

The Hemipenes of Some Snakes of the Semifossorial Genus *Atractus*, with Comments on Variation in the Genus

WALTER E. SCHARGEL¹ AND TODD A. CASTOE²

Department of Biology, The University of Texas at Arlington, Box 19498, Arlington, Texas 76019, USA

ABSTRACT.—The hemipenes of seven species of *Atractus* (*Atractus emigdioi*, *Atractus major*, *Atractus marisela*, *Atractus poeppigi*, *Atractus torquatus*, *Atractus univittatus*, and *Atractus ventrimaculatus*) are described. Hemipenial morphology in this poorly known genus of snakes is found to be particularly variable among the species studied. Additionally, the primitive unicapitate hemipenial condition is more widespread among *Atractus* than was previously thought. Given the drastic variation in hemipenial morphology observed in *Atractus*, it is likely that characters derived from studying this organ may prove especially useful for future work on intrageneric relationships among members of this genus.

RESUMEN.—Los hemipenes de siete especies de *Atractus* (*Atractus emigdioi*, *Atractus major*, *Atractus marisela*, *Atractus poeppigi*, *Atractus torquatus*, *Atractus univittatus* y *Atractus ventrimaculatus*) son descritos. La morfología de los hemipenes en este género de serpientes poco conocido es particularmente variable entre las especies estudiadas. Adicionalmente, la condición primitiva unicapitada del hemipene tiene una distribución en *Atractus* más amplia que lo que se pensaba anteriormente. Debido a la gran variabilidad en la morfología de hemipenes observada en *Atractus* es muy probable que el estudio de este órgano obtenga caracteres útiles para trabajos futuros sobre las relaciones intragénicas entre los miembros de este género.

For more than a century many of the attempts to construct a natural classification for New World colubrid snakes have relied heavily on characters derived from hemipenial morphology (Cope, 1895; Dunn, 1928; Dowling and Duellman, 1978; Jenner and Dowling, 1985; Zaher, 1999). Despite this, only recently have major groups (e.g., subfamilies) been successfully defined based on relatively unambiguous hemipenial characters (Zaher, 1999). The Dipsadinae are a primarily Neotropical subfamily initially recognized on the basis of immunological evidence (Cadle, 1984). Subsequently, this group has been diagnosed by the possession of hemipenes with reduced or lost of bilobation, unicapitation, and with a distal division of the sulcus spermaticus (Myers and Cadle, 1994; Zaher, 1999). Currently, 22 genera are placed in the subfamily Dipsadinae, and a number of additional genera may also belong in this subfamily (listed as "Xenodontinae and Dipsadinae incertae sedis" by Zaher, 1999:table 1). Among dipsadine genera, *Atractus* is the most diverse, with more than 80 species currently recognized (Savage, 1960; Fernandes, 1995a). Members of this genus are distributed from Panama to southern Brazil and northern Argentina (Peters and Orejas-Miranda, 1970). At present, the taxonomy of *Atractus* is in a confused state, and virtually nothing is known about the evolutionary relationships among the members of this genus.

Savage (1960) defined two hemipenial types in *Atractus*: undifferentiated and differentiated. Undifferentiated hemipenes were defined as being completely

covered with spines except for the basal area; the differentiated type was characterized by possessing scalloped transverse flounces that replace spines in the distal portion of the organ. These characters, in combination with scutellation and dentition, were used by Savage (1960) to define three putatively monophyletic groups within the genus. Although the majority of dipsadine snakes have unicapitate hemipenes, most species of *Atractus* apparently have non-capitate hemipenes. Fernandes (1995b) and Fernandes et al. (2000), however, reported that a group of *Atractus* restricted to southern South America possesses unicapitate hemipenes. Accordingly, they regarded the unicapitate condition plesiomorphic and concluded that this character did not necessarily support the monophyly of that group of *Atractus*.

Examination of the hemipenes of *Atractus ventrimaculatus* from the Andes of Venezuela, showed that this species possesses the primitive unicapitate condition as well. This finding prompted us to examine additional species to better comprehend the variation present in the genus. In this paper, we describe or comment on the hemipenes of seven species of *Atractus* and demonstrate that there is considerable variation within the genus. Although our survey is by no means comprehensive, we were able to examine the everted hemipenes of specimens of species allocated to all three groups defined by Savage (1960).

