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Hemipenis descriptions of *Mastigodryas* (Serpentes: Colubrinae) from northern Middle America, with comments on the use of hemipenial data in phylogenetics

Robert C. Jadin* and Richard V. Parkhill

Abstract. A greater number of studies are including hemipenial morphology as a tool to investigate phylogenetic relationships and reproductive behaviour. Few studies however have included hemipenis descriptions for species of *Mastigodryas*, a genus for which evolutionary relationships have not been proposed using modern methodology. Here we describe and illustrate the hemipenes of three species of *Mastigodryas* from northern Middle America. Within these species we found some features that appear constant, while others are considerably variable, such as shape and ornamentation. We believe some features may be evolutionarily constrained whereas more plastic characters may be selected by reproductive behaviour. Therefore, numerous hemipenial characters, with their various evolutionary histories, may provide a variety of support for different levels of phylogenetic inference.

Keywords. Hemipenes, Evolution, Morphology, Reproduction, Snakes

Introduction

Mastigodryas is a genus of the family Colubridae and includes species previously assigned to the genus *Dryadophis* (see Dixon and Tipton (2004) for systematic review). Although the majority of *Mastigodryas* species occur in South America, several species occur in Middle America. Among the Middle American taxa are *M. cliftoni* (Hardy, 1964)—endemic to western Mexico, *M. dorsalis* (Bocourt, 1890)—which occurs in Guatemala, Honduras, and Nicaragua, *M. sanguiventris* (Taylor, 1954)—from Punta Arenas, Costa Rica, *M. pleei* (Duméril, Bibron, and Duméril, 1854)—which only just enters Panama from South America, and *M. melanolomus* (Cope, 1868)—a potential species complex, which ranges from Mexico to Ecuador (Savage, 2002; Köhler, 2003). Evolutionary relationships among these species remain unresolved, as no intrageneric phylogenetic studies have been published.

Hemipenis descriptions provide many useful characters for descriptive morphology (Branch, 1981), phylogenetics (Keogh, 1999; Jadin et al., 2010), sexual selection (Böhme and Ziegler, 2009), and copulatory behaviour (King et al., 2009). Dowling (1967) and Böhme and Ziegler (2009) suggested that hemipenial characters offer more evolutionary information about relationships than other morphological characters because they are not influenced by ecological selection and it has been reported in some studies (e.g., Arnold, 1986; Keogh, 1999) that characters can also be highly stable. Because there is much convergence in many external features of colubrid snakes (e.g., head scales) it is especially useful to describe hemipenes of these species in an attempt to provide more phylogenetic data for investigating their relationships. Few studies have included detailed descriptions of *Mastigodryas* hemipenes and therefore we describe and illustrate the hemipenial features of three species of *Mastigodryas* (i.e., *M. cliftoni*, *M. dorsalis*, *M. melanolomus*) from northern Middle America.

Materials and Methods

Hemipenes of three adult specimens (Appendix) from the Museum of Natural History at the University of Colorado at Boulder (UCM) and the Amphibian and Reptile Diversity Research Center at the University of Texas at Arlington (UTA) were examined. The right hemipenis was removed at the base and prepared following the procedures of Myers and Cadle (2003) and Zaher and Prudente (2003). Additionally, blue petroleum jelly was inserted into the hemipenis during eversion as described and illustrated in Smith and Ferrari-Castro (2008) and Jadin and Smith (2010). Hemipenial descriptions, measurements and counts were obtained from these preparations, using a dissecting scope with an ocular micrometer or a ruler. Hemipenial terminology follows Dowling and Savage (1960), Keogh (1999), and Savage (2002).

Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, Boulder, CO 80309, USA;

