extend distally more than one-third the length of the lobe; the latter feature is also shared with C. cerastes (Campbell and Lamar 1989, 2004). However, C. stejnegeri is unique in that the hemipenial lobes are greatly compressed mediolaterally (Campbell and Lamar 1989, 2004), an interesting feature that does not occur in other viperids to our knowledge. Although C. stejnegeri was described nearly nine decades ago, some features of its unique hemipenis have not been published. In addition, the recent description of C. ericsmithi addressed only a few of these characters and did not include hemipenial measurements or comparisons to C. stejnegeri (Campbell and Flores-Villela 2008). Because only a single female (BYU 23800-Holotype) was available of C. lannomi (Tanner 1966, Campbell and Lamar 1989, 2004), a hemipenial analysis was not possible until an adult male was found recently (Reyes-Velasco et al. 2010). The lack of molecular data and scant morphological evidence supporting the monophyly of the long-tailed rattlesnakes, suggests that a more thorough examination, comparison, and illustration of the hemipenes for these three species would be useful. Herein, we describe and compare the morphologies of the hemipenes of the three longtailed rattlesnakes to ascertain whether the unique features of the copulatory organ of C. stejnegeri are shared with the other two species and whether there are additional hemipenial characters that further distinguish the three taxa.

We examined adult male specimens of *Crotalus* ericsmithi (UTA R-55372–Holotype), *C. lannomi* (MZFC 22941) and *C. stejnegeri* (UTA R-6234) deposited at the Amphibian and Reptile Diversity Research Center, University of Texas at Arlington

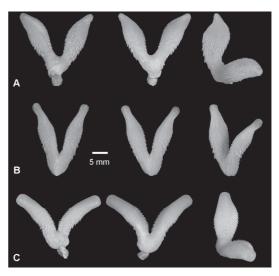


Figure 1. Sulcate (left), asulcate (middle), and medial (right) views of the left hemipenes of (A) Crotalus ericsmithi, (B) C. lannomi, and (C) C. stejnegeri. Scale bar applies to all images.

(UTA) and the Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC) (Appendix I). In addition to the specimen examined above, a subadult C. stejnegeri (UTA R-5926) was examined in much less detail but was found to share similar hemipenial characters (e.g., many small spines on lobes, mediolateral compression) as the adult. The left hemipenis of C. stejnegeri was previously prepared by J. A. Campbell; therefore, we removed and prepared the left hemipenes of C. ericsmithi and C. lannomi, following the methods of Myers and Cadle (2003), Zaher and Prudente (2003), and Smith and Ferrari-Castro (2008). Terminology follows Dowling and Savage (1960) and Savage (2002). Hemipenial measurements were taken using a dissecting scope and optical micrometer.

The hemipenes of *Crotalus stejnegeri*, *C. ericsmithi*, and *C. lannomi* are remarkably similar to each other and dissimilar to those of other rattlesnakes; nonetheless there are distinctions among the three species. First, the presence of mediolateral compression of the lobes (Figure 1), a possibly unique feature among viperids

which results in a lateral biconic shape, provides additional evidence supporting Campbell and Flores-Villela's (2008) assertion that the taxa form a clade. All three hemipenes have lobes of similar length, about 17 mm long, allowing for accurate comparison. In each of these species, the mostly naked base of the hemipenis bifurcates into a naked crotch. The *sulcus spermaticus* is relatively deep, extends to the tip of the hemipenis, and is closely bordered by spines or calyces at proximal and distal sections of the lobes, respectively.

In spite of the similarities in hemipenial ornamentation of the three long-tailed rattlesnakes, many distinctions exist (Appendix II). As mentioned by Campbell and Flores-Villela (2008), the transition from spines to calyces is abrupt in C. ericsmithi and more gradual in C. stejnegeri and C. lannomi. Crotalus lannomi has the slimmest hemipenis; it also probably has more spines than any other rattlesnake species known, with more than 220 per lobe. The biconic lateral lobe shape of C. ericsmithi is asymmetrical and S-shaped (Figure 1A), whereas the lateral biconic shape of the hemipenes of C. lannomi and C. stejnegeri are more symmetrical and C-shaped (Figure 1B, C). The tips of the hemipenial lobes are rounded in C. stejnegeri, tapered in C. ericsmithi, and slightly bulbous and rounded in C. lannomi.

