OBSERVATIONS ON THE VERTEBRAL HYPAPOPHYSES AND ASSOCIATED MUSCULATURE IN SOME SNAKES, WITH SPECIAL REFERENCE TO THE COLUBRIDAE

by

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With three tables

Hypapophyses are reported to be present on the anterior precaudal vertebrae of representatives of all snake families, except the Typhlopidae, Leptotyphlopidae, and Uropeltidae. The processes occur on all precaudal vertebrae in the Acrochordidae, Colubridae (auct.), Elapidae, Viperidae, and two subfamilies of the Boidae, the Bolyerinae and Tropidophinae. Among the numerous genera of the Colubridae caudal extent of the presence of the hypapophyses is variable, even within a genus or species.

Cope (1864) associated hypapophyses on the posterior precaudal vertebrae with the Homalopsinae. In the years following he utilized the character to distinguish the Homalopsinae (1886), the Colubrinae (1887), the Natricidae (1893); in his last classification (1900), Cope divided the families Colubridae and Dipsadidae into two informal series of genera based on the presence or absence of hypapophyses on the posterior precaudal vertebrae.

Boulenger (1893-96) used the presence or absence of posterior hypapophyses in a similar manner to separate the genera of two subfamilies of the Colubridae, the Colubrinae and Dipsadomorphinae. Several authors since have used the character in organizations of the confusing array of colubrid genera (Dunn, 1928; Bogert, 1940; Smith, 1943, who suggested the terms Hypophysia and Anhypophysia for the two basic types; Underwood, 1967). Malnate (1960) suggested a possible evolutionary sequence for the character in the Colubridae. Auffenberg (1963) recommended that more detailed observations be made of the hypapophyses.

Rosén (1905a, b) took exception to Boulenger's statements regarding posterior hypapophyses in some genera. Brongersma (1938) reviewed Rosén's work, confirmed his findings, and added that hypapophyses are present on the posterior vertebrae of *Psammodynastes pictus*, *Helicops bicolor* (= *Rhabdops bicolor*), *H. schistosus* (= *Atretium schistosum*), and *Langaha cristi-galli* (= *L. nasuta*). He reported posterior hypapophyses absent in *Ahaetulla prasina, Oxybelis fulgidus*, and *Boiga cynodon, jaspidea, multimaculata* and present or absent in *B. irregularis*. Malnate reported the absence of posterior hypapophyses in two forms previously assumed to possess them: *Tropidonotus baileyi* (= *Thermophis baileyi*; 1953) and *Tropidonotus ornaticeps* (= *Amphiesmoides ornaticeps*; 1961).

Smith (1943) pointed out that examination of the hypapophyses is not complete without an accounting of the attending muscle, the M. transversohypapophyseus. Mosauer (1935) showed a positional relationship of this muscle with the M. costalis internus superior and the M. transversus dorsalis, and that each of these may be associated with the hypapophyses.

A survey of a number of colubrid genera reported to possess hypapophyses on the posterior vertebrae was initiated to determine, if possible, 1) a more useful definition of hypapophyses; and, 2) what variations may exist that would be helpful in a taxonomic evaluation of the character. Representatives of a number of colubrid genera with hypapophyses on the anterior vertebrae only and certain non-colubrid genera also were examined.

Methods and materials

Vertebrae and musculature were examined in situ. Posterior vertebrae (at a level 5 to 25 ventrals anterior to the cloaca) were examined in every specimen. Where hypapophyses were found to be absent at that level the most caudal point of their presence was determined. Observations were made of the general profile of the hypapophyses, the extent of ventral and posterior projection from the centrum, and the form of the posteroventral (distal) tip. Development of the M. transversohypapophyseus and the length of individual bundles (in terms of vertebrae spanned) was noted, as was its relation to the M. costalis internus superior. Cephalic extent of the M. transversus dorsalis also was determined. Specimens examined are listed in table 1; observations of the hypapophyses and musculature are summarized in tables 2 and 3, respectively. Muscle terminology is from Mosauer (1935), and is abbreviated as follows: Mthy (M. transversohypapophyseus), Mcis (M. costalis internus superior), Mtd (M. transversus dorsalis). Gasc (1967) uses the name M. parapophyso-hypapophyseus for M. transversohypapophyseus Mosauer, and defines the muscle as a differentiation of the M. subvertebralis.