MATERIALS AND METHODS

For descriptions of hemipenes, we largely follow the terminology of Dowling and Savage (1960) and, where appropriate, use terms and modifications proposed elsewhere by other authors (e.g., Myers, 1974; Myers and Campbell, 1981; Keogh, 1999; Zaher, 1999). The use of the term hemipenial body is adopted from Zaher (1999) and is here defined as all the hemipenis excluding the lobes and the capitulum or the distal

¹ Corresponding Author. E-mail: wschargel@yahoo.com

² Present address: Department of Biology, University of Central Florida, 4000 Central Florida Boulevard, Orlando, Florida 32816-5769, USA.

region that differs in ornamentation (e.g., calyces and flouces) from the rest of the organ. Specimens examined were *Atractus emigdioi* (MCNG 2110), Trujillo, Venezuela; *Atractus major* (KU 175399), Napo, Ecuador; *Atractus mariselae* (MCNG, uncataloged specimen), Trujillo, Venezuela; *A. poeppigi* (UTA R3536), Vaupés, Colombia; *Atractus torquatus* (UTA R3597), Vaupés, Colombia; *Atractus unioittatus* (UTA R3819), Meta, Colombia; and *A. ventrimaculatus* (MCNG 2127), Mérida, Venezuela. Museum abbreviations are listed in the Acknowledgments.

RESULTS AND DISCUSSION

Among the species studied, capitate hemipenes were observed in *A. ventrimaculatus* (Fig. 1A) and *A. unioittatus*. The organ of *A. ventrimaculatus* is slightly bilobed, uncapitate, extending to the seventh subcaudal when adpressed to the tail. The sulcus spermaticus is centrolineal and divides at the base of the capitulum, with a tendency to become centrifugal in the distal region of the lobes. The capitulum is completely encircled by spinulate flouces. Moderate-size spines are present on the sulcate and lateral surfaces of the hemipenial body. Small spines are occasionally present on the surface between the large spines. The asulcate surface is sparsely covered with very small spines that increase in size distally and laterally. The organ is nude in the basal region with a small pocket lateral to the sulcus. The hemipenes of *A. unioittatus* are rather complex compared to most other *Atractus*. They are slightly bilobed, uncapitate, extending to the fifth subcaudal when adpressed to tail. The sulcus spermaticus is centrifugal and divides at the base of the capitulum. The capitulum is completely covered by papillate calyces. The hemipenial body is covered, on the sulcate side, by spines that become large and fleshy laterally and basally. The asulcate surface is divided into two distinct regions that differ in ornamentation. Directly below the capitular groove there are three transversal rows of conical spines, which are replaced proximally by fleshy protuberances that form the swollen bases of spines. A small basal pocket is present lateral to the sulcus.

Among *Atractus*, the capitate condition has only been reported in *Atractus maculatus*, *Atractus reticulatus*, *Atractus serranus*, *Atractus taeniatus*, *Atractus trihedrus*, and *Atractus zebrinus*, (Fernandes, 1995b; Fernandes et al., 2000). Fernandes (1995b) thought that this condition was exclusively found in this group of species, and he suggested that these taxa might represent a "basal grade" in relation to all other *Atractus*, in which capitation is lost. The hemipenes of *A. ventrimaculatus* and *A. unioittatus* differ from those of the aforementioned species by having spinulate flouces and papillate calyces, respectively, versus spinulate calyces in the capitulum. Fernandes (1995b) described the asulcate side of the hemipenis of *A. reticulatus* as bearing spines slightly larger than those on the sulcate side, which contrasts with the condition found in *A. ventrimaculatus*. The characteristics of the asulcate side of the remaining species, however, were not described.

The hemipenes of *Atractus emigdioi* and *Atractus mariselae* are undifferentiated (sensu Savage, 1960), which appears to be typical for the majority of the genus. The hemipenes of *A. emigdioi* (Fig. 1B) are slightly bilobed, noncapitate, extending to the fifth

subcaudal when adpressed to the tail. The sulcus spermaticus is centrolineal, dividing slightly below the middle of the organ. The organ is completely covered by small spines. Below the division of the sulcus the spines become larger in the lateral regions. Above the sulcus division the spines become slightly smaller and occur in greater density. Small ridges are occasionally present on the lobes, connecting the base of the spines. No basal pocket present. The hemipenes of *A. mariselae* are similar to that of *A. emigdioi*. The hemipenes of *A. mariselae* differs by having the sulcus spermaticus dividing in the upper half of the organ and by possessing spines in the distal region noticeably smaller than the ones below the sulcus division. Furthermore, these spines gradually decrease in size toward the apex of the lobes.