Although it may seem as if the hemipenes of the long-tailed rattlesnakes and C. polystictus are very similar (see above), we examined hemipenes of two specimens of C. polystictus (UTA R-4916 & 5667) and observed several drastic differences. These differing hemipenial features of C. polystictus include: most of the spines occurring on the base rather than the lobes of the hemipenes; almost the entire lobes covered by calyces; and hemipenes terminating in an awn or soft papilla at the tip, similar to *Daboia russellii* (RCJ, pers. obs.) or species of Porthidium (Gutberlet 1998: figure 2). Therefore, hemipenial morphology does not suggest a close relationship between C. polystictus and the long-tailed rattlesnakes but provides many supporting characters for the monophyly of the latter.

Acknowledgments.—We thank O. Flores-Villela and E. Perez Ramos (MZFC), and J. A. Campbell and C. J. Franklin (UTA) for allowing us access to material under their care. Helpful comments to this manuscript were provided by J. A. Campbell and S. A. Orlofske. Funding for this study was provided by grants to ENS from Bioclon and NSF (DEB-0416160) and J. A. Campbell from NSF (DEB-0613802).

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Appendix I. Specimens Examined.

Crotalus ericsmithi: MEXICO: Guerrero: Carretera La Laguna-Bajitos de la Laguna: UTA R-55372. Crotalus lannomi: MEXICO: Jalisco: Colima: 42 km by road SE of Cuautitlán: MZFC 22941. Crotalus polystictus: MEXICO: Jalisco: Rancho San Francisco, 2.4 km NW Tapalpa: UTA R-4916 & 5667

Crotalus stejnegeri: MEXICO: SINALOA, Ejido Tebaira near Plomosas: UTA R-6234; Plomasas: UTA R-5926.

Appendix II. Morphological features of the hemipenes of the three species of long-tailed rattlesnake.

Character	Species		
	Crotalus ericsmithi UTA R-55372	Crotalus lannomi MZFC 22941	Crotalus stejnegeri UTA R-6234
Snout-vent length (mm)	468	470	541
Tail length (mm)	70	71	82
Mediolateral compression of hemipenial lobes	Present	Present	Present
Biconic lateral lobe shape	S-shaped	C-shaped	C-shaped
Maximum width of hemipenial base (mm)	7.0	6.3	7.2
Maximum width at the middle of hemipenial lobe (mm)	7.5	6.3	8.0
Narrowest width at the middle of hemipenial lobe (mm)	5.5	3	4.5
Ratio of narrowest/maximum width at the middle of lobe	0.733	0.4615	0.5625
Naked mesial region (mm) ¹	3.5-4.0	1.5	0.9
Spines on each lobe left/right	~202/~205	~225/~233	~172/~186
Length of spines (mm)	0.7-2.0	0.5–1.2	0.6–1.5
Rows of calyces on sulcate side	11–13	13	16
Length of calyx region on sulcate side (mm)	7.5	7.5	8.0
Rows of calyces on asulcate side	15	19	18
Length of calyx region on asulcate side (mm)	7.0	7.9	9.0
Rows of spines on sulcate side	9	9	11–12
Length of spinous region on sulcate side (mm)	7.5	9.0	7.5
Rows of spines on asulcate side	9	7–9	7–8
Length of spinous region on asulcate side (mm)	9.5	9.0	6.5–7.0
Sulcus spermaticus bifurcates before bilobation (mm)	2.3	3.3	2.3
Proximal calyces	Raised and spinulate	Low and spinulate	Weakly papillate
Distal calyces	Papillate	Papillate	Reduced with low and smooth ridges
Shape of crotch	U-shaped	V-shaped	V-shaped
Tips of hemipenial lobes	Tapered	Slightly bulbous and rounded	Rounded

¹ Naked mesial region is measured from the center of the crotch to the most proximal spines on the lobes.