Hypapophyses

In its most simple form the hypapophysis is narrow and projects ventroposteriorly in straight, spine-like form. An anterior keel usually is present, reaching forward to the rim of the cotyle. The distal tip is pointed or bluntly so, and extends caudally to near or beyond the level of the condyle tip. This form of hypapophyses was found in *Agkistrodon* and *Crotalus*. Auffenberg (1963) associates this form with the viperids. The *Bitis* examined does not exhibit this type of hypapophyses.

The most common form of hypapophysis among the genera examined is blade-like (sigmoid, Auffenberg, 1963); i.e., a more or less broad ventral process with an anterior keel and the posteroventral (distal) region produced caudally. The anterior keel is a low, forward extension of the hypapophysis and may or may not reach the rim of the cotyle. The body of the hypapophysis may be narrow (*Chersydrus, Chrysopelea, Enhydris, Lycognathophis, Lycophidion*) but a caudal projection of the distal tip always is present, in contrast to the spine-like type. Variation in ventral depth and extent of caudal projection occurs. In some forms (*Lamprophis, Macropisthodon, Trachyboa*) the caudal process may be absent, the posterior edge of the hypapophyses being vertical or nearly so, at the level of the condyle base. Commonly, however, it is produced to some extent below the condyle, terminating in a sharp or rounded point at a level near or at the tip of the condyle; it thus overlaps the anterior portion of the vertebrae next caudal. The ventral edge (sometimes horizontal) of the hypapophysis may be thin, flattened or somewhat expanded laterally (as in *Amastridium*).

In those genera wherein hypapophyses are present only on the anterior vertebrae reduction and loss of the process occurs in the region of the heart. Cephalic to this region the hypapophyses may be strongly or weakly developed. Loss is accomplished rapidly over a short span of vertebrae (2 to 5). Two specimens of *Chrysopelea ornata* (ANSP 5238 and 5241), however, show a gradual reduction of the hypapophyses over approximately two-thirds of the precaudal vertebrae. Anterior to the heart level (60th ventral), the hypapophyses are well-developed. Reduction of the hypapophyses begins caudal to the heart and in the region of the 150th-155th ventrals the hypapophyses are reduced to a low, stout keel extending the length of the centrum; this keel is present on the remaining vertebrae to the cloaca (221st ventral).

The anterior hypapophyses of *Lycodon* are weakly developed and the posterior vertebrae bear a low but well-defined median keel not strikingly different in development from the anterior hypapophyses. *Tretanorhinus variabilis* possesses a strong keel on the posterior vertebrae which, however, is quite different in form from the hypapophyses present on the anterior vertebrae (in *T. nigroluteus* the keel is much reduced and the anterior hypapophyses weakly developed). Both *Lycodon* and *Tretanorhinus* have been reported to possess posterior hypapophyses.

Intracolumnar variation in the form of hypapophyses, when these are present on all precaudal vertebrae, appears slight; those anterior in the series usually are somewhat more strongly developed than those posterior. Sexual variation may occur but it cannot be shown in this sample; nor can ontogenetic development.

Musculature

The M. transversohypapophyseus (Mthy) is composed of subvertebral bundles of muscle fibers. Individual bundles arise from the parapophysial process of the vertebrae and insert, via a strong tendon, on the distal tip of a hypapophysis three to eight vertebrae anterior (cf. Mosauer, 1935; Gasc, 1967). In general, the Mthy is more strongly developed anteriorly than posteriorly; it is most highly developed in association with strong hypapophyses, and to a lesser degree in forms with weak hypapophyses. Exception is shown by *Chersydrus*, *Enhydris*, and *Gerardia*, each with well-developed hypapophyses but a weakly or moderately developed Mthy.

Colubrid genera show a positive correlation between development of the Mthy and the presence of hypapophyses. In all forms with the hypapophyses absent on the posterior precaudal vertebrae the Mthy is reduced and lost with the hypapophyses. An excellent example of this positive correlation is provided by the gradual reduction and loss of the muscle in conjunction with the condition of the hypapophyses in the two specimens of *Chrysopelea ornata* described above. The Mthy is present throughout the body length in all elapid and viperid genera examined, as are hypapohyses. It was not found in *Cylindrophis*, *Trachyboa*, *Tropidophis*, and *Xenopeltis*, all of which possess hypapophyses. It is absent also in *Leptotyphlops* and *Typhlops*; hypapophyses also are absent.

