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FOSSIL SNAKES OF NORTH AMERICA

BY
CHARLES W. GILMORE

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INTRODUCTION

In 1868 Cope described *Palaeophis littoralis*, the first fossil snake named from North America. Since then 24 species pertaining to 13 genera have been described by various authorities, although Cope and Marsh were the principal contributors to our knowledge of the extinct Serpentes of this continent.

Such information as has accumulated concerning the extinct snakes of North America is the result of spasmodic and uncorrelated studies, a research that was made difficult by the extreme rarity and the usually fragmentary state of the available specimens. The scarcity of snake remains in the fossil record, aside from their small size, may perhaps be attributed to the fact that with comparatively few exceptions they are terrestrial in habit, and for that reason their skeletons were less apt to be preserved as fossils.

The present study was made possible through the co-operation of the author's colleagues who upon request, without exception, generously turned over their serpent materials for his use. Thus he was enabled to bring together in the United States National Museum practically all the ophidian specimens known from North America, consisting of all the original types, except *Coluber acuminatus* (Cope), *Ogmophis oregonensis* Cope, and *Palaeophis littoralis* Cope, which appear to be lost, as well as all unstudied material. Of the latter, however, it was disappointing to find so few specimens among the accumulations of many years of explorations.

The very fragmentary character of the original types, consisting at best of a few vertebrae, makes their study very specialized and difficult. The study of extinct serpents is rendered still more arduous because of the dearth of adequate description of the osteological anatomy of the living forms, aside from the crania, which are seldom found in the fossil state. The characterization of genera and species in modern Serpentes has, as in the Sauria, been largely based on the arrangement, and number, of the head and body scales, together with other features of the soft anatomy, all characters which are useless for the purposes of the paleontologist.

However, in a few instances, through the discovery of better and more fully preserved specimens the author has been enabled to establish certain described forms and to demonstrate their relationships to living members of the suborder.

ACKNOWLEDGMENTS

Special attention has been given to the assembling and recording in this one article of all available information and facts relating to the extinct Serpentes of North America.

The author wishes to express his appreciation to the following individuals and institutions with which they are connected for their generous response to his request for the loan of specimens: Dr. R. S. Lull, Director, Peabody Museum of Natural History; Dr. M. R. Thorpe, of the Peabody Museum of Natural History; Dr. Barnum Brown, of the American Museum of Natural History; Dr. A. Avinoff, Director, Carnegie Museum; Mr. C. M. Sternberg, of the National Museum of Canada; Dr. E. Troxell, of Trinity College; Dr. E. C. Case, of the University of Michigan; Mr. Edgar S. Weinberg, of New York; Dr. J. M. Sullivan, of Millsap College; Mr. Herman Gunter, State Geologist of Florida; Mr. C. J. Hesse, of the University of California; Dr. Thomas Barbour, Director, Museum of Comparative Zoology; and Mr. Thomas E. White, of the Museum of Comparative Zoology.

Thanks are due Dr. C. E. Resser for the photographs of *Boavus idelmani* and to Mr. Charles East for the preparation and loan of recent ophidian specimens from his private collection. To Miss Doris M. Cochran, the author is under special obligation for the loan of specimens and assistance on numerous occasions.

The drawings are by Mr. Sydney Prentice.

Great obligation is due the Geological Society of America for the financial support which made this research possible.

GEOLOGICAL DISTRIBUTION OF SERPENTES IN NORTH AMERICA

The oldest known ophidian is the *Pachyophis woodwardi* described by Nopcsa (1923, p. 118–151, pls. 7 and 8) from the Neocomian (Lower Cretaceous) of Hercegovina. It seems to have comparatively rigid jaws, a small zygosphene, and ribs not completely adapted for the mode of progression characterizing the typical snakes. In North America the oldest ophidian specimen known at present is *Coniophis precedens* Marsh from the Lance, Upper Cretaceous of Wyoming. Known only from a single thoracic vertebra, it does not display any outstanding primitive characteristics but appears to have already developed most of those features characteristic of the typical ophidian vertebrae. More complete materials, however, would doubtless show characteristics in harmony with its early geological occurrence.

From the Upper Cretaceous up to the present, ophidian remains are found in all the main geological subdivisions.

In the Tertiary (Paleocene) the first undoubted ophidian is the genus *Helagras* found in the Puerco formation. Its family relationships are unknown at this time. Snakes are present in the Wasatch, but the known remains are too scanty for closer identification. No Serpentes is known from the Wind River. In the eastern region of the United States the family Palaeophidae makes its first appearance in the Jackson formation of Alabama (*Pterosphenus*) and in the Eocene of New Jersey and Virginia (*Palaeophis*). A single specimen, the type of a new genus of snake (*Cheilophis huerfanoensis*), has been found in the Huerfano of Colorado. The Green River and Bridger, Middle Eocene, mark the first appearance of the Boidae on this continent, but associated genera cannot be certainly evaluated as to family.

With the advent of the Oligocene three new genera are introduced—*Ogmophis, Calamagras,* and *Neurodromicus.* The first two are tentatively regarded as pertaining to the Boidae. The genus *Ogmophis* is of unique interest due to the fact that one species, *O. compactus,* occurs in Canada, somewhat outside the climatic zone of the present range of this family.

Venomous snakes first appear in the Upper Miocene. Viperidae were found by Lartet in the Miocene of France, and the Crotalidae, according to Cope, were found in the Loup Fork beds of Kansas. The earliest occurrence of *Crotalus* as indicated in the assembled North American materials is a specimen from the Lower Pliocene of Nebraska. It is also in the

Lower Pliocene that the first Colubrid snake (*Palaeoelaphe*) is found. Therefore, the paleontological evidence is that the Peropoda appeared earlier than the Solenoglypha, which is in accord with modern systematic

TABLE 1.—*Geological distribution of Serpentes in North America*

Pleistocene	*Coluber acuminatus, Thamnophis* sp., *Crotalus adamanteus, Crotalus* sp., *Pituophis* sp., *Natrix?* sp., *Farancia?* sp., *Drymarchon* cf. *corais couperi*				
Pliocene	Upper	Hagerman Lake Beds	*Thamnophis* sp. Colubrid (Curtiss Ranch)		
	Lower	Republican River Beds	*Crotalus* sp., *Palaeoelaphe kansensis*		
Miocene	Upper Lower	Flint Creek	*Ogmophis arenarum*		
Oligocene	Upper	John Day	*Ogmophis oregonensis*		
	Middle	Cedar Creek	*Calamagras murivorus, C. angulatus, C. talpivorus, Neurodromicus dorsalis*		
	Lower	Cypress Hills	*Ogmophis compactus*		
Eocene	Upper	Uinta			
	Middle	Bridger	*B. occidentalis, B. brevis* *Lithophis sargenti*	Eastern region	
		Huerfano	*Cheilophis huerfanoensis*	*Palaeophis grandis* *P. halidanus* *P. littoralis*	New Jersey
		Green River	*Boavus idelmani*	*P. virginianus*	Virginia
		Wind River		*Pterosphenus schucherti*	Alabama
	Lower	Wasatch	*Ophidian*		
Paleocene		Torrejon	*Helagras prisciformis*		
		Puerco	*Helagras prisciformis*		
Cretaceous		Lance	*Coniophis precidens*		

classification of the Ophidia. With the exception of *Bothrodon* from the silt of Paraguay, all known Pleistocene remains are identifiable with existing genera. The following genera have now been recognized—*Coluber, Pituophis, Drymarchon, Thamnophis, Natrix? Farancia?*, and *Crotalus.* The geological distribution of the Serpentes in North America is graphically shown in Table 1.

SERPENTES SKELETON

The skeleton of recent serpents, aside from the skull, has been little utilized in their systematic study. There is so much uniformity in the character of the skeleton that, although peculiarities characterize the principal divisions of the Serpentes, apparently no definite groups can be traced in the great number of harmless snakes on skeletal characters alone. A dearth of literature on the osteology of living snakes renders it an exceedingly difficult group with which to contrast fossil specimens. Since vertebrae are usually the only remains available to the paleontologist it is with these structures that he is most concerned. Their study is a specialized one with a descriptive technique and terminology differing somewhat from other branches of paleontology, and for that reason an outline of the nomenclature used is introduced here.

In this connection, free use has been made of the excellent outline compiled by Simpson (1933, p. 2–4) which, with a few emendations, adequately covers the subject. The skull characters have been drawn from many sources, and no claim is made to the introduction of original matter. The limited number of recent skulls at the author's disposal has permitted only a spasmodic checking of characters, but an attempt has been made to harmonize differences of opinion as to the homologies of certain elements of the cranium so as to bring about a uniform and workable nomenclature.

The limited number of recent skeletons available for this study has made it impossible to form definite conclusions as to the taxonomic limitations of vertebrae by themselves. It is quite certainly determined, however, that in many groups species cannot be recognized on vertebrae alone. In some instances it is possible to recognize genera on vertebral characters, but in a family like the Colubridae, there are decided limitations.

SKULL: The bones of the snake skull are dense, ivory-like, and united by smooth sutures. In all ophidian skulls the frontals are distinct and the parietals are always fused. According to Cope, the nasals, except in *Charina*, are always distinct. The brain cavity is elongate, and its lateral walls to mid-length are formed by descending processes of the parietal and frontal.

The cranium of serpents differs from those of lizards in the constant absence of both temporal arches and epipterygoids and in the strong development of the ectopterygoids which join the maxillary and palatopterygoid arches. There is no parietal foramen. There are movable connections not only between the bones last mentioned but also between

the squamosal and occipital region and between the rami of the lower jaw.

The premaxillary bone is reduced and constantly edentulous except in some of the Boidae, Ilysiidae, and *Xenopeltis*. The maxillary is loosely

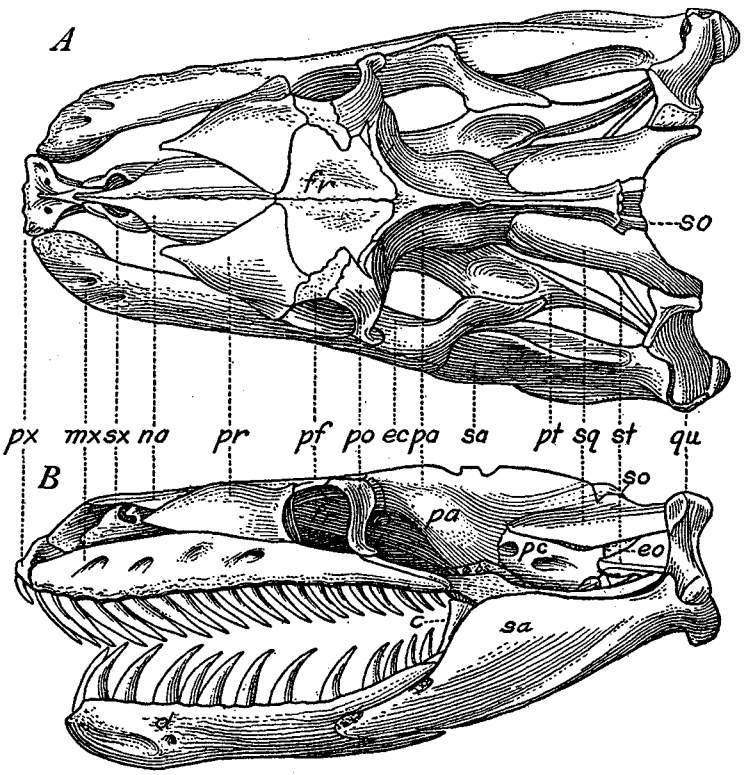


FIGURE 1.—*Skull of Python*

A, superior view; *B*, lateral view; *bs*, basisphenoid; *c*, coronoid; *d*, dentary; *ec*, ectopterygoid; *eo*, exoccipital; *fr*, frontal; mx, maxillary; *na*, nasal; *pa*, parietal; *pc*, proötics; *pf*, postfrontal; *po*, postorbital; *pr*, prefrontal; *pt*, pterygoid; *px*, premaxillary; *qu*, quadrate; *sa*, surangular; *so*, supraoccipital; *sq*, squamosal; *st*, stapes; *sx*, septomaxillae. Natural size. After Williston.

attached, having a close articulation only with the prefrontal, except in the Epanodonata when it is fixed firmly, as in lizards, to the premaxillary and vomers. This bone is usually solid but in the Crotalidae it is deeply excavated on the posterior external side (Fig. 29). It is rarely edentulous.

There are no lachrymal, jugal, or quadratojugal bones in the skull of serpents. The prefrontals are articulated above with the frontals, and in some genera with the nasals. Postfrontals are present, but are small and often lost in the preparation of recent specimens. In the Pythonidae there is a supraorbital element. According to Williston (1925, p. 72), the squamosal bone, of most authors, is absent in the serpent skull, and the

tabulare functions in its stead to furnish the articulation for the quadrate. Boulenger designates this element as supratemporal. In the present work, following Owen, the term squamosal will be used. The quadrate bone presents some diversities of form. According to Cope, in *Typhlops* it is short and flat, with a free angular process anteriorly. In *Leptotyphlops* it is long and slender and without anterior process. In the *Tortricina* it is very short, and has in the Ilysiidae a cylindric shaft. In *Asinea* it is generally flat and expanded at the proximal end and has no angular process of the shaft, but in *Eryx* it is not expanded and has a triangular section. In *Xenopeltis* it is short, with a short posterior projection, proximally as in lizards. In the boas and pythons there is a short anterior process on the inner side with which the columella auris articulates.

The supraoccipital never participates in the boundary of the foramen magnum, being excluded above by the exoccipitals. The exoccipital and opisthotic are always fused. The vomers are constantly toothless.

The palatine bones differ considerably in the principal forms. The characters are seen in the presence or absence of external (maxillary) or internal (vomerine) processes. Both may be present, one may be present, or both absent. The pterygoids are elongate and extend to the quadrate except in the Scolecophidae, where they are short. There is an imperfectly developed interorbital septum, the ventral part of which is formed by the presphenoid.

Lower Jaw: In the lower jaw the dentary is fully articulated with the posterior elements which are closely fused. According to Williston (1925, p. 72), the coronoid is prearticular and the articular is in part surangular. In the present paper the small bone that lies upon the surangular and abuts the upper posterior end of the dentary will be called the coronoid, as its relationships to the other elements is precisely that of the coronoid in other reptilian jaws, where the prearticular is present. The author regards the prearticular bone as being absent or fused in the ophidian jaw. In the light of paleontological evidence Williston is probably correct in calling the upper part of the articular of authors the surangular, and that determination is accepted as being the correct homology of this portion of the mandible. The angular is small and far anterior to the angle of the jaw which is formed by the articular. The splenial is always present and, except in *Typhlops*, is confined to the inside of the jaw. It usually ends far short of the median symphysis. In many snakes Meckel's groove is open, but in others it is closed by the splenial. According to Cope (1900, p. 691), it is open in the Crotalidae, Viperidae, Hydrophidae, Ilysiidae, Boidae, Pythonidae, Charinidae, and Xenopeltidae. It is also open in many genera of Colubridae, but closed in a lesser number of genera of this same family. In the Typhlopidae the mandible is toothless.

DENTITION: The dentition consists of slender, recurved acrodont teeth usually present on the maxillary, premaxillary, pterygoids, palatines, and dentary bones. Occasionally they are lacking on the palatines (Uropeltidae), and often on the rudimentary premaxilla. In certain genera (*Opisthoglypha*) there is a groove on the anterior or external face (*Ogmius*) of the posterior one or two teeth of the maxillary bone. In *Ogmodon* all the maxillary teeth are grooved. In the venomous snakes, however, it is the anterior maxillary teeth which have undergone modification. These teeth are traversed by either a canal or groove ending in a slit-like opening near the point of the tooth for the transmission of the venom. In *Crotalus*, this external slot is on the front of the tooth slightly above the point.

Some of the nonpoisonous snakes have grooved teeth.

The teeth of snakes are adapted for piercing, tearing, and holding. As in other reptiles, they are replaced by others which are developed close to the bases of the old teeth.

VERTEBRAE: According to Woodward (1932, p. 341), the complete vertebral column in some serpents exceeds 500 in number, with as few as 138 in *Cerastes*. The vertebrae of snakes are always procoelous and the neural arches always provided with zygosphene and zygantrum. Many of the vertebrae, especially in the anterior thoracic region, are provided with simple hypapophyses. In some, as the Crotalidae, these processes persist throughout the entire precaudal region. In all the Madagascar Colubrinae the hypapophysis is developed throughout the vertebral column, thus differing from the American genera *Liophis*, *Heterodon*, and *Dromicus*. The neural arches are always thoroughly co-ossified with their centra. Transverse processes (diapophyses) are short and tumid.

The vertebrae of ophidians can be distinguished from those of lizards, which they most closely resemble, by the presence in the lizard vertebrae of small diapophyses with a simple, convex sessile tubercle, shallow zygantra when present, and chevrons on the caudal vertebrae.

There is a great difference of usage among authorities in the grouping of these divisions of the backbone, as well as a lack of uniformity in the names used. Except in rare instances, this fact need not deeply concern the paleontologist, since most of his materials consist of scattered vertebrae.

Rochebrune divides the vertebral column into five regions which he calls cervical, thoracic, pelvic, sacral, and coccygeal. Janensch uses only three divisions, cervical, presacral, and postsacral. Some authorities recognize only two divisions, caudal and precaudal. For the purposes of the paleontologist, the following grouping proposed by Simpson is adequate:

1. Cervical. Usually two in number. Without ribs and modified in form.
2. Thoracic. By far the greater number. With movable ribs.

A. Anterior thoracic. Usually fewer than posterior thoracic, with long hypapophyses.
B. Posterior thoracic. With hypapophyses short or absent.

3. Caudal. Always fewer than thoracic and usually only a fourth or a fifth as many. Without movable ribs.
A. Anterior caudal. Never more than ten in number. With bifid diapophyses and no lymphapophyses.
B. Much more numerous than the anterior caudals. With single diapophyses and strong lymphapophyses.

Ophidian vertebrae are complex structures consisting of no less than 12 articular surfaces and numerous processes and muscular attachments.

The principal terms used in describing them, together with their meaning, have been extracted from Simpson with a few additions and emendations and are as follows:

ALIFORM PROCESSES—wing-like posterior projections, one on each side of the neural arch.

CENTRUM—actual body of the vertebra, below the neural canal and between the condyle and glenoid cavity. In snakes, the centrum is usually much outweighed in bulk by the various processes arising from it.

CONDYLE—approximately hemispherical posterior articular process of the centrum. Often called ball.

DIAPOPHYSES—paired processes on the two sides of the vertebra, below the prezygapophyses. On the thoracic vertebrae they bear ribs and on the caudals are variously produced. One division, where these processes are bifid, is sometimes called the parapophysis. Although "diapophysis" in so broad a sense undoubtedly includes various non-homologous structures, the homologies are so uncertain that it is convenient to use the term descriptively to include all lateral processes on this part of the vertebra, its exact application being sufficiently clear from the context. Some authorities use the synonymous term transverse process.

EPAPOPHYSIS—a median ridge on the floor of the neural canal.

GLENOID CAVITY—anterior concavity on the centrum, for the reception of the condyle of the preceding vertebra. Often called cup.

HYPAPOPHYSIS—a median ventral process, sometimes double (in tandem) but very seldom distinctly paired (transversely).

LYMPHAPOPHYSES—laterally paired ventral processes (occurring only in the posterior caudal region).

NEURAL ARCH—two plates arising from the top of the centrum, surrounding the neural canal, and meeting in the mid-line above.

NEURAL CANAL—canal for the spinal cord.

NEURAL SPINE—median dorsal projection above the neural arch.

POSTZYGAPOPHYSES—posterior processes similar to the prezygapophyses bearing articular facets facing downward (and generally somewhat outward) for articulation with the prezygapophyses of the following vertebra.

PREZYGAPOPHYSES—paired anterior processes arising near the junction of the neural arch and centrum on each side, bearing articular facets facing upward (and generally somewhat inward).

ZYGANTRUM—mortise-like depression on the posterior part of the neural arch above the neural canal, articulating with the zygosphene of the following vertebra.

ZYGOSPHENE—somewhat wedge-shaped median anterior process from the union of the neural arch above the neural canal, bearing two articular processes facing outward and downward.

Most snake vertebrae, when viewed from the side, present three main surfaces between the hypapophyses and neural spine. The most ventral of these is usually concave, generally bounded on the midline by the

hypapophysis or median keel, and usually ending above at a rounded ridge running posteriorly from the diapophysis toward the condylar end. Above this ridge, which may be either absent or greatly reduced in length, is a larger surface that looks outward, backward, and somewhat downward. It is bounded above by the more or less horizontal ridge which usually joins the pre- and postzygapophyses. Above this ridge is a still larger surface on the neural arch which faces upward, outward, and forward. If present, it is produced posteriorly into the aliform process and anteriorly extends into the base of the neural spine.

As in *Coniophis*, the neural spine may be entirely missing but it is usually present as a thin rectangular plate of bone with slight dilation of its upper truncated extremity. The height of spine varies much in the different genera. This process may be thickened with tubercle-like extremities as in *Helagras*, or with thin and plate-like extremities as in *Boavus*.

The vertebrae of snakes are strongly articulated, there being five articulations with each adjacent vertebra, a large cup and ball joint, and four inclined planes that form the zygapophysial, zygantral, and zygosphenal articulations. The zygosphene almost completely fills the zygantrum, leaving only a slight space at its deepest middle part.

Although the vertebrae are strongly and closely interlocked by these various articulations, lateral motion is relatively free. There is some possibility of arching the back but little or no possibility of making it concave ventrally.

RIBS: Ribs are almost always present in the trunk region beginning with the third vertebra. Freely articulated by a single head, they assist in propelling the body. The ribs are long, curved, and frequently hollow. They are with and without *tuber costae*; this process, where present, is on the side of the proximal end.

A list of recent snakes, including representatives of the various families and giving the figures of the three categories of vertebrae and their total number, has been compiled from Janensch and de Rochebrune as follows.

	Cervical	Thoracic	Caudal	Total
TYPHLOPIDAE:				
Typhlops lumbricalis Dumeril	2	176	10	188
BOIDAE:				
Python sebae Gmelin	2	306	62	370
Python molurus Gray	2	372	61	435
Liasis amethystinus Gray	2	330	92	424
Constrictor constrictor (Linnaeus)	2	256	44	302
XENOPELTIDAE:				
Xenopeltis unicolor Schlegel	2	188	20	210
COLUBRIDAE:				
(a) Aglypha				
Natrix natrix Schlegel	2	211	45	258
Elaphe aesculapii Daudin	2	226	68	296
Zamensis viridi flavus Wagler	2	239	73	314
Dendrophis picta Boie	2	196	87	285
Acrochordus javanicus Hornstedt	2	191	55	248

	Cervical	Thoracic	Caudal	Total
(b) Opisthoglypha				
Passerita prasina Boie	2	237	176	415
Homalopsis buccatus Fitzinger	2	171	58	231
Dipsas annulata Linnaeus	2	182	71	255
(c) Proteroglypha				
Platurus fasciatus Daudin	2	147	42	191
Pelamis bicolor Daudin	2	158	32	192
Enhydris hardwickii Gray	2	130	32	164
VIPERIDAE:				
Pelias berus Merrem	2	150	51	203
Cerastes aegyptiacus Schlegel	2	120	16	138
Crotalus horridus Linnaeus	2	184	24	210

GENERA AND SPECIES

A complete alphabetical list of all North American serpent genera and species described up to the close of 1934 has been compiled. A reference is cited for the original description of each, its present disposition in the synonymy, the present location of the type specimen, and its catalogue number.

Aphelophis COPE, Synop. new Vert. Tert. Colo. (October 1873) p. 16, Washington. = *Calamagras talpivorus* COPE, *ibid.*, p. 16. Type no. 1598, A. M. N. H. (= *Calamagras talpivorus*).

Boavus MARSH, Am. Jour. Sci., 3d ser., vol. 1 (1871) p. 372. = *agilis* MARSH, *ibid.*, p. 373, 374. Cotype nos. 467, 2765, 2766, P. M. N. H. (= *Boavus occidentalis*).
brevis MARSH, *ibid.*, p. 374, 375. Type no. 468, P. M. N. H.
occidentalis MARSH, *ibid.*, p. 373. Type no. 511, P. M. N. H.

Calamagras COPE, Synop. Vert. Tert. Colo. (October 1873) p. 15. Washington.
angulatus COPE, *ibid.*, p. 16. Type no. 1654, A. M. N. H.
murivorus COPE, *ibid.*, p. 15. Type no. 1603, A. M. N. H.
truxalis COPE, *ibid.*, p. 15, 16. Type no. 1657, A. M. N. H. (= *C. murivorus*).

Coluber (*Zamenis*) *acuminatus* COPE, Philadelphia Acad. Nat. Sci., Jour., 2d ser. (1899) vol. 11, p. 197. Type lost.

Coniophis MARSH, Am. Jour. Sci., 3d ser., vol. 43 (1892) p. 450.
precedens MARSH, *ibid.*, p. 450. Type no. 2134, U. S. N. M.

Dinophis MARSH, Am. Jour. Sci., 2d ser., vol. 48 (1869) p. 397–400. (= *Palaeophis*).
grandis, *ibid.*, p. 397–400. Type no. 2762, P. M. N. H. (= *Palaeophis grandis*).

Helagras COPE, Am. Philos. Soc., Pr., vol. 20 (1883) p. 545.
prisciformis COPE, *ibid.*, p. 545. Type no. 1628, A. M. N. H.

Lestophis MARSH, Am. Jour. Sci., 3d ser., vol. 29 (1885) p. 169.

Limnophis MARSH, Am. Jour. Sci., 3d ser., vol. 1 (1871) p. 328 (= *Lestophis*).
crassus MARSH, *ibid.*, p. 328. Type no. 531, P. M. N. H. (= *Lestophis crassus*) = Sauria

Lithophis MARSH, Am. Jour. Sci., 3d ser., vol. 1 (1871) p. 325.
sargenti MARSH, *ibid.*, p. 325. Type no. 2719, P. M. N. H.

Neurodromicus COPE, Synop. new Vert. Tert. Colo. (October 1873) p. 15. Washington.
dorsalis COPE, *ibid.*, p. 15. Type no. 1599, A. M. N. H.

Ogmophis COPE, U. S. Geol. Surv. Terr., 3d Rept., vol. 3 (1884) p. 782.
angulatus COPE, *ibid.*, p. 783, 784, pl. 58-a, fig. 12. (= *Calamagras angulatus*).
arenarum DOUGLASS, Ann. Carnegie Mus., vol. 2 (1903) p. 153, 171. Type no. 744, Carnegie Mus.
compactus LAMBE, Contrib. Canad. Paleont., vol. 4, pt. 4 (1908) p. 9, 20; pl. 1, figs. 26–30. Type no. 6237, Nat. Mus. Canada.
oregonensis COPE, Rept. U. S. Geol. Surv. Terr., vol. 3 (1884) p. 783, pl. 58-a, figs. 9–11. Type temporarily lost. A. M. N. H.

Palaeboa SCHMIDT, Copeia, issue 163 (1927) p. 58. (=*Lestophis*).

Palaeophis OWEN, Geol. Soc. London, Tr., 2d ser., vol. 6 (1839) p. 209, pl. 22.
grandis MARSH, Am. Jour. Sci., 2d ser., vol. 48 (1869) p. 397–400. Type no. 2762, P. M. N. H.
halidanus COPE, Philadelphia Acad. Nat. Sci., Pr. (1868) p. 234. Type no. 2763, P. M. N. H.
littoralis COPE, *ibid.*, p. 147. Type no. 2392, A. M. N. H.
virginianus LYNN, Johns Hopkins Univ., Geol. Stud. no. 11 (1934) p. 45–49, pl. 17. Cotype nos. 13640, 13641, U. S. N. M.

Protagras COPE, Am. Philos. Soc., Pr., vol. 12 (1872) p. 471. (= *Boavus*).
lacustris COPE, *ibid.*, p. 471. Type no. 4126, U. S. N. M. (= *Boavus occidentalis*).

Pterosphenus LUCAS, U. S. N. M., Pr., vol. 21 (1899) p. 637, 638, pl. 45, 46.
schucherti, LUCAS, *ibid.*, p. 637, 638. Type no. 4047, U. S. N. M.

As shown in the preceding list five genera are regarded as synonyms, as follows:

Aphelophis = *Calamagras*
Dinophis = *Palaeophis*
Limnophis = *Lestophis*
Palaeboa = *Lestophis*
Protagras = *Boavus*

The following species are regarded as synonyms: *Boavus agilis* = *B. occidentalis; Calamagras truxalis* = *C. murivorus; Protagras lacustris* = *Boavus occidentalis.*

After revision of the described extinct Serpentes and the addition of two new genera and three new species herein described, it is found that 18 genera and 24 species are now recognized as constituting the ophidian fauna of North America. Fragmentary remains found in the various collections clearly indicate that this list will be much increased by continued explorations.

LIST OF FAMILY ASSIGNMENTS OF GENERA AND SPECIES

Due to meager materials many of these are tentative.

Family Boidae
- *Boavus occidentalis* Marsh
  - *brevis* Marsh
  - *idelmani* Gilmore
- *Ogmophis oregonensis* Cope
  - *arenarum* Douglass
  - *compactus* Lambe
- *Calamagras murivorus* Cope
  - *angulatus* Cope
  - *talpivorus* (Cope)

Family Palaeophidae
- *Palaeophis grandis* (Marsh)
  - *halidanus* Cope
  - *littoralis* Cope
  - *virginianus* Lynn
- *Pterosphenus schucherti* Lucas

Family Colubridae
- *Coluber acuminatus* (Cope)
- *Palaeoelaphe kansensis* Gilmore
- *Drymarchon* cf. *corais couperi* (Holbrook)
- *Pituophis* sp.
- *Thamnophis* sp.
- *Farancia* sp.
- *Natrix* sp.

Family Crotalidae
- *Crotalus adamanteus* Beauvois
- *Crotalus* sp.
- *Neurodromicus dorsalis* Cope

Family Unknown
- *Coniophis precedens* Marsh
- *Lithophis sargenti* Marsh
- *Helagras prisciformis* Cope
- *Cheilophis huerfanoensis* Gilmore

SYSTEMATIC DESCRIPTION OF GENERA AND SPECIES

GENERAL STATEMENT

In the pages to follow all the genera and species of extinct North American Serpentes are discussed. The original descriptions, being comparatively short, are quoted in their entirety so that all information leading up to the designation and assignment of the species is available to future students without the necessity of searching the literature for this preliminary information. All the available type specimens have been illustrated, several for the first time. The complete bibliography of all species is given, as are the present location of the type specimen and its catalogue number, a list of the parts constituting the type, and the type locality and geological horizon, with, if known, the name of the collector and date of collection.

While the distinctive characters of genera and species rest primarily on the original types, every opportunity has been taken to elucidate these characters further by the description of such additional materials as has come to hand. Care has been exercised to distinguish clearly between this material and the original types, and all specimens are definitely located by their catalogue numbers and a reference to the museum or organization to which they belong.

Class REPTILIA

Subclass DIAPSIDA

Order SQUAMATA

Squamata, OPPEL, Ordn. Rept. (1811) p. 14.

Body elongate, covered with corneous or, more rarely, dermal scales or scutes. Quadrate movably attached to the skull, the lower temporal arcade always and upper temporal arcade frequently wanting. Palatal vacuities large, pterygoids not in contact with vomer; external nares separated; teeth acrodont, subthecodont, or pleurodont. Vertebrae well ossified, usually procoelous, rarely amphicoelous; sacral vertebrae not more than two in number; postcervical intercentra wanting; abdominal ribs or parasternum often present; dorsal ribs single headed. Limbs adapted for ambulation or natation, absent in nearly all ophidians and a few Sauria.