A noncapitate differentiated (sensu lato) condition was observed in the hemipenes of *A. major* and *Atractus torquatus*; however, they differ in so many aspects that without a more extensive survey we do not perceive the differentiated condition to be homologous in these species. Savage (1960) described and figured the hemipenis of *A. major*, defining it as characteristic of the *badius* group. Hoogmoed (1980) described the hemipenis of *A. torquatus* from Surinam as undifferentiated, which conflicts with our observations. However, it is important to point out that both these authors based their descriptions on retracted hemipenis, which may potentially obscure certain features that are best appreciated on fully everted organs (Dowling and Savage, 1960; Branch, 1986).

Some authors (e.g., Myers, 1974; Myers and Cadle, 1994) have suggested that a full understanding of the snake hemipenis requires the study of this organ in its retracted as well as in its everted condition. Therefore, we here provide the first description of the hemipenes of both species based on everted organs. In *A. major* (Fig. 1C), the hemipenes are slightly bilobed, noncapitate, and extend to the sixth subcaudal when adpressed to the tail. The sulcus spermaticus divides below the right lobe (right hemipenis), with the right branch extending longitudinally to the tip of the lobe, whereas the left branch diverts to the left lobe extending to the tip in a centrifugal arrangement. Small papillate transverse flouces appear at the level of the sulcus division and extend to the tip of the lobes. Three rows of large spines are present in the sulcate side below the sulcus division and disappear proximally, leaving a large nude surface. The number of rows of spines increases gradually toward the asulcate side; therefore, the nude surface becomes reduced in that region. Most spines are very large, somewhat compressed, and very close to one another. A large naked pocket is present basally on the asulcate side. The asymmetric condition of the sulcus spermaticus described in the right organ is mirrored in the left organ. The hemipenes of *A. torquatus* (Fig. 1D) are bilobed, extending to the sixth subcaudal when adpressed to the tail. The lobes are well defined and separated from one another by a short interspace at their bases. The sulcus spermaticus is centrifugal and divides at the middle of the organ. The lobes are smooth and lack ornamentation. The hemipenial body is covered, except basally, with spines that extend to the base of the lobes, including the intrasulcar region. The organ is nude in the basal region with a naked pocket lateral to the sulcus.