Lateral or dorsolateral to the Mthy is the M. costalis internus superior (Mcis). In those genera with a strongly developed Mthy (e.g., viperids), that muscle projects well ventral to the flat Mcis. Where the Mthy is moderately or weakly developed, the fibers of the Mcis lie adjacent (lateral) to or may overlap the lateral surface of the Mthy. The Mcis arises from a broad aponeurosis from the lateral surface of the hypapophysis, vertebral keel or the centrum (when ventral processes are absent); the aponeurosis passes ventral to the Mthy. Mosauer (1935) has described the condition in the viperids wherein the Mcis develops from slips from an aponeurotic sheath enclosing the strongly developed Mthy.

Ventral to both the Mthy and Mcis is the M. transversus dorsalis (Mtd). This is a very thin, delicate, and often difficult to distinguish, sheet lying immediately dorsal to the peritoneum. The Mtd also arises from a broad aponeurosis attached to the lateral surface of the hypapophysis, vertebral keel or from the centrum. The muscle is present forward to the region of the heart, with slight variation in the level of its disappearance observed, in all genera examined, except *Leptotyphlops* and *Typhlops* (see Mosauer, 1935, for discussion of the condition in *Typhlops*).

Discussion

Hypapophyses, by definition, are processess produced from the ventral surface of the vertebrae. In practice, the term generally has been used in reference to prominent projections, those of low configuration being referred to as haemal keels or simply keels. This distinction is subjective and, presumably, is the basis for the confusion in the reported presence or absence of hypapophyses, especially on the posterior precaudal vertebrae.

The colubrid, elapid, and viperid species examined show, with no exception noted, a positive correlation between the development of the hypapophyses and the development of the M. transversohypapophyseus. Two other hypaxial muscles, the M. costalis internus superior and the M. transversus dorsalis develop from aponeuroses arising from the lateral surface of the hypapophyses when these structures are present. In the absence of hypapophyses these muscles arise from ventral keeling or the lateroventral surface of the centrum and, thus, are not dependent on the hypapophyses.

A second vertebral process appears also to be positively correlated with the presence of the Mthy: the parapophysial process, produced ventrally and anteriorly from the paradiapophyses of the vertebrae (Hoffstetter, 1939). The Mthy originates on this process; the process has not been found in the absence of the Mthy.

Four genera examined possess well-developed hypapophyses but lack the Mthy. *Cylindrophis* and *Xenopeltis* have stout hypapophyses present on the vertebrae anterior to the heart level. *Trachyboa* and *Tropidophis* have broad, low hypapophyses present, with slight reduction posteriorly in the series, on all precaudal vertebrae. Parapophysial processes are not developed in any of the four genera. The function of the hypapophyses in these genera is not clear. In *Trachyboa* and *Tropidophis* the well-developed Mcis arises from broad, tough aponeuroses attached the full length of the hypapophyses, suggesting an association of the somewhat unusual form of the hypapophyses with the development of the Mcis. No association between musculature and hypapophyses has been ascertained in *Cylindrophis* and *Xenopeltis*.

With the exception of *Chersydrus* (Acrochordidae) presence of the M. transversohypapophyseus appears to be restricted to the advanced snakes (see also Mosauer, 1935). Hypapophyses, however, are known from several groups of snakes. The functional difference between hypapophyses which support the Mthy and those processes present in the absence of the Mthy would seem to give the former a strong biological distinction. Knowledge of this function of the hypapophyses seems necessary to any taxonomic consideration of the structures. The presence of parapophysial processes in correlation with hypapophyses suggests that presence of Mthy may be determined from skeletal material; this should be further confirmed.

An understanding of the variation in form of the hypapophyses, blade-like or spine-like, is elusive with the present data. A relationship appears to exist between spine-like hypapophyses and a strongly developed Mthy, most notably in the viperids. The simple spine-like form may be a more primitive type than the elaborate blade-like form but the data do not yet provide sufficient evidence in support of this conjecture.

Presence of hypapophyses, or more correctly the M. transversohypapophyseus, on all precaudal vertebrae has been suggested (Malnate, 1960) as the primitive condition among colubrids (and, presumably, all advanced snakes). Greater knowledge of variation in other characters of colubrid snakes has led to the acceptance of the fact of several phyletic lineages and that loss of the Mthy posteriorly has occurred in more than one of them. Secondary development of ventral vertebral processes may have occurred on the posterior vertebrae in some genera. On the basis of observations made here it appears unlikely that the Mthy/hypapophyses system has reappeared once lost.