The two suborders Sauria and Serpentes are classed under the Squamata.

Suborder SERPENTES

LINNAEUS, Syst. Nat., ed. 10, vol. 1 (1758) p. 214.

Temporal arches of skull absent; columella absent. Quadrate bone articulated to the skull; brain capsule entirely osseous; parietal impaired and without pineal

foramen the sides extended downward and fused with the prootic, alisphenoid, and orbitosphenoid; rami of the mandible united by ligament. Vertebrae procoelous, with zygosphene-zygantrum articulation, and the anterior centra with strong simple hypapophyses.

Family BOIDAE

This family, consisting of about 20 genera, has a wide distribution ranging through practically all the tropical and subtropical parts of the world. The great number of all described fossil serpents has been referred to the Boidae, but it is quite evident that the present list will be much curtailed by the discovery of more adequate specimens.

The more important skeletal features characterizing this family are as follows:

Both jaws having teeth, simple and nearly equal; pterygoid reaching the quadrate; ectopterygoid present; coronoid present; prefrontal strongly in contact with the nasal; squamosal present, and not intercalated in the cranial wall. Vertebrae seldom show any marked compression or aberrant development of processes. Vestigial hind limbs and pelvis.

Some classifications separate the boas, pythons, and their allies into two or more families, but there is a difference of opinion as to the validity of this procedure. Since these divisions cannot be recognized in the materials available to paleontologists, the term Boidae will be used here in its broad sense. The boids are a relatively primitive group. Their known history as fossils extends back to the Eocene and also covers the world. In Canada and Patagonia they occur considerably outside the limits of the climatic zones in which they are now found.

Simpson (1933, p. 5) writes:

"In dealing with fossils, there has been a strong tendency to consider those from the western hemisphere as boids and from the eastern as pythonids, but even if these groups are valid the distributional anomalies of recent forms prove that at one time or another both have spread widely over both hemispheres."

The term Boidae as used paleontologically is much broader and more inclusive than as used by modern herpetologists.

The recent as well as the fossil forms range from about 2 to 30 or more feet in length. It seems quite probable that none of the extinct forms much exceeded the greatest size reached by modern pythons and anacondas. *Madtsoia*, recently described by Simpson from South America, is one of the largest and probably the most satisfactorily known form. *Boavus* from the Bridger and Green River Eocene of Wyoming is now the best-known North American boid. Tentatively the American genera *Ogmophis* and *Calamagras* are retained in this family. The genera from Europe are *Paleryx*, *Palaeopython*, *Scytalophis*, *Scaphophis*, *Botrophis*; from Sardinia, *Heteropython*; from Asia, *Python*; from Burma, *Daunophis*; from Australia, *Python*; from Africa, *Gigantophis*; from England, *Paleryx*.

Genus *Boavus* Marsh

Boavus MARSH, Am. Jour. Sci., 3d ser., vol. 1, May (1871) p. 323.
Protagras COPE, Am. Philos. Soc., Pr., vol. 12 (1872) p. 471.

GENOTYPE: *Boavus occidentalis* Marsh.

The genus *Boavus* was founded on vertebral characters alone, but owing to the scantiness of the type materials no attempt was ever made to define it. Through the discovery in recent years of better preserved specimens a diagnosis of the important characters is now made possible, and *Boavus* becomes the best known of all North American fossil serpents.

In the diagnosis given below the skull characters have been derived almost entirely from the type of *Boavus idelmani*, and the vertebral characters from the type of *B. occidentalis* and referred specimens.

DIAGNOSIS: Skull; thin saggital crest extending about half the length of parietal bones; frontals rectangular, three times as long as greatest width. Prefrontal large and principal contact apparently with the frontals. Postorbital bones appear to be present. Quadrate above articular end triangular in outline. Ectopterygoid seems to be present. Pterygoids reaching quadrate, with a longitudinal row of minute teeth. Teeth extending full length of maxillary and dentary bones. Teeth largest in front decreasing posteriorly. Coronoid appears to be present. Inner vertical plate of posterior half of ramus highest.

VERTEBRAE: Centrum of vertebrae relatively short and stout. Condyle moderately oblique. Anterior thoracic vertebrae with well-developed compressed hypapophyses; posterior thoracic vertebrae with a sharp longitudinal hypapophysial ridge or haemal carina. This carina begins at the edge of the cup and ends just before reaching the ball in an obtuse projection. Neural arch elevated and massive. Zygosphene wider than cup, slightly convex above, deep, and without median tubercle. Neural spine compressed, plate-like, with truncated extremity, front border receding from below backward. Diapophyses heavy, auriform, and projecting below the inferior margin of the centrum. Pre- and postzygapophyses subtriangular in outline moderately large. Lateral emargination between zygapophyses of moderate depth. Neural canal with median epapophysis and sharp lateral ridges, giving it a trifoliate outline.

The family affinities, as indicated by the name *Boavus*, were originally considered related to the modern *Boas*, a viewpoint which appears to be substantiated by this study of more complete specimens, and it is here referred to the family Boidae, as an isolated but very distinct genus.

The cranial characters that appear especially significant as indicating böid relationships are the moderately high, but thin saggital crest, the presence of ectopterygoid and coronoid bones, and pterygoid reaching the quadrate; teeth largest in front and decreasing posteriorly. The inner vertical plate of the posterior half of the ramus shows definite relationship with the *Boas* in distinction to the *Python* in which the opposite condition obtains. The presence of a massive zygosphene and the absence of aberrant processes on the vertebrae gives additional support to its affinities being in the family Boidae.

In contrasting the vertebrae with other described forms they appear to approach nearest those of *Palaeopython* from the Phosphorites of Quercy. The slender spine, more circular cup, greater inclination of the

condyle, and other characters in *Palaeopython*, exclude it from generic relationship with *Boavus*.

The supposed fossil böids from the Eocene and Oligocene of North America, *Ogmophis* and *Calamagras*, may be distinguished at once from *Boavus* by the short stout form of their spines and by their thinner zygosphenes. *Protagras*, also from the Eocene, is a synonym of *Boavus*. Insofar as it is possible to contrast *Boavus* with the so-called böids of Europe, there is no evidence to indicate any close affinity between them.

Cope (1872, p. 471) briefly described the new genus and species *Protagras lacustris*, basing his description on a fragmentary specimen found in the Bridger formation along Cottonwood Creek, Bridger Basin, Uinta County, Wyoming. The type materials, No. 4126 U. S. N. M., as now preserved in the paleontological collections of the United States National Museum, consist of the zygosphene, illustrated by Cope (1884, pl. 23, fig. 18) and the anterior half of a centrum, presumably a portion of the vertebra, illustrated in Figure 17 of the same publication. The other parts of this vertebra have been lost.

ORIGINAL DESCRIPTION: A serpent of about the size of the existing "Pine Snake" (*Pituophis melanoleucus*), and allied to the water snakes of *Tropidonotus* and allied genera.

"A vertebra before me has the longitudinal hypapophysial groove [keel] of that group, which terminates in a very obtuse point. The ball looks extensively upwards. The upper articular extremity of the parapophysis is short and obtuse, and the inferior equally so, and directed shortly downwards. The articular face being continuous with each other. It sends an obtuse keel backwards, which terminates in front of the ball. The angle connecting the diapophysis and zygapophyses is strong, while the former was narrow; in the specimens it is broken.

Measurements	m	m[1]
"Length of centrum below	0.009	.0090
Depth to base of neural spine, in front	.011	.0119
Width cup	.0054	.0054
Depth cup	.0045	.0043
Expanse parapophyses above	.012	
" " below	.008	

"From the Badlands of Cottonwood Creek, Wyoming."

In 1884 Cope pointed out that *Protagras* is distinguished from *Boavus* by two important differences,

"One is that in *Boavus* the diapophyses are said to be "convex throughout," while here they present a median constriction, giving a figure eight outline. The other is, that the cup and ball are "more nearly vertical" than in Boa; the ball is very oblique in *Protagras*."

Comparison of *Protagras* with the type of *Boavus occidentalis* shows that neither of the differences pointed out by Cope exists, and since these vertebrae show the closest resemblances, when their similar geological occurrence is taken into consideration, it leaves no doubt of their being

[1] The measurements of the type in this column were published in F. V. Hayden: Rept. U. S. Geol. Surv. Terr., vol. 3 (1884) p. 103.

congeneric, and as *Boavus* has priority by a year, *Protagras* must be abandoned as a synonym of the former. Since the type vertebra cannot be distinguished from those of *B. occidentalis*, the species *lacustris* also becomes a synonym of *B. occidentalis*.

Three species of this genus are now recognized: *B. occidentalis* Marsh, *B. brevis* Marsh, and *B. idelmani* Gilmore. *B. agilis* Marsh is here regarded as a synonym of *B. occidentalis*.

Boavus occidentalis Marsh

(Plate 3)

Boavus occidentalis MARSH, Am. Jour. Sci., 3d ser., vol. 1 (1871) p. 323—KING, U. S. Geol. Surv. 40th Par., vol. (1878); vol. 3, p. 405—DE ROCHEBRUNE, Nouv. Arch. Mus. Hist. Nat., 2d ser., vol. 3 (1880) p. 289—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 479; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 268.

Boavus agilis MARSH, Am. Jour. Sci., 3d ser., vol. 1 (1871) p. 324—KING, U. S. Geol. Surv. 40th Par., vol. 1 (1878) p. 405—DE ROCHEBRUNE, Nouv. Arch. Mus. Hist. Nat., 2d ser., vol. 3 (1880) p. 289—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 479; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 268.

Protagras lacustris COPE, Am. Philos. Soc., Pr., vol. 12 (1872) p. 471; Paleontol. Bull., no. 3 (1872) p. 3; U. S. Geol. Surv. Terr. (Hayden), 6th Ann. Rept., 1872 (1873) p. 632; U. S. Geol. Surv. Terr. (Hayden) Rept., vol. 3 (1884) p. 103, pl. 23, figs. 17, 18—DE ROCHEBRUNE, Nouv. Arch. Mus. Hist. Nat. 2d ser., vol. 3 (1880) p. 289—HAY, U. S. Geol. Surv., Bull., 179 (1902) p. 479; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 271—MERRILL, U. S. Nat. Mus., Bull. 53, pt. 2 (1907) p. 76.

TYPE SPECIMEN: P. M. N. H., Cat. no. 511. Consists of a single dorsal vertebra. Collected by O. C. Marsh, 1870.

TYPE LOCALITY: Grizzly Buttes, Uinta County, Wyo.

HORIZON: Middle Eocene, Bridger (horizon B).

ORIGINAL DESCRIPTION: "This species is established on eight vertebrae, nearly all from the middle dorsal region. They evidently represent several individuals, as they differ considerably in size, and were found at three separate localities. They indicate constricting serpents between six and eight feet in length. The neural arch in this species is elevated and massive. The neural spine is short, and triangular at its base, which rests on the posterior three-fourths of the arch. The zygosphene is convex above, slightly excavated in front, and without a median tubercle. The neural canal has a distinct median epapophysis on its floor, and sharp lateral ridges, which give it a sub-trifoliate outline. The diapophyses are auriform, and project below the inferior margin of the cup. The hypapophysis is a sharp ridge, beginning at the margin of the cup, and ending, just before reaching the ball, in an obtuse projection."

"The principal dimensions of one of the largest vertebrae of this species are as follows:

			Mm
Length of centrum from edge of cup to convexity of ball	4.50	lines	[9.45]
Transverse diameter of cup	2.80	"	[5.88]
Vertical diameter of cup	2.50	"	[5.25]
Transverse diameter of zygosphene at base	3.50	"	[7.35]
Distance from top of zygosphene to lower margin of cup	5.00	"	[10.50]
Vertical diameter of ball	2.45	"	[5.14]
Width of neural canal in front	1.75	"	[3.67]
Height of neural canal in front	1.10	"	[2.31]

"The various specimens representing this species were found in September last by H. B. Sargent, A. H. Ewing and the writer, at Grizzly Buttes, near Fort Bridger, Wyoming Territory. The geological horizon is probably Eocene."

Although Marsh mentions eight dorsal vertebrae, pertaining to several individuals, as being the materials upon which he based his descriptions

of *Boavus occidentalis*, a search of the Peabody Museum collection failed to produce more than three vertebrae thus labeled. These were in two glass vials, one containing a single vertebra labeled "Type *Boavus occidentalis*, G. Buttes, Wyo., 1870", the other containing parts of two, and

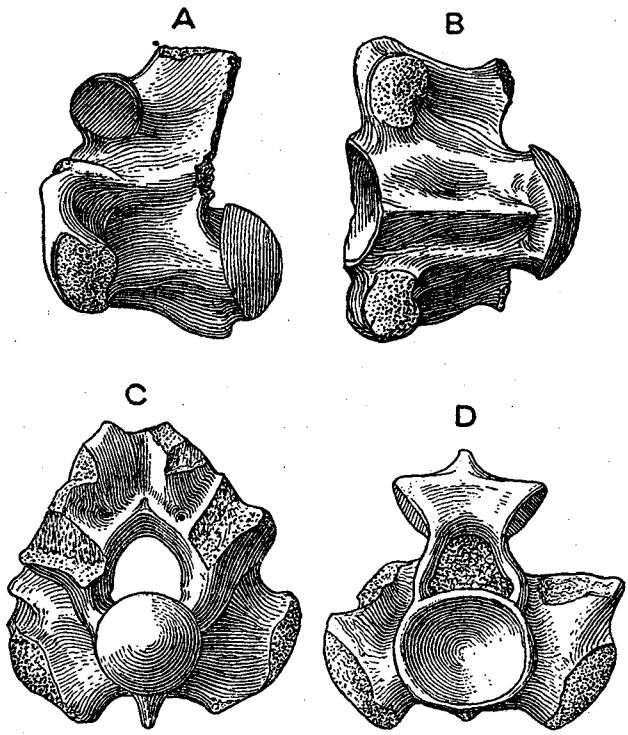


FIGURE 2.—*Posterior thoracic vertebra of Boavus occidentalis Marsh*

Type no. 511 P. M. N. H. *A*, lateral view; *B*, ventral view; *C*, posterior view; *D*, anterior view. ×3.

possibly three, vertebrae and marked "*B. occidentalis*, M. Fork, A. H. E." Other vertebrae in the collection can be identified as pertaining to this species, but there is no way of determining which of these was originally used by Marsh.

Since the original authority obviously selected a type, this species must rest upon the characters displayed by the single dorsal vertebra so labeled.

The type specimen is here illustrated for the first time (Fig. 2).

A specimen, No. 12980 U. S. N. M. in the National Museum collections, having vertebrae identical in size and other characteristics with the type of *Boavus occidentalis*, permits of its definite reference to this genus and species. This specimen consists of the complete left ramus with teeth,

quadrate of the same side, fragment of a maxillary, and 70 or more vertebrae with many ribs. Several segments of the backbone remain in an articulated condition in the matrix as shown in Plate 3. The longest segment with attached ribs is lying ventral side up, but some of the shorter sections have only the dorsal side exposed; two short sections of the anterior thoracic region are lying on the side, thus exposing the long hypapophysis. With one exception this is the most complete snake skeleton yet discovered in North America and it contributes much to our knowledge of the skeletal anatomy of this little-known genus and species.

This specimen comes from practically the same locality and geological horizon as the type, having been found by George B. Pearce, of the Smithsonian Expedition of 1930, in the breaks between Levitt and Little Spring Creek, Bridger Basin, Uinta County, Wyoming.

A second specimen, No. 2770 P. M. N. H., consisting of 80 or more disarticulated vertebrae and numerous portions of ribs, is also referred to *B. occidentalis*. Many of the vertebrae are completely preserved, and, as all sections of the backbone except the caudal region are free from the matrix, they furnish more detailed information than the more complete specimen previously mentioned. It is presumed that all these vertebrae pertain to a single individual. This specimen was collected by Frederick Mead in 1873, in the Bridger Basin halfway between Lodge Pole and Henry's Fork road.

A comparison of the cotypes (Nos. 2765 and 2766 P. M. N. H.), on which *B. agilis* was established (Fig. 3), with the corresponding vertebrae of the more complete specimens now available, shows such close resemblance as to indicate their being the same species. Therefore, on the ground of priority, *B. agilis* becomes a synonym of *B. occidentalis*, to which it is now referred.

Marsh's original description is as follows:

"This species, which was nearly the same in length as the preceding, [*B. occidentalis*] although apparently much more slender, is indicated by five vertebra, all from the dorsal region, and representing two or more individuals. They may readily be distinguished from the corresponding vertebrae of *B. occidentalis*, by the proportionally more elongated centrum; by the rounder and more inclined cup; by the more expanded anterior zygapophyses; by the diapophyses, which do not extend below the inferior surface of the centrum; and by the hypapophysial ridge, which is more obtuse, and in its anterior portion expands rapidly until it disappears in the margin of the cup.

"The largest vertebra of this series has the following dimensions:—

			Mm
Length of centrum from edge of cup to convexity of ball	4.25	lines	[8.9]
Transverse diameter of cup	2.50	"	[5.2]
Vertical diameter of cup	2.40	"	[5.0]
" " " ball	2.35	"	[4.9]
Width of neural canal, in front	1.75	"	[3.6]

"The specimens on which this species is based were discovered by the writer, near Fort Bridger, [Grizzly Buttes], in the same formation as the remains above described [*B. occidentalis*]."

Only four of the five vertebrae mentioned by Marsh were found so labeled in the collections of the Peabody Museum, and these now bear the catalogue numbers 467, 2765, and 2766.

After assorting the keeled vertebrae of No. 2770, P. M. N. H., now identified as pertaining to *B. occidentalis*, it was found that, taken as a whole, the obtusely keeled vertebrae were somewhat smaller than the

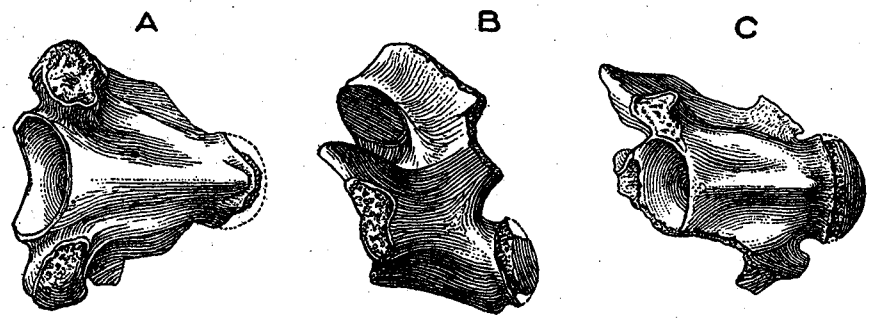


FIGURE 3.—*Thoracic vertebrae of Boavus occidentalis Marsh*

Cotypes of *B. agilis* Marsh. *A*, ventral view of No. 2765 P. M. N. H.; *B*, lateral view; *C*, ventral view (both of No. 2766 P. M. N. H.). ×3.

typical sharp keeled type. The obtusely keeled vertebrae of No. 2770 correspond in size and in all other characteristics with the cotypes on which *B. agilis* was founded. Marsh's statement regarding the diapophyses not extending below the inferior surface of the centrum cannot be accurately judged since all the available cotypes have this portion missing or have the surfaces badly abraded and worn (Fig. 3). Insofar as the cup of the centrum is more inclined or the prezygapophyses more expanded, direct comparison fails to disclose any appreciable differences. After reviewing all the characters used for distinguishing *B. agilis* the author concludes that these cotypes are from a more posterior position in the vertebral column than the type of *B. occidentalis*, but that both forms occur in the backbone of a single individual is clearly indicated by specimen No. 2770 in the Peabody Museum of Natural History.

OSTEOLOGY OF THE SKELETON: The detailed description of the osteological structure of the *Boavus occidentalis* is based primarily on specimen No. 12980 U. S. N. M., but is supplemented by specimen No. 2770 of the Peabody Museum.

SKULL: The skull is known only from the right quadrate, and fragmentary portion of the maxillary. The quadrate was preserved at the end of the right ramus almost in its proper articulated relationship, as shown in Plate 3. As lying in the matrix only the anterior view is visible. Some of the proximal end appears to be missing (Fig. 4). In this aspect the bone is subtriangular in outline, with a ridge of bone that rises from

the inner edge of the lower articular end and extends upward merging into the general level of the surface of the widened upper end. This ridge is at right angles to the triangular-shaped plate which forms at the main mass of the bone. At the center, this ridge is notched for articulation with the stapes (Fig. 4). It is quite unlike the quadrate of *Boa* which is more quadrangular in its general shape.

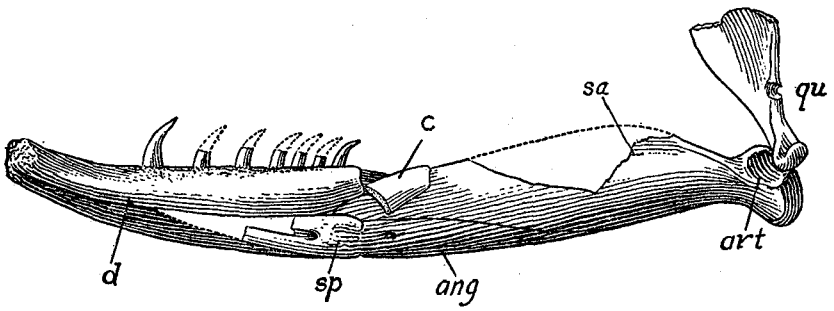


FIGURE 4.—*Right ramus and quadrate of Boavus occidentalis Marsh*

No. 12980 U. S. N. M. Internal view. *Ang*, angular; *art*, articular; *c*, coronoid; *d*, dentary; *qu*, quadrate; *sa*, surangular; *sp*, splenial. ×2.

In the general triangular outline, with constricted shaft above the articular end, and truncated upper extremity, the quadrate bones of *B. occidentalis* and *B. idelmani* have a close resemblance. Owing to the fact that in *B. occidentalis* only the front of this bone is available for study, it cannot be properly contrasted with the quadrate of *B. idelmani* which has only the opposite side exposed.

A fragment of the anterior end of the left maxillary containing the broken bases of two upper teeth shows no features that would be of aid in the characterization of this genus.

LOWER JAW: The right ramus containing two complete, and the basal portions of five other, dentary teeth is shown in Plate 3, lying in the matrix with the internal side exposed. For fear that permanent injury might result from an attempt to detach this delicate fossil from its bed, it was deemed inexpedient to attempt its removal. On that account the description to follow is of the internal side only (Fig. 4).

In general the ramus shows many resemblances to the lower jaw of *Boa constrictor*, the most marked distinction being found in the proportions of the two halves of the ramus. In *Boa constrictor* the vertical suture between the ends of the splenial and angular is exactly at mid-length, whereas in *B. occidentalis* the posterior portion is considerably longer than the dentary part. The inner flange of the surangular, although incompletely preserved in the fossil, rises rapidly in front of the cotylus as in *B. constrictor*, whereas in *Python* it widens little anteriorly. The pos-

terior end of the articular bone is truncate and thickened transversely, with a decided downward inflection as in *Boa*. The dentary gradually narrows anteriorly with a slight inward bend of the anterior end. On the lower internal side the bone is channelled by the Meckelian groove. This groove is covered in part by the splenial, the anterior end of which is missing in this specimen. The posterior end of the splenial, as in the

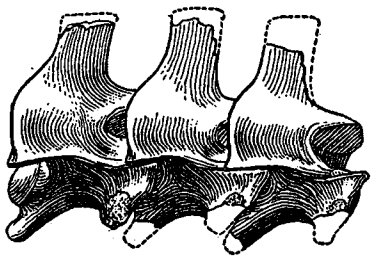


FIGURE 5.—*Anterior thoracic vertebrae of Boavus occidentalis Marsh*
No. 12980 U. S. N. M. Viewed from right side. ×3.

Boa and *Python*, is perforated by a foramen. As in snakes generally, it joins the angular posteriorly by a vertical suture. As shown in Fig. 4, a small foramen perforates the anterior end of the angular, and a small fragment of the coronoid bone is attached to the forward end of the surangular.

Measurements of ramus

	Mm
Greatest length over all	52.0
Greatest depth of posterior end of dentary	4.0
Greatest depth of anterior end of dentary	2.7
Greatest depth posterior to last tooth	6.0

TEETH: The dentition of *Boavus occidentalis* is represented by two complete, and the basal portions of five, dentary teeth, and the basal portions of two maxillary teeth. As in modern ophidians, these were ankylosed to the jaw. The teeth indicate that the series gradually diminish in size from the front toward the back. They are of the typical simple Boid type, slender, recurved, with delicate sharp tips. It is estimated that the complete dentary series would consist of from 15 to 17 teeth.

THORACIC VERTEBRAE: Two short segments, with four and five vertebrae respectively, of specimen No. 12980 U. S. N. M., give the first information as to the character of the anterior thoracic vertebrae of *Boavus occidentalis*. As shown in Plate 3, the longer section of five vertebrae lies in the matrix immediately to the right of the quadrate bone. Their small size with simple compressed hypapophyses that are shorter than the spines indicates their position in the column as being well forward, if not closely following the cervicals which are missing. As shown by the

presence of simple hypapophyses, the second segment of four vertebrae at the extreme top of Plate 3 also belongs to the anterior thoracic region. The most posterior centrum has a maximum length of 11.5 mm., whereas the posterior vertebrae of the section mentioned above are only 6 mm. long. Some of the other segments shown in Plate 3 may pertain to the

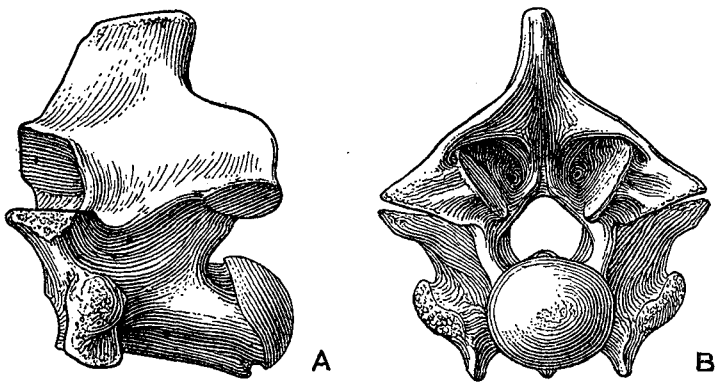


FIGURE 6.—*Thoracic vertebra of Boavus occidentalis Marsh*

No. 2770 P. M. N. H. *A*, lateral view; *B*, posterior view. Reconstructed from four vertebrae. ×3.

anterior thoracic region, but, since they are to be seen only from the top, their position in the column cannot be determined at this time.

These anterior vertebrae differ from the posterior thoracic vertebrae only in the presence of simple spine-like hypapophyses, narrower spines, lower position of zygapophyses, and their smaller size.

The detailed description of the posterior thoracic vertebrae is based primarily on the type specimen but supplemented by vertebrae of specimens No. 12980 U. S. N. M. and No. 2770 P. M. N. H. The centrum is triangular in outline, moderately long, and not depressed. The glenoid fossa is subcircular, being slightly wider than high and slightly narrower than the zygosphene. These proportions prevail in all the vertebrae available for measurement. Condyle is moderately oblique, with short neck. Inferior surface of centrum is divided by a sharp, median ridge that begins at the margin of the cup and ends just before reaching the ball in an obtuse projection. This correctly describes the type and other vertebrae, but the character of this hypapophysial ridge changes in different parts of the vertebral column. Among the disarticulated vertebrae of specimen No. 2770 P. M. N. H. are three distinct types of hypapophyses; (1) thin, sharp ridge without obtuse projection; ridge extending downward prominently below the ventral border of the centrum; (2) sharp ridge, ending in an obtuse projection behind and extending downward slightly below ventral border; (3) transversely rounded ridge that widens from mid-length toward both ends, more especially toward the anterior which

is flattened. These modifications of the hypapophyses take place in the order named from front to rear, as shown by the articulated series of *B. idelmani*. No caudal vertebrae have been recognized in any of the disarticulated specimens referred to this genus. Those of the second type are well shown in Figure 6, as is the third type in Figure 3.

The hypapophysis divides the ventral surface into a pair of distinct concave surfaces that at mid-length are usually perforated by a pair of small foramina as shown in B of Figure 2.

The diapophyses, especially when viewed from the front, are prominent and heavy. They extend well downward on the sides of the centrum near the anterior end immediately below the anterior zygapophyses, and their inferior borders, unless abraded and worn, always extend below the level of the centrum The outer articular ends of these processes present a heavy rounded superior surface and a narrower somewhat flattened inferior surface. These articular faces are continuous, not divided by a notch as in some Boids (*See* Fig. 6). These articular surfaces in the type have lost the hard, smooth surface of a perfect bone, and consequently Figure 2 does not illustrate perfectly the character of these articular surfaces.

The lateral surface, between the rounded edge which runs from the lower end of the diapophysis to the condyle and the more prominent ridge that connects the zygapophyses, is flattened and slightly sculptured, with a vascular foramen below the middle of the last-mentioned ridge.

Since the zygosphene is slightly incomplete in the type, this process will be described from vertebrae of No. 2770 P. M. N. H. The nonarticular anterior face of the zygosphene is flattened, massive, with diagonal raised lateral edges. Above it is moderately convex from side to side. Below the flattened anterior surface it passes smoothly into the roof of the neural canal. In an average-sized thoracic vertebra this flattened area between the top of the canal and the top of the zygosphene measures 2 mm. in depth.

In the type vertebra the spine, much of the zygantra, and all of the postzygapophyses are missing. (*See* Fig. 2 C.) As shown by other specimens, (*See* Fig. 6), the zygantrum is excavated in the posterior expansion of the neural arch, the two flattened articular surfaces being separated at the center by a nonarticular surface that is continuous with the slightly thickened posterior border of the spine. The spine is of moderate height, compressed with a squarely truncate extremity. The front border is acutely edged, the hinder border slightly thickened and rounded. Both borders are inclined backward. (Fig. 6.) At its base the spine is triangular in section.

The neural canal has a distinct epapophysis on its floor, with sharp lateral ridges.

The triangular zygapophyses are joined by a moderately stout ridge. The lateral emargination between them is fairly symmetrical, with the deepest part above the middle of the centrum. The neural arch is relatively high, its lateral borders cut well back from the ball.

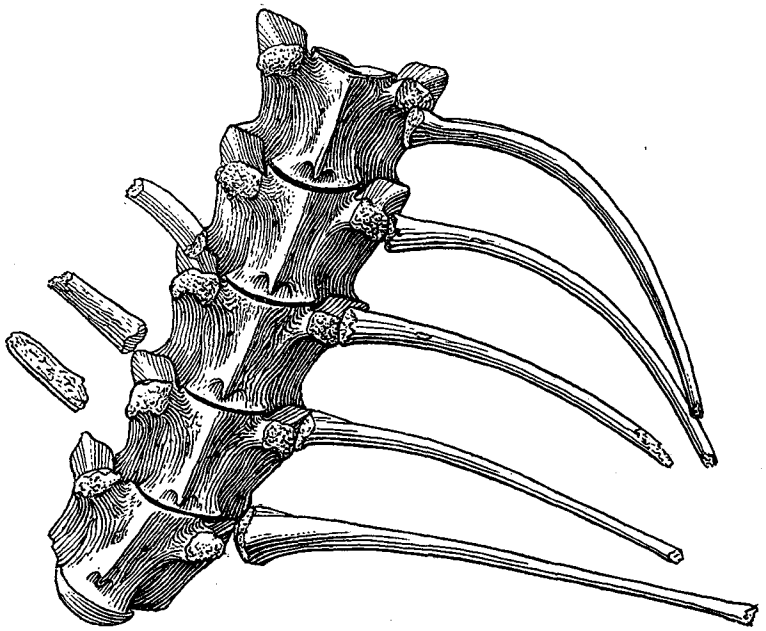


FIGURE 7.—*Thoracic vertebrae and ribs of Boavus occidentalis Marsh*

No. 12980 U. S. N. M. Shown as they were found articulated. (*See* longest segment, Pl. 3.) X2.