* Corresponding author. e-mail: rcjadin@gmail.com

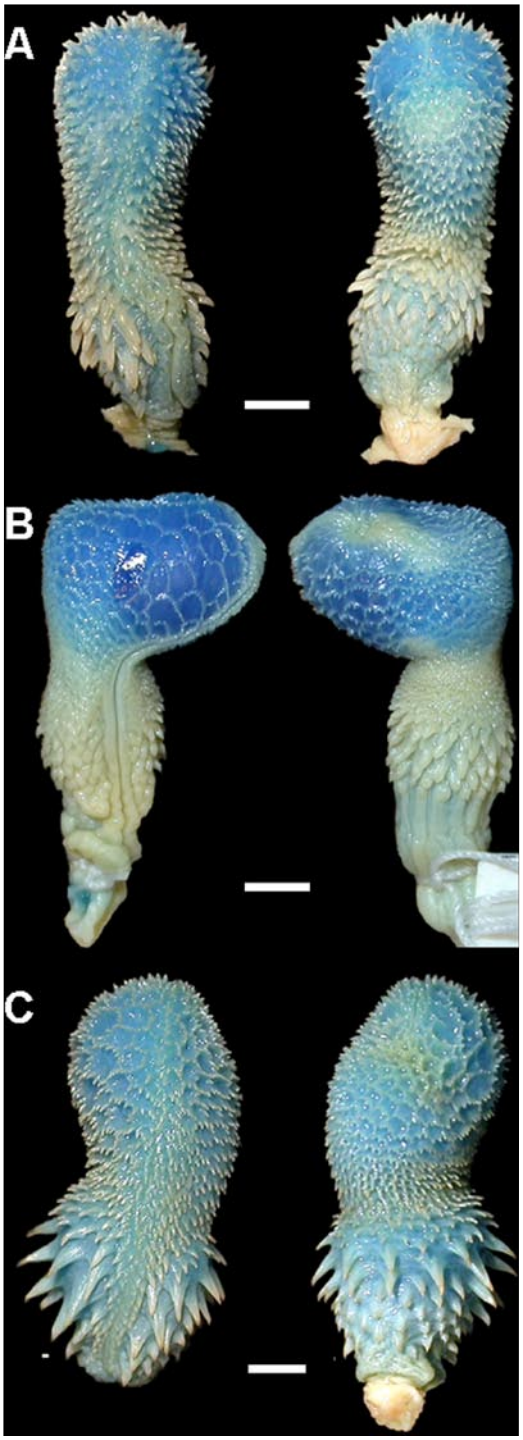

Figure 1. Sulcate (left) and asulcate (right) views of (A) *Mastigodryas cliftoni* (JLE 14111); (B) *M. dorsalis* (UTA R-37284); and (C) *M. melanolomus* (UCM 30652). Scale bars equal 4 mm.

Results

Mastigodryas cliftoni (JLE 14111; Fig. 1A)

Adult male specimen (SVL 740 mm, tail length 545 mm, 146 divided subcaudals). The hemipenis is cylindrical and noncapitate, ca. 27 mm in length and 9 mm at its maximum width. The base is covered with miniscule spines, extending approximately 4 mm. The spinous region follows the base and occupies approximately 7 mm of the sulcate and 4.5 mm of the asulcate side of the hemipenis; it has 94 spines between 0.5 to 2.5 mm in length, most being roughly 1 mm. Following the spines is the spinous calyx region which occupies the remainder 16 mm of length; it includes 23 rows of calyces on the sulcate side. The *sulcus spermaticus* is simple and extends over the tip of the hemipenis slightly into the asulcate side. The *sulcus spermaticus* has large, fleshy borders at the base and spinous region, and a single row of miniscule spines bordering the calyx region.

Mastigodryas dorsalis (UTA R-37284; Fig. 1B)

Adult male specimen (SVL 778 mm, tail length 364 mm, 138 divided subcaudals). While still attached and partially everted the right hemipenis had spines beginning at the level of the proximal edge of the 3rd subcaudal and ending at the distal edge of the 5th subcaudal, where the calyces begin. The hemipenis is noncapitate and unbifurcated. After dissection and expansion the hemipenis is approximately 30 mm in length, 7 mm at its maximum width at the spinous region, and ca. 14 mm its maximum width in the calyx region. The base is broad and nude, extending approximately 11 mm in length. The spinous region follows the base and occupies approximately 5 mm of the length in the sulcate side and 4.5 mm of the length of the asulcate side of the hemipenis; there are ca. 126 spines in this area, ranging from 0.7 to 2.3 mm in length, most being roughly 1.9 mm. Following the spinous region is the calyx region, which is spinulated and occupies 13 mm of the length and has more than 23 rows of calyces on the sulcate side. The *sulcus spermaticus* is simple and extends to the uneverted top of the hemipenis. The *sulcus spermaticus* is bordered by large and fleshy borders at the base, spinous, and a quarter of the calyx region; there is a single row of miniscule spines bordering the *sulcus spermaticus*, on each side, for the remainder of the calyx region. The apical region of the calyx has very thin walls and the internal pressure from expansion tore holes on the internal lining (external when everted) of the organ, preventing full eversion.