Literature cited

Auffenberg, W., 1963. The fossil snakes of Florida. — Tulane Studies Zoology, 10 (3): 131-216, 51 figs.

Bogert, C. M., 1940. Herpetological results of the Vernay Angola expedition, with notes on African reptiles in other collections. Pt. 1. Snakes, including an arrangement of African Colubridae. — Bull. Amer. Mus. Nat. Hist., 77: 1-107, pl. 1, 18 figs.

Boulenger, G. A., 1893-1896. Catalogue of the snakes in the British Museum (Natural History), 1 (1893): xii, 1-448, 28 pls., 26 figs.; 2 (1894): xi, 1-382, 20 pls., 25 figs.; 3 (1896): xiv, 1-727, 25 pls., 37 figs.

Brongersma, L. D., 1938. On the presence or absence of hypapophyses under the posterior precaudal vertebrae in some snakes. — Zool. Meded. Leiden, 20: 240-242, 1 fig.

Cope, E. D., 1864. Contributions to the herpetology of Central America. — Proc. Acad. Nat. Sci. Phila.. 16: 166-181.

——, 1886. An analytical table of the genera of snakes. — Proc. Amer. Philos. Soc., 23: 479-499.

——, 1887. Catalogue of batrachians and reptiles of Central America and Mexico. — Bull. U.S. Nat. Mus., 32: 7-98.

——, 1893. Prodromus of a new system of the non-venomous snakes. — Amer. Nat., 27: 477-483.

——, 1900. The crocodilians, lizards and snakes of North America. — Rept. U.S. Nat. Mus., 1898: xviii, 1-1143, 36 pls., 347 figs.

Dunn, E. R., 1928. A tentative key and arrangement of the American genera of Colubridae. — Bull. Antiv. Inst. Amer., 2 (1): 18-24.

GASC, J.-P., 1967. Introduction à l'étude de la musculature axiale des squamates serpentiformes. — Mém. Mus. Nat. Hist. nat., (A) Zool., 48 (2): 69-125, 3 pls., 46 figs.
HOFFSETTER, R., 1939. Contribution à l'étude des Elapidae actuels et fossiles et de l'Ostéologie des Ophidiens. — Arch. Mus. Hist. nat., Lyon, 15: 1-78, 2 pls., 13 figs.
MALNATE, E. V., 1953. The taxonomic status of the Tibetan colubrid snake Natrix baileyi. — Copeia, 1953 (2): 92-96, 1 fig.
——, 1960. Systematic division and evolution of the colubrid snake genus Natrix, with comments on the subfamily Natricinae. — Proc. Acad. Nat. Sci. Phila., 112 (3): 41-71, 2 figs.
——, 1961. Amphiesmoides, a new genus for Tropidonotus ornaticeps Werner (Serpentes; Colubridae). — Notulae Naturae, 341: 1-7.
MOSAUER, W., 1935. The myology of the trunk region of snakes and its significance for ophidian taxonomy and phylogeny. — Univ. Cal. Publ. Biol. Sci., 1 (6): 81-120. 15 figs.
ROSÉN, N., 1905a. List of snakes in the Zoological Museums of Lund and Malmö, with descriptions of new species and a new genus. — Ann. Mag. Nat. Hist., (7) 15: 168-181, 2 pls., 2 figs.
——, 1905b. Reply to Mr. G. A. Boulenger. — Ann. Mag Nat. Hist., (7) 16: 126-129.
SMITH, M. A., 1943. The fauna of British India, Reptilia and Amphibia, 3, Serpentes: xii, 1-583, 166 figs.
UNDERWOOD, G., 1967. A contribution to the classification of snakes. Trustees Brit. Mus., publ. 653: x, 1-179, 14 figs.