RIBS: A few ribs, as shown in Plate 3 and Figure 7, were found articulated with the vertebrae. None of these has the distal end complete. The longest measures 36 millimeters from end to end. The heads are nearly twice as wide dorsoventrally as anteroposteriorly. On the dorsal side, a projecting process (*tuber costae*) extends backward and upward, a process that is present in the ribs of most living snakes. All the ribs are hollow.

Referred specimens

No. 2706, P. M. N. H. Consists of portions of two thoracic vertebrae. From Bridger, Eocene, Millers Fork, Bridger Basin, Uinta Co., Wyo. Collected by A. H. Ewing, 1870.

No. 2717, P. M. N. H. Consists of a single dorsal vertebra. From Bridger, Eocene, Grizzly Buttes, Uinta Co., Wyo. Collected by O. C. Marsh, Sept. 5, 1870.

No. 6058, A. M. N. H. Consists of portions of 28 thoracic vertebrae. From Bridger, Eocene, Church Buttes, Uinta Co., Wyo. Collected by Expedition, August 18, 1903. Small specimen.

Boavus brevis Marsh

Boavus brevis MARSH, Am. Jour. Sci., 3d ser., vol. 1 (1871) p. 324—KING, U. S. Geol. Surv. 40th Par., vol. 1 (1878) p. 405—DE ROCHEBRUNE, Nouv. Arch. Mus. Hist. Nat., 2d ser., vol. 3 (1880) p. 289—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 479; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 268.

TYPE SPECIMEN: P. M. N. H., Cat. no. 468. Consists of a single thoracic vertebra, collected by H. B. Sargent, Sept. 3, 1870.

TYPE LOCALITY: Grizzly Buttes, Uinta Co., Wyo.

HORIZON: Bridger, Middle Eocene.

ORIGINAL DESCRIPTION: "The serpents representing this species were considerably smaller than those described above, [*B. agilis*] and evidently much shorter in proportion to their bulk, being probably not more than four or five feet in length. The only remains obtained consist of three dorsal vertebrae, all in good preservation, and evidently belonging to two different individuals. These vertebrae have the centrum unusually short, its extent measured on the inferior surface scarcely exceeding the transverse diameter of the zygosphene. The neural arch is low, and bears on its posterior two-thirds the neural spine, which is quite short and truncated. The zygosphene is less massive than in the preceding species, and has a slight median swelling on the anterior margin of its base.

"The dimensions of the most perfect of these vertebrae are as follows:

			Mm
Length of centrum from edge of cup to convexity of ball	2.20	lines	[4.6]
Transverse diameter of cup	1.60	"	[3.3]
Vertical diameter of cup	1.25	"	[2.6]
Transverse diameter of zygosphene at base	1.85	"	[3.7]
Distance from top of zygosphene to lower margin of cup	2.80	"	[5.6]
Width of neural canal in front	1.00	"	[2.1]
Height of neural canal in front	.90	"	[1.8]

"The specimens here described were found by H. B. Sargent, in the same freshwater Tertiary deposits, and near the same locality, as the two preceding species."

Mention is made by Marsh of three vertebrae pertaining to two individuals, but in the Peabody Museum serpent materials submitted to the author for study only one vertebra corresponding to the description and measurements given by Marsh was found. This vertebra was in a glass vial, the cork plainly marked "Type *Boavus brevis* H. B. S." It seems quite evident that Marsh selected this specimen as the type, even though no direct reference to that fact was made in his description. Since no measurements or illustrations of the other vertebrae have been published, it is no longer possible to recognize them even though they should eventually be found.

The type specimen is illustrated here for the first time (Fig. 8).

The prezygapophyses and diapophyses of the right side are missing from the type vertebra, and the articular diapophysial surfaces are so bandly abraded as to render their shape and extent somewhat uncertain. On the ventral surface the centrum is traversed for its entire length by an obtusely rounded keel, which apparently indicates this vertebra to belong in the posterior thoracic region of the vertebral column. The angularly rounded outline of the glenoid fossa is unique (Fig. 8, C). The illustration depicts the shape of the fossa correctly, but it may be that edges of the cup are broken away, and since, through abrasion, have been rounded so as to have the appearance of being complete. A determina-

tion of this point, however, must await the discovery of additional specimens. The same uncertainty exists regarding the completeness of the top of the neural spine.

The short centrum, with low neural arch, glenoid fossa angularly ovate transversely, less massive zygosphene with a slight median swelling on the anterior margin, and the short narrow, truncated spine are character-

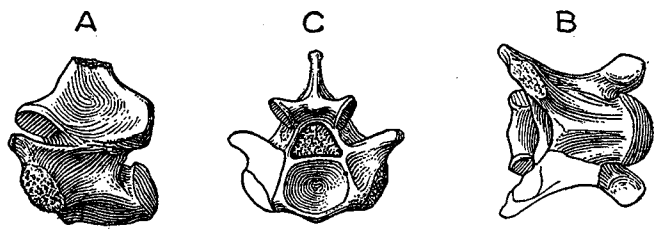


FIGURE 8.—*Thoracic vertebra of Boavus brevis Marsh*

Type no. 468 P. M. N. H. *A*, lateral; *B*, ventral; *C*, anterior views. ×3.

istics distinguishing *B. brevis* from *B. occidentalis*, which occurs in this same formation. As a whole these characteristics constitute more than specific distinction, but in the absence of corroborative materials it seems best for the present to retain the species in the genus *Boavus* as originally assigned until such time as the discovery of additional specimens shall disclose its true relationships.

Boavus idelmani, n. sp.

(Plates 1 and 2)

TYPE: A nearly complete articulated skeleton. Private collection of E. S. Weinberg, New York, N. Y.

LOCALITY: Fossil Basin, probably near Fossil, Uinta Co., Wyo.

HORIZON: Green River formation, Eocene.

The specimen on which the present species is based is the most complete fossil snake specimen ever found in North America. Its history is slightly obscure. It originally belonged to the late Max Idelman, a merchant of Cheyenne, Wyoming, but after his death in 1913 it came into the hands of his son-in-law, Edgar S. Weinberg of New York, and it was through the latter's generosity and understanding of its scientific importance that the specimen was loaned to the author for study and description. Judging from the manner of its preservation on a slab of shale it was presumed that Mr. Idelman obtained the specimen from a professional collector of Green River fossils, of which he had a considerable series of fish specimens. In an attempt to verify the supposed Green River origin of the specimen, W. H. Bradley of the United States Geological Survey was consulted, and he was not only able to recognize the shale as being from the Green River formation, but a peculiar crinkling of the laminae indi-

cated it was from the Fossil Basin area, as that particular type of lamination is not known elsewhere in the Green River formation.

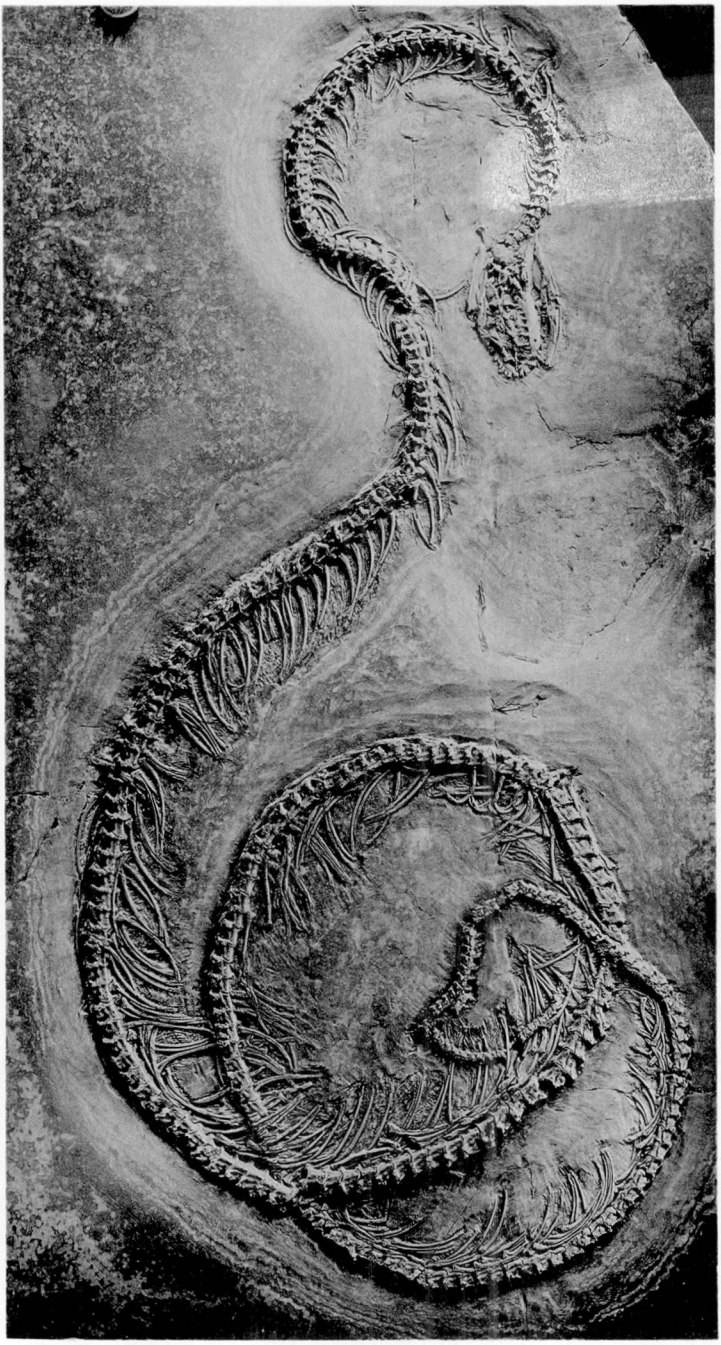
The specimen as exposed on the slab (Plate 1) is lying ventral side up with the head turned backward along the thorax. The long thoracic region extends backward in sinuous curves peculiar to serpents, the tail portion forming two complete circles one within the other. It is probable that a few terminal caudals are missing from the tip of the tail. Most of the ribs are present, though somewhat disarranged. The skull is ventral side up, with the right ramus lying in the matrix parallel with the skull, and with its inner side exposed (Pl. 2). The maxillary bones, quadrate, pterygoid, basisphenoid, and basioccipital, are clearly recognizable, and the ectopterygoid appears to be present, but the other palatal elements are so badly broken and intermingled as to be difficult of recognition and valueless from a systematic standpoint. In a straight line, as preserved, this specimen has a total length of 960 millimeters (37 $\frac{13}{16}$ inches).

Skull: In the hope that the top of the skull would show characters disclosing the affinities of this specimen, the top of the cranium was laid bare by removing the matrix from the under side of the slab of shale on which the specimen rests. This delicate task was so skilfully accomplished by N. H. Boss, Chief Preparator in the Division of Vertebrate Paleontology of the United States National Museum, that none of the skull elements was in the least disturbed from its original position in the matrix.

It is disappointing, however, to find that the top of the skull was not intact, but that, like the palate, it had suffered post-mortem injuries (Fig. 9). Some elements are missing, while others have been shifted out of position and are otherwise disarranged.

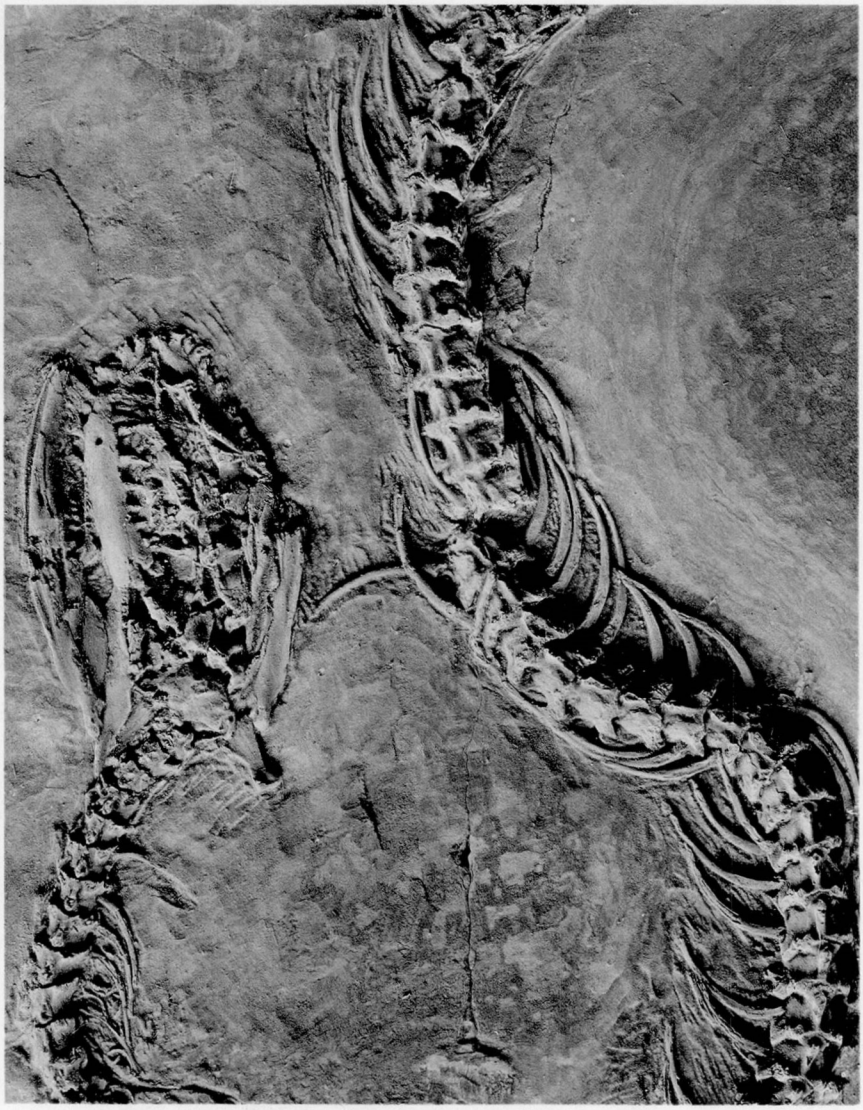
The top of the brain case is preserved fairly complete and is surmounted by a moderately high, thin saggital crest that in its development closely resembles the crest of a *Boa constrictor* of equivalent size. In front of this crest the parietal widens into a flattened area, the length of which is about equal to the crested portion. This is quite unlike the condition found in the *Boa* and *Python* where the broad, flattened area in front of the crest is composed of the paired frontal bones (Fig. 1). That this portion of the *Boavus* skull is parietal and not frontal is indicated by the absence of all sutures, there being no trace of a median suture separating the elements of opposite sides. According to Cope the frontals are always separate in the ophidian skull. Verification of this observation is apparently shown by an examination of the ophidian skulls available to the author for this study, all of which show this suture to be distinctly present. This area is bordered on either side by a lateral element identified as the postorbital, which is entirely in contact with the parietal when in position (Fig. 9). The sutural border for the nasals is broadly scalloped with a short median projection at the center.

A rectangular plate-like element lying in contact, but slightly twisted



SKELETON OF *BOAVUS IDELMANI* GILMORE

Type. Shown as found preserved on a slab of Green River Shale. About 7/11 natural size.



SKULL AND SEGMENTS OF VERTEBRAL COLUMN OF *BOAVUS IDELMANI* GILMORE
Type. Enlarged. About twice natural size.

out of alignment, is regarded as the right frontal bone. Its length is about three times the breadth of the posterior end. The anterior end is broadly rounded from side to side but subequal in width to the posterior. Further verification of its being properly identified as the frontal is indicated by the long emargination of the outer border which forms the upper boundary of the orbit.

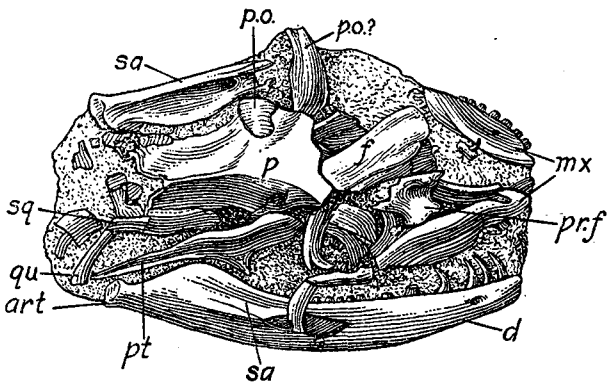


FIGURE 9.—*Disarranged top of the skull of Boavus idelmani Gilmore as found in the matrix*

Type. *Art*, articular; *D*, dentary; *F*, frontal; *Mx*, maxillary; *P*, parietal; *Po*, postorbital; *Pr.f*, prefrontal; *Pt*, pterygoid; *Qu*, quadrate; *Sa*, surangular; *Sq*, squamosal. About ×2.

No trace has been found of the nasal bones which, because of the great lengthening of the frontals, must necessarily have been short.

The rectangular form of the frontal of *Boavus* at once distinguishes it from the nasal bones of *Boa* and *Python* which are subquadrangular in shape. It closely resembles the frontal of *Natrix rhombifer* in shape and proportions, as it does those of *Dimlysia patagonia* Woodward.

Adjoining the right frontal along its outer side is a subtriangular element, provisionally identified as the prefrontal. That it is the prefrontal appears to be indicated by a wide inwardly projecting surface at its posterior end, which probably formed the anterior wall of the orbit. There is a thin raised wall along what would be the top and lateral sides of this end, if in normal position, almost precisely the conditions found in the prefrontal of *Boa* and *Natrix*.

On the other hand the author fails to find any trace of the longitudinal foramen which perforates the lower part of this bone in most living snakes and which would positively identify it if present. It may be that this lower portion is broken off and missing.

A detached bone lying in the matrix at right angles to the parietal near its external-anterior border may represent the postorbital of the left side. It is subtriangular in outline with a comparatively broad proximal extremity tapering rapidly below mid-length to a bluntly pointed end.

The maxillaries are both present and little disturbed from their normal relationships. Only their upper surface can be seen from the dorsal view (Fig. 9), but in the palatal view the maxillary of the left side is free and contains the bases of 10 teeth. There may have been one or two more at the posterior end of the series, but this point is obscure. A thin, flattened but badly crushed bone overlapping the brain case on the right side may be the squamosal, but its preservation is such as to make its identification uncertain. At the posterior end of the squamosal the edge of a bone extends outward and terminates close to the posterior ends of the right ramus and pterygoid; it is presumed to be the edge of the right quadrate. The extreme thinness of the matrix surrounding the quadrate prevented its further development lest permanent damage be done to the specimen. On the upper side this bone is covered by the overlapping bones of the palate.

The basioccipital is without hypapophyses as in *Boa* and *Python*. So far as it can be compared it resembles the basioccipital of *Boa* more closely than that of the *Python*. The basisphenoid can be recognized but is so broken that its features cannot be clearly determined. The left quadrate bone is plainly visible in the palatal view of the skull, lying in the matrix at the posterior end of the left ramus as clearly shown in Plate 2. It appears to be the posterior side that is exposed. In this aspect the shaft immediately above the lower articular end is constricted, but above this constriction it continues to widen until the upper truncated end is reached. In general form it closely rsembles the quadrate of *Boavus occidentalis* (Fig. 4).

Both the pterygoid bones are present, the right element being most clearly recognizable. However, it is partially hidden by the overlying right dentary. The pterygoid is relatively long and in all probability reached the quadrate. The basal portions of a longitudinal row of minute teeth are present on its anterior half.

On the left side, in the palatal view, a short but much damaged bone lies in contact with the posterior end of the maxillary anteriorly and in contact with the pterygoid posteriorly. Because of these relationships it is provisionally identified as the ectopterygoid.

The remaining palatal elements are so badly broken and crushed as to be unrecognizable.

Measurements of skull elements

	Mm
Greatest length of parietal at the center	10.6
Greatest width of anterior end	6.6
Greatest length of nasal	6.0
Greatest width of posterior end	1.9
Greatest width across top of orbits	4.0
Greatest length of left quadrate	6.0

LOWER JAW: The right ramus is preserved almost in its entirety, whereas the left ramus has been broken apart, the dentary portion lying over upon the palate (Pl. 2), the articular half being at the side and parallel with the skull in nearly its proper relationships. (*See* Fig. 9.) From a study of the two rami it has been possible to determine practically the entire structure of the mandible.

The dentary bears teeth on its entire length, there being evidence of not less than seventeen in the complete series. As in *B. occidentalis*, the teeth decrease in size from the front toward the back. The inner ventral side is channelled by Meckel's groove which is open. A thin triangular bone on the inner posterior side of the dentary quite certainly represents the splenial which sends a tapering point forward for more than half the length of the dentary. It is relatively longer and more fully developed than in either *Boa* or *Python*.

Although it cannot be positively determined, a coronoid seems to have been present. In this region of the right ramus the bone surfaces are somewhat damaged, but a tapering bone pressed down upon the surangular part of the ramus may represent a portion of the slightly displaced coronoid bone. Furthermore, on the anterior end of the posterior half of the left ramus there is a decided upward turn of the dorsal border as in other serpent rami which have the coronoid, so that although the evidence is not positive it all points to the presence of this important element.

The posterior half of the ramus shows Boid affinities that are definitely distinct from *Python*. Reference is made to the two vertical parallel plates that form the boundaries of the trough that leads to the Meckelian orifice. In this specimen the inner plate is the higher, with an upwardly curved superior border, whereas the outer plate is low with a straight upper border as in *B. occidentalis*. This is almost precisely the condition found in *Boa constrictor*, but in the genus *Python* this condition is reversed, the outer plate being the higher. The elements of the posterior portion of the ramus are all fully fused and cannot be differentiated.

Measurements

	Mm
Greatest length of ramus (right)	27.7
Greatest depth of dentary (left)	3.4
Greatest length of dentary (right)	15.7

The close similarity of the ramus of *B. idelmani* to that of *B. occidentalis* is clearly shown by comparing Figures 4 and 10, the chief distinctions of *B. idelmani* being its much smaller size and the less robust nature of the posterior or articular end. The latter difference, however, may be more apparent than real since this end has been damaged and on that account its full shape cannot be determined. *Boavus* appears to differ from both *Python* and *Boa* in the presence of a more fully developed splenial bone.

The lower jaw of *B. idelmani* furnishes strong confirmatory evidence of the correctness of the assignment of this species to the genus *Boavus*.

VERTEBRAE: As shown in Plate 1, the vertebral column is practically complete. The vertebrae, except for slight dislocations here and there, are in a continuous series from the atlas to the two hundred and fifty-third vertebra. At this point a break in the series, combined with the badly damaged condition of two or more vertebrae, renders the total count somewhat uncertain. There is evidence of 282 vertebrae in all, but the total number is somewhat greater since an undetermined number of terminal caudals are quite certainly missing.

Most of the backbone lies on the shale slab ventral side up, thus hiding from view the more important features of the vertebrae. This is most unfortunate, as so complete a specimen would be of great assistance in showing the changes that take place in the several segments of the vertebral column and would enable one to allocate more accurately the scattered vertebrae that comprise most fossil snake specimens. The preparation of the specimen was roughly done, as practically all the projecting processes have either been damaged or entirely cut away.

Considering the vertebral column as a whole, because of the missing processes which determine the points of division, it cannot be divided into the several regions outlined on p. 8. Tentatively the main divisions are as follows: Cervicals 2; thoracic 225±, caudal 55+.

The anterior thoracic vertebrae have hypapophysial processes. These begin as a rounded ridge slightly posterior to the border of the glenoid fossa and end posteriorly before reaching the margin of the condyle in a relatively short subacute process that projects downward below the general level of the centrum (Pl. 2). The first complete hypapophysial process is found on the fifteenth vertebra posterior to the skull. From a study of these mutilated processes it is quite evident that none was spine-like as in *B. occidentalis*. In a posterior direction the hypapophyses gradually decrease in length, until in the vicinity of the seventieth vertebra they persist only as an acute longitudinal keel or ridge, with faint extension downward at the posterior end. More posteriorly, however, this keel in front becomes rounded, while the posterior half remains acute. In a posterior direction the rounded border extends forward more and more, until, near the one hundred and fortieth vertebra, the keel presents a rounded ventral surface bordered by shallow longitudinal depressions. The keel throughout is more widely rounded toward the anterior end; thus, when viewed vertically, it is subtriangular in outline. Beginning at the two hundredth vertebra the posterior end of the keel begins to pinch together to form an obtuse edge. The extent of this style of keel cannot be accurately determined because of the damaged condition of the remaining posterior vertebrae.

The diapophyses seem to have been prominent and heavy in development, though very few of these processes are preserved intact. Their outer articular ends present a heavy, rounded, upper articular surface, and a narrower, flatter, articular surface that extends somewhat below the level of the intervening centrum. There is no perceptible division between these two surfaces except a slight indentation on the posterior side, as in *B. occidentalis.*

The pre- and postzygapophyses are joined by a prominent longitudinal ridge that appears to be slightly emarginated at the mid-length of the vertebra. The lateral surface between the rounded ridge, which runs from the lower end of the diapophysis to the condyle, and the more prominent ridge joining the zygapophyses are flattened with a vascular foramen below the middle of the last-mentioned ridge, as in *B. occidentalis.*

A short section of nine vertebrae, Nos. 166 to 174, are lying on their sides, thus bringing the spinous processes into view. These vertebrae have relatively short spines with truncated tops, the anterior border strongly receding from the bottom upward, the posterior border slightly overhanging. These spines are relatively wide at the bottom, extending nearly the full length of the neural arch.

Slight displacement of the column between the thirtieth and thirty-first vertebra, and again between the one hundred and fifty-sixth and one hundred and fifty-seventh vertebra, shows the cup and ball to be subovate in transverse diameter. How much this feature has been exaggerated by vertical pressure it is of course impossible to determine.

The first vertebra bearing fused ribs is either the two hundred and twenty-second or the two hundred and twenty-third, thus indicating the beginning of the caudal series. The former presence of lymphapophyses seems to be indicated by paired broken bases on the ventral surfaces of a few of the caudals. These vertebrae gradually reduce in size posteriorly, but most of them have been so badly mutilated in preparation that their structural details can no longer be determined. For this reason it is impossible to determine the point of division between anterior and posterior caudals.

The close resemblance of the ramus to that of *B. occidentalis* in the similar shape of quadrate bones and the similar structure of vertebrae, insofar as they can be contrasted, points to the propriety of the reference of this species to the genus *Boavus.*

The much smaller size of the present specimen, coupled with the absence of long compressed hypapophyses in the anterior thoracic region, apparently indicates its specific distinctness from *B. occidentalis*; henceforth it will be known as the type of *Boavus idelmani*, named in honor of the late Max Idelman, in whose collection of fossil specimens it was found.

Genus *Ogmophis* Cope, 1884

Ogmophis, COPE, U. S. Geol. Surv. Terr., Rept. 3 (1884) p. 783, pl. 58a, figs. 10–12.

GENOTYPE: *Ogmophis oregonensis.*

Known only from thoracic vertebrae.

The type specimens on which this genus and species were founded have been temporarily misplaced in the American Museum of Natural History

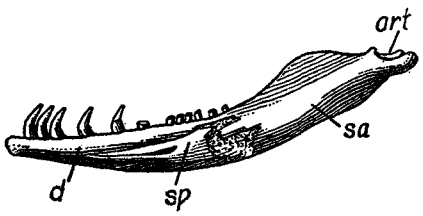


FIGURE 10.—*Right ramus of Boavus idelmani Gilmore*

Type. Internal view. *Art*, articular; *d*, dentary; *sa*, surangular; *sp*, splenial. ×2.

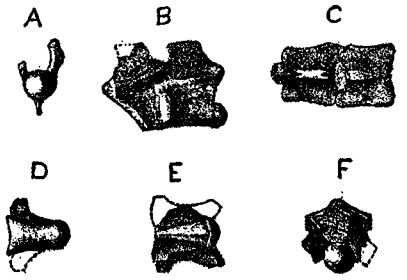


FIGURE 11.—*Thoracic vertebrae of Ogmophis oregonensis Cope*

Type. *A*, An anterior centrum from behind; *B*, two consecutive vertebrae, lateral view; *C*, same, superior view; *D*, same, inferior view; *E*, another vertebra, inferior view; *F*, same, posterior view. Natural size. After Cope.

and are therefore not available at this time so that one has to rely on Cope's description and published figures for the characters of the genus. The original characterization of the genus is as follows:

"Neural spine of vertebra short and obtuse. No process below the prezygapophyses. Rib surface single, uninterrupted; rib [ridge] extending posteriorly from its inferior extremity. Inferior face of centrum without hypapophyses on the dorsal region, but probably furnished with one on the cervical region. This genus resembles *Aphelophis* in most respects, and probably has similar general affinities. It is distinguished by the ridge which extends from the parapophysis, and the groove which is included between this and the middle line of the centrum."

This diagnosis does not satisfactorily distinguish *Ogmophis* from the closely related *Calamagras*, but until the type materials come to light it appears best to retain the genus as valid. The presence in *Ogmophis* of a neural spine occupying more than half the length of the neural arch gives additional support to the idea that *Ogmophis* is distinct from *Calamagras.*

The genera *Calamagras* and *Ogmophis* are very close in their relationships, as first recognized by Cope, and in all probability have similar affinities. After study and comparison of the type materials the author must confess to his inability to find characters that will satisfactorily distinguish them. The loss of the type of *Ogmophis oregonensis* is especially

unfortunate, since the illustrations are not entirely adequate (Fig. 11). The principal distinctions are, in *Ogmophis*, the more rounded obtuse nature of the hypapophysial keel, the presence of a short ridge running posteriorly from the parapophyses, relatively larger zygapophysial articular surfaces, and the wider fore and aft diameter of the short truncated spine. Most of these distinctions are not greater than might be found in different sections of the same vertebral column. Although *Calamagras* and *Ogmophis* may eventually prove to be congeneric, for the present the author proposes to continue their use as being distinct. It is anticipated that the recovery of the type materials and the discovery of more complete specimens will eventually clear up the taxonomic relationships of *Ogmophis*.

As known at present, the three species referred to *Ogmophis*—*O. oregonensis* Cope, *O. compactus* Lambe, and *O. arenarum* Douglass—may be distinguished as follows:

O. arenarum. Flint Creek Beds, Upper Miocene.
Ball and cup depressed, ovate transversely; obliquity of ball strong; ridge connecting zygapophyses inconspicuous; ridge extending outward and downward from side of glenoid fossa to support diapophyses not clearly defined. Parapophyses on the level of the centrum.

O. compactus. Cypress Hills, Oligocene.
Ball and cup wider than high, subovate; no obliquity of ball; ridge connecting zygapophyses inconspicuous; ridge extending outward and downward from side of glenoid fossa to support diapophyses well defined. Parapophyses on level with centrum.

O. oregonensis. John Day, Upper Oligocene.
Ball and cup subround; obliquity of ball moderate; ridge connecting zygapophyses very prominent. Parapophyses apparently above ventral surface of centrum.

Ogmophis oregonensis Cope

Ogmophis oregonensis, COPE, U. S. Geol. Surv. Terr., Rept. 3 (1884) p. 783, pl. 58a, figs. 10–12—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 480; Carnegie Inst. Washington, vol. 2 (1930) p. 268—MERRIAM AND SINCLAIR, Univ. Calif. Publ., Bull., Dept. Geol., vol. 5 (1907) p. 187.