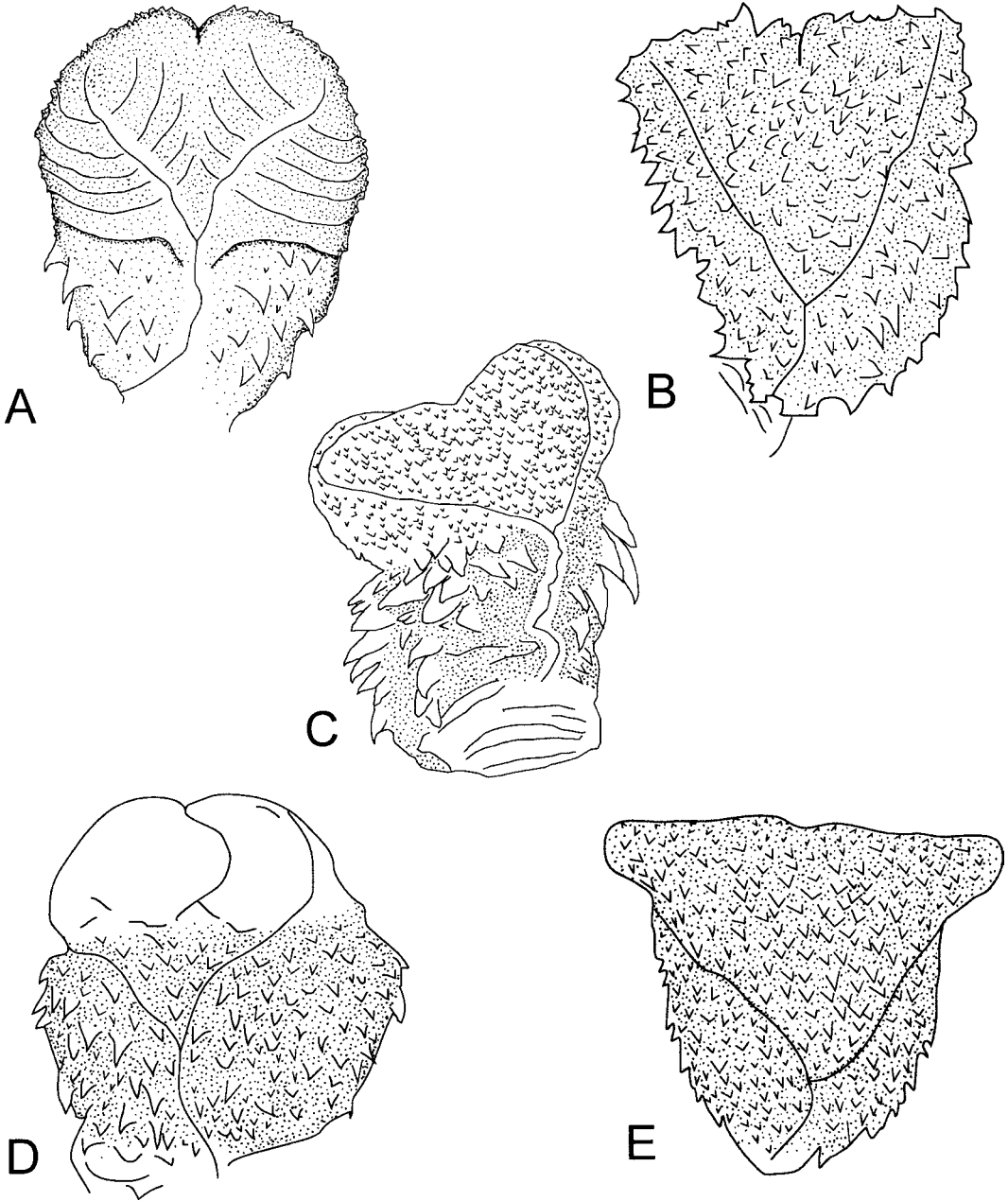


FIG. 1. Diagrammatic illustrations of the sulcate side of the hemipenes of the *Atractus* discussed in the text. (A) *Atractus ventrimaculatus*, (B) *Atractus emigdioi*, (C) *Atractus major*, (D) *Atractus torquatus*, (E) *Atractus poeppigi*.

The hemipenes of *Atractus poeppigi* were described by Dixon et al. (1976). We reexamined the specimen on which these workers based their description and observed a distinctive condition (relative to the majority of species within the genus *Atractus*) that Dixon and collaborators did not describe. The lobes in *A. poeppigi* are very small and separated from each other by a large interspace (Fig. 1E). Dixon et al. (1976)

described the hemipenis as "bilobed at tip," which does not accurately describe this condition. *Atractus poeppigi* has been placed with *A. elaps* and *A. latifrons* into the *A. elaps* group, which seems to be monophyletic (Savage, 1960; Fernandes, 1995a). Additionally, the *elaps* group may in fact be more closely related to the genus *Adelphicos* than to other *Atractus* (Fernandes, 1995a), thus rendering *Atractus* polyphyletic as currently

defined. Savage (1960) and Hoogmoed (1980) described the hemipenes of *Atractus elaps* and *Atractus latifrons*, respectively. They did not find the condition in the lobes that we found in *A. poeppigi*. Both authors based their description on retracted organs, however, which may complicate recognition of this condition.

The use of hemipenial morphology as a source of phylogenetically informative characters has recently regained support based on the monographic works of Keogh (1999) and Zaher (1999). Phylogenetic studies of snakes have often been considered difficult given that their external morphology is generally conservative, plagued by homoplasy, and reduced in easily assessable features relative to other squamates (Dowling, 1967; Savage, 1997). Especially in the diverse family Colubridae, hemipenial morphology appears to be of tremendous taxonomic utility. Although external morphology in *Atractus* is conservative (except for color pattern) and provides few informative characters, the great variation observed in the hemipenes of the species of *Atractus* discussed herein illustrates the potential information that can be provided by this organ in taxonomic and phylogenetic studies of this genus.

Acknowledgments.—We are most grateful to J. A. Campbell, University of Texas at Arlington (UTA), L. Trueb, University of Kansas (KU) and J. E. García-Pérez, Museo de Zoología, Biocentro, UNELLEZ (MCNG), Guanare, Venezuela, for letting us examine specimens under their care. D. C. Taphorn provided working space to one of us (WES) at the MCNG in Venezuela. R. and A. Schargel have supported WES in Venezuela. M. Hoogmoed kindly sent us valuable information to clarify matters regarding the methods he used for describing hemipenes in his work on *Atractus* from Surinam. We thank E. Smith for helping with the figures. J. Campbell, T. Doan, J. Meik, C. Myers, and an anonymous reviewer provided helpful criticisms on the manuscript.