TABLE I
List of specimens examined

Agkistrodon contortrix (ANSP 10715, Texas, U.S.A.)
Alsophis portoricensis (ANSP 19630, Virgin Islands)
Amastridium veliferum (ANSP 3738, Nicaragua)
Aspidura brachyorrhus (ANSP 3309, Ceylon)
Amphiesma pryeri (ANSP 27244, Okinawa, Riukiu Islands)
Amphiesma stolata (ANSP 11434, Hainan, China)
Atretium schistosum (ANSP 6636, locality unknown)
Bitis lachesis (ANSP 20300, Belgian Congo)
Boaedon fuliginosus (ANSP 15379, Zanzibar; ANSP 20709, Cameroons)
Boiga cynodon (ANSP 26420, Borneo)
Boiga irregularis (ANSP 26101, New Guinea)
Boiga kraepelini (ANSP 27147, Taiwan)
Boiga pulverulenta (ANSP 10142, Liberia)
Bothropthalmus lineatus (ANSP 20336, Fr. Equatorial Africa)
Bungarus ceylonicus (ANSP 6864, Ceylon)
Chersydrus granulatus (ANSP 6729, Philippine Islands)
Chrysopelea ornata (ANSP 5238, Philippine Islands; ANSP 5241, East Indies; ANSP 15006, Sumatra)
Coluber constrictor (ANSP 16421, Pennsylvania, U.S.A.)
Crotalus horridus (ANSP 7108, Missouri, U.S.A.)
Cylindrophis rufus (ANSP 26351, Borneo)
Dendrelaphis caudolineatus (ANSP 26441, Borneo)
Enhydris enhydris (ANSP 5091, India)
Gerardia prevostiana (ANSP 5090, Philippine Islands)
Helicops carinicaudus (ANSP 16419, South America)
Helicops danieli (ANSP 12174, locality unknown)

Hydraethiops melanogaster (ANSP 20701, Cameroons)
Lamprophis aurora (ANSP 10263, South Africa)
Langaha nasuta (ANSP 5289, Madagascar)
Laticauda colubrina (ANSP 6755, Marquesas Islands)
Leptotyphlops dulcis (ANSP 10944, Texas, U.S.A.)
Lycodon laoensis (ANSP 19971, Thailand)
Lycognathophis seychellensis (ANSP 5206, Seychelles Islands)
Lycophidion capense (ANSP 20301, Belgian Congo)
Macropisthodon flaviceps (ANSP 15036, Sumatra)
Macropophis dendrophiops (ANSP 27245, Philippine Islands)
Mehelya capensis (ANSP 20715, Fr. Equatorial Africa)
Micrurus fulvius (ANSP 6824, Louisana, U.S.A.)
Natriciteres olivaceus (ANSP 4701, Lake Rudolph)
Natrix annularis (ANSP 27247, Taiwan)
Natrix natrix (ANSP 6429, Italy)
Natrix sipedon (ANSP 16614, Kansas, U.S.A.)
Ninia atrata (ANSP 3351, Ecuador)
Ninia sebae (ANSP 11716, Mexico; ANSP 22872, Nicaragua; ANSP 26661, Honduras)
Psammodynastes pictus (ANSP 26346, Borneo)
Psammodynastes pulverulentus (ANSP 26343, Borneo)
Pseudaspis cana (ANSP 5149, South Africa)
Regina alleni (ANSP 18966, Florida, U.S.A.)
Regina grahami (ANSP 6035, Illinois, U.S.A.)
Rhabdophis subminiatus (ANSP 27073, Thailand)
Rhabdophis swinhonis (ANSP 27347, Taiwan)
Seminatrix pygaea (ANSP 25874, Florida, U.S.A.)
Storeria dekayi (ANSP 16625, Pennsylvania, U.S.A.)
Thamnophis sirtalis (ANSP 12415, Pennsylvania, U.S.A.)
Trachyboa boulengeri (ANSP 25073, Colombia)
Tretanorhinus nigroluteus (ANSP 10217, Panama)
Tetranorhinus variabilis (ANSP 5108, Cuba)
Tropidophis pardalis (ANSP 10282, locality unknown)
Tropidophis wrighti (ANSP 9886, locality unknown)
Typhlops acutus (ANSP 3301, locality unknown)
Virginia striatula (ANSP 10802, Texas, U.S.A.)
Virginia valeriae (ANSP 20605, Pennsylvania, U.S.A.)
Xenochrophis piscator (ANSP 26609, Assam)
Xenopeltis unicolor (ANSP 26399, Borneo)