TYPE SPECIMEN: A. M. N. H. (temporarily misplaced). Consists of four dorsal vertebrae and possibly a fifth from the region near the skull. Collected by J. L. Wortman.

TYPE LOCALITY: Near the John Day River, Ore.

HORIZON: John Day, Upper Oligocene.

ORIGINAL DESCRIPTION: "This snake is represented by four dorsal vertebrae and probably by a fifth from the region near the skull. The last-named vertebra has a smaller centrum than the others, as is usual with those from the anterior part of the column, but the details of its structure are much as in the others. It has an acute hypapophysial ridge which extends posteriorly into a short subacute process. In the other centra, the median inferior ridge bounded by the lateral grooves, is obtuse, and has different forms. It is wide at both extremities and the surface is equally convex; in two others it is much narrower medially and widened posteriorly. In all of these the posterior part is slightly angulate medially. The articular faces are nearly round, and the obliquity of the ball is only moderate. The ridge from the inferior extremity of the rib surface terminates a short distance from the articular

ball. The ridge connecting the zygapophyses is very prominent. The rib articular face is one-half deeper than wide; the superior half is convex, the remainder gently concave, the inferior border, projecting slightly outwards.

"The only specimen of this species preserved rather exceeds in size the others here described, except the *Neurodromicus dorsalis*.

Measurements

	m.
"Length of centrum with ball	.0050
Transverse diameter of ball	.0026
Total elevation of vertebra	.0060
Elevation of neural spine	.0019
Width of interzygapophysial ridge	.0044
Vertical diameter of rib surface	.0023
Width of ball of a "cervical" centrum	.0020"

Our knowledge of this species rests entirely on the original description and figures of Cope, as no additional specimens have come to the author's attention from this region.

Ogmophis arenarum Douglass

Ogmophis arenarum, DOUGLASS, Ann. Carnegie Mus., vol. 2 (1903) p. 153, 171—LAMBE, Contrib. Canad. Paleont., vol. 4, pt. 4 (1908) p. 21—HAY, Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 268.

COTYPES: Carnegie Mus., Cat. no. 744. Consists of three vertebrae. Collected by Earl Douglass, 1899.

TYPE LOCALITY: Near New Chicago, Granite Co., Mont.

HORIZON: Flint Creek Beds, Upper Miocene.

ORIGINAL DESCRIPTION: "Three vertebrae of a snake from the Flint Creek beds were associated with many small bones and teeth, among which were the humeri of moles described in this paper.

"The vertebrae not so long as broad. Centrum small, with no keel but a broad convexity on lower side. Ball transversely elliptical and facing somewhat upward as well as forward; neural canal arch-shaped with a median ridge or convexity on floor; the articular surfaces of the zygosphenes quite narrow and facing outward and downward; neural spine low and not reaching to the anterior part of the neural arch; neural arch large and zygosphenes almost as far apart as its width; protuberance for articulation of the rib quite prominent, higher than wide, convex above and in front, and slightly concave on the posterior inferior surface. The interzygapophysial ridges almost die out midway between the anterior and posterior zygapophyses.

"Compared with *O. angulatus* Cope (Terr. Vert. p. 783, Pl. LVIIIa, fig. 13) the protuberance for the articulation of the rib is larger, the vertebra proportionally lower, and there is no hypapophysial angle or ridge."

Measurements

Length of centrum of vertebra	4 mm
Width of vertebra	5 mm

It is quite evident from Douglass' remarks that the three vertebrae ascribed to the present genus and species were found intermingled with many small bones and teeth, and therefore cannot be certainly regarded as belonging to a single individual. In fact the disparity in size between the three vertebrae points to their pertaining to an equal number of individuals, and they must therefore be regarded as cotypes.

For the purpose of illustration, the most perfectly preserved vertebra has been selected as a subject here illustrated for the first time in Figure 12.

The vertebrae of *Ogmophis arenarum* can be at once distinguished from the other species of the genus by the depressed ovate form of the articular ends of the centra. It is further separated from *O. compactus* by its much smaller size, the vertebrae being only about one-half the dimensions of the Canadian species.

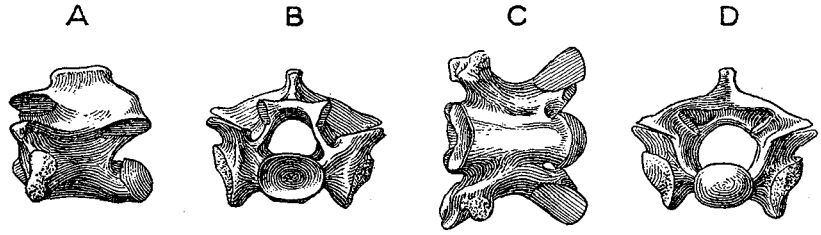


FIGURE 12.—*Thoracic vertebra of Ogmophis arenarum Douglass*

No. 744 Carnegie Mus. Cotype. *A*, lateral; *B*, anterior; *C*, ventral; *D*, posterior views. ×5.

Ogmophis compactus Lambe

Ogmophis compactus, LAMBE, Contrib. Canad. Paleont., vol. 4, pt. 4 (1908) p. 9, 20, pl. 1, figs. 26-30—HAY, Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 268—OSBORN, U. S. Geol. Surv., Mon. 55 (1929) p. 118.

Ophidian vertebrae, LAMBE, Geol. Surv. Canada, Summ. Rept. 1904 (1905) p. 366.

TYPE: Nat. Mus. Canada, Cat. no. 6237. Consists of one dorsal vertebra. Collected by L. M. Lambe, 1904.

PARATYPES: Cat. nos. 6238, 6239, 6240.

TYPE LOCALITY: 4 miles above east end of Post Office, Cypress Hills, Saskatchewan, Can.

HORIZON: Oligocene.

ORIGINAL DESCRIPTION: "Four dorsal vertebrae apparently belonging to the same species were found separately. They are all of different sizes, and probably, are from different individuals. The maximum breadth is across the zygapophyses, which are broadly expanded laterally; it apparently exceeds the maximum height (unobtainable on account of the abrasion of the neural spine in all the specimens) and greatly exceeds the length measured so as to include the pre- and postzygapophyses. A marked character is the shortness of the centrum. The cup is wider than high, with a well-defined sharp rim, and is directed very slightly downward. The ball is as slightly inclined upward. The zygosphene is broader than the neural canal is wide, and has a plane upper surface, and a straight sharp front margin that slightly overhangs the upper rim of the cup. The neural spine starts as an angular ridge behind the upper surface of the zygosphene. The neural canal is subtriangular in cross section, the angles being rounded with the apical one the most obtuse; its sides are slightly incurved. A low rounded ridge occupies the center of the floor of the canal longitudinally, corresponding in shape with the hypapophysial keel of the lower surface of the centrum. An angular interzygapophysial ridge is feebly developed, the surfaces above and below the ridge being shallowly concave. The front margin of the neural arch between the postzygapophyses is, in outline as seen from above, deeply emarginate, restricting the span available for the base of the neural spine. The facets of the zygapophyses and the zygosphene and zygantrum are inclined at a slight angle to each other, those of the zygapophyses being the less removed from the horizontal. The costal tubercle is not prominent; its articular

face in all the specimens is a little worn, but sufficiently well preserved to show that it is single. Its face is higher than broad, and is directed obliquely outward and downward from beneath the prezygapophyses at a level corresponding with that of the cup. In the largest vertebra (No. 3) [Cat. No. 6239] the articular face is seen to be convex above and slightly concave below posteriorly. A rounded ridge is developed near the base of the tubercle, and passes backward almost to the side of the ball at its mid-height. This ridge leaves a longitudinal depression on either side of the hypapophysial ridge which passes from the ball to the cup and is well

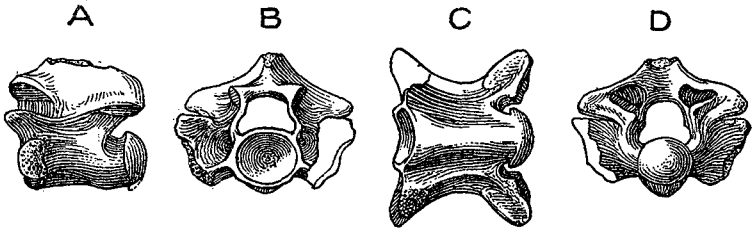


FIGURE 13.—*Thoracic vertebra of Ogmophis compactus Lambe*

Type no. 6237 Nat. Mus. Can. *A*, lateral; *B*, anterior; *C*, ventral; *D*, posterior views. ×3.

rounded and distinct but not prominent. There are slight variations in the above vertebrae but their general proportions are similar. The vertebra figured on Plate I [Fig. 13] is No. 2, [Cat. No. 6237 marked type] of the table of measurements given below.

Measurements in mm.

	"Length of centrum	Breadth of vertebra		Height of vertebra	
		ant.	post.	ant.	post.
No. 1	4.3	9.5	....	....	8.0
No. 2	5.0	....	7.75	....	6.0
No. 3	...	11.0	....	6.75	...
No. 4	4.3	....	6.00	....	6.4

"This species is distinct from *O. angulatus* described by Cope from the White River (Oligocene) beds of northeastern Colorado. The vertebrae of Cope's species approach more closely in general form those of the Cypress Hills species than do those of other described species of the genus. *O. arenarum* Douglass from the Flint Creek beds (Miocene) of Montana differs in important particulars."

All the vertebrae ascribed to this species have been much rounded and worn, and in none is the neural spine completely preserved. Lambe failed to designate a type in his original description, but his having written "Type" on the container of No. 6237 N. M. C. would seem sufficient to indicate his intention.

O. compactus is at once distinguished from the other species of the genus by its much larger size, being nearly twice their dimensions. The deep grooves which parallel the angularly rounded keel on either side are much more pronounced than in either *O. oregonensis* or *O. arenarum*. The distinct ridge joining the lower end of the diapophyses with the side of the glenoid fossa is also distinctive of this species.

Two articulated vertebrae, No. 13675 U. S. N. M., from the Oligocene of Sioux County, Nebraska, except for their smaller size, have the closest resemblance to *O. compactus* and are provisionally referred to it. If

correct in this identification it marks the first record of this species outside of Canada. The neural spine of this specimen is very short and confined to the posterior half of the neural arch. The truncated tops of these vertebrae are slightly expanded laterally.

Referred specimens

No. 4241, N. M. C. Consists of one thoracic vertebra. From east end of Cypress Hills, Saskatchewan, Can. Collected by L. M. Lambe, July 25, 1904.
No. 13675, U. S. N. M. Two thoracic vertebrae. From the Oligocene, Sioux Co., Neb. Collected by J. B. Hatcher, 1888.

Genus *Calamagras* Cope

Calamagras, COPE, Synop. new Vert. Tert. Colo. (October 1873) p. 15. Washington.
Aphelophis, COPE, Synop. new Vert. Tert. Colo. (October 1873) p. 16. Washington.

GENOTYPE: *Calamagras murivorus*.
Known only from thoracic vertebrae.

DIAGNOSIS: Centrum relatively short. Glenoid fossa, suboval. Condyle moderately oblique. Haemal carina represented by an inferior keel, which is probably produced into a true hypapophysis on the anterior part of the column, but which almost disappears in the posterior thoracic region. Neural spine short and stout, occupying less than half the length of the neural arch. Neural arch low, wide with deep lateral emarginations, with deepest part anterior to mid-length. Zygosphene wider than glenoid fossa, with slightly convex superior border, and thin dorsoventrally. Zygapophyses joined by a short inconspicuous ridge. No process below prezygapophyses. Diapophyses prominent, articular surfaces continuous, slightly convex above, slightly flattened below, but without distinct separation. Parapophyses extend slightly below the level of the centrum, with faint ridge extending backward.

The genus *Aphelophis* Cope is here regarded as a synonym of *Calamagras*, for a comparison of the types of *C. murivorus* and *A. talpivorus* failed to disclose any characters that could possibly be interpreted as being of generic importance. The faintly developed vertebral keel in the type of *Aphelophis talpivorus*, the slightly more ovate glenoid fossa, and the less differentiated articular surfaces of the diapophyses, are the more important differences between the two types and, although they may in part be accounted for by coming from different parts of the vertebral column, for the present it seems best to retain the species which will now be known as *Calamagras talpivorus* (Cope).

Originally three species were assigned to this genus. Named in chronological order these were: *Calamagras murivorus*, *C. truxalis*, and *C. angulatus*. *C. truxalis* was later found by Cope to be a synonym of *C. murivorus*. Thus at the present time *C. murivorus*, *C. angulatus*, and *C. talpivorus* are here recognized as pertaining to this genus. With the discovery of better-preserved specimens it would occasion no surprise if this number was further reduced.

The genus *Calamagras* known only from vertebral characters closely

resembles the genus *Ogmophis*, and it may eventually be shown that no generic distinctions exist. Cope was the first to recognize their close affinities and ventured the suggestion that both might belong to the existing family Erycidae or Lichamuridae. For the present, however, this genus will be retained in the Boidae.

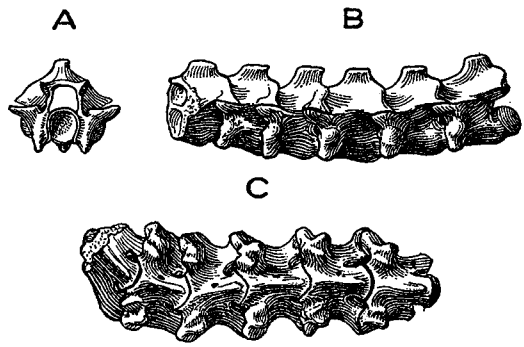


FIGURE 14.—*Articulated thoracic vertebrae of Calamagras murivorus Cope*

Type no. 1603 A. M. N. H. *A*, anterior, much restored; *B*, lateral; *C*, ventral views. ×3.

Calamagras murivorus Cope

Calamagras murivorus, COPE, Synop. new Vert. Tert. Colo. (October 1873) p. 15. Washington; U. S. Geol. Geog. Surv. Terr. (Hayden), 7th Ann. Rept., 1873 (1874) p. 517; U. S. Geol. Surv. Terr. (Hayden), 3d Rept. (1884) p. 784—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 480; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 268.

Calamagras truxalis, COPE, Synop. new Vert. Tert. Colo. (October 1873) p. 15. Washington; U. S. Geol. Geog. Surv. Terr. (Hayden), 7th Ann. Rept., 1873 (1874) p. 517—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 480.

TYPE SPECIMEN: Am. Mus. Nat. Hist., Cat. no. 1603. Consists of six articulated vertebrae. Collected by E. D. Cope, 1873.

TYPE LOCALITY: Cedar Creek, northeastern Colorado.

HORIZON: Oligocene. Oreodon Beds.

ORIGINAL DESCRIPTION: "*Char. gen.* An obtuse hypapophysial keel most prominent posteriorly. No ridge from the zygosphene; that from parapophysis wanting or rudimentary. Neural spine posterior, short, and obtuse. Neural arch not produced posteriorly; zygosphene wider than articular cup. Articular surfaces moderately oblique. A concavity separating the articular surfaces of the dia- and parapophyses.

"This genus differs from *Boavus*, as described by Marsh, in the absence of ridges and concavity of parapophysis.

"*Char. specif.*—Articular surfaces a broad transverse ellipse. Hypapophysis terminating in an appressed point. No inferior lateral ridge on centrum; a trace of one on the posterior part of neural arch."

Measurements

	m.
"Length of centrum	.0030
Width of ball	.0017
Depth of ball	.0013
Width between parapophyses	.0023
Depth of entire vertebra	.0040

"Represented by six consecutive vertebrae. Size that of the water snake (*Tropidonotus sipedon*)."

Cope (1884, p. 784) included the species *C. truxalis* Cope as a synonym under *C. murivorus*, and on the basis of the two types, Nos. 1603 and 1657 A. M. N. H., and a third specimen No. 1658 A. M. N. H., making 13 vertebrae in all, he published a revised description as follows:

"The zygosphene is a little wider than the articular cup. The ball, viewed directly in the line of the axis of the centrum, has a wide, transversely placed oval outline. The balls of a set of three vertebrae [No. 1658 A. M. N. H.] in which the

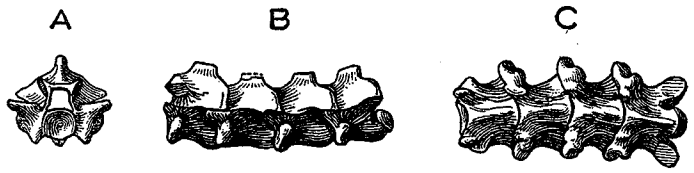


FIGURE 15.—*Thoracic vertebrae of Calamagras murivorus Cope*

Type of *C. truxalis* Cope. No. 1657 A. M. N. H. *A*, anterior; *B*, lateral; *C*, ventral views. ×3.

hypapophyses are best developed, and which I therefore supposed to belong to the anterior part of the series, are more nearly round. The ridge connecting the zygapophyses is deeply emarginate. In the anterior vertebrae the hypapophyses are acute keels supporting an angular prominence near the center; further posteriorly there is a slight prominence at the base of the ball. More posteriorly the hypapophysis forms a narrow but somewhat obtuse ridge, terminating posteriorly in an apical angle at the inferior side of the ball. The neural arches are separated by spaces equal to the lengths of their bases. The rib articulations present the peculiarity of other members of this group, of a single surface, of which the superior half is convex, and the inferior slightly concave."

Measurements

"No. 1—More anterior [No. 1658 A. M. N. H.] m.

Length of centrum	0.0027
Width of ball	.0016
Depth of ball	.0011
Width between parapophyses	.0020
Depth of entire vertebra	.0034

No. 2—More posterior [No. 1603 A. M. N. H.]

Length of centrum	0.0030
Width of ball	.0017
Depth of ball	.0013
Width between parapophyses	.0023
Depth of entire vertebra	.0040

From the beds of the White River Epoch in northeast Colorado."

Comparison of the above-mentioned specimens leaves no doubt of the correctness of Cope's final conclusion that all are co-specific. (Compare Figs. 14 and 15.)

The differences in the three vertebral series pointed out by Cope in his final diagnosis of the species are almost precisely those modifications that take place in the different parts of the column of a single individual.

Referred specimen

No. 13824, U. S. N. M. Consists of three thoracic vertebrae, Oligocene. Sioux Co., Neb. Collected by J. B. Hatcher, 1888.

Calamagras angulatus Cope

Calamagras angulatus, COPE, Synop. new Vert. Tert. Colo. (October 1873) p. 16. Washington; U. S. Geol. Geog. Surv. Terr. (Hayden), 7th Ann. Rept., 1873 (1874), p. 518.

Ogmophis angulatus, COPE, U. S. Geol. Surv. Terr. (Hayden), 3d Rept., vol. 3

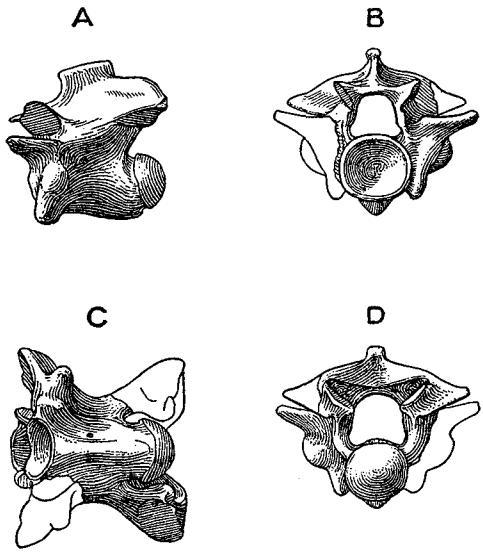


FIGURE 16.—*Thoracic vertebra of Calamagras angulatus Cope*

Type no. 1654 A. M. N. H. *A*, lateral, restored from opposite side; *B*, anterior; *C*, ventral; *D*, posterior views. ×5.

(1884) p. 783, 784, pl. LVIII a., fig. 13—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 480; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 268—LAMBE, Contrib. Canad. Paleont., vol. 3, pt. 4 (1908) p. 21.

TYPE SPECIMEN: A. M. N. H., Cat. no. 1654. Consists of a single vertebra collected by E. D. Cope, 1873.

TYPE LOCALITY: ? Cedar Creek, Colorado.

HORIZON: Oligocene, Oreodon Beds.

ORIGINAL DESCRIPTION: "The largest species, distinguished by the presence of a low ridge on the centrum from the parapophysis to the middle of the centrum. Neural spine on the posterior half of the neural arch short, truncate. Hypapophysis short, ending in an obtuse point. Parapophysis larger than in other species, nearly equal to the diapophysis."

Measurements

	m.
"Length of centrum	.0030
Diameter of ball, transverse	.0017
Diameter of ball, vertical	.0016
Width between parapophyses	.0024
Depth of entire vertebra	.0045"

Cope first referred this species to the genus *Calamagras* but later assigned it to *Ogmophis*. The author now proposes to transfer the species back to

Calamagras because in its main features, such as short, truncated spine, confined to posterior half of the arch; zygosphene wider than glenoid fossa; hypapophysis short, ending in an obtuse point; and articular surfaces of the diapophysis but slightly differentiated, the type vertebra is in complete agreement with the type of *C. murivorus*. It differs in the presence of a low ridge on the centrum from the parapophysis to the middle of the centrum, and a slightly larger parapophysial articular surface. A faint suggestion of the parapophysial ridge is present on some of the type vertebrae of *C. murivorus* which leads to the suggestion that in another part of the vertebral column this ridge may also be present in that species. For the present, however, it seems best to continue the species although undoubtedly, with the discovery of adequate specimens, it will eventually be shown to be a synonym of *C. murivorus*.

Calamagras talpivorus (Cope)

Aphelophis talpivorus, COPE, Synop. new Vert. Tert. Colo. (October 1873) p. 16. Washington; U. S. Geol. Geog. Terr. (Hayden), 7th Ann. Rept., 1873 (1874) p. 517; U. S. Geol. Surv. Terr. (Hayden), 3d Rept., vol. 3 (1884) p. 782, pl. 60, fig. 21—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 480; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 268.

TYPE SPECIMEN: A. M. N. H., Cat. no. 1598. Consists of three vertebrae. Collected by E. D. Cope, 1873.

TYPE LOCALITY: Cedar Creek, northeastern Colo.

HORIZON: Oligocene, Oreodon Beds.

ORIGINAL DESCRIPTION: "*Char. gen.* Similar to the preceding [*Calamagras angulatus*] in the absence of acuminate diapophysial process, the zygosphene exceeding the articular extremity in width, and the simplicity of the posterior border of the neural arch. There are no longitudinal ridges, the hypapophysis being entirely wanting. The articular faces of the para- and diapophysis continuous without intervening concavity.

"*Char. specif.*—Vertebrae short and wide, the neural spine stouter and more obtuse than in any other species here described, occupying less than half the neural arch with its basis. Zygosphene wide, depressed, with nearly straight posterior margin, not sending any ridge backward from the posterior face. Articular faces of centrum a depressed oval; ball looking upward, its axis making 45° with that of the centrum. Parapophysis not projecting below centrum."

Measurements

	m.
"Length of centrum	.0026
Diameter of cups, transverse	.0018
Diameter of cups, vertical	.0012
Width between parapophyses	.0017
Depth of entire vertebra	.0034
Width of zygosphene	.0020

Represented by three vertebrae of an individual about the size of *C. truxalis*."

In the original description Cope states, "the hypapophyses being entirely wanting." This statement is entirely correct insofar as there is a true process, but there is a faint keel whose presence leads to the belief that these vertebrae may pertain to the posterior thoracic region of *C.*

murivorus. The changes observed in the ventral structure of these series of *Calamagras* vertebrae are not greater than those in the vertebral column of *Boavus idelmani*, and all might well pertain to the vertebral column of a single individual.

The short and more obtuse spine, ovate articular ends, and less globular diapophyses, may for the present be used to distinguish *C. talpivorus* from the other described species.

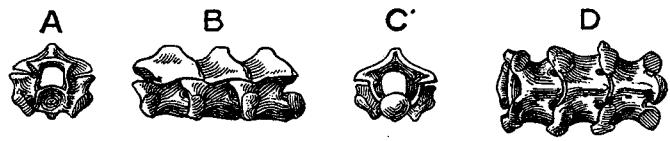


FIGURE 17.—*Thoracic vertebrae of Calamagras talpivorus (Cope)*

Type no. 1598 A. M. N. H. *A*, anterior; *B*, lateral; *C*, posterior; *D*, ventral views. ×3.

Family PALAEOPHIDAE

Palaeophidae LYDEKKER, Cat. Foss. Reptilia and Amphibia Brit. Mus., pt. 1 (1888) p. 256.

Large snakes, probably of marine habits, including the two genera *Palaeophis* and *Pterosphenus*, both of Eocene age. Representatives of this family have been found as follows: *Palaeophis* Owen, Lower and Middle Eocene of England, Belgium, and Nigeria; *Pterosphenus* Lucas (*Moeriophis* Andrews), Upper Eocene of Alabama and top of Middle Eocene, Fayum, Egypt. In both localities they are associated with the remains of the sea-living mammal *Basilosaurus* (*Zeuglodon*). The type genus was referred by Owen to the Hydrophidae, but de Rochebrune, Cope, Marsh, and Andrews considered the family allied to the *Pythons*.

The family is characterized by Lydekker, with slight emendations, as follows:

> Vertebrae with very tall neural spines, which have no backwardly directed processes at the summit; costal articulations placed low down on the centrum, and the zygapophyses not expanded and scarcely reaching beyond the lateral borders of the costal articulations; hypapophyses single or double, occasionally joined by a sharp ridge. Ribs without *tuber-costae*.

The outstanding differences between the two genera constituting the family Palaeophidae may be enumerated as follows:

In *Pterosphenus* the aliform processes are more strongly developed; zygosphene wider than glenoid fossa; with articular faces that look more strongly downward than outward; and the more ventral position of the articular surfaces of the prezygapophyses.

Genus *Palaeophis* Owen

Palaeophis OWEN, Geol. Soc. London, Tr., 2d ser., vol. VI (1839) p. 209, pl. 22.
Dinophis MARSH, Am. Jour. Sci., 2d ser., vol. 48 (1869) p. 397–440.

Titanophis MARSH, Am. Assoc. Adv. Sci., Pr., Nashville meeting, 1877 (1878) p. 223—LYDEKKER, Cat. Foss. Reptilia and Amphibia Brit. Mus. Pt. I (1888) p. 257.

Paleophis LYNN, Johns Hopkins Univ. Geol. Ser. no. 11 (1934) p. 345–349, pl. 17.

GENOTYPE: *Palaeophis toliapicus* Owen.

Known only from vertebrae and ribs.

DIAGNOSIS: Aliform processes present, but small. Centrum relatively long, posterior half usually compressed. Glenoid fossa as wide or wider than zygosphene. Condyle moderately oblique. Inferior surface of centrum with either one or two hypapophyses, sometimes connected by a thin, sharp, median keel. Diapophyses placed low down on side of centrum, prominent, heavy, and projecting below level of centrum. Zygosphenes stout and deep, articular surfaces looking strongly outward. Zygantrum rather shallowly excavated. Zygapophyses usually joined by an inconspicuous horizontal ridge. Lateral emarginations between zygapophyses wide and relatively shallow. Anterior zygapophyses with a wide (vertically) projecting plate below the level of the articulating surface. Neural arch elevated or depressed. Neural canal nearly as wide as zygosphene. Well-defined epapophyses. Neural spines tall, with base extending from one-half to nearly the entire length of the neural arch.

Nine species have been named for the genus *Palaeophis*, four of which are American. Professor Owen established the genus for the species *toliapicus* and subsequently described *P. typhaeus*, *P. porcatus*, and *P. longus*, all from the London Clay, Eocene of England. Pomel set up the species *P. giganteus*, from the Sanden, Cuise de la Motte. The American species in chronological order are: *P. littoralis* Cope, *P. halidanus* Cope, *P. grandis* (Marsh), and *P. virginianus* Lynn. The first three mentioned are from the Eocene of New Jersey, the last from the Eocene of Virginia.

The British materials are much more numerous and better known than the American, but at least, as pointed out by Janensch (1906, p. 335), it is quite probable that too many species have been named. Lydekker (1888b, p. 258) has already indicated his belief that *P. porcatus* is a synonym of *P. typhaeus*.

On the basis of the differences displayed by the type specimens, the American species can be distinguished from one another, but how many of these characters may be modifications attributable to changes taking place in different sections of the same vertebral column cannot be positively determined from known specimens. For that reason it appears best to retain all the named species until the discovery of better-preserved specimens will disclose their true relationships.

Key to American species

Smallest size. Vertebrae with double hypapophyses, joined by a sharp median keel. Neural arch elevated. Base of spine extending short of anterior margin of the arch.

P. littoralis

Medium size. Vertebrae with double hypapophyses, anterior member reduced, median keel rounded. Neural arch depressed.

P. halidanus

Large size. Vertebrae with double hypapophyses, joined by a sharp median keel. Neural arch elevated. Base of spine extending short of anterior margin of the arch.

P. grandis

Large size. Vertebrae with single posterior hypapophysis. Neural arch depressed. Base of spine occupying only the anterior half of the neural arch.

P. virginianus

Palaeophis littoralis Cope

Palaeophis littoralis, COPE, Philadelphia Acad. Nat. Sci., Pr. (1868) p. 147, 234; Appendix B, Geol. N. J. (1869) p. 737. Newark; Am. Philos. Soc., Tr., vol. 14 (1869) p. 227, pl. 5, fig. 1; Philadelphia Acad. Nat. Sci., Pr. (1872) p. 14; Am. Nat., vol. 16 (1882) p. 981, fig. 1—MARSH, Am. Jour. Sci., 2d ser., vol. 48 (1869) p. 400, (*Dinophis*)—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 479; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 267—JANENSCH, Arch. Biontol., vol. 1 (1906) p. 337, 339, 343.

TYPE SPECIMEN: A. M. N. H., Cat. no. 2392. Consists of three vertebrae. Collected by Dr. Knieskern.

TYPE LOCALITY: Squankum, Monmouth Co., N. J.

HORIZON: Manasquan marl, Eocene.

ORIGINAL DESCRIPTION: "Cope called attention of the Academy to the rarity of Ophidian remains and to the fact that none had been discovered in North America up to the present time. He then exhibited two vertebrae of a serpent of or near the family of the Boas, from the greensand of Squankum, Monmouth Co., N. J., which had been discovered by Dr. Knieskern.

"Peculiar interest attached to these specimens, from the fact that they came from a bed which has recently been stated, by Conrad, to be an equivalent of the older Eocene or London clay of the Thames Valley. They confirm this identification exactly, since they belong to Owen's genus *Palaeophis*, which is characteristic of these beds in England. They indicate a species intermediate between the two larger described by Prof. Owen, and of some fifteen feet in length. It was associated with remains of crocodiles, sting-rays, and saw-fishes, and was named from its geographical and geological location, *Palaeophis littoralis* Cope."

On October 27, 1868, Cope published the additional information and description as follows:

"The specimens consist of three vertebrae, neither of them perfect; the most so with neural arch, but with diapophyses broken off.

"The more perfect is an anterior dorsal, with two hypapophyses, the anterior small and directed forwards, the posterior larger, and directed vertically downwards. The ball has some superior up-look, though the groove which bounds it is but little oblique. Centrum much compressed behind the middle. Plane of basis of zygapophysis opposite floor of neural arch; zygapophysis directed slightly upwards and outwards, continuous by a broad wing running posteriorly with the diapophysis. Neural arch well elevated, (broken off behind). The basis of the neural spine is narrow on the anterior part of the arch, and does not reach the anterior margin.