LITERATURE CITED

- BRANCH, W. R. 1986. Hemipenial morphology of African snakes: a taxonomic review part 1. Scolecophidia and Boidae. *Journal of Herpetology* 20:285–299.
- CADLE, J. E. 1984. Molecular systematics of Neotropical xenodontine snakes. II. Central American xenodontines. *Herpetologica* 40:21–30.
- COPE, E. D. 1895. The classification of the Ophidia. *Transactions of the American Philosophical Society* 18:186–219.
- DIXON, J. R., R. A. THOMAS, AND H. G. GREENE. 1976. Status of the Neotropical snake *Rhabdosoma poeppigi* Jan, with notes on variation in *Atractus elaps* (Günther). *Herpetologica* 32:221–227.
- DOWLING, H. G. 1967. Hemipenes and other characters in colubrid classification. *Herpetologica* 23:138–142.
- DOWLING, H. G., AND W. E. DUELLMAN. 1978. Systematic herpetology: a synopsis of families and higher categories. *Herpetology Information Search System (HISS)*, New York.
- DOWLING, H. G., AND J. M. SAVAGE. 1960. A guide to snake hemipenis: a survey of basic structure and systematic characteristics. *Zoologica* 45:17–28.
- DUNN, E. R. 1928. A tentative key and arrangement of the American genera of Colubridae. *Bulletin of the Antivenin Institute of America* 2:18–24.
- FERNANDES, R. 1995a. Phylogeny of the dipsadine snakes. Unpubl. Ph.D. diss., Univ. of Texas, Arlington.
- . 1995b. Variation and taxonomy of the *Atractus reticulatus* complex (Serpentes: Colubridae). *Comunicações do Museu de Ciências da PUCRS, Série Zoologia* 8:37–53.
- FERNANDES, R., E. M. X. FREIRE, AND G. PUERTO. 2000. Geographic variation of the Brazilian Atlantic rain forest snake *Atractus maculatus* (Günther, 1858) with the revalidation of *Rhabdosoma zebrinum* Jan, 1862 (Serpentes: Colubridae). *Boletim do Museu Nacional, Zoologia* 419:1–8.
- HOOGMOED, M. S. 1980. Revision of the genus *Atractus* in Surinam, with the resurrection of two species (Colubridae, Reptilia). Notes on the herpetofauna of Surinam VII. *Zoologische Verhandlungen* 175:1–47.
- JENNER, J. V., AND H. G. DOWLING. 1985. Taxonomy of American xenodontine snakes: the tribe Pseudoboini. *Herpetologica* 41:161–172.
- KEOGH, J. S. 1999. Evolutionary implications of hemipenial morphology in the terrestrial Australian elapid snakes. *Zoological Journal of the Linnean Society* 125:239–278.
- MYERS, C. W. 1974. The systematics of *Rhadinaea* (Colubridae), a genus of New World snakes. *Bulletin of the American Museum of Natural History* 153:1–262.
- MYERS, C. W. AND J. E. CADLE. 1994. A new genus for South American snakes related to *Rhadinaea obtusa* (Colubridae) and resurrection of *Taeniophallus* Cope for the "*Rhadinaea brevirostris*" group. *American Museum Novitates* 3102:1–33.
- MYERS, C. W. AND J. A. CAMPBELL. 1981. A new genus and species of colubrid snake from the Sierra Madre del Sur of Guerrero, Mexico. *American Museum Novitates* 2708:1–20.
- PETERS, J. A. AND B. OREJAS-MIRANDA. 1970. *Catalogue of the Neotropical squamata. Part I. Snakes*, Smithsonian Institution Press, Washington, DC.
- SAVAGE, J. M. 1960. A revision of the Ecuadorian snakes of the colubrid genus *Atractus*. *Miscellaneous Publications of the Museum of Zoology, Univ. of Michigan* 112:1–86.
- . 1997. On terminology for the description of the hemipenes of squamate reptiles. *Herpetological Journal* 7:23–25.
- ZAHER, H. 1999. Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. *Bulletin of the American Museum of Natural History* 240:1–168.

Accepted: 13 June 2003.