TABLE 2

Observed characteristics of hypapophyses

Genus	Present precaudal vertebrae	Profile	Anterior keel	Distal tip: form, caudal projection	Ventral edge
Agkistrodon	all	narrow, deep; spine-like	to cotyle rim	pointed, to condyle tip; slightly thickened	
Alsophis	anterior	broad, low	strong, to cotyle rim	pointed, to condyle tip	
Amastridium	all	broad, deep	stout, to cotyle rim	pointed, to condyle tip	flattened, expanded laterally
Aspidura	all	broad, low	low, to cotyle rim	pointed, to condyle base	
Amphiesma	all	broad, deep	to cotyle rim	pointed, to condyle tip	flattened
Atretium	all	broad, deep	sharp, to cotyle rim	posterior edge condyle base	
Bitis	all	broad, low	strong, to cotyle rim	pointed, slightly caudal to condyle base	
Boaedon	all	moderately broad and deep	thin, to cotyle rim	flatly rounded, to condyle base	
Boiga	anterior	moderately broad and deep; caudal to heart reduced to low, stout keel	absent	sharply pointed, no projection	
Bothropthalmus	all	broad, deep	short	rounded, to condyle base	slightly thickened
Bungarus	all	broad, low	stout, to cotyle rim	pointed, to near condyle tip	
Chersydrus	all	narrow, deep; spine-like	low, to cotyle rim	blunt, to condyle tip	

TABLE 2 (continued)

Genus	Present precaudal vertebrae	Profile	Anterior keel	Distal tip: form, caudal projection	Ventral edge
Chrysopelea	all	stout, narrow and deep	strong, to cotyle rim	pointed, to condyle tip	
	anterior	narrow and deep; caudal to heart gradual reduction to low, stout keel	short	blunt, caudal to condyle tip; caudal to heart reduced to very short, free point	
Coluber	anterior	broad, deep; caudal to heart reduced to low keel	sharp, to cotyle rim	rounded, thickened, to condyle tip	
Crotalus	all	narrow, deep; spine-like	strong, to cotyle rim	rounded, to slightly caudal of condyle tip	
Cylindrophis	anterior	stout, moderately broad, deep; absent caudal to heart	low, stout, to cotyle rim	blunt, thickened, to condyle base	
Dendrelaphis	anterior	moderately broad and deep; caudal to heart reduced to very low keel	to cotyle rim	rounded, to condyle base	
Enhydris	all	narrow, deep	heavy, to cotyle rim	squarish, to slightly caudal condyle base	
Gerardia	all	stout, broad, deep	to cotyle rim	pointed, to condyle tip	
Helicops	anterior	broad, deep; caudal to heart reduced to strong, low keel	to cotyle rim	rounded, to condyle base; caudal to heart reduced to slight projection	

TABLE 2 (continued)

Genus	Present precaudal vertebrae	Profile	Anterior keel	Distal tip: form, caudal projection	Ventral edge
Hydraethiops	all	moderately broad, deep	to cotyle rim	pointed, to condyle tip	
Lamprophis	all	broad, deep	short	posterior edge vertical at condyle base	
Langaha	all	broad, moderately deep	thin, to cotyle rim	pointed, to level slightly caudal to condyle base	
Laticauda	all	broad, low	to cotyle rim	pointed, to condyle base	expanded, lanceolate
Leptotyphlops	absent				
Lycodon	anterior	broad, shallow; caudal to heart reduced to low keel	low, to cotyle rim	pointed, to slightly caudal of condyle base	
Lycognathophis	all	narrow, deep	to cotyle rim	pointed, to condyle tip	
Lycophidion	all	narrow, deep	absent	pointed, to condyle tip	
Macropisthodon	all	broad, deep	to cotyle rim	posterior edge vertical, distal projection slightly caudal to condyle base	
Macropophis	all	moderately broad, deep	strong, to cotyle rim	rounded, to condyle tip	
Mehelya	all	broad, deep		rounded, to condyle tip	

TABLE 2 (continued)