			Mm.
"Length centrum (ball to edge cup)	8.25	lines	[17.3]
Depth ball	4.25	"	[8.9]
Width ball	5.00	"	[10.5]
Width between extremities of zygapophyses	8.00	"	[16.8]
Depth cup and neural arch	7.50	"	[15.7]
Width neural arch behind	2.25	"	[4.7]

"A strong ridge extends from the zygapophysis posteriorly parallel with the centrum. There is no ridge continued from the zygosphene. Except a slight ridge below the fossa, which is above and back of the diapophysis, the surface of the vertebra is smooth.

"Another vertebra is rather broader in proportion to its length, and less compressed.

			Mm.
"Length (as above)	7.8	lines	[16.3]
Width ball	5.0	"	[10.5]

"In both the ball has a subtriangular outline. In the more perfect, the base of the neural canal is divided by a narrow longitudinal epapophysis."

The type of *Palaeophis littoralis* has been temporarily misplaced in the American Museum of Natural History and hence was not available for this study. Fortunately, Cope published illustrations of the best-preserved vertebra (Fig. 18) which clearly depicts the principal features of this species. The relatively small size of the vertebra and the presence of a double hypapophysis with elevated neural arch clearly indicate a

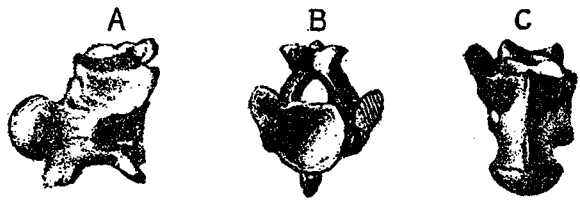


FIGURE 18.—*Anterior thoracic vertebra of Palaeophis littoralis Cope*

Type no. 2392 A. M. N. H. *A*, lateral; *B*, anterior; *C*, ventral views. Natural size. After Cope.

position well forward in the vertebral column. In this connection attention is directed to the close resemblance of the type vertebra of *P. littoralis* Cope to that of *P. grandis* (Marsh). Except for the much larger size of the *P. grandis* vertebra, and the higher elevation of the prezygapophyses, the two specimens are closely similar. Such minor differences as are noted can be accounted for by slightly different positions in the anterior thoracic series. The chief distinction between these species as known at the present time, therefore, is that of size, the *P. grandis* vertebra having a bulk fully three times that of *P. littoralis*.

A specimen, No. 11753 in the National Museum collections, clearly pertains to this species. It is slightly larger than the type vertebra, having a length of 20 mm. from the ball to edge of the cup, width of ball 11 mm.; width of zygosphene 11 mm. This vertebra is deficient in almost precisely the same way as the type specimens and on that account does not contribute anything new to our knowledge of the structural features of this species.

Referred specimen

No. 11753, U. S. N. M. Consists of a single anterior thoracic centrum with anterior portion of neural arch lacking the spine and prezygapophyses. From Vincentown, Durlington Co., N. J. Eocene, Vincentown lime. Collected by Charles Schuchert, 1892.

Palaeophis halidanus Cope

Palaeophis halidanus, COPE, Philadelphia Acad. Nat. Sci., Pr. (1868) p. 234; Appendix B, Geol. N. J. (1868) p. 738. Newark; Am. Philos. Soc., Tr., vol. 14 (1869) p. 227, pl. 5, fig. 2; Philadelphia Acad. Nat. Sci., Pr. (1872) p. 14; Am. Nat., vol. 16 (1882) p. 981, fig. 2; (1891) p. 52, fig. 28-b—MARSH, Am. Jour. Sci., 2d ser., vol. 48 (1869) p. 400 (*Dinophis*)—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 479; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 267—COOKE AND STEPHENSON, Wash. Acad. Sci., Jour., vol. 18 (1928) p. 143—HOFFMAN, *in* BROWN, *Klassen und Ordnungen des Thierreichs* (1890) p. 1812—JANENSCH, Arch. Biontol., vol. 1 (1906) p. 337, 343.

TYPE SPECIMEN: P. M. N. H., Cat. no. 2763. Consists of a single vertebral centrum with one anterior zygapophysis. Collected by O. B. Kinney.

TYPE LOCALITY: In excavations of the Squankum Marl Company, Squankum, about 3 miles south of Farmingdale, Monmouth Co., N. J.

HORIZON: Manasquan marl, Eocene.

ORIGINAL DESCRIPTION: "A single vertebra represents this species. It indicates one of the largest of the genus, being little different from the *P. typhaeus* of Owen in size. The bulk of the vertebra is double that of *P. littoralis*. In addition to this point, it differs from the latter in the greater transverse diameter of the cup and ball; these are transversely oval; in the *P. littoralis* subtriangular ovate; the centrum is naturally less constricted and broader in the former. The articular face of the zygapophysis is broadly ovate in *P. halidanus*, narrowly in the smaller species; while there are indications of similar posterior hypapophysis in both, the anterior in the *P. halidanus* appears to have been smaller.

"As compared with the species described by Owen, the cup and ball are more transverse than in any noticed in the British Fossil Reptiles, approaching that figured by him in Pl. 3, fig. 22–24; the ball has not the oblique, up-looking profile of that species, but forms a nearly regular arc, with its posterior margin superiorly a little behind its position inferiorly. The hypapophysial ridge is considerably interrupted, as in the *P. typhaeus*, while *P. littoralis* agrees with the *P. toliapicus* in having it continuous. The two last named species differ in the development of their hypapophyses; in the American species both are large, especially the posterior; in the English, the anterior process is weak or wanting; the ridge connecting the zygapophyses disappears in the *P. toliapicus*, and continues in the *P. littoralis*. The general proportions of the centrum are slender, as in *P. toliapicus* and not so stout as in *P. porcatus* Owen.

"The diapophyses in the *P. halidanus* are not so pedunculate as in *P. typhaeus*, though they are separated above by a notch from the vertical ala which descends from the zygapophysis, which I do not find in the *P. littoralis*. They approach near the margin of the cup in their transverse extent below.

"The horizontal ridge between the zygapophyses is strongly marked, and in the specimen in hand comes off from the anterior vertical ala below the zygapophysis, rather than from the plane of that process, as in *P. littoralis*. The neural canal is depressed behind, below the margin of the ball, and has an obtuse epapophysis along the median region of its median line. There is no ridge parallel to the hypapophysis. The cup is partially broken, but its transverse diameter appears to have been one-fourth greater than the vertical. The transverse plane of the face of the zygapophysis is transverse. A large part of the neural arch is broken away.

			Mm.
Length from edge up to convexity of ball	12.75	lines	[26.7]
Width between anterior zygapophyses	13.5	"	[28.3]
Width of cup	8.4	"	[17.6]
Depth of cup	6.2	"	[13.0]
Least width centrum at middle	5.3	"	[11.1]
Width neural canal	4.0	"	[8.4]

"*Locality:* This serpent was found by my friend, O. B. Kinney in the excavation of the Squankum Marl Company, at Squankum, Monmouth Co., N. J., a few miles south of Shark River. The horizon is Eocene.

"This animal was probably a sea-serpent distantly allied to the Boas, and far exceeding in dimensions those at present inhabiting the Indian Ocean. Its size was similar to that of the very largest of terrestrial serpents of the modern era, and was probably proportioned to a length of twenty feet."

The type of *Palaeophis halidanus* in the original paper describing the species was said to be in the collection of the New Jersey Geological Survey. Correspondence with the State Geologist, Dr. Henry B. Kümmel, developed the fact that it could not be found in the state collections; nor was there any record of it in the catalogue of specimens.

Among the ophidian materials received from the Peabody Museum of

Natural History was a large but poorly preserved snake vertebral centrum, accompanied by a slip of paper, on which was written, apparently in Cope's handwriting: "*Palaeophis halidanus*. Type. Squankum." That this is the type was further verified by comparison with the illustrations of the specimen (Cope, pl. 5, fig. 2). The type consists of a poorly preserved centrum to which remains attached a small portion of the neural

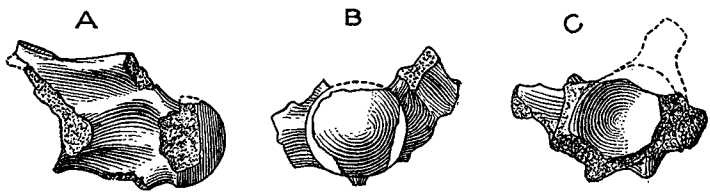


FIGURE 19.—*Posterior thoracic vertebra of Palaeophis halidanus Cope*

Type no. 2763 P. M. N. H. *A*, lateral; *B*, posterior; *C*, anterior. Natural size.

arch including the right prezygapophyses. Since it was originally illustrated, the specimen has suffered the loss of minor pieces (Fig. 19).

The fragmentary condition of the type and only known specimen of this species makes it extremely doubtful that other specimens can ever be positively identified with it. Its intermediate size, with rounded keel, reduced anterior hypapophyses, and wider cup, are modifications that might be expected in vertebra posterior in position to those of the *P. littoralis* type. With the discovery of more adequate specimens, it would not be surprising if both styles were found in the vertebral column of a single individual.

While Cope's original description fully describes the features of the type specimen, as now preserved practically all evidence of the former existence of a small hypapophysis on the anterior end of the centrum has been lost. The beginning of a slight upward turn of the median ventral surface at the broken edge strongly suggests the authenticity of Cope's original observation that the hypapophysis was double.

Palaeophis grandis (Marsh)

Dinophis grandis, MARSH, Am. Jour. Sci., 2d ser., vol. 48 (1869) p. 397-400—DE ROCHEBRUNE, Nouv. Arch. Mus. Hist. Nat., 2d ser., vol. 3 (1880) p. 289.

Palaeophis grandis, COPE, Am. Philos. Soc., Tr., vol. 14 (1869) p. 228; Philadelphia Acad. Nat. Sci., Pr. (1872) p. 14—DE ROCHEBRUNE, Nouv. Arch. Mus. Hist. Nat., 2d ser., vol. 3 (1880) p. 289—HAY, U. S. Geol. Surv., Bull 179 (1902) p. 479; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 267—JANENSCH, Arch. Biontol., vol. 1 (1906) p. 337—LYNN, Johns Hopkins Univ., Stud. Geol., no. 11 (1934) p. 247, 248.

TYPE SPECIMEN: Peabody Mus. Yale Univ. Cat. no. 2762. Consists of a single dorsal vertebra. Collected by W. S. Kimball.

TYPE LOCALITY: Near Shark River, Monmouth Co., N. J.

HORIZON: Probably Shark River formation, Eocene.

ORIGINAL DESCRIPTION: "The earliest remains of *Ophidia* both in Europe and this country have been found in the Eocene, and nearly all the species from strata older than the Post Pliocene appear to be more or less related to the constricting serpents. Remains of this character are not uncommon in European rocks, but in this country two species only, one founded on a single vertebra, have been described hitherto, and both of these were discovered in the Tertiary greensand of New Jersey. An interesting specimen from the same formation, recently presented to the Museum of Yale College, indicates a third species, much larger than either of the others, in fact, superior in size to any known fossil Ophidian, and not surpassed by the largest of modern serpents.

"This species is represented by a single dorsal vertebra, somewhat injured, but with the neural arch well preserved. The general form of the centrum is elongate, and considerably compressed behind the middle. The articular cup and ball are subtriangular ovate, and their faces are much more nearly vertical than is usual in ophidian vertebrae, the cup looking but very slightly downward. The neural arch is elevated, and massive. The neural canal is broader than high, and its floor depressed posteriorly, with indications of a slight medial epapophysis. The sides of the canal are marked by a sharp longitudinal ridge which, in connection with the arched roof above, gives a trifoliate outline to a transverse section of the opening, as in some species of *Python*. The floor of the neural canal is somewhat below the plane of the anterior zygapophyses. The zygosphene is much elevated, and its summit concave. It is narrower than the articular cup, a feature which appears to be peculiar to fossil serpents alone. Its anterior surface is deeply excavated, and the lateral margins extend from the base downward and outward to the superior edge of the cup, thus continuing the sides of the neural canal forward. The zygantrum is comparatively shallow, and has its greatest depth on the medial line. Its base extends downward and backward until directly over the superior margin of the ball, protecting also from above the neural canal posteriorly. The neural spine is much compressed, triangular in outline at its base, and does not extend to the anterior margin of the zygosphene. The base of the neural arch is strengthened by a thick rounded ridge, which unites the zygapophyses on each side. It begins below the plane of the anterior zygapophysis, and ascending slightly, joins the posterior zygapophysis above the articular face. Remnants of two hypapophyses connected by a prominent ridge exist, and show that the anterior process was much the smaller, and its base somewhat separated from the margin of the cup.

"The principal dimensions of this vertebra, which is apparently an anterior dorsal, are as follows:—

			Min.
Length of centrum from edge of cup to convexity of ball	14.25	lines	[29.00]
Transverse diameter of cup	9.10	"	[18.00]
Vertical diameter of cup	7.5	"	[14.00]
Distance from top of zygosphene to lower margin of cup	13.25	"	[28.00]
Vertical diameter of ball	7.25	"	[14.50]
Width of neural canal in front	3.75	"	[8.00]
Height of neural canal in front	2.50	"	[5.25]

"The present species is quite distinct from *Palaeophis halidanus* Cope, which somewhat resembles it in size. The original specimen on which the latter species was founded is now in the Museum of Yale College, and a comparison shows that the centrum is much more depressed, the cup and ball more transverse, and the ridge uniting the zygapophyses narrower in proportion, and less rounded. From the vertebrae of *Palaeophis littoralis* Cope, which it most nearly resembles in general form, outline of cup, and hypapophyses, the present specimen differs especially, judging from the description and figures [Cope, 1868, p. 234; 1869, pl. 5] in having the plane of the anterior zygapophyses above the floor of the neural canal, and the ridge between the zygapophyses not parallel with the centrum. The zygosphene is also more elevated, and the top of the neural canal more rounded in front. The bulk of the present vertebra, is, moreover, at least three times that of *Palaeophis halidanus*, and five or six times that of *P. littoralis*. It is also considerably larger than any vertebra described by Professor Owen in his valuable memoir on the Tertiary Ophidia of England (1850) as well as quite distinct from any of the species there defined.

"The present specimen is evidently identical generically with the two species already described by Professor Cope, but in comparing these various remains with typical specimens and figures of the species placed by Professor Owen in his genus

Palaeophis, several marked differences between the two groups will be observed, which would seem to justify their separation. For the reception of the American species, therefore, the genus *Dinophis* is proposed. Among the most apparent differences between this genus and *Palaeophis*, to which it is closely related, are the following:—The base of the neural spine in *Dinophis is not* coextensive with the supporting arch, but rises a short distance back of the anterior margin of the zygosphene,

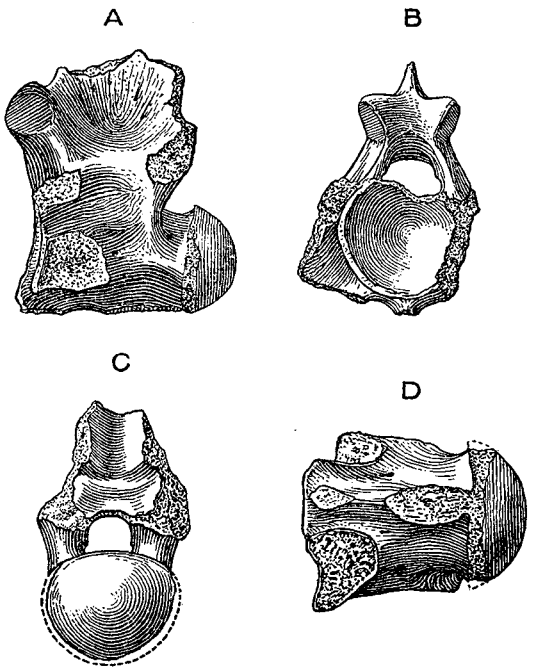


FIGURE 20.—*Thoracic vertebra of Palaeophis grandis (Marsh)*

Type no. 2762 P. M. N. H. *A*, lateral; *B*, anterior; *C*, posterior; *D*, ventral views. Natural size.

as in the existing *Python*. The ridge connecting the anterior and posterior zygapophyses is much more developed, and its continuous crest more rounded. The sloping sides of the arch above the neural canal are more deeply concave, and an obtuse ridge separates the concavity from the anterior zygapophysial notch. The neural canal has a sharp longitudinal ridge on each side, which gives its transverse section a trifoliate outline, as in *Python*. The zygosphene is more excavated anteriorly, and its summit is concave. The zygapophyses are more extended outwardly, and the hypapophysial ridge is more prominent.

"The vertebra here described would indicate an animal not less than thirty feet in length, probably a sea-serpent allied to the Boas of the present era. In view of its superior size, the species may appropriately be named *Dinophis grandis*."

The type specimen has been accurately and adequately described by Marsh. The type is here illustrated for the first time (Fig. 20).

In proposing the new genus *Dinophis*, Marsh distinguished it from *Palaeophis* by a number of features all of which are comparative in nature, the most clean-cut character being the noncoextensive extent of the neural spine with the length of the neural arch. In Owen's description of

Palaeophis, he mentions spines that are coextensive with the arch and those that are not. *P. typhaeus*, for example, has vertebrae with a well-defined space in front of the spine. After making careful comparison of the type of *P. grandis* with *Palaeophis* as described by Owen, the author agrees fully with Cope, who writes: "until the limits of the proposed genus [*Dinophis*] if valid, can be more fully defined, I retain the genus in *Palaeophis*."

Palaeophis virginianus Lynn

Palaeophis virginianus LYNN, Johns Hopkins Univ., Stud. Geol., no. 11 (1934) p. 245–249, pl. 17.

COTYPES: U. S. N. M. Cat. nos. 13640 and 13641. Consists of two posterior thoracic vertebrae. Collected by W. G. Lynn, 1933.

TYPE LOCALITY: Belvedere Beach, Va.

HORIZON: Aquia Creek, Eocene.

ORIGINAL DESCRIPTION: "On two successive collecting trips to the Eocene exposures at Belvedere Beach, Virginia, December 2, 1933, and March 27, 1934, single vertebrae of a large snake were found. These were not *in situ* but they lay on the beach within a short distance of each other so that there seems every probability that they belong to the same individual. The first specimen (Cat. No. 13640 U. S. N. M.) is complete except for the tip of the neural spine,[1] the distal portions of both diapophyses and the greater part of the left postzygapophysis. The second specimen (Cat. No. 13641 U. S. N. M.) consists of the centrum alone with the entire neural arch missing. Both are apparently posterior thoracic vertebrae, the former being one of the anterior members of this group while the latter is probably from a region considerably posterior.

"In both, the centrum is elongate in form and somewhat compressed behind the middle (see measurements). The median ventral process, the hypapophysis, is a rather blunt tubercle situated posteriorly. There is no anterior hypapophysial tubercle and no sign of a ridge extending anteriorly from the posterior process. Prominent nutrient canals are present, one on each side of the ventral surface of the centrum. The articular cup and ball (glenoid cavity and condyle) have their faces only slightly inclined from the vertical, and are sub-triangular in shape. The neural arch is massive, and flattened dorso-ventrally, the neural canal being broader than high (see measurements). The floor of the neural canal is depressed posteriorly and is traversed by a well-defined median longitudinal ridge, the epapophysis, which is interrupted, however, both anteriorly and posteriorly. There are two similar prominent ridges on the lateral walls of the canal so that the structure has a decided "trifoliate" appearance in section. The floor of the neural canal is below the plane of the prezygapophysis. The summit of the zygosphene is somewhat concave and it is but slightly narrower than the glenoid cavity (see measurements); its anterior excavation is shallow and smooth surfaced. The zygantrum is broadly excavated with a pair of nutrient canals leading into the neural arch. The stump of the neural spine shows that it had a triangular base, broad at the dorsal border of the zygantrum and narrowing anteriorly. It runs only to the base of the zygosphene anteriorly and is, therefore, not coextensive with the neural arch. There is a well-marked concavity on each side of the neural arch at the base of the neural spine. A low rounded ridge connects the pre- and postzygapophyses on each side running directly in the plane connecting the articular facets of these processes. The prezygapophyses are continuous with the diapophyses on each side. A slight ridge above and behind the diapophysis is directed postero-dorsally and becomes confluent with the ridge connecting pre- and postzygapophyses. The principal dimensions of the two type specimens are given herewith.

[1] The terminology used in describing the vertebrae is that given by Simpson (1933).

Measurements

	Vert. I *Mm*	*Vert. II* *Mm*
"Length of centrum (edge of glenoid cavity to convexity of condyle)	24.0	20.5
Distance from summit of zygosphene to lower margin of glenoid cavity	23.5	....
Transverse diameter of glenoid cavity	15.5	12.0
Vertical diameter of glenoid cavity	11.5	9.5
Transverse diameter of condyle	14.5	11.5
Vertical diameter of condyle	12.0	10.0
Distance between extremities of pre- and postzygapophyses	30.5	....
Distance between extremities of right and left postzygapophyses	32.0	....
Width of neural canal in front	8.0	....
Height of neural canal in front	5.0	....
Least width of centrum (near middle)	12.0	11.0
Greatest width of zygosphene (distance between tips)	14.0	....
Length of hypapophysis	7.0	5.0

"The genus *Palaeophis* was described by Owen ('41) for the reception of certain snakes from the Eocene of England. Three American species referable to this genus have been described: *P. littoralis* (Cope) ('68), *P. halidanus* (Cope) ('68), and *P. grandis* (Marsh) ('69), all from the Eocene greensands of New Jersey. The present specimens, as has been stated, were obtained at Belvedere Beach, Virginia, in Eocene deposits of the Aquia Creek stage.

"Examination of the type specimens reveals several outstanding characteristics in which the species under consideration differs from all three of those previously described from America. (1) *P. virginianus* possesses a posterior hypapophysial tubercle only; in this it resembles some of the English species figured by Owen. (2) In *P. virginianus* the ridge connecting pre- and postzygapophyses begins and ends on a level with the plane of the articular surfaces and is not parallel to the axis of the centrum since it ascends slightly posteriorly. (3) The neural arch in *P. virginianus* is compressed dorso-ventrally as compared with the condition in the other three species. (4) *P. virginianus* is unlike *P. littoralis* and *P. grandis* but resembles *P. halidanus* in that the centrum is not so strikingly compressed behind the middle. In addition to these general differences there are many other features in which the present species differs from particular other forms. In *P. littoralis* the plane of the base of the prezygapophysis is on a level with the floor of the neural canal, in *P. virginianus* considerably above it. In *P. grandis* the zygosphene is much narrower as compared with the width of the condyle than is the case in *P. virginianus*. Moreover, the prezygapophyses in the former are set almost immediately beneath the articulating facets of the zygosphene and, therefore, do not extend so far laterally as in *P. virginianus*. In *P. halidanus* the shape of the condyle and glenoid cavity differs from that in *P. virginianus*, in the former they are "transversely oval," in the latter sub-triangular in outline. In the former the articular face of the prezygapophysis is broadly ovate, in the latter narrowly ovate. Moreover, the neural spine is laterally compressed in *P. halidanus* and its base approaches the anterior end of the zygosphene much more nearly than is the case in *P. virginianus*.

"Certain of these characters are clearly features which vary with position in the column. In the skeleton of a recent *Python molurus* the neural spine approaches nearly to the tip of the zygosphene in the vertebrae of the central part of the column, but ends considerably behind the zygosphene in vertebrae lying more anteriorly as well as in those more posteriorly placed. The degree of development of the neural spine and the position of the articulating facets of the zygapophyses also vary with position in the column. However, when these facts are considered there still remain a number of differences which serve to distinguish the various species.

"Marsh ('69) in connection with his description of *P. grandis* calls attention to certain characteristics by which the three American species, *P. littoralis*, *P. halidanus* and *P. grandis*, differ from the forms described by Owen from England. Marsh considered these differences sufficiently important to warrant creation of a new genus *Dinophis*, for the American forms but this has not been generally accepted. In most of these points outlined by Marsh *P. virginianus* agrees with the other American

species but in two respects it differs from them and resembles the British forms. One character, the absence of the hypapophysial ridge, has already been noted. In addition, the other American species are characterized by a prominent ridge running from the zygosphene to the base of the prezygapophysis. This is practically absent in *P. virginianus* just as it is in Owen's types. This would seem to be an added indication that Cope's original conclusion that the English and American forms are generically identical is a correct one."

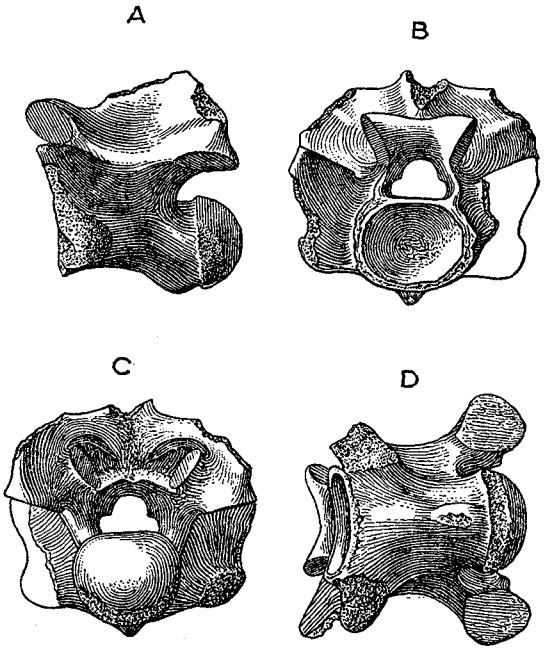


FIGURE 21.—*Thoracic vertebra of Palaeophis virginianus Lynn*

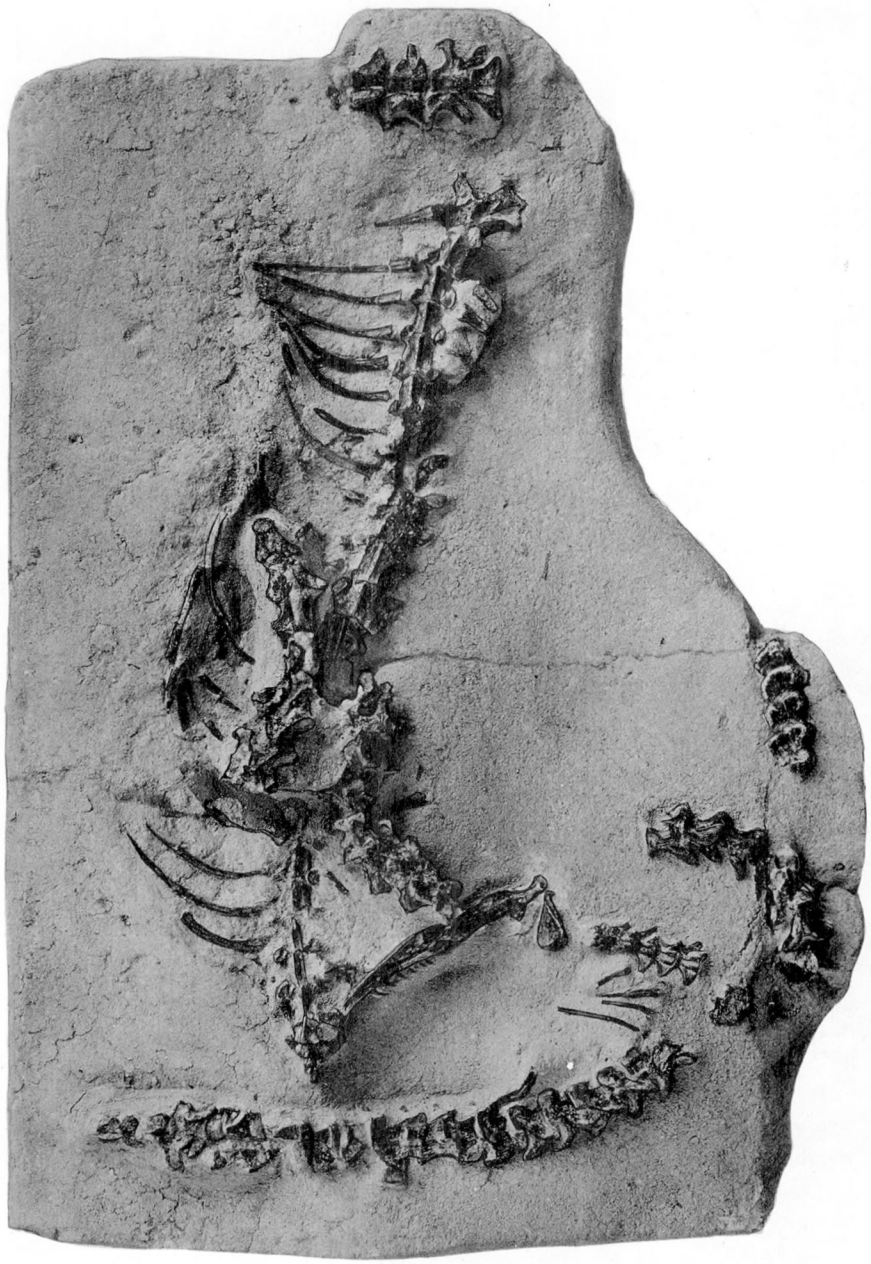
Cotype no. 13640 U. S. N. M. *A*, lateral; *B*, anterior; *C*, posterior; *D*, ventral views. Natural size.

Palaeophis virginianus has been so fully and accurately discussed in the original description that there is little need for further comment. In the light of present knowledge of the genus *Palaeophis*, the species *virginianus* is adequately distinguished but, as fully recognized by Lynn, many of the distinguishing characteristics may be modifications attributable to the posterior position in the vertebral column to which the type vertebrae belong. It is therefore quite possible that the discovery of more perfect specimens will show *P. virginianus* to pertain to one of the earlier described species.

Genus *Pterosphenus* Lucas

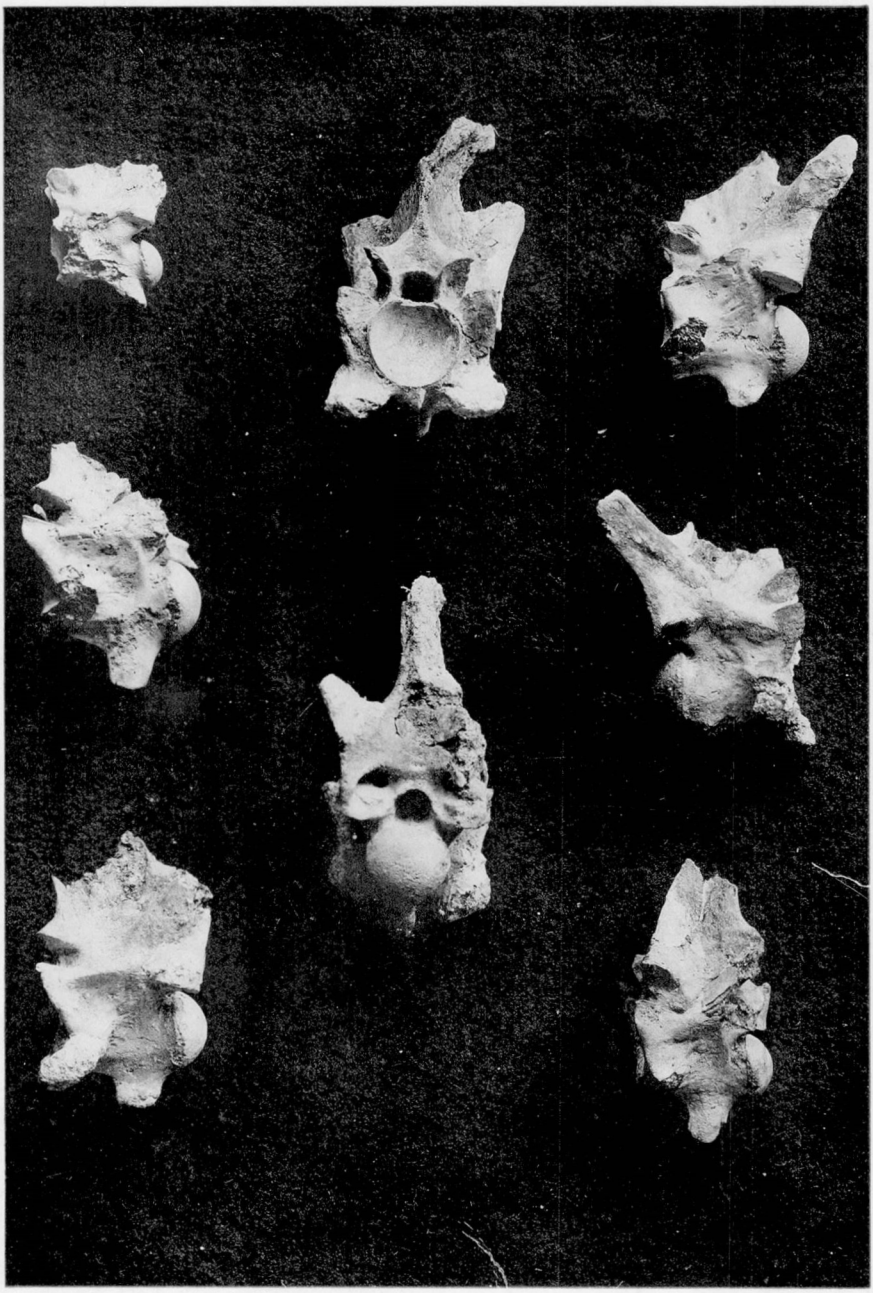
Pterosphenus LUCAS, U. S. Nat. Mus., Pr., vol. 21 (1899) p. 637.
Mocriophis ANDREWS, Geol. Mag., 4th ser., vol. 8 (1901) p. 438.

