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Hemipenial morphology in the North American snake genus *Phyllorhynchus* (Serpentes: Colubridae), with a review of and comparisons with natricid hemipenes

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Abstract

Hemipenes of species in the North American colubrid genus *Phyllorhynchus* are described. Contrary to previous reports of a divided sulcus spermaticus, both species have an unusual morphology in which the lips of the sulcus diverge near the apex so that the sulcus groove opens into an extensive apical nude region. Two distinctive hemipenial morphologies were discovered within *P. browni*, which may signal unresolved systematic issues. *Phyllorhynchus* hemipenes are additionally unusual for colubrids in having calyces reduced (*P. decurtatus*) or absent (*P. browni*). These features resemble some natricid hemipenes, which are reviewed in order to make detailed comparisons. That review led to a reassessment of some hemipenial characters of natricids and the recognition of several novelties, including calyces in *Rhabdophis* and a peculiar lobular pocket in *Xenochrophis cerasogaster.*

I conclude that the resemblance of the sulcus configurations in *Phyllorhynchus* and natricids is only superficial and therefore convergent. Other evidence supports the phylogenetic placement of *Phyllorhynchus* with Colubridae, for which the sulcus configuration, highly reduced calyces, and extensive apical nude areas are unusual. Relationships of *Phyllorhynchus* within Colubridae are unclear, but the genus shares with *Salvadora* an unusual morphology of the rostral scale and nude hemipenial apices. However, in other respects *Salvadora* and *Phyllorhynchus* differ greatly in morphology and ecology.

Key words: Hemipenis, Natricidae, North America, Asia, Africa, *Afronatrix*, *Amphiesma*, *Macropisthodon*, *Natrix*, *Nerodia*, *Rhabdophis*, *Salvadora*, *Xenochrophis*, Systematics

Introduction

Hemipenial characters have played an important role in characterizing major clades of alethinophidian snakes, sometimes to the near exclusion of other character systems. The Colubridae, used here in the narrow sense of Zaher *et al.* (2009; = Colubrinae auctorum) has been characterized by two hemipenial characters: a simple (nonbifurcate) sulcus spermaticus and a calyculate apex (McDowell 1987; Zaher 1999; Zaher *et al.* 2009). The sulcus morphology is apomorphic at the level of Colubridae and hypothesized to be derived in a manner distinct from other simple sulci (review and references in Zaher *et al.* 2009: 139). On the other hand, calyces are apomorphic at a more inclusive level, Colubroidea (Zaher *et al.* 2009: 138).

While reviewing some literature on hemipenial morphology I became puzzled by two explicit reports of a bifurcate sulcus spermaticus in the North American genus *Phyllorhynchus* Stejneger. Klauber (1935: 14) described the everted hemipenis of *P. decurtatus perkinsi* as having the "sulcus divided distally". Savage & Cliff (1954: 72), examining the retracted hemipenis of *P. arenicola* (= *P. decurtatus* [Cope]), reported the sulcus as "divided at the very tip of the organ". These reports were surprising because recent classifications and molecular phylogenies associate *Phyllorhynchus* with Colubridae (e.g., Zaher 1999, Zaher *et al.* 2009, Vidal *et al.* 2007, Lawson *et al.* 2005) and a simple sulcus is usually considered universal within this group. However, Dowling & Duellman (1974–1978: 112b.2) had questionably placed *Phyllorhynchus* in their "Lycodontinae", presumably based in part on the earlier reports of a divided sulcus since they stated elsewhere that all "Lycodontinae" except Psammophiini

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