

SHORT NOTES

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ON TERMINOLOGY FOR THE
DESCRIPTION OF THE HEMIPENES
OF SQUAMATE REPTILES

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The use of morphological differences of the hemipenes as systematic characters in the Squamata dates from the seminal papers of Cope (1893, 1895, 1896). Subsequently, the hemipenial features of snakes have been widely used as a basis for higher classification and in species recognition (e.g. Dunn, 1928; Bogert, 1940; Myers, 1974; Branch, 1986).

While utilization of the characteristics of snake hemipenes in systematic studies is now *de riguer*, until recently little attention has been given to these structures in lizards. This is partially because the streamlined habitus of snakes provides a reduced set of features for phylogenetic reconstruction that are plagued by extensive homoplasy. The search for additional informative structures has thus taken advantage of the substantial variation in the relatively large snake hemipenes. In contrast, lizards have a wider range of external and internal characters that are thought to be subject to less homoplasy, and hemipenes are generally smaller structures than in snakes.

Renewed attention to lizard hemipenes as a rich mine of data (Uzzell, 1965, Presch, 1978; Branch, 1982; Arnold, 1986; Böhme, 1988, 1991; Frost & Etheridge, 1989) confirms Cope's (1896) perspicacity in identifying their value in systematics. However, this revival of interest raises questions of homology and the need for a uniform terminology applicable to all squamate hemipenes. Dowling & Savage (1960) presented an overview of the variation in snake hemipenes and an updated standardized terminology for description that has been further refined by McDowell (1961), Myers & Campbell (1981), and Branch (1986), especially with regard to the position of the sulcus spermaticus. Generally, lizard hemipenes may be described utilizing the same set of terms as these authors. However, Klaver & Böhme (1986) and Böhme (1988), in the most comprehensive review of lizard hemipenes to date, proposed a number of new descriptors for specialized features not found in snakes. Böhme (1988) also provided a revised set of definitions for uniform description of lizard hemipenes.

The present paper is intended to clarify definitions, resolve inconsistencies and integrate the terminology applied to hemipenial variation for lizards and snakes into a broader scheme applicable to all squamates. Issues to be treated relate primarily to regional

characterization and differentiation, details of ornamentation and apical specialization. Terms that are concordant between Dowling & Savage (1960) and Böhme (1988) are not discussed but are accepted as standardized descriptors. The terminology for variation in the sulcus spermaticus of snakes provided by McDowell (1961), Myers & Campbell (1981) and Branch (1986) also should be applied to conditions in lizards, including amphisbaenians, when appropriate.

Most squamate hemipenes are differentiated into two or three regions by the degree and kinds of ornamentation (e.g. calyces, papillae, spines). The basal one-fifth to one-half is often naked but may have some distinctive features (e.g. hooks, naked pocket, small spines). A central zone consisting of about one-half to one-third of the penial length is usually differentiated from both the basal sector and the distal one-third to one-fourth of the organ. Klaver & Böhme (1986) introduced the terms pedicel, truncus and apex for the proximal (basal), central and distal areas, respectively. The very tip (apex) of the hemipenes often has a distinctive terminal structure (e.g. papilla, awn, disk) while the rest of the distal region is differentiated (e.g. spinous, calyculate, papillate). For this reason it seems best to refer to the distal sector as the apical region and describe the terminal specializations separately.

Other terminal specializations include structures called "horns" and "cups" by Branch (1982), and a series of bizarre features, which will be discussed below, found only in chamaeleons (Klaver & Böhme, 1986). The "horns" (Branch, 1982) of varanid lizards are extensions of the divided retractor muscle that do not evert and lie in the lumen of the retracted hemipenis. The terminal papillae and awns of the few snakes having them appear to be similar structures. Terminal papillae and awns also occur on the hemipenes of some macroteiid lizards (Böhme, 1988, Fig. 24). Nevertheless the varanid structures are so distinctive that it seems best to recognize them separately as hemipenial *cornua* (sing. *cornus*).

The "cups" described by Branch (1982) in varanids are substantially different from those that he subsequently recognized in some boid snakes (Branch, 1986). The latter are the same paired structures called apical disks by Cope (1895) and Dowling and Savage (1960) and may be terminal or lateral to the apex. The varanid lateral "cups" form slight depressions to strongly concave areas demarcated by a thick fleshy ridge surrounding a hemipenial cornus. They occur in relatively few species and are paired or only one is present. (Branch, 1982; Böhme, 1988). There appears no need to coin any special terms for these features which may be simply described.

Klaver & Böhme (1986) described and standardized terminology for the remarkable apical pedunculi, auriculae and rotulae unique to chamaeleons. These authors also described two kinds of unusual features in members of the chamaeleon genus *Brookesia* as terminal "horns" and "crests". Species in this genus have

either a pair of "horns" or a pair of "crests" terminally. There is considerable similarity between "horns" and pedunculi and "crests" and auriculae or rotulae. Because of the uncertainty of homology or lack thereof it seems inappropriate to coin any new terms for these structures following Klaver & Böhme (1986).