GENOTYPE: *Pterosphenus schucherti.*
Known only from vertebrae.



SKELETON OF *BOAVUS OCCIDENTALIS* MARSH

No. 12980 U. S. N. M. From Bridger formation. Eocene. Bridger Basin, Wyoming. About 8/13 natural size.



THORACIC VERTEBRAE OF *PTEROSPHENUS SCHUCHERTI* LUCAS
No. 4047 U. S. N. M. Type. About ¾ natural size. After Lucas.

DIAGNOSIS: Aliform processes strongly developed. Procoelous centrum relatively long, posterior half strongly compressed. Zygosphene wider than glenoid fossa. Obliquity of condyle slight. Inferior surface of centrum with either one or two hypapophyses (in tandem). Hypapophysis compressed, when double usually connected by a rounded keel. Diapophyses placed low on centrum, prominent, robust, projecting prominently below level of centrum. Zygosphene stout, moderately deep, articular surfaces looking strongly downward. Zygantrum shallowly excavated. Anterior zygapophyses usually on a level with the floor of neural canal, occasionally below. Zygapophyses joined by a prominent horizontal ridge. Little or no lateral emarginations between zygapophyses. Anterior zygapophyses connected by a vertical plate that projects outward and forward below the level of the articulating surface. Neural arch relatively low. Neural canal narrower than zygosphene. Epapophyses present. Neural spines tall, with bases usually extending the entire length of the neural arch.

This genus was established by Lucas for the species *P. schucherti*, a very large snake found in the Jackson, a marine formation of Alabama, where it occurred in association with the remains of *Basilosaurus* (*Zeuglodon*) and *Zygarhiza*. Subsequently Andrews described a second species, *P. schweinfurthei* from the Eocene of Egypt, likewise associated with the remains of *Basilosaurus*.

Pterosphenus schucherti Lucas

(Plate 4)

Pterosphenus schucherti LUCAS, U. S. Nat. Mus., Pr., vol. 21 (1899) p. 637, 638, pls. 45, 46—SCHUCHERT, U. S. Nat. Mus., Pr., vol. 23 (1900) p. 328—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 479; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 267—ANDREWS, Descr. Cat. Tert. Vert. of the Fayum, Egypt, vol. 25 (1906)—COOKE AND STEPHENSON, Jour. Geol., vol. 36 (1928) p. 143—JANENSCH, Arch. Biontol., vol. 1 (1906) p. 330-331, pl. 26, fig. 5—MERRILL, U. S. Nat. Mus., Bull. (1907) vol. 53, pt. 2, p. 76—SAUVAGE, Rev. Crit. Paléozool., vol. 3 (1899) p. 150—SIMPSON, Am. Mus. Nat. Hist., Bull., vol. 67, art. 1 (1933) p. 6 (genus only).

TYPE SPECIMEN: U. S. N. M., Cat. no. 4047. Consists of about 40 vertebrae. Collected by Charles Schuchert, 1896.

TYPE LOCALITY: About 2 miles southeast of Melvin (Cocoa), Choctaw Co., Ala.

HORIZON: Jackson formation, Eocene.

ORIGINAL DESCRIPTION: "The most striking feature of the vertebrae, and the one on which the generic name is based, is the prolongation of the metapophysis upward and outward into a wing-like process. This character distinguishes the genus from all others. The species is named in honor of Mr. Charles Schuchert, by whom it was obtained.

"The bodies of the vertebrae are slightly shorter than in *Palaeophis* and the spinous processes, as shown by the only perfect example are very high and their bases coextensive with the neural arch.

"The height of the spinous process, however, is but little more than in *Boa* or *Ancistrodon*, although it *looks* higher from the shortness of the centrum.

"Hypapophyses are present or indicated on all the vertebrae. On the foremost, which from its size must be very close to the skull, the hypapophysis, arises as usual from the posterior portion of the vertebra and is directed as usual backward. The next complete hypapophysis, ten or fifteen vertebrae back of the foremost, extends directly downward. All succeeding hypapophyses are directed downward or incline slightly *forward*, a totally different arrangement from that found in other serpents.

"About twenty or twenty-five vertebrae behind the foremost the hypapophyses are doubled in number—one, quite low and pointing forward, arising from the anterior part of the centrum, the second, or principal hypapophysis, being on the posterior part of the centrum. The two processes are connected by a low ridge. The

facets for the ribs are pedunculate, as in *Palaeophis*, and, as in that genus, a ridge extends from the anterior zygapophysis to the costal facet.

"The sockets are as wide as, or in some cases slightly wider than, high. The balls are slightly triangular in outline, although in most cases this is exaggerated by the abrasion of their edges.

"The articular faces look more directly backward and forward than they do in modern snakes with which this specimen has been compared, the difference between this species and *Python* being very marked. The zygapophyses agree with those of *Palaeophis* in their slight lateral extent, a feature which gives the body of the vertebra a compact, compressed appearance, and contrasts with the wide-spread facets of *Python*. The facets of the zygosphene look more or less downward, contrasting very strongly with those facets in *Python* which look obliquely outward, as they do in *Palaeophis*. The facets of the anterior zygapophyses and zygosphene and those of the posterior zygapophyses and zygantrum lie nearly in parallel planes instead of converging, as in *Python*.

"On each side of the zygantrum, just above the facet, is a foramen communicating with a cavity running well up toward the anterior zygapophysis, and this in turn communicates with a cavity at the base of the neural spine and one on each side of the body of the vertebra. (See Plates XLV and XLVI.) [Fig. 22] This feature exaggerates a character found in *Python* and other snakes as well, but in *Python* the foramen is minute and the cavities smaller.

"This species may be provisionally included in the *Palaeophidae*, although, as we know nothing of the structure of skull of either *Palaeophis* or the present species, the exact relations of both are uncertain.

"This species may not have been marine, although found with *Zeuglodon*, for a large Emyd was also found associated with it. It does, however, appear probable that it was aquatic.

"The spinous processes are high, as in the semiaquatic *Boa* and *Ancistrodon*, but the force of this is weakened by the fact that in the strictly aquatic *Pelamys* the spinous processes are low. On the other hand, the low point of articulation of the ribs, as in *Pelamys*, and the comparatively high compressed character of the vertebrae generally indicate a correspondingly compressed body, such as would be best adapted for swimming.

"From the size of the vertebrae it is evident that the specimen was from 20 to 25 feet in length."[1]

The 40 vertebrae constituting the type materials quite certainly pertain to a single individual, and, although not stated by Lucas, it is quite apparent that no considerable number were found articulated. Lucas has regarded these vertebrae as forming the forward part of the column, the smallest being the most anterior. Since the foremost, as in the hindmost region of the body of snakes, are the smaller, the difficulty of determining the position of disarticulated vertebrae is at once apparent. Although there is no reason for seriously questioning Lucas' determination, it seems important to call attention to the possibility of their being posterior thoracic instead of anterior, a question that can only be positively decided by the finding of an articulated series.

The smallest vertebra has a single hypapophysis that arises from the posterior ventral surface, but the anterior ventral surface between the downwardly projecting parapophyses is flattened and without trace of a median keel. However, in the next type of vertebra posterior (Fig. 22 A, B, and C), the hypapophysis is much compressed and directed almost directly downward. From its anterior edge an incipient ridge is developed that extends forward and bisects the flat area previously mentioned. This ridge or keel grows stronger and more prominent in a posterior direction,

and in the largest vertebrae of those present a second hypapophysial projection appears at the extreme anterior end of the keel, which is always smaller than the posterior one (Fig. 22 E). Janensch finds these same modifications in the hypapophyses in the Egyptian species *P. schweinfurthei.*

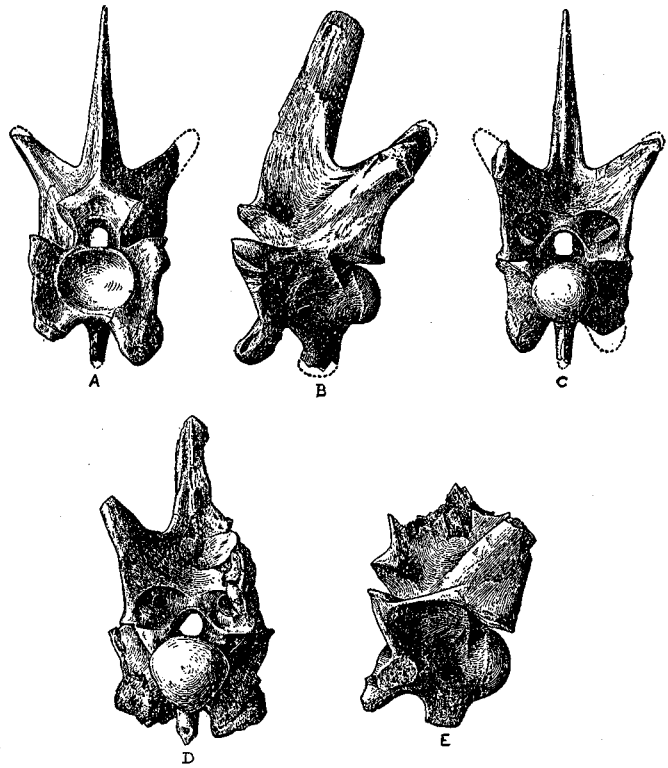


FIGURE 22.—*Thoracic vertebrae of Pterosphenus schucherti Lucas*

Type no. 4047 U. S. N. M. *A*, *B*, and *C*, anterior, lateral, and posterior views of an anterior thoracic vertebra; *D*, posterior view of one of the largest vertebra, showing the large foramina on either side of the zygantrum; *E*, lateral view of a thoracic vertebra showing the double hypapophyses. About ⅔ natural size. After Lucas.

In all these vertebrae the relationships of the zygosphene to the floor of the neural canal remain fairly constant, being relatively lower than in *Palaeophis.* The prezygapophyses have the plane of their articular facets on a level with the floor of the neural canal in all the type vertebrae. However, a vertebra, No. 5085 A. M. N. H., of *Pterosphenus* from the Fayum has a reduced posterior hypapophysis only and presumably it is from the posterior thoracic region and shows these facets of the zygapophyses elevated much above the floor of the canal.

The principal features of some of the better-preserved vertebrae are clearly depicted in Plate 4 and in Figure 22.

In all the type vertebrae having the arch preserved, the base of the spines extends the full length of the arch.

Measurements

	Largest *Mm.*	Smallest *Mm.*
Length of centrum, ball to edge of cup	24.0	16.5
Width of ball, transversely	23.8	9.0
Width of cup, transversely	24.0	9.0
Width of zygosphene	29.0	11.0

Although the American and Egyptian species are very close to one another, Janensch (1906b, p. 340) has pointed out that important differences distinguish them. In *P. schweinfurthei* the neural spines are narrower than in *P. schucherti*, the aliform processes are longer and more posteriorly directed, the zygapophysial facets more extensive and somewhat longer, and the parapophysial portions of the diapophyses are more robust.

Referred specimens

In the private collection of J. Magruder Sullivan, Millsap College, Jackson, Miss. Consists of 23 thoracic vertebrae. From the Jackson formation, Eocene, on the property of Robert Land, near Melvin, Choctaw Co., Ala. Collected by J. M. Sullivan, 1934.

Family COLUBRIDAE

The family Colubridae is said to include more than one-half of all living snakes, and they are world wide in distribution.

The following synopsis of skull characters has been largely extracted from Boulenger.

Facial bones movable; prefrontal not in contact with nasal; ectopterygoid present; pterygoid extending to mandible or quadrate; squamosal present and attached scale-like to the skull and suspending quadrate; maxillary horizontal, not movable perpendicularly to the ectopterygoid; postorbital not produced forward; mandible without coronoid bone. Both jaws toothed. Teeth solid.

Anterior thoracic vertebrae usually with simple hypapophyses in same genera as *Natrix* and *Thamnophis*, developed throughout the thoracic region.

On vertebrae alone, usually the only skeletal parts available to the paleontologist, species cannot be distinguished in many of the genera. This same observation seems to apply to some of the genera. All the Madagascar Colubridae have the hypapophyses developed throughout the vertebral column as in *Natrix*, which distinguishes them from the American genera *Liophis*, *Heterodon*, and *Dromicus*.

The known geological history of this family extends back to the Miocene in Europe and to the Lower Pliocene in North America. The following genera are recognized:

Miocene. *Elaphe, Thamnophis, Pylemophis,* and *Periops,* Europe.
Pliocene. *Thamnophis,* North America.
Pleistocene. *Coluber,* Europe and North America
Thamnophis, Drymarchon, Pituophis, and *Natrix?, Farancia?,* North America.

Genus *Coluber*

Coluber LINNAEUS, Syst. Nat., ed. 10, vol. 1 (1758) p. 16.

GENOTYPE: *Coluber constrictor.*

The presence of the genus *Coluber* in the Pleistocene of North America was first recognized by Wheatley (1871, p. 237). Although 16 living species are listed by Stejneger and Barber as occurring in North America, only two species, *C. acuminatus* Cope and *C. constrictor* Linnaeus are recognized in the fossil record. As previously mentioned, it is exceedingly doubtful if species of this genus can be distinguished from vertebral characters alone.

Coluber acuminatus (Cope)

Zamenis acuminatus COPE, Philadelphia Acad. Nat. Sci., Jour., 2d ser., vol. 11 (1899) p. 197.
Bascanion acuminatus HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 480—BAKER, Univ. Ill., Bull., vol. 17, no. 41 (1920) p. 208, 213, 394.
Coluber acuminatus HAY, Carnegie Inst. Washington, Publ. no. 322 (1923) p. 312, 314; Publ. no. 390, vol. 2 (1930) p. 269.

TYPE: Lost. Consists of fractured skull and 25 anterior thoracic vertebrae.
LOCALITY: Port Kennedy Cave, Montgomery Co., Pennsylvania.
HORIZON: Pleistocene.

ORIGINAL DESCRIPTION: "Represented by a fractured skull and twenty-five vertebrae from the anterior part of the column. The vertebrae display rather long, compressed, and obliquely truncate hypapophyses as far as they are preserved; and small protuberances project from the inferior side of the anterior zygapophyses. The upper portion of the costal articular face is the more convex; the inferior the more longitudinal.

"Of the skull, the premaxillary, the maxillary, proötic and mandibular bones are preserved, so as to be available for study. The first named is subconic, being narrower and more protuberant than in *Z. constrictor* and *Z. testaceus,* with which I have compared it. It formed an obtusely conical body, the lateral borders enclosing less than a right angle. The maxillary has a distinct external margin on the posterior half, which is interrupted by a long open excavation above the posterior internal process. The anterior internal process is continuous with the superior border. The maxillary foramen is large and is situated just anterior to the latter process. The posterior internal process is truncate at the extremity. The two processes and the space between them measure the bases of eight teeth. The latter are subequal except on the anterior part of the bone, where they are a little smaller. In the same space there are nine teeth in a skull of *Zamenis constrictor* with which I compare it.

"The mandible displays the characteristics of the genus. The pterygoid fossa is deep and wide and the lateral laminae well developed; the inner lamina is not so convex as in *Z. constrictor* and *Z. testaceus.* As in those species, the basis of the outer lamina continues for a short distance along the ramus as a low ridge, and on the outer side of this, a short distance in front of the fossa, the mandibular foramen issues. The cotylus for the os quadratum is large, and wider than in either of the species named. The proötic displays the large maxillary and smaller ophthalmic divisions of the foramen ovale, with a smaller foramen below the latter as in *Z. constrictor;* but the bridge separating the former two is narrower than in the specimens of the two species with which I have compared it.

"In size this species is similar to the common black snake. The ramus of the mandible measures .035 m. in length; and is .0045 in depth at the inner side of the pterygoid fossa. The maxillary measures .0087 in length from the front of the anterior to the posterior border of the posterior, inner, transverse process. The length of a vertebral centrum is .006. The various details of structure already mentioned indicate the specific distinctness of this snake from the two species of the genus to which it is most nearly allied, and with which I have compared it. Its pertinence to the genus *Zamenis* is demonstrated by the cranial bones fortunately preserved.[1]"

[1] These specimens have not been found in the collection as transferred to the Academy.

The original specimens on which Cope based this species were apparently lost years ago, as indicated by the editorial footnote at the end of the original description. Since the type has never been illustrated, the authenticity of this species rests upon the characters enumerated by Cope in his original description. As it is distinguished principally for its cranial and mandibular characters, the species is here retained as valid. Few if any species of the genus *Coluber* can be differentiated on vertebral characters alone.

Coluber cf. *constrictor constrictor* (Linnaeus)

Coluber constrictor (part) LINNAEUS, Syst. Nat., ed. 10, vol. 1 (1758) p. 216.

LOCALITIES: 2 miles west of Melbourne, Brevard Co., Fla., and Conard Fissure, Willcockson Co., Ark.

HORIZON: Pleistocene.

A vertebra (No. 13777 U. S. N. M.) found at the "Golf Course locality" near Melbourne, Florida, by J. W. Gidley in 1928 is so precisely similar in size and other characteristics to the middle thoracic vertebrae of an extant specimen of *Coluber constrictor constrictor* collected near Gainesville, Florida, that it is tentatively referred to that genus and species. Should this assignment eventually prove to be erroneous as to species, it will at least serve temporarily to indicate the presence of a Colubrid snake distinct from *Drymarchon* which occurs in these same deposits.

Numerous vertebrae found with those of *Crotalus* sp. in the Conard Fissure fauna in Arkansas are also referred to this genus but less certainly to the species *constrictor* since there are slight differences, especially in the development of the hypapophysial keel, which in the extinct forms is more widened at the posterior end. In other particulars they are very similar.

The chief characteristics of the *Coluber constrictor* vertebrae are: Vertebral centrum tapering, with strong longitudinal keel that terminates as a blunt end short of the condylar end; ventral surface on either side of keel flattened; spine low, thin, top slightly overhanging especially on the posterior side. Small spur-like process projecting from posterior border immediately above the postzygapophyses; long slender process projecting outward and forward below the level of the articular surfaces of the prezygapophyses; rib articulations having the peculiarities of other members of this group of an upper globular surface and a lower flattened face. These surfaces are quite distinctly set off from each other by a constric-

tion at the center but are not well preserved in the extinct form. Zygosphene is much wider than the glenoid fossa. Most of these features are clearly shown in Figure 23.

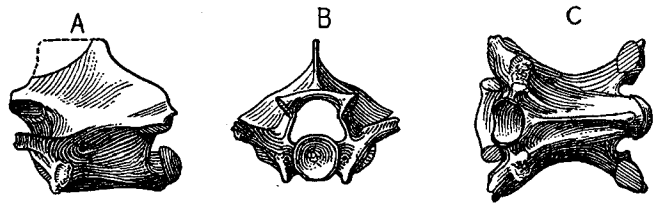


FIGURE 23.—*Middle thoracic vertebra of Coluber constrictor constrictor (Linnaeus)*
No. 13777 U. S. N. M. *A*, lateral; *B*, anterior; *C*, ventral views. ×3.

Coluber sp.

Coluber, WHEATLEY, Am. Jour. Sci., 3d ser., vol. 1 (1871) p. 237—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 480; Carnegie Inst. Washington, Publ. no. 322 (1923) p. 314; Publ. no. 390 (1930) p. 269.

LOCALITY: Port Kennedy Cave, Montgomery Co., Pa.
HORIZON: Pleistocene.

In 1871 Wheatley published a short paper reviewing briefly the fauna of the Port Kennedy Cave in which he listed two species of *Coluber*. No mention was made of the character of the material on which the identifications were based. It is presumed that one of the specimens so listed was later described as *Coluber acuminatus* by Cope, but the other insofar as the author can find, was not afterward mentioned in the literature.

Since the specimen is apparently lost, the authenticity of the determination by Wheatley will always remain in doubt.

Palaeoelaphe, n. gen.

GENOTYPE: *Palaeoelaphe kansensis*

A colubrid snake that in its vertebral structure bears a striking resemblance to the extant genus *Elaphe*. The generic characters are drawn from vertebrae only and will be found in the diagnosis given below. The outstanding generic features are found in the shape of the hypapophyses and the haemal carina. It is possible that the European forms *Elaphe atavus* and *E. oweni* may also fall in this genus. Both are from the Miocene of Germany and are therefore older than the species here described from the Lower Pliocene, which is the most ancient member of the Colubridae yet recognized in North America.

Palaeoelaphe kansensis, n. sp.

TYPE SPECIMEN: U. S. Nat. Mus. Cat. no. 13500. Collected by J. B. Hatcher, October, 1884.
TYPE LOCALITY: "Quarry E", Long Island, Phillipps Co., Kans.
HORIZON: Republican River formation, Lower Pliocene.

The vertebrae selected as the type of the present genus and species were found disarticulated, and it is therefore not positively known that all are of a single individual. They were found intermingled with the scattered remains of *Teleoceras fossiger*.

DIAGNOSIS: Vertebrae typically Colubroid. Centrum triangular, moderate length, slightly depressed. Glenoid fossa circular in anterior thoracic, wider than high in posterior thoracic region. Glenoid fossa narrower than zygosphene. Condyle moderately oblique. Hypapophyses on anterior thoracic vertebrae, strong, compressed, and extending downward and slightly backward from the posterior half of the centrum; its truncated extremity is slightly expanded transversely but more especially in an antero-posterior direction. Hypapophyses subequal in length to the spine. Posterior thoracic vertebrae with a low haemal carina, having a flattened ventral surface on the posterior half; the carina begins at the margin of the cup and ends before reaching the condyle in a blunt, transversely rounded projection; at the front end the carina expands rapidly, but in the opposite direction the widening is gradual but continuous to the very end. On either side of the carina the surface of the centrum is flattened, thus causing this keel to stand out boldly in relief. Heavy, low rounded ridge between condyle and diapophyses. Diapophyses below, but set posterior to the overlying prezygapophyses; articular surfaces looking outward and downward; upper articular surface subglobular, lower articular surface flattened, widened antero-posteriorly and extending strongly below the inferior margin of the glenoid fossa. Zygapophyses slender, with sharp borders, and oblique oval facets. Zygosphene thin dorso-ventrally, facets 45 degrees to the vertical, wider than glenoid fossa. Lateral emargination between zygapophyses joined by a sharp ridge, but not prominent. Bluntly pointed process extending outward and forward from below the level of the articular facets of the prezygapophyses. Spine quadrangular, moderate height, upper truncated border slightly overhanging posteriorly. Neural canal nearly as wide as zygosphene.

Associated with the type materials of *Palaeoelaphe* were a number of much smaller vertebrae, indicating the presence of an undescribed snake in this fauna. The diseased condition of many of these vertebrae and their poor preservation as a whole prevent description. Their small size and much flattened haemal keel distinguish them from the present species.

Among extant ophidians, *Palaeoelaphe* appears to have its closest affinities with the genus *Elaphe* from which it is distinguished by its larger size, more robust hypapophyses with dilated distal end that is truncate, and by the flattened haemal carina.

The principal features of the vertebrae are clearly shown in Figures 24 and 25.

Genus *Drymarchon* Fitzinger

Drymarchon FITZINGER, Syst. Rept. (1843) p. 26.

GENOTYPE: *Drymarchon corais*.

The occurrence of this genus in the Pleistocene of North America was first recognized by Hay (1917, p. 44) on vertebrae found near Vero Beach, St. Lucie County, Florida. In all probability the extinct form here referred to *D. corais couperi* represents a distinct species, but it cannot be satisfactorily distinguished on vertebral characters alone. The living members of this genus are commonly called Gopher or Indigo snakes.

Since there are only two subspecies of this genus known from North America, *D. corais couperi*, ranging from the Carolinas to Florida and westward to Texas, and *D. corais melanurus*, ranging from southeastern Texas to northwestern South America, the reference of an extinct form to the former appears to be a reasonable assignment. The author has not seen a skeleton of the last-mentioned species.

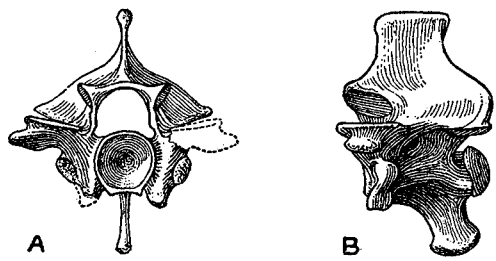


FIGURE 24.—*Anterior thoracic vertebra of Palaeoelaphe kansensis Gilmore*

Type no. 13500 U. S. N. M. *A*, anterior view; *B*, lateral view. ×3.

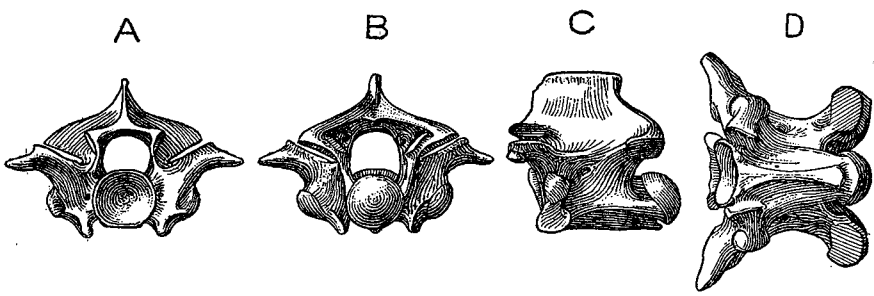


FIGURE 25.—*Posterior thoracic vertebrae of Palaeoelaphe kansensis Gilmore*

Type no. 13500 U. S. N. M. *A*, anterior; *B*, posterior; *C*, lateral; *D*, ventral views. ×3.

Drymarchon cf. *corais couperi* (Holbrook)

Coluber couperi HOLBROOK, N. Am. Herp., ed. 2, vol. 3 (1842) p. 75, pl. 16.
Drymarchon corais HAY, Fla. Geol. Surv., Rept., Ann. Rept. 9 (1917) p. 44.
Drymarchon corais couperi HAY, Carnegie Inst. Washington, Publ. no. 322 (1923) p. 382; Carnegie Inst. Washington, Publ. no. 390, vol. 2 (1930) p. 269, 270.

LOCALITY: Vero Beach, St. Lucie Co., and near Melbourne, Brevard Co., Fla.
HORIZON: Pleistocene (Stratum no. 3).

In the collections made from the Pleistocene of Florida, vertebrae of *Drymarchon* are equally abundant with those of *Crotalus adamanteus* with which they are often found intermingled. Subsequent to their discovery at Vero Beach, St. Lucie County, in 1917, identical vertebrae were collected for the United States National Museum in the Pleistocene deposits near Melbourne, Brevard County, by J. W. Gidley in 1929, and still

later at the same locality by C. P. Singleton for the Museum of Comparative Zoology, Cambridge, Massachusetts. In all, more than 100 vertebrae are known of this one snake.

When these vertebrae are compared with those of *Drymarchon corais couperi*, which lives in Florida today, with one exception, the closest re-

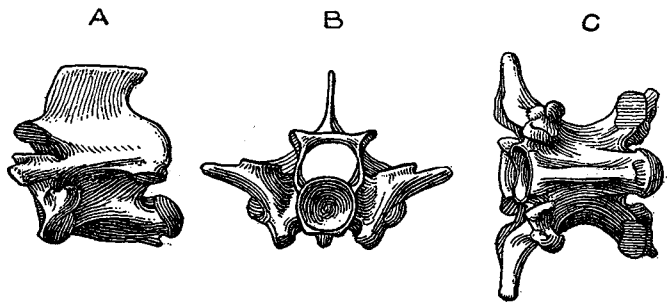


FIGURE 26.—*Thoracic vertebra of Drymarchon corais couperi (Holbrook)*
No. 13671 U. S. N. M. *A*, lateral; *B*, anterior views; *C*, ventral.

semblances are found. The hypapophysial keel in many of the Pleistocene vertebrae has flattened ventral surfaces, whereas it is rounded in the skeleton of the living form. The principal features of one of these thoracic vertebrae is well shown in Figure 26.

Referred specimens

No. 13671, U. S. N. M. Consists of 15 thoracic vertebrae. From "Golf Course," 2 miles west of Melbourne, Brevard Co., Fla. Collected by J. W. Gidley, 1928.
No. 13775, U. S. N. M. Consists of 30 thoracic vertebrae. From "Golf Course," 2 miles west of Melbourne, Brevard Co., Fla. Collected by J. W. Gidley, March 2, 1928. Several individuals.
No. V 1630, Fla. Geol. Surv. Consists of two thoracic vertebrae. From Bank of Canal, Vero Beach, St. Lucie Co., Fla.
No. V 1546, Fla. Geol. Surv. Consists of three thoracic vertebrae. From Vero Beach, St. Lucie Co., Fla.
No. V 2163, Fla. Geol. Surv. Consists of two vertebrae. From Vero Beach, St. Lucie Co., Fla.
No. V 6774, Fla. Geol. Surv. Consists of two vertebrae. From Florida.
(Not catalogued) Mus. Comp. Zool. Numerous vertebrae from near Melbourne, Brevard Co., Fla.

Genus *Pituophis* Holbrook

Pituophis HOLBROOK, N. Am. Herp., ed. 2, vol. 4 (1842) p. 7.

GENOTYPE: *Pituophis melanoleucus.*

On the basis of vertebral characters the author is unable to distinguish species of this genus, although the limited number of specimens available for study does not render this conclusion altogether authoritative. A common name often applied to the serpents of this genus is that of "Bull-Snake."

Pituophis sp.

A specimen, No. 7083 U. S. N. M., consisting of the left ramus, disarticulated portions of the skull, 39 vertebrae and numerous rib portions is identified as pertaining to the genus *Pituophis*. It was found in the loess, about a quarter of a mile south of the main entrance to the Chippianock Graveyard, near Rock Island, Illinois, by J. A. Udden, more than 30 years ago.