Mastigodryas melanolomus laevis (UCM 30652; Fig. 1C)

Adult male specimen (SVL 723 mm, tail length 343 mm, 111 divided subcaudals). When everted in situ, spines of the right hemipenis end at the level of the 3rd subcaudal, where the calyces begin, and the hemipenis in its entirety extends to the beginning of the 7th subcaudal. The hemipenis is asymmetric, weakly bilobed, and noncapitate. After the hemipenis was dissected and expanded it attained 34 mm in length and 11 mm in maximum width. The base is broad and covered with miniscule spines, extending approximately 7–8 mm of the length. The spinous region follows the base and occupies approximately 12 mm of the sulcate side and 9 mm of the asulcate side of the hemipenis; the spinous region has ca. 73 spines ranging from 1.0 to 4 mm in length, most being 2–3 mm. Following is the spinous calyx region which occupies 20 mm of the total length and includes 20–22 rows of calyces on the sulcate side. The *sulcus spermaticus* is simple and extends beyond the tip of the hemipenis into the asulcate side. At the base and spinous region the *sulcus spermaticus* has thick and fleshy borders covered by two rows of miniscule spines, which fragment on the calyx region, then the *sulcus spermaticus* is only bordered by calyces.

Discussion

The hemipenes of these three species share several similarities (e.g., simple *sulcus*, no capitation, numerous spines followed by spinous calyces) but are also considerably different from one another in shape and ornamentation (Fig. 1A–C). *Mastigodryas dorsalis* differs from the other two by having a bulbous apical region, a long and naked base, a greater number of spines and rows of calyces, and a very thin calyx wall. The weakly bilobed hemipenis, larger spines, and double columns of miniscule spines on the fleshy borders of the *sulcus* of *M. melanolomus* differ from the other two species.

Our results coincide with conclusions by Schargel et al. (2005) and Jadin et al. (2010) who showed much intrageneric variation of hemipenial morphology in *Taeniophallus* and *Atropoides*, respectively. Schargel et al. (2005:18) cautioned that "hemipenial characters may not be as conserved as often thought." Although differing morphologies could suggest distant relationship, some studies suggest that drastically different morphologies may reflect very different reproductive behaviours. King et al. (2009) found that hemipenis shape is evolutionarily plastic within *Thamnophis* and fluctuates greater due to copulatory behaviour than phylogeny. Therefore, variations in hemipenial shape, as well as increases and decreases in numbers and size of spines and calyces, among these three species represent characters which are not phylogenetically conserved and could be selected for by reproductive behaviour. Reproductive behaviours suggested by King et al. (2009) include the necessity of holding a female in place during copulation in species where females conduct shorter copulations and dislodge males by rolling. Other characters, such as the presence of a simple *sulcus* and noncapitate hemipenis, also shared by *M. amarali*, *M. boddaerti*, *M. bruesi*, *M. heathi*, *M. moratoi*, and *M. pleei* from South America (Stuart, 1932; Montingelli and Zaher, 2011), appear more phylogenetically conserved and common among species of this clade.

Hemipenial morphology provides an adequate way to evaluate evolutionary relationships among species (e.g., Dowling and Savage, 1960; Böhme and Ziegler, 2009; Jadin et al., 2010). When combined with morphological data for additional species, some features listed above that are potentially constrained by phylogeny (e.g., simple *sulcus*, no capitation) may provide useful phylogenetic information at the intergeneric level. More plastic characters, those selected by reproductive behaviours or neutral mutations (e.g., hemipenis shape, number of spines), may be more useful in generating phylogenetic signal for resolving intrageneric relationships.

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Appendix

Specimens examined.

Mastigodryas cliftoni: MEXICO: Chihuahua: Chinipas, 469 m (Field Number: JLE 14111, specimen to be catalogued in UCM).

Mastigodryas dorsalis: GUATEMALA: Escuintla: Finca El Rosario Vista Hermosa, Sur Volcan de Agua, 900 m (UTA R-37284).

Mastigodryas melanolomus laevis: GUATEMALA: Izabal: Tenedores (UCM 30652).

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