Genus	Present precaudal vertebrae	Profile	Anterior keel	Distal tip: form, caudal projection	Ventral edge
Micrurus	all	broad, moderately deep	strong, to cotyle rim	pointed. to slightly caudal of condyle tip	slightly thickened
Natriciteres	all	moderately broad and deep	strong, to cotyle rim	rounded, to slightly caudal of condyle tip	
Natrix	all	broad, low to deep	strong, to cotyle rim	roundly pointed, to condyle base or tip	flattened
Ninia	all	very broad, low	to cotyle rim	sharply pointed, to condyle tip	
Psammodynastes	all	broad, deep	to cotyle rim	pointed, thickened, to condyle tip	
Pseudaspis	anterior	broad, deep; caudal to heart, reduced to heavy, deep keel	strong, to cotyle rim	rounded, to condyle base	expanded, lanceolate on posterior vertebrae
Regina	all	broad, deep	stout, to cotyle rim	rounded, to slightly caudal of condyle tip	
Rhabdophis	all	broad, shallow; or narrow and moderately deep	stout, to cotyle rim	pointed or rounded, to condyle base or tip	flattened
Seminatrix	all	moderately broad, deep	stout, short of cotyle rim	rounded, to caudal of condyle tip	
Storeria	all	broad, low	to cotyle rim	pointed, to condyle base	thickened, flattened
Thamnophis	all	moderately broad, deep	thin, to cotyle rim	rounded, to condyle tip	

TABLE 2 (continued)

Genus	Present precaudal vertebrae	Profile	Anterior keel	Distal tip: form, caudal projection	Ventral edge
Trachyboa	all	moderately broad, deep	to cotyle rim	posterior edge vertical, at condyle base	
Tretanorhinus	anterior	broad, deep; or low and keel-like; caudal to heart reduced to low, strong keel or very low median ridge	absent	rounded, no projection; or pointed with slight projection	thin, or flattened and splayed distally
Tropidophis	all	broad, low, rounded both ends	absent	absent	
Typhlops	absent				
Virginia	all	broad, low	low, to cotyle rim	pointed, to condyle base or tip	flattened
Xenochrophis	all	moderately broad, deep	to cotyle rim	pointed, to condyle tip	
Xenopeltis	anterior	broad, low; thick; absent caudal to heart	strong, low to cotyle rim	pointed, to condyle base	flattened, thick

TABLE 3
Characteristics of the M. transversohypapophyseus

Genus	Development	Length of segment	Relation to Mcis
Agkistrodon	strong	8 v.	ventral
Alsophis	moderate; lost at heart level	5 v.	lateral
Amastridium	strong	3 v.	ventral
Aspidura	moderate	4 v.	ventral
Amphiesma	strong	4 v.	lateral
Atretium	moderate	4 v.	lateral
Bitis	strong	8 v.	ventral
Boaedon	moderate	4 v.	ventral
Boiga	moderate; lost at heart level	4 v.	lateral
Bothropthalmus	strong	4 v.	ventral
Bungarus	moderate	8 v.	lateral
Chersydrus	weak	4 v.	dorsal
Chrysopelea	strong; present entire body length or reduced caudally	4 v.	ventral
Coluber	moderate; lost at heart level	4 v.	lateral
Crotalus	strong	8 v.	ventral
Cylindrophis	absent		
Dendrelaphis	strong; lost at heart level	4 v.	ventral
Enhydris	weak	4 v.	lateral
Gerardia	moderate	5 v.	lateral
Helicops	weak; lost at heart level	4-5 v.	lateral
Hydraethiops	moderate	4 v.	ventral
Lamprophis	strong	4 v.	ventral
Langaha	strong	4 v.	ventral
Laticauda	weak	6 v.	dorsal
Leptotyphlops	absent		

Genus	Development	Length of segment	Relation to Mcis
Lycodon	weak; lost at heart level	3 v.	dorsal
Lycognathophis	strong	4 v.	ventral
Lycophidion	strong	4 v.	lateral
Macropisthodon	strong	4 v.	ventral
Macropophis	strong	5 v.	ventral
Mehelya	strong	4 v.	ventral
Micrurus	moderate	7 v.	lateral
Natriciteres	strong	4 v.	ventral
Natrix	moderate to strong	4 v.	lateral or ventral
Ninia	weak	4 v.	lateral
Psammodynastes	strong	4 v.	ventral
Pseudaspis	moderate; lost at heart level	4 v.	dorsal
Regina	strong	4 v.	ventral
Rhabdophis	moderate	4-5 v.	lateral
Seminatrix	moderate	4 v.	lateral
Storeria	strong	4 v.	lateral
Thamnophis	moderate	5 v.	lateral
Trachyboa	absent		
Tretanorhinus	weak; lost at heart level	5 v.	dorsal
Tropidophis	absent		
Typhlops	absent		
Virginia	weak	4 v.	dorsal
Xenochrophis	strong	5 v.	lateral
Xenopeltis	absent		