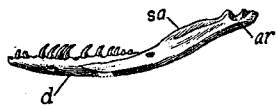


FIGURE 27.—*Left ramus of Pituophis sp.*

No. 7083 U. S. N. M. *Ar*, articular; *d*, dentary; *sa*, surangular. Natural size.

Comparison of this specimen with a skeleton of *Pituophis sayi sayi* of nearly equal size shows such close agreement in skull, mandible, and vertebral characters that the author does not hesitate to refer it to this genus.

The ramus (Fig. 27) is identical in every respect with the jaw of the living species *P. sayi sayi*, but species of this genus cannot be recognized on skeletal characters alone, and for that reason no assignment of this specimen to species has been attempted; although, on the grounds of geographical occurrence it would appear logical to assign it to *P. sayi sayi*.

Vertebrae from the Pleistocene of Conard Fissure, Willcockson County, Arkansas, are indistinguishable from those discussed above and are therefore provisionally referred to *Pituophis* sp.

Natrix

Tropodonotus WHEATLEY, Am. Jour. Sci., 3d ser., vol. 1 (1871) p. 237, 384—HAY, Carnegie Inst. Washington, Publ. no. 390, vol. 2 (1929) p. 270. (*Natrix*.)

LOCALITY: Port Kennedy Cave, Montgomery Co., Pa.
HORIZON: Pleistocene.

Wheatley in 1871 reported *Tropodonotus* (*Natrix*) as being present in the Port Kennedy Cave fauna in Montgomery County, Pennsylvania.

These specimens have now been lost. No mention of this genus was made by Cope in his subsequent papers discussing this fauna so that the presence of this genus in this fauna and in the fossil record rests entirely upon the evidence of Wheatley's statement.

Genus *Thamnophis* sp.

Thamnophis FITZINGER, Syst. Rept. (1843) p. 26.
Thamnophis sirtalis PETERSON, Ann. Carnegie Mus., vol. 16 (1926) p. 253—HAY, Carnegie Inst. Washington, Publ. no. 390, vol. 2 (1930) p. 370.

LOCALITY: Frankstown Cave, Blair Co., Pa., and near Hagerman, Twin Falls Co., Idaho.

HORIZON: Pleistocene and Upper Pliocene.

The occurrence of the genus *Thamnophis* in the fossil record was first reported by Peterson in 1926 as follows:

"Some remains of *Thamnophis sirtalis* were in the general mass of material in the Frankstown Cave. The right maxillary, No. 11,322 [C. M.] though smaller than an average sized garter snake, is recognized by actual comparison with specimen No. 1754 in the osteological series of the Museum. A second specimen No. 11319, also fragments of jaws represent a snake somewhat larger than No. 11,322 but perhaps of the same species.

"Remains of larger snakes (? *Coluber constrictor* Linneaus) were also found. In all there are seven fragments of jaws and many vertebrae, indicating at least two varieties of snakes. The fragmentary condition of the remains prevents detailed study."

After an examination of all these specimens, now preserved in the Carnegie Museum, the author agrees with Peterson's conclusion that at least two kinds of snakes are present in this cave fauna. Also, he was correct in referring the smaller specimens to the genus *Thamnophis*, since the maxillary and vertebrae agree with those of the living species down to the smallest detail. On geographical grounds the reference of these Pleistocene specimens to the species *sirtalis* may be correct, but after comparing the maxillae and vertebrae of *T. ordinoides vagrans*, *T. sirtalis sirtalis*, *T. radix*, *T. marcianus*, and *T. sauritus proximus*, and finding the closest correspondence between them, except for differences in size, the author concludes that species of this genus cannot be differentiated on these isolated bones, and for that reason the extinct form cannot be recognized as to species.

Eight vertebrae, No. 13,688 U. S. N. M., collected by the 1934 Smithsonian Paleontological Expedition to Idaho, under the direction of C. L. Gazin, are provisionally referred to the genus *Thamnophis*. These vertebrae are from several individuals but are of the same general character (Fig. 28).

As in the living species, all these vertebrae are provided with compressed backward projecting hook-like hypapophyses whose obtuse termination extends backward beyond the condyle of the centrum. The parapophyses extend well below the level of the centrum and, in many of the vertebrae, have the peculiarity of turning strongly inward toward the median line at the distal end. These processes also project forward beyond the edge of the glenoid fossa. The neural spine is low, plate-like, and with the truncated upper border overhanging both in front and back. In all these particulars the vertebrae of *Thamnophis* are in accord with those of *Natrix*, but the small size of the fossil vertebrae are more in keeping with the first-mentioned genus. Both the genera mentioned above have well-developed hypapophyses throughout the thoracic series, and it

is presumed that the extinct forms had a similar development of these processes.

Because of the Upper Pliocene age of the Hagerman vertebrae, there is every reason for thinking they pertain to a distinct species but, in view of the fact that only vertebrae are known, and since these cannot be distinguished from either the Pleistocene or Recent specimens, there is no object in naming them.

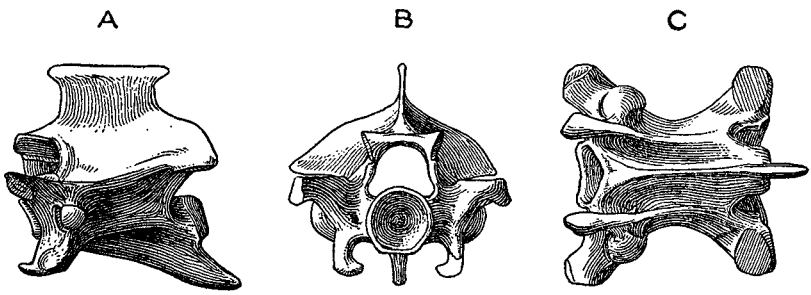


FIGURE 28.—*Thoracic vertebra of Thamnophis sp.*

No. 13,688 U. S. N. M. *A*, lateral view; *B*, anterior view; *C*, ventral view. All ×5.

Referred specimens

No. 13776, U. S. N. M. Consists of one vertebra. Lower Pliocene. From Castle Butte, Twin Falls Co., Idaho. Collected by Smithson. Paleont. Exped., 1934.

No. 11321, Carnegie Mus. Consists of about 34 vertebrae. Pleistocene. From Frankstown Cave, Blair Co., Pa. Collected by O. A. Peterson.

Farancia abacura (Holbrook)

Coluber abacura HOLBROOK, N. Am. Herp., ed. 1, vol. 1 (1836) p. 119.

Farancia abacura HAY, Fla. Geol. Surv., Ann. Rept. 9 (1917) p. 44, 48; Carnegie Inst. Washington, Publ. no. 322 (1923) p. 382; Carnegie Inst. Washington, Publ. no. 390, vol. 2 (1930) p. 269.

LOCALITY: Vero, St. Lucie Co., Fla.

HORIZON: Pleistocene (Stratum no. 3).

The occurrence of this genus and species at Vero, Florida, rests upon an articular bone identified by Hay. His comments on the specimen follow:

"In the collection made by Dr. Sellards in Stratum No. 3 at Vero, is the articular bone of a snake which seems to have belonged to this species. The bone has a length of 41 mm. but a small piece is broken from the front end. It has been compared with an articular of a skull which belongs to Dr. R. W. Shufeldt, and which, as he reports, he took from a *Farancia*, 6 feet and 3 inches long, found near New Orleans. This bone is 44 mm. long. Three other bones considerably smaller, belonging to the National Museum have been used for comparison.

"In the New Orleans specimen the two plates which enclose the insertion of the masseter muscle are of equal height, 7 mm. In all the other bones, including the fossil the outer plate is much lower. In the fossil the inner plate is 8 mm. high while the fossil presents some peculiarities, they are probably due to individual variation. The snake which possessed this bone was probably about 6 feet long.

"The lower jaw of *Abastor* is similar to that of *Farancia*, but the dentary extends backward only a short distance behind the front of the articular; while in *Farancia*

the dentary, with teeth, is carried back more than half-way to the groove for the masseter muscle."

The failure to find among the Florida serpent materials any vertebrae which can be referred to the genus *Farancia* leads me to question the authenticity of Hay's reference of a single articular bone, no longer available, to *F. abacura*. One of the outstanding characteristics of the thoracic vertebrae of *Farancia* is the heavy truncated character of the process which projects outward below the level of the articular surface of the prezygapophyses. A low rectangular spine, and heavy broadly rounded keel, bordered by longitudinal grooves, are other distinguishing features of these vertebrae. This combination of vertebral characters is sufficient to make the vertebrae of *Farancia* readily distinguishable from the other ophidian materials with which they might be found in Florida.

In the absence of the articular bone on which Hay made his original identification, it is impossible to verify his determination, although the author believes that the differences pointed out by Hay between the fossil and the jaw of a recent *Farancia* are not individual variations, as thought by Hay, but are probably normal features of another genus. It is therefore doubtful that the genus *Farancia* is present in the Pleistocene of Florida. There is only a single living species of this genus, so that the temporary expedient of referring the extinct form to it is logical.

Colubrid

Vertebrae found in the Pliocene of Curtiss Flats, Cochise County, Arizona, quite certainly pertain to a member of the Colubridae. The long, tapering centrum with distinct ventral keel, and the presence of processes projecting outward and forward from the prezygapophyses, are features found in that family. The materials are too fragmentary for closer determination. Their chief interest is in recording a new locality for ophidian remains.

Referred specimens

No. 13687, U. S. N. M. Consists of three thoracic vertebrae. From Pliocene, Curtiss Flats, Cochise Co., Ariz. Collected by J. W. Gidley, 1921.
No. 3251, A. M. N. H. Consists of two vertebrae. From Pliocene, Curtiss Flats, Cochise Co., Ariz. Collected by Mus. Exped., 1924.

Family CROTALIDAE

Venomous snakes make their first appearance in Europe in the Miocene, and Cope (1900, p. 706) has reported the Crotalidae as occurring in the Miocene, Loup Fork of Kansas. The fossil record shows this family to have had a wide geographical distribution in Pleistocene time in North America, skeletal remains having been found in no less than 10 States. The living species are predominantly American. They have the highest

efficiency of venom apparatus and thus have developed the most specialized type of ophidian structure.

The extant genera, *Crotalus*, *Sistrurus*, and *Agkistrodon*, are the important North American representatives of this family. The extinct genera, *Neurodromicus*, *Helagras*, and *Coniophis*, were assigned to the Crotalidae by Hay (1902, p. 480–481) with the possible exception of *Neurodromicus*. No evidence is found favoring such an assignment.

A brief synopsis of the skeletal characteristics of this family is as follows:

Maxillary bone vertical, excavated by a deep fossa which opens externally; ectopterygoid present; pterygoid reaching quadrate or mandible. Coronoid absent; fang slotted in front. All thoracic vertebrae bearing long hypapophyses subequal in length with neural spines; diapophyses with a small circumscribed articular tubercle from its upper convexity and a short process from its under part extending downward and forward below the level of the centrum; a short, obtuse process projects from below and a little beyond the end of the prezygapophyses.

Genus *Crotalus*

Crotalus, LINNAEUS, Syst. Nat., ed. 10, vol. 1 (1758) p. 214.

GENOTYPE: *Crotalus horridus* Linnaeus.

Largely on the basis of geographical distribution, Pleistocene specimens of *Crotalus* have been referred to the extant species, *C. horridus*, *C. adamanteus*, and *C. atrox*. All the extinct specimens so referred consist of scattered vertebrae only. After a study and comparison of all available specimens, the author concludes that, excepting *C. adamanteus*, which may be recognized on account of its large size, other species of *Crotalus* cannot be identified by vertebrae alone. Furthermore, with vertebrae of equal size, it is exceedingly difficult, if not impossible, to differentiate between *Crotalus* and the closely allied *Sistrurus* and *Agkistrodon*. Comparison of entire specimens seems to show the skeleton of *Agkistrodon* to be of more slender proportions, with more delicately constructed processes, but in isolated vertebra those differences are exceedingly difficult to detect. It is for that reason that scattered vertebrae are here referred to the genus *Crotalus* sp. with reservations. It is quite possible that some of the specimens so referred may pertain either to *Sistrurus* or *Agkistrodon*, or both.

Crotalus sp.

Crotalus WHEATLEY, Am. Jour. Sci., 2d ser., vol. 1 (1871) p. 287—SINCLAIR, Univ. Calif. Publ., Am. Arch. Ethn., vol. 2 (1904) p. 18—BROWN, Am. Mus. Nat. Hist., Mem., vol. 9 (1908) p. 207, pl. 22—MILLER, Univ. Calif. Publ., Bull., Dept. Geol., vol. 7 (1912) p. 71—HAY, Carnegie Inst. Washington, Publ. no. 322 (1923) p. 314, 353; Publ. no. 390, vol. 2 (1930) p. 271.

Crotalus horridus, HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 481; U. S. Nat. Mus., Pr., vol. 58 (1920) p. 96; Carnegie Inst. Washington, Publ. no. 322 (1923) p. 348; Publ. no. 390 (1930) p. 271.

Crotalus atrox HAY, U. S. Nat. Mus., Pr., vol. 58 (1920) p. 135, pl. 10, fig. 2.

LOCALITY: Arkansas, California, Florida, Georgia, Iowa, Maryland, Nebraska, Tennessee, Texas, and Virginia.

HORIZON: Pleistocene and Lower Pliocene?

In the assembled collection of fossil Serpentes materials are a considerable number of specimens consisting principally of vertebrae which are referred with some reservation to the genus *Crotalus* sp. They cover a wide geographical distribution, coming from many sections of the United States. In the literature certain of these specimens have been identified

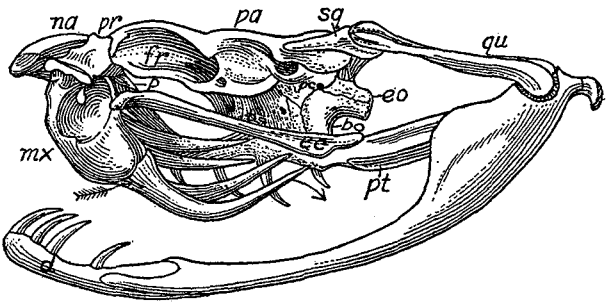


FIGURE 29.—*Skull of Crotalus*

Bo, basioccipital; *bs*, basisphenoid; *d*, dentary; *ec*, ectopterygoid; *eo*, exoccipital; *fr*, frontal; *mx*, maxillary; *na*, nasal; *pa*, parietal; *pc*, proötics; *pr*, prefrontal; *pt*, pterygoid; *qu*, quadrate; *sq*, squamosal. Natural size. After Williston.

as pertaining to the species *C. horridus* and *C. atrox?* (Hay, 1920, p. 96; 135, pl. 10, fig. 2), but after a critical comparison of a considerable number of extant *Crotalus* skeletons, representing the species *C. horridus*, *C. confluentus confluentus*, *C. adamanteus*, and *C. atrox*, it is my conclusion that these species cannot be differentiated on vertebral characters. Furthermore, on vertebrae alone the author is unable to find characters that would distinguish *Crotalus* from the other American members of the Crotalidae, as *Sistrurus* and *Agkistrodon*. Owing to the difference in size of the fossil vertebrae, there are proportional differences in the length of spines and hypapophyses but these disparities, in all probability, can be accounted for by differences in age of the individuals compared. When an individual vertebra is contrasted with vertebrae of corresponding size of an extant species, they are found to be in accord down to the smallest detail.

Therefore, those specimens referred to *C. horridus* and *C. atrox?* cannot be identified as to species, and hereafter they should be indicated as *Crotalus* sp. only, and reference to genus should be regarded as provisional.

The practice of referring Pleistocene Crotalid specimens to species of *Crotalus* occurring in the same locality, therefore, should be discontinued, especially where two or more living species occur in the same area.

Geologically, the most ancient specimens referable to *Crotalus* found in the assembled ophidian materials are Nos. 1637, 1638, and 1639 A. M. N. H. labelled as coming from the Lower Pliocene?, Driftwood Creek, Hitchcock County, Nebraska, and collected by R. Hill in 1879. It may be that these specimens are equivalent in age to the Crotalid mentioned

by Cope as coming from the Miocene of Kansas, since authorities in the past have disagreed as to whether these formations along the Republican River were Upper Miocene or Lower Pliocene in age.

The better-preserved specimen (No. 1639) consists of two fangs and about 90 vertebrae. The fangs are identical in every respect to those of a small *C. horridus*, and the vertebrae are likewise indistinguishable.

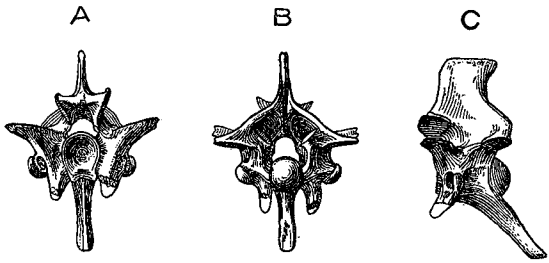


FIGURE 30.—*Thoracic vertebra of Crotalus sp.*

No. 9223 U. S. N. M. Originally referred by Hay to *C. atrox*. *A*, anterior; *B*, posterior; *C*, lateral views. Natural size.

In all probability these specimens pertain to a species distinct from any now living, but, since the known remains show no distinguishing characteristics, they are referred to the genus *Crotalus* sp. und.

Referred specimens

No. 4887, U. S. N. M. Consists of 54 thoracic vertebrae. From Pleistocene, Ladd's Lime Kiln, near Cartersville, Ga. Presented by Robert H. Coupler, 1900.

No. 9157, U. S. N. M. Consists of two thoracic vertebrae. From Pleistocene, Bushey Cavern, about 8 miles east of Hagerstown, near Cavetown, Washington Co., Md. Identified by O. P. Hay (1920, p. 96) as *C. horridus*. Collected by Charles Peabody.

No. 13772, U. S. N. M. Consists of 10 thoracic vertebrae. From Pleistocene, Cumberland Cave, near Cumberland, Md. Collected by J. W. Gidley.

No. 13686, U. S. N. M. Consists of 18 thoracic vertebrae, and a few rib fragments. From Pleistocene, Big Pigeon River, near Newport, Cocke Co., Tenn.

No. 9223, U. S. N. M. Consists of about 50 thoracic vertebrae, ramus, fang, and numerous ribs. From Pleistocene, Bulverde, Bexar Co., Texas. Collected by D. V. Schuchardt, 1915. Identified by O. P. Hay (1920, p. 135, pl. 10, fig. 2) as *C. atrox*.

No. 1637, A. M. N. H. Consists of one fang and 35 vertebrae. From Pliocene?, Driftwood Creek, Hitchcock Co., Neb. Collected by R. Hill, 1879.

No. 1638, A. M. N. H. Consists of 6 thoracic vertebrae. From Pliocene?, Driftwood Creek, Hitchcock Co., Neb. Collected by R. Hill, 1879.

No. 1639, A. M. N. H. Consists of 2 fangs and about 90 thoracic vertebrae. From Pliocene?, Driftwood Creek, Hitchcock Co., Neb. Collected by R. Hill, 1879.

No. 6404, A. M. N. H. Consists of left articular. From Pleistocene, Conard Fissure, 4 miles west of Willcockson, Newton Co., Ark. Collected by Barnum Brown.

No. 13685, U. S. N. M. Consists of 7 thoracic vertebrae. From Pleistocene?, Andrews' Stone Quarries, above Sioux City, Iowa. Collected by Orestes St. John, 1869.

(Not catalogued) Univ. Calif. Consists of numerous vertebrae. Pleistocene. Rancho La Brea, Los Angeles Co., Calif. Collected in 1911 and 1912.

(Not catalogued) Univ. Calif. Consists of a few vertebrae. Pleistocene. McKittrick Asphalt Pit (Loc. no. 7139) Kern Co., Calif.

Nos. 1009–1010, Univ. Mich. Consists of two vertebrae. Pleistocene. Seminole Co., Fla. Collected by E. H. Hubbell.

Crotalus adamanteus Beauvois

Crotalus adamanteus BEAUVOIS, Am. Philos. Soc., Tr., vol. 4 (1799) p. 368—COPE, Rept. Smithson. Inst. 1898, U. S. Nat. Mus., pt. 2 (1900) p. 1161, fig. 333—HAY, Fla., Geol. Surv., 9th Ann. Rept. (1917) p. 44; Carnegie Inst. Washington, Publ. no. 322, vol. 2 (1923) p. 382; Publ. no. 390, vol. 2 (1929) p. 271.

LOCALITY: Vero St. Lucie Co., Melbourne, Brevard Co., Ocala, Marion Co., and Pinellas Co., Fla.

HORIZON: Pleistocene.

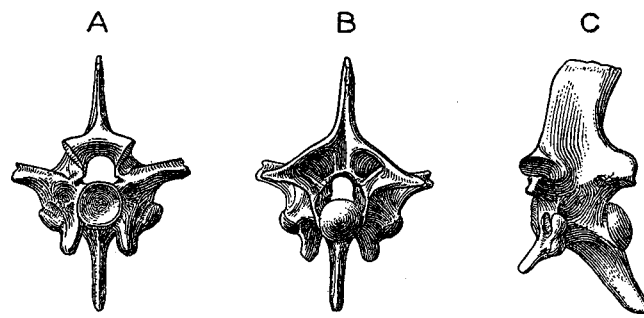


FIGURE 31.—*Thoracic vertebra of Crotalus adamanteus Beauvois*

No. 11333 U. S. N. M. *A*, anterior; *B*, posterior; *C*, lateral views. Natural size.

The presence of a large *Crotalus* in the Pleistocene deposits of Florida is indicated by numerous vertebrae found at Vero, St. Lucie County, and at Melbourne, Brevard County. It is on size alone that they are referred to *C. adamanteus*, for the fossil vertebrae are identical in every respect with those of other living species. According to Cope (1900, p. 1161), "*C. adamanteus* is the largest and most formidable species of the genus." A record specimen killed near Jacksonville, Florida, measured 8 feet 9 inches in length. The fossil vertebrae are nearly as large as those of a specimen in the U. S. National Museum that was 7 feet in length, indicating that the extinct form rivaled the living species in size. In all probability these Pleistocene vertebrae represent a species distinct from any of those now living, but, since the materials available do not disclose characters that will distinguish them, their assignment to the largest living species which inhabits this same area appears logical. This assignment was originally made by O. P. Hay.

A typical vertebra selected from a lot of 46 collected from the north side of the drainage canal near Vero Beach, St. Lucie County, Florida, is illustrated in Figure 31.

It is quite evident from the relatively wide geographical distribution of the specimens found that remains of *C. adamanteus* may occur in Florida anywhere that Pleistocene fossils are found.

The largest fossil vertebra (No. 13679 U. S. N. M.) found with a com-

plete neural spine has the dimensions given below, as contrasted with measurements of a vertebra from a 7-foot *C. adamanteus* specimen.

Measurements

	No. 13679 U.S.N.M. *Mm.*	No. 110497 U.S.N.M. *Mm.*
Greatest height from top of spine to bottom of centrum	29.0	35.0
Greatest expanse across prezygapophyses	25.5	27.5
Greatest diameter of zygosphene	11.0	11.8
Greatest length of centrum cup to convexity of ball	12.0	13.3
Greatest transverse diameter of glenoid fossa	5.6	7.0
Greatest vertical diameter of glenoid fossa	6.4	6.0

Referred specimens

No. 11333, U. S. N. M. Consists of 46 thoracic vertebrae. Pleistocene. North side of drainage canal near Vero Beach, St. Lucie Co., Fla. Collected by J. W. Gidley, 1925.

No. 11220, U. S. N. M. Consists of two thoracic vertebrae. Pleistocene. From 2 miles west of Melbourne, Brevard Co., Fla. Collected by J. W. Gidley, 1924.

No. 11856, U. S. N. M. Consists of 12 thoracic vertebrae. Pleistocene. From 2 miles west of Melbourne, Brevard Co., Fla. Collected by J. W. Gidley, 1926.

No. 13677, U. S. N. M. Consists of 3 thoracic vertebrae. Pleistocene. From "Golf Links locality, near Melbourne, Brevard Co., Fla." Collected by J. W. Gidley, March 1928.

No. 13678, U. S. N. M. Consists of 19 thoracic vertebrae. Pleistocene. From 2 miles west of Melbourne, Brevard Co., Fla. Collected by J. W. Gidley, 1930. Probably more than one individual represented by these vertebrae.

No. 13679, U. S. N. M. Consists of 5 thoracic vertebrae. Pleistocene. From near Melbourne, Brevard Co., Fla. Collected by J. W. Gidley, 1929.

(Not catalogued), Cambridge Mus. Zool. Consists of several hundred thoracic vertebrae. Pleistocene. From near Melbourne, Brevard Co., Fla. Representing many individuals.

No. V 2414, Fla. Geol. Surv. Consists of one vertebra. Pleistocene. From Canal near Vero Beach, St. Lucie Co., Fla.

No. V 2411, Fla. Geol. Surv. Consists of two vertebrae. Pleistocene. From north bank of Canal near Vero Beach, St. Lucie Co., Fla.

No. V 2399, Fla. Geol. Surv. Consists of one vertebra. Pleistocene. From west of railroad bridge, Vero Beach, St. Lucie Co., Fla.

No. V 2412, Fla. Geol. Surv. Consists of two vertebrae. Pleistocene. From north bank of canal near Vero Beach, St. Lucie Co., Fla.

No. V 1702, Fla. Geol. Surv. Consists of one vertebra. Pleistocene. From west of railroad bridge, Vero Beach, St. Lucie Co., Fla.

No. V 191, Fla. Geol. Surv. Consists of one vertebra. Pleistocene. From south bank of canal, Vero Beach, St. Lucie Co., Fla.

No. V 1712, Fla. Geol. Surv. Consists of one vertebra. Pleistocene. From Vero Beach, St. Lucie Co., Fla.

No. V 1765, Fla. Geol. Surv. Consists of one vertebra. Pleistocene. From south bank of canal, Vero Beach, St. Lucie Co., Fla.

No. V 4014, Fla. Geol. Surv. Consists of two vertebrae. Pleistocene. From Seminole Field, Pinellas Co., Fla.

No. V 2987, Fla. Geol. Surv. Consists of one vertebra. Pleistocene. From Pit no. 2, Florida Lime Co., 2 miles south of Ocala, Fla.

No. 28910, Univ. Calif. Consists of two vertebrae from Seminole Field. Pleistocene. Lecanto Co., Fla. Collected by W. W. Holmes.

Genus *Neurodromicus* Cope, 1873

Neurodromicus, COPE, Synop. new Vert. Tert. Colo. (October 1873) p. 15. Washington.

GENOTYPE: *Neurodromicus dorsalis*.

Known only from a single anterior thoracic vertebra.

Cope's last and most complete characterization of the genus is as follows:

DIAGNOSIS: "Centrum small, with a prominent truncate, hypapophysis. Neural arch capacious, the zygantrum wider than the articular cup. Neuropophyses bounding the canal laterally below the zygosphene; its border not angulate behind. Parapophyses projecting acutely below centrum. An elevated neural spine. No process below the prezygapophysis. No prominent ridge connecting the zygapophyses."

Neurodromicus was included by Hay (1902) in the Crotalidae, and by Williston (1925) in the Viperidae. Neither authority has advanced any reasons for this assignment, although it may be inferred that it was based on the presence of a compressed hypapophyses. Comparison of the type and only known specimen with the various ophidian vertebrae available show its closest resemblances to be with those of *Crotalus*, and it may be that such differences of structure as exist are not greater than might be expected in a Crotaline of Oligocene age. But, on the evidence furnished by a single vertebra, its taxonomic relationships cannot be certainly determined. However, in order to direct attention to its Crotaline resemblances, such as the presence of a compressed hypapophysis, paired parapophyses projecting acutely below the centrum, and plate-like spine, the author proposes to retain it in the Crotalidae until such time as the discovery of additional materials shall disclose its true family affinities.

Neurodromicus dorsalis Cope

Neurodromicus dorsalis, COPE, Synop. new Vert. Tert. Colo. (October 1873) p. 15. Washington; U. S. Geol. Geog. Surv. Terr. (Hayden), 7th Ann. Rept., 1873 (1874) p. 517; U. S. Geol. Surv. Terr. (Hayden), 3d Rept., vol. 3 (1884) p. 786, pl. 58, figs. 7, 8—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 481; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 271.

TYPE SPECIMEN: A. M. N. H., Cat. no. 1599. Consists of a single anterior thoracic vertebra. Collected by E. D. Cope, 1873.

TYPE LOCALITY: Cedar Creek, Pawnee Buttes, northeast Colo.

HORIZON: Oreodon beds, Oligocene.

ORIGINAL DESCRIPTION: "*Char. gen.* Centrum small, with a prominent truncate hypapophysis. Neural arch capacious, the zygantrum wider than the articular cup. Neuropophyses bounding the canal laterally below the zygosphene; its border not angulate behind. Parapophyses projecting acutely below centrum. An elevated neural spine.

"*Char. specif.* Articular surfaces of centrum round; the ball with a slight upward-looking obliquity. Hypapophysis continued to cup as a prominent carina. A ridge connecting zygapophyses. Neural spine extending its base forward, so as to stand on the entire length of the neural arch.

Measurements

	Mm.
"Length of centrum	.0045
Diameter of cup, vertical	.0020
Diameter of cup, transverse	.0021
Elevation of neural spine above centrum	.0055
Elevation of neural spine above neural arch	.0029
Length of hypapophysis below centrum	.0012
Width of hypapophysis	.0011

"The zygantrum is capacious, and the whole neural arch open and light. The species was about the size of the black snake (*Bascanium constrictor*)."

The principal structural features are adequately described in the original description, but the author wishes to direct special attention to the large size of the neural canal (Fig. 32), a feature that at once distinguishes this vertebra from those of all other described fossil ophidians. The vertical diameter of the neural canal is equal to this same measurement of the

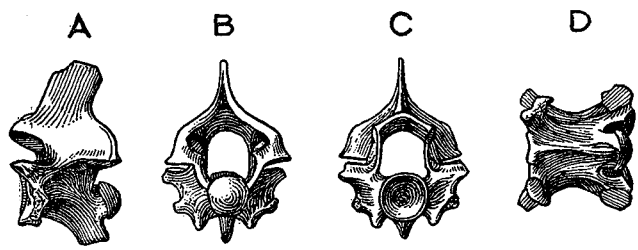


FIGURE 32.—*Anterior thoracic vertebra of Neurodromicus dorsalis Cope*
Type. no. 1599 A. M. N. H. *A*, lateral; *B*, posterior; *C*, anterior; *D*, ventral views. X3.

glenoid fossa, whereas in other extinct Serpentes the canal diameter is less than that of the cup.

SERPENTES OF UNKNOWN FAMILY REFERENCE

Genus *Lithophis* Marsh 1871

Lithophis, MARSH, Am. Jour. Sci., 3d ser., vol. 1 (1871) p. 325.

GENOTYPE: *Lithophis sargenti.*
Known only from an incomplete anterior thoracic vertebra.

DIAGNOSIS: Compressed centrum, articular cup and ball subcircular in transverse outline and standing at nearly right angles to the axis of the centrum. Anterior zygapophyses much extended outward. Diapophyses with articular faces divided by horizontal groove. No lateral ridge extending from diapophyses to articular ball. Hypapophyses, a wedge-shaped ridge, extending practically the whole length of centrum with its apex below the level of the inferior margin of the glenoid fossa.

The genus *Lithophis* was included by Hay (1902) in the Boidae, but this assignment was probably made as a matter of expediency rather than on account of any basic reasons. On the evidence furnished by a single incomplete vertebra, a conclusion as to its taxonomic relations cannot be reached, and for that reason it shall be included with others under the heading of Serpentes of Unknown Family Reference.