Cope's (1893) descriptions are based on uneverted hemipenes, which led him to adopt an ambiguous terminology for the longitudinal and transverse or pinnate folds that he observed in his preparations. He referred to these folds collectively as laminae. In addition he called both the longitudinal and transverse or pinnate folds plicae. Dowling & Savage (1960) standardized Cope's terms to "flounce" for non-calyculate transverse or pinnate folds because they could make no distinction between flounces and plicae in this context. In addition they pointed out that Cope's longitudinal plicae are folds of membranous tissue that disappear when the organ is everted. Peters (1974) obfuscated the situation by equating flounces with plicae and stating that flounces disappear when the hemipenes are everted. As shown by Dowling & Savage (1960) and Böhme (1988), flounces are definite structures but what Cope called longitudinal plicae are not. Although the latter disappear as the hemipenes are everted there are other structural differentiations of the pedicel (e.g. fleshy ridges, naked pockets) that may be present in both inverted and everted states.

Cope (1895) described the truncus and apical region of macro- and microteiids as covered by thin transverse, slightly overlapping folds which he called "transverse laminae". He contrasted this condition with the fleshy flounces observed in many other lizards. Böhme (1988) recognized the differences between "laminae" and flounces and coined the term paryphasmata as a descriptor for the latter. Unfortunately, he chose to use "plicae" for the laminate structures. Because of the dual and confusing usage of "plicae" for flounces and transitory longitudinal folds (Cope, 1893, 1895; Peters 1974) and "laminae" for flounces, longitudinal "plicae" and Böhme's (1988) plicae (Cope 1896), I recommend that these terms not be used in squamate hemipenial descriptions. I propose that the descriptive and unambiguous term *petalum* (pl. *petala*) be applied to the thin transverse overlapping folds found in lizards and called plicae by Böhme (1988).

Petala and flounces of lizards may exhibit differences in micro-ornamentation as described for snakes (Dowling and Savage, 1960). The surface of the petala in some species is covered with minute spines (Böhme, 1988). In several microteiids (Gymnophthalmidae) the petala have an internal skeleton of closely packed small calcified spines. Böhme (1988) proposed the term spiculae for these structures to distinguish them from other spinous features of the hemipenes. Although Branch (1982) coined the term "frill" to denote deeply scalloped flounces that are characteristic of many varanid lizards, these flounces do not differ sig-

nificantly from similar structures found in other squamates.

It should be noted that petala have not been reported for any snake. Also unknown in snakes are the hemibacula (Böhme, 1988), unique internal supportive mineralizations within the large apical cornua of the hemipenes of some varanid lizards (Branch, 1982; Card & Kluge, 1995).

Böhme (1988) concluded that the basic kinds of ornamentation found on the apical region and/or truncus of hemipenes was characteristic of major groups of lizards: Iguania and Gekkota having calyces but lacking petala and flounces; Scincomorpha having petala and lacking calyces and flounces; Anguimorpha having flounces but lacking calyces and petala.

Subsequently, Böhme (1989) reviewed the structure of the hemipenes in amphisbaenians. They resemble those of teiid lizards in ornamentation by having petala and lacking calyces and flounces, or are nude. Partially on the basis of the penial characteristics, Böhme regarded them as scincomorphs fitting into his overall generalizations on hemipenial features for major lizard groups.

While these generalizations have much merit it needs to be pointed out that flounces occur sporadically in Iguania and Scincomorpha as well. In the former the distal calyculate area may gradually grade into a series of transverse ridges (Böhme's *Randleisten*) toward the base as the number of longitudinal connecting ridges are reduced. In some representatives of the scincomorph families Xantusiidae (Böhme, 1988, Fig. 23), Gymnophthalmidae (Böhme, 1988, Figs. 24, 28) and Scincidae (Noble and Bradley, 1933, Fig. 12) a portion or most of the ornamentation consists of thick fleshy transverse folds (called *Ringfalten* and *Ringwülste* by Böhme) differing only slightly from the flounces found in the Anguimorpha.

The distinction between petala and flounces is one of degree. The former are thin, closely set and slightly imbricate, and the latter fleshy, more widely spaced and non-overlapping. Somewhat intermediate conditions seem to occur in some scincomorphs (e.g. Presch, 1978, Fig. 2) suggesting that a character transformation from flounces to petala or vice versa has occurred more than once among lizards.

Another area needing clarification is the use of the term capitate for the hemipenes of some lizards (Branch, 1982; Frost & Etheridge, 1989). In snakes capitate describes organs in which a distinct transverse naked groove, or a pair of grooves in some bilobed forms, completely encircles the organ (or each lobe), except where the sulcus spermaticus passes through the groove(s). The groove separates the differentiated apical region(s), called a capitulum (pl. capitula), from the truncus.

No known lizard has the capitate condition. Branch's (1982) usage is ambiguous. Frost & Etheridge (1989) used capitate to describe lizard hemipenes that have the apical region calyculate and

distinctly differentiated in ornamentation from the truncus or truncus plus pedicel. Since there is no bounding naked groove in these cases and consequently no capitulum, this term should not be applied in lizard hemipenial descriptions.

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