Lithophis sargenti Marsh

Lithophis sargenti MARSH, Am. Jour. Sci., 3d ser., vol. 1 (1871) p. 325—KING, U. S. Geol. Expl., 40th Par., vol. 1 (1878) p. 405—DE ROCHEBRUNE, Nouv. Arch. Mus. Hist. Nat., 2d ser., vol. 3 (1880) p. 289—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 479; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 268.

TYPE SPECIMEN: Peabody Mus. Nat. Hist., Cat. no. 2719. Consists of a single thoracic vertebra. Collected by H. B. Sargent, 1870.
TYPE LOCALITY: Grizzly Buttes, Uinta Co., Wyo.
HORIZON: Bridger. Middle Eocene.

ORIGINAL DESCRIPTION: "This species and genus are at present represented by three trunk vertebrae, only one of which, however, is sufficiently well preserved to show all its more important characters. The specimens indicate a small serpent about four feet in length, and probably, like the preceding species, allied to the constrictors. From the vertebrae of *Boavus*, as well as from those of the other fossil Ophidians discovered in this country, the present specimens may be readily distinguished by the more compressed centrum, and especially by the articular cup and ball, which are circular in transverse outline, as in the African *Eryx*, and stand nearly at right angles to the axis of the centrum. The anterior zygapophyses, also, are more extended outward, and their articular faces have a greater antero-posterior expansion than in any of the described species. The diapophyses have their articular surfaces divided by a horizontal groove, having a rounded tubercle above, and a pointed projection below, as in the modern *Bascanion*. There is no lateral ridge extending from the diapophyses to the articular ball, as in *Boa* and *Boavus*, the converging sides of the centrum being nearly flat. The hypapophysis is reduced to a wedge-shaped ridge, extending the whole length of the centrum, and having its sharp apex below the inferior margin of the cup. The floor of the neural canal has a prominent, obtuse median ridge throughout its whole length, but no lateral ridges are apparent.

"The principal measurements of the best-preserved vertebra are as follows:

			Mm.
Length of centrum from edge of cup to convexity of ball	2.80	lines	[5.4]
Transverse diameter of cup	1.35	"	[2.7]
Vertical diameter of cup	1.35	"	[2.2]
Vertical diameter of ball	1.30	"	[2.5]
Width of neural canal in front	.90	"	[2.0]
Distance from end of anterior zygapophysis to hypapophysis	3.00	"	[6.0]
Distance between ends of the anterior zygapophysis	4.50	"	....

"For the extinct genus manifestly indicated by the fossils here described, the name *Lithophis* is proposed, and the species they represent may appropriately be called *Lithophis sargenti*, after the discoverer, H. B. Sargent, of the Yale Scientific party, who found the specimens in the Eocene "Mauvaises Terres" beds at Grizzly Buttes, near Fort Bridger."

Three vertebrae are mentioned by Marsh in the original description, but only one of these can now be recognized in the Peabody Museum collections. This vertebra was in a glass vial on whose cork was the inscription "Type *Lithophis sargenti*," evidently placed there by the original authority. Since the vertebra marked type agrees with the description and fairly well with the measurements, it may safely be regarded as the specimen on which the genus and species were originally characterized.

The zygosphenal and zygantral portions are missing, as are all the zygapophyses except the left prezygapophysis.

With few exceptions, the original description accurately describes all the important features of this vertebra. As shown by the corrected measurements above, the cup and ball are not precisely circular, as both are slightly wider than high. The zygapophyses are nearly horizontal transversely and on a level with the floor of the neural canal (Fig. 33 B). The median portion of the neurapophyses is roof-like, broadly rounded from side to side in front, but developing a median ridge more posteriorly. It is quite evident that if a neural spine was ever present it was very small and confined entirely to the posterior third of the arch which is missing in this specimen.

The vertebra of *Lithophis* may be distinguished at once from those of *Boavus* which occurs in these same beds, by the following characteristics: More compressed centrum; more nearly circular form of cup and ball; wedge-shaped hypapophyses; divided diapophysial articular facets; absence of lateral ridge between diapophyses and articular ball; lower and more horizontal position of the anterior zygapophyses; apparent absence of a neural spine.

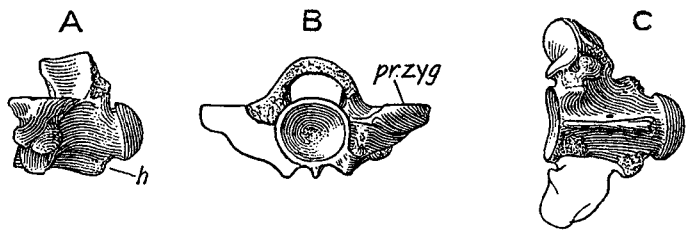


FIGURE 33.—*Thoracic vertebra of Lithophis sargenti Marsh*

Type no. 2719 P. M. N. H. *A*, lateral; *B*, anterior; *C*, ventral views; *H*, hypapophysis; *pr. zyg*, prezygapophysis. ×3.

Cheilophis n. gen.

GENOTYPE: *Cheilophis huerfanoensis.*

The characters distinguishing this new genus will be found in the diagnosis given below.

Cheilophis huerfanoensis, n. sp.

TYPE SPECIMEN: No. 5195 A. M. N. H. Consists of about 157 anterior and posterior thoracic vertebrae and numerous rib fragments. Collected by the 1918 American Museum Expedition.

TYPE LOCALITY: Two miles north of Gardner, Custer Co., Colo.

HORIZON: Upper Huerfano, Middle Eocene.

The vertebrae of the specimen selected as the type were found largely disarticulated, but it is presumed that all pertain to a single individual. The characters distinguishing this genus and species, as given below, have been derived chiefly from the posterior thoracic vertebrae.

DIAGNOSIS: Centrum relatively long, with condyle looking strongly upward. Hypapophyses on anterior thoracic, but none is intact; posterior thoracic with a haemal carina forming a deep keel having a blunt ventral edge, and terminating posteriorly as a blunt wedge-shaped end before reaching the condyle. This keel widens, especially at its base toward the posterior end.

On either side of the keel the surface of the centrum is flattened. Heavy rounded ridge between condyle and diapophyses. Zygosphene shallow with a median horizontal, lip-like projection on its anterior face; zygosphene wider than glenoid fossa and concave on superior surface. Neural arch moderately depressed, and bearing a short spine, with transversely expanded top. Diapophyses moderately strong, prominent, with a convex superior part and a flattened inferior part, but without distinct division; the lower part projecting prominently below the level of the centrum. Zygapophyses with sharp borders, and oblique, angularly oval facets. Short, blunt process extending outward from below the level of the articular surface of the zygapophyses.

The outstanding features of the present genus and species are the lip-like projection on the zygosphene and the short, moderately thin spine with expanded extremity. The principal dimensions of an average-sized posterior thoracic vertebra is as follows:

	Mm.
Length of centrum from edge of cup to convexity of ball	6.0
Transverse diameter of ball	2.3
" " " cup	2.7
Vertical " " ball	2.1
" " " cup	2.3
Transverse " " zygosphene	3.5
Height over all	6.5

The rib fragments show them to be hollow, but no other features are worthy of mention.

When compared with the snakes of the Bridger formation which is practically the equivalent of the Huerfano in age, no close resemblance is found. *Cheilophis huerfanoensis* is at once distinguished from *Boavus occidentalis* by its smaller size, thinner zygosphene, less massive diapophyses, and by the median lip-like process on the zygosphene. Although *B. brevis* shows resemblances such as the thin zygosphene with an incipient median process, the relatively short centrum and absence of processes on the prezygapophyses at once distinguish it from *Cheilophis huerfanoensis*. It is likewise distinguished from *Lithophis* by the longer, more slender centrum, more oblique cup and ball, and prezygapophyses above the floor of the neural canal. The Oligocene genera *Ogmophis* and *Calamagras* are distinguished by their smaller size, less developed haemal carinae, and absence of a projecting process on the prezygopophyses.

The relatively long, slender centrum, with strongly developed haemal carina, and the presence of a short but projecting process extending outward from below the articular face of the prezygopophyses, are characteristics in common with *Coluber*, and it may eventually be shown that the affinities of *Cheilophis* lie in the Colubridae.

A single incomplete vertebra, No. 13779 U. S. N. M., collected by J. B. Hatcher in 1888 from the Oligocene of Sioux County, Nebraska, is referred to the present genus. It is of about the same size, and shows the same deep keel and a lip-like process on the anterior face of the zygosphene. In all probability it pertains to a distinct species, but from the scanty materials now available that point cannot be positively determined.

Genus *Helagras* Cope 1883

Helagras, COPE, Am. Philos. Soc., Pr., vol. 20 (1883) p. 545.

TYPE: *Helagras prisciformis*.

Known only from vertebral characters.

DIAGNOSIS: Vertebrae with low, thickened, truncate, tubercle-like spines entirely over the posterior half of the arch; keeled and nonkeeled vertebrae; hypapophyses on the anterior vertebrae; diapophyses heavy, wide, and projecting below level of centrum; hyposphene thickened.

Hay, in 1902, included *Helagras* in the Crotalidae, and Williston, in 1925, referred it with a question to the Viperidae. Both of these references are quite in error, as indicated by the absence of all aberrant processes on the vertebrae. The absence of such processes, the presence of a thickened

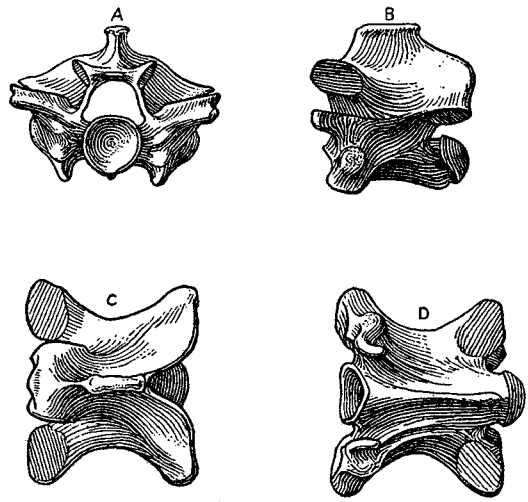


FIGURE 34.—*Posterior thoracic vertebra of Cheilophis huerfanoensis Gilmore*

Type no. 5195 A. M. N. H. *A*, anterior; *B*, lateral; *C*, dorsal; *D*, ventral views. ×3.

zygosphene and stout spines, are features strongly suggestive of Boid affinities, but the elongated centrum seems opposed to such an assignment. On the information furnished by vertebrae alone, a conclusion as to its family affinities has not been reached and, for the present, it shall be included under *Serpentes of unknown family reference.*

Helagras prisciformis Cope

Helagras prisciformis, COPE, Am. Philos. Soc., Pr., vol. 20 (1883) p. 545; Am. Nat., vol. 17 (1883) p. 545; U. S. Geol. Surv. Terr. (Hayden), 3d Rept., vol. 3 (1884) p. 731, pl. 24-g, fig. 2; Am. Philos. Soc., Tr., vol. 16 (1888) p. 302—ZITTEL, Handbuch der Paläont., vol. 3 (1890) p. 632—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 481; Carnegie Inst. Washington, Publ. 390 (1930) p. 271—GARDNER, Jour. Geol., vol. 18 (1910) p. 731—GILMORE, U. S. Geol. Surv., Prof. Paper 119 (1920) p. 10—MATTHEW, Geol. Soc. Am., Bull., vol. 25 (1914) p. 383—REESIDE, U. S. Geol. Surv., Prof. Paper 134 (1924) p. 42.

GENOTYPE: A. M. N. H., Cat. no. 1628. Consists of two posterior thoracic vertebrae. Collected by D. Baldwin, 1881.

TYPE LOCALITY: Northwestern New Mexico.

HORIZON: Puerco, Paleocene.

ORIGINAL DESCRIPTION: *Char. gen.* "The generic characters are drawn from vertebrae only. These display a modified form of the zygosphene articulation as follows: The roof of the zygantrum is deeply notched on each side of the median line so as to expose the superior lateral angles of the zygosphene. This separate median portion of the roof of the zygantrum forms a wedge-shaped body which may be called the *episphen*. It is surmounted by a tuberosity, which constitutes the entire neural

spine. The latter is thus entirely different in form from that of other serpents. Articular extremities of centrum round, the ball looking somewhat upwards. Costal articulation 8-shaped, the surface convex and continuous. Hypapophyses none on the two vertebrae preserved. Zygapophyses prominent. Free diapophyses none.

"This genus is readily distinguished by the presence, now first observed, of the episphen in addition to the zygosphen, and by the peculiar form of the neural spine. We have now several vertebral articulations originally discovered in American vertebrata. These are the *episphen* as above; the *hyposphen*, which characterized the Opisthocoelous Dinosauria (*Sauropoda* Marsh), and the *Diadectidae* of the Permian period; and the *zygantrapophysis*, which is present in the Diplocaulid family of Batrachia.

"*Char. specif.* A section of the vertebra at the middle is pentagonal, the inferior side slightly convex downwards. The lateral angle is the section of the angular ridge which connects the zygapophyses. The episphen has a shallow rounded groove on its infero-posterior side, which is bounded by a projecting angle on each at its middle. The episphen does not project so far posteriorly as the postzygapophyses, and the degree of its prominence differs in different parts of the vertebral column. In one of the two vertebrae in my possession its prominence is small. The tuberosity on its summit is a truncate oval with the long diameter anteroposterior and equaling two-fifths the length of the arch above. It is elevated above the rest of the median line, which is roof-like, with obtuse angle. The tubercular articular facet is entirely below the prezygapophysial surface, but the free part of the prezygapophysis extends well in front of it. It is distinguished from the capitular surface by a very slight constriction. A slight ridge extends from the capitular articulation to the edge of the ball of the centrum. Below this the surface is slightly concave, and the middle line is gently convex. The latter terminates in an obtuse-angled mark just in front of the edge of the ball. This edge is also slightly free from the ball. The capitular costal surfaces do not project inferiorly quite to the line of the inferior surface of the centrum."

Measurements of a Vertebra

	Mm.
"Length of centrum (with ball)	.0070
Diameter of ball, vertical	.0035
Diameter of ball, transverse	.0040
Elevation of vertebra at episphen	.0085
Elevation of vertebra at middle	.0062
Width at prezygapophyses	.0120
Width of tubercular costal faces	.0105
Width of zygantrum	.0058
Vertical diameter costal faces	.0040
Transverse diameter tubercular costal face	.0028

"This snake was about the size of the black snake, *Bascanium constrictor*. It is an interesting species for two reasons: First, it is the oldest serpent known from North America. Second, in the imperfection of the zygantrum we observe an approximation to the ordinary reptilian type of vertebra from which the ophidian type was no doubt derived. In the former there is no zygosphen or zygantrum."

In the original description Cope stressed the modified form of the zygosphene articulation as being the principal feature distinguishing the genus *Helagras*. He regarded the roof of the zygantrum as notched, and thus exposing the superior lateral angles of the zygosphene. Examination of the type specimen (Fig. 35) shows that he was in error in this conclusion. On the right side of the type vertebrae there are notches as described, but it is clearly evident they were formed by the breaking through of the roof by the sharp edges of the zygosphene of the next vertebra posterior. That this was the case is shown by one of the vertebra which has the roof of the left side intact and gives no indication of a notch. Furthermore,

three specimens, Nos. 1629, 1650, and 5185 of the American Museum of Natural History, that are clearly referable to this genus and consist of a considerable number of well-preserved vertebrae, do not show any indication of notching of the zygantral roof as originally described by Cope.

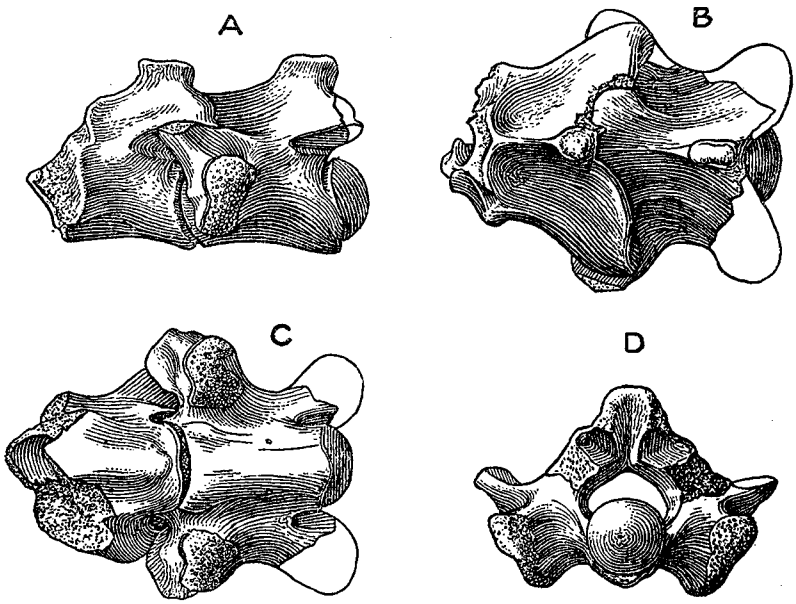


FIGURE 35.—*Posterior thoracic vertebrae of Helagras prisciformis Cope*
Type no. 1628 A. M. N. H. *A*, lateral; *B*, superior; *C*, ventral; *D*, posterior views. ×3.

Thus, this feature of the *Helagras* vertebrae may be dismissed from further consideration as it is non-existent. The so-called "*episphene*" of Cope is nothing more than the spinous process, and under this interpretation this term is no longer applicable.

DESCRIPTION OF VERTEBRAE: The outstanding feature of the *Helagras* vertebrae is the presence of a short, thickened, tuberous-like neural spine. Its summit is truncate, suboval in cross section, with the long diameter anteroposterior. It is entirely confined to the posterior half of the arch, and slightly elevated above the rest of the median line which is obtusely roof-like. In the type and in specimen No. 5185 A. M. N. H., the tops of the spines are set off by a circumscribing groove that gives the cap the appearance of being an epiphysis that had not fully coalesced. This feature, which is only of trivial importance, is not so apparent in the other known specimens. The peculiar form of the neural spine appears to distinguish the vertebrae of *Helagras* from those of other serpents.

Although there is some difference in size between the most anterior and

the most posterior, they do not vary much in proportions or in structure. The only changes noted are a slight lengthening of the neural spines and the progressive change usually found in the development of the hypapophyses. The flattened inconspicuous nature of the keel in the type vertebrae indicates that they pertain to the posterior thoracic part of the vertebral column. Precisely similar vertebrae are present with Nos. 1629 and 5185 A. M. N. H. When the vertebrae of these specimens are assorted according to the development of the hypapophyses it is found that they form a graduated series from the low rounded keel of the largest vertebrae to the compressed pendant type that occur on the smallest vertebrae and clearly pertain to the anterior thoracic region. On the more anterior of these, the posterior half of the hypapophyses projects well below the level of the articular end as a compressed, obtusely truncated hypapophysis. The anterior end in all the vertebrae widens transversely with a gentle convexity and merges smoothly into the rim of the glenoid fossa.

The diapophyses are relatively heavy and extend slightly below the ventral surface of the centrum. The tubercular articulation is prominent, hemispherical, and separated from the capitular surface by a slight constriction. The form of these articulating surfaces are not well shown in the type, being slightly abraded as on many vertebrae of the other specimens now available. They are placed directly below the prezygapophyses, but the free part of the latter extends well in front of the diapophyses. The condyle is moderately oblique, with an unusually short neck, subovate, longest diameter transverse.

The non-articular anterior face of the zygosphene is thickened and on some vertebrae shows a slightly raised transverse ridge on the lower median face. The top of the zygosphene is shallowly concave from side to side. The zygosphene is slightly wider than the glenoid fossa.

Referred specimens

No. 1629, A. M. N. H. About 90 anterior and posterior thoracic vertebrae. From the Puerco formation. Locality not given, but probably New Mexico. Collected in 1884. Part of the Cope collection.

No. 1650, A. M. N. H. 12 posterior thoracic vertebrae. From the Torrejon formation, West Fork Arroyo, Torrejon, N. Mex. Collected by W. J. Sinclair, 1913.

No. 5185, A. M. N. H. About 109 anterior and posterior thoracic vertebrae. From the Torrejon formation, West Fork Arroyo, Torrejon, N. Mex.

Genus *Coniophis* Marsh 1892

Coniophis Marsh, Am. Jour. Sci., 3d ser., vol. 43 (1892) p. 450, fig. 1a–e.

Genotype: *Coniophis precedens*.

Known from a single thoracic vertebrae.

Diagnosis: Neuropophyses greatly extended posteriorly, overhanging the ball; and with shallow emargination; without neural spine; zygosphene wider than glenoid fossa.

Coniophis from the Lance, Upper Cretaceous of Wyoming, is the most ancient snake known from North America.

There is nothing in common between *Coniophis* and *Symoleophis* from the Cretaceous (Lenonian) of France. Williston (1925, p. 276) regarded the type vertebrae of the last-mentioned genus as more probably pertaining to a dolichosaur lizard.

It is quite probable that *Coniophis* pertains to a distinct family, but the evidence is still too meager to determine that point.

Coniophis precedens Marsh

Coniophis precedens, MARSH, Am. Jour. Sci., 3d ser., vol. 43 (1892) p. 450, figs. 1a–e—WALCOTT, Science, 2d ser., vol. 11 (1900) p. 23—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 481; Carnegie Inst. Washington, Publ. no. 390 (1930) p. 271—BOWEN, U. S. Geol. Surv., Prof. Paper 90 i (1915) p. 129—MERRILL, U. S. Nat. Mus., Bull. 53, pt. 2 (1907) p. 66—OSBORN, Contrib. Canad. Paleont., vol. 3 (1902) p. 13.

TYPE SPECIMEN: U. S. N. M., Cat. no. 2134. Consists of a single thoracic vertebra, collected by J. B. Hatcher, 1892.

TYPE LOCALITY: "Peterson Quarry," Niobrara Co., Wyo.

HORIZON: Lance, Upper Cretaceous.

ORIGINAL DESCRIPTION: "The earliest serpents hitherto known in this country are included in the genera *Titanophis* (*Dinophis*) from the marine Eocene of New Jersey and *Boavus* from the fresh-water Dinoceras and Coryphodon beds of the West, both described by the writer. None have hitherto been found in the American Cretaceous and but one species is known from Europe. The type specimen of the present genus and species is the vertebra represented below in figure 1. [Fig. 36] Several others were found at the same locality, but may not pertain to this individual.

"In the type specimen figured above the zygosphene articulation is fully developed and all the characteristic Ophidian features are distinctly shown. The nearer affinities of the genus will be discussed in a later communication. All the known remains of the species are from the Ceratops beds of Wyoming."

The several other vertebrae mentioned by Marsh have not been located in the Peabody Museum collections so that our knowledge of *Coniophis precedens* rests entirely on the single type vertebra. The type, as has been determined, is from the famous mammal sand locality of Niobrara County (formerly Converse), Wyoming, designated by the collectors as "Peterson's quarry," after the late O. A. Peterson. It was one of those sandy areas from which the late J. B. Hatcher and his assistants obtained a large collection of isolated teeth, jaws, and other bones of diminutive mammals and reptiles.

In the hope that additional snake vertebrae might be found among the detrital materials from these sands, of which there is a considerable quantity in the U. S. National Museum collections, a systematic search of these materials was made, but without success. At present our knowledge of the Upper Cretaceous Serpentes rests entirely upon the single type vertebra.

This vertebra is in a perfect state of preservation, except for the lack of the smooth, hard diapophysial articular surfaces for the ribs, and a tiny abrasion of the surface on the median posterior border of the neural arch which may have been the seat of a small projecting spur (Fig. 37). Otherwise the vertebra is without a neural spine and, as a whole, is low and wide. The centrum has a median keel that may have developed into a distinct hypapophysis more anteriorly; this keel begins at the edge of the cup and terminates short of the articular surface of the ball. Anteriorly it presents an obtusely acute edge, gradually widening posteriorly where it has a truncated ventral surface that projects downward below the level of the centrum (Fig. 36).

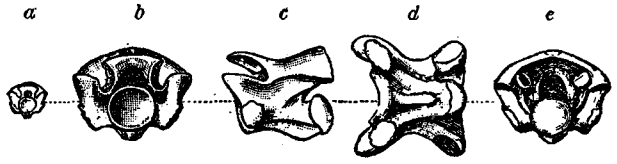


FIGURE 36.—*Thoracic vertebra of Coniophis precedens Marsh*

Type no. 2134 U. S. N. M. *A*, natural size; *B*, anterior; *C*, lateral; *D*, ventral; *E*, posterior views. ×3. After Marsh.

FIGURE 37.—*Thoracic vertebra of Coniophis precedens Marsh*

Type no. 2134 U. S. N. M. Superior view. ×3.

Cup and ball are transversely elliptical and slightly oblique. Diapophyses quite prominent but, as previously mentioned, with articular surfaces abraded. That the articular face was divided into a tubercular and capitular facet appears to be indicated by an indentation on the posterior side of the diapophyses. Faint longitudinal ridges run backward from each facet, disappearing at mid-length on the side of the centrum. Between these ridges the surface is slightly hollowed out.

The zygosphene is wider than the glenoid fossa, slightly convex above with a comparatively thin and straight transverse border, without median tubercle. Edges of the articular facets project backward slightly beyond the intermediate border. The zygantrum is deeply excavated and more extensively roofed over than is found in modern serpents. The posterior neuropophysial border is broadly but shallowly notched, not deeply incised as in most ophidians (Fig. 37), This posterior extension of the neuropophyses has its nearest counterpart in the type of *Lestophis* (*Limnophis*) *crassus*, but more extreme than in that species.

Interzygapophysial ridges practically die out in the center, the region of greatest lateral emargination. The zygapophyses have nearly horizontal, articular surfaces that are somewhat elongate, oval facets.

Measurements

	Mm.
Length of centrum from edge of cup to convexity of ball	3.5
Vertical diameter of cup	1.5
Transverse diameter of cup	1.8
Transverse diameter of zygosphene at top	2.2
Distance from top of zygosphene to bottom of cup	3.0
Vertical diameter of ball	1.4
Transverse diameter of ball	1.7

SUPPOSED SERPENTES REFERRED TO SAURIA

Lestophis crassus Marsh

Limnophis crassus MARSH, Am. Jour. Sci., 3d ser., vol. 1 (1871) p. 328—KING, U. S. Geol. Expl. 40th Par., vol. 1 (1878) p. 405—DE ROCHEBRUNE, Nouv. Arch. Mus. Hist. Nat., 2d ser., vol. 3 (2) III, (1880) p. 289.

Lestophis crassus MARSH, Am. Jour. Sci., 3d ser., vol. 29 (1885) p. 169—HAY, U. S. Geol. Surv., Bull. 179 (1902) p. 480; Carnegie Inst. Washington, Publ. 390, vol. 2 (1930) p. 268.

Paleoboa crassa (MARSH) SCHMIDT, Copeia, issue 163 (1927) p. 58.

TYPE SPECIMEN: Peabody Mus. Yale Univ., Cat. no. 531. Consists of a single cervical vertebra. Collected by A. H. Ewing, Sept. 1870.

TYPE LOCALITY: Marsh Fork, about 15 miles from Fort Bridger, Uinta Co., Wyo.

HORIZON: Bridger, Middle Eocene.

ORIGINAL DESCRIPTION: "One of the most interesting of the Ophidian fossils obtained during our explorations in Wyoming was a single anterior dorsal vertebra, very well preserved, and quite unlike any hitherto described. It indicates a moderately sized constricting serpent, perhaps six feet in length, but evidently of a very different type from the species already characterized. On comparing it with the corresponding vertebrae of *Boavus* and *Lithophis*, a striking difference is at once seen in the dimensions of the articular cup, which considerably exceeds in width the parallel diameter of the base of the zygosphene, a feature only observed heretofore in a few fossil serpents from the Eocene and quite unknown in modern species. The cup and ball have a subtriangular, ovate outline, the greatest transverse diameter being above the center; they are also placed nearly at right angles to the axis of the centrum. Another marked peculiarity of this vertebra is the unusual posterior extension of the neurapophyses which project some distance beyond the articular ball. Their nearly flat sides slope downward and outward like a gable roof, without any indication of the angle so characteristic of the vertebrae of *Palaeophis?* which in several other respects the present specimen strongly resembles. The neural spine is unfortunately not preserved, but it was evidently short and confined to the posterior two-thirds of the neural arch. The anterior zygapophyses had only a moderate expansion. The diapophyses have, for the attachment of the rib, a single rounded, and prominent tubercle, with its lower border above the inferior margin of the cup, and with no indication of a dependent process. There is also no ridge extending from the diapophysis to the articular ball. The hypapophysis consists of a single, compressed, obtuse tubercle, which descends from the middle of the centrum downward and slightly forward; its base occupying rather more than half of the median line. The more important dimensions of this vertebra are as follows:

			Mm.
"Length of centrum from edge of cup to convexity of ball	3.20	lines	[6.7]
Transverse diameter of cup	2.30	"	[4.8]
Vertical diameter of cup	1.80	"	[3.7]
Vertical diameter of ball	1.70	"	[3.5]
Distance from posterior summit of neurapophysis to inferior margin of ball	3.50	"	[7.3]
Length of hypapophysis below inferior margin of cup	.90	"	[1.8]"

A study of the type specimen shows that the very characters used by Marsh to distinguish this genus and species are those that appear to indicate its affinities to be with the Sauria and not with the Serpentes. Reference is made to the wide, ovate articular cup, the great posterior extension of the neuropophyses, the presence of a single rounded tubercle for the articulation of the rib, and the absence of a zygosphene-zygantrum articulation.

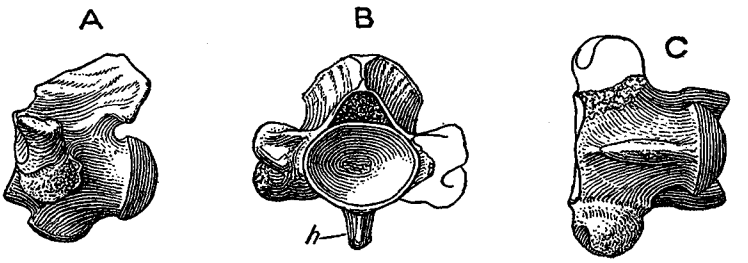


FIGURE 38.—*Anterior vertebra of Lestophis crassus Marsh*

Type no. 531 P. M. N. H. *A*, lateral; *B*, anterior; *C*, ventral views; *H*, hypapophysis. ×3.

Substantiation of this conclusion (Gilmore, 1928, p. 46, 47) is found when the specimen is contrasted with the type of the Amphisbaenoid, *Ototriton anceps* (Marsh), which shows many likenesses all the more significant when it is known that both specimens came from the same geological horizon and the same general locality. The two vertebrae are in full agreement as to the apparent absence of a neural spine, the sculpturing of the surface on either side of the superior median ridge by longitudinal ridges, the short and slightly depressed centrum, and the low neural arch and articular ball looking more forward than upward.

The only character not in accord with its assignment to the Sauria appears to be the presence of a well-developed hypapophysis. Among the extinct Sauria exogenous processes for hypapophyses are found on the cervical vertebrae of *Saniwa ensidens* and in the Mosasauria. A similar condition is found in the living *Varanus*, but nowhere has the author been able to find hypapophyses on the dorsal vertebrae of a lizard, either living or extinct. It would therefore appear to indicate the type vertebra to be a posterior cervical.

In view of the Sauria characters, pointed out above, the author proposes to remove this genus and species from Serpentes to the Sauria, and, because of the resemblances cited to assign *Ototriton anceps* (Marsh) to the genus *Lestophis* (Gilmore, 1928, p. 46), to be known hereafter as *Lestophis anceps* (Marsh).

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INDEX*

* Numbers in **boldface type** indicate detailed description of genera and species.

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