malachiticus (12), *megalepidurus* (1), *melanorhinus melanorhinus* (1), *melanorhinus stuarti* (1), *merriami merriami* (3), *mucronatus* (1), *nelsoni* (1), *occidentalis biseriatus* (6), *occidentalis occidentalis* (61), *olivaceus* (4), *orcutti licki* (3), *orcutti orcutti* (12), *ornatus* (5), *parvus* (4), *poinsetti* (15), *prezygus* (1), *pyrocephalus* (2), *scalaris scalaris* (10), *scalaris slevini* (10), *siniferus siniferus* (2), *spinosus spinosus* (4), *squamosus* (3), *torquatus torquatus* (2), *undulatus consobrinus* (13), *undulatus hyacinthinus* (14), *undulatus undulatus* (3), *utiformis* (2), *variabilis olloporus* (2), *variabilis variabilis* (3), *virgatus* (6), *woodi* (1).

Uma: *exsul* (2), *notata inornata* (6), *notata notata* (4), *notata rufopunctata* (6), *paraphygas* (2), *scoparia* (24).

Urosaurus: *auriculatus* (1), *bicarinatus bicarinatus* (2), *clarionensis* (1), *graciosus* (7), *microscutatus* (3), *nigricaudus* (34), *ornatus caeruleus* (1), *ornatus lateralis* (1), *ornatus ornatus* (4), *ornatus schmidti* (1), *ornatus symmetricus* (13).

Uta: *concinna* (1), *martinensis* (1), *stansburiana elegans* (2), *stansburiana hesperis* (140), *stansburiana stejnegeri* (3), *stellata* (3).

Phrynosoma: *asio* (1), *cornutum* (9), *coronatum blainvillii* (12), *douglassi hernandesi* (7), *mcalli* (7), *modestum* (8), *orbiculare cortezi* (1), *orbiculare orbiculare* (4), *platyrhinos calidiarum* (10), *platyrhinos platyrhinos* (6), *solare* (3).

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Department of Zoology, San Diego State College, San Diego, California.

Fossil Snakes from the Valentine Formation of Nebraska

J. Alan Holman

The Valentine formation of Brown County, Nebraska, apparently represents a period transitional between upper Miocene and lower Pliocene. The snake fauna is the earliest known that is essentially modern. Snake vertebrae from the Valentine are identified as: Boidae, Boinae gen. et sp. indet.; Colubridae, *Paleoheterodon tiheni* gen. et sp. nov., *Elaphe nebraskensis* sp. nov., *Lampropeltis similis* sp. nov., Colubrinae indet., and Natricinae gen. et sp. indet.

Introduction

MOST of our knowledge of late Tertiary snakes is based on a handful of specimens from lower Miocene and middle Pliocene deposits. Thus, the discovery of fossil snake remains from beds considered transitional between the Miocene and Pliocene series offers a unique opportunity for study. This report is based on these fossil remains, and details the earliest essentially modern North American snake fauna known.

The fossils listed in this paper were collected at the Norden Bridge local fauna of the Valentine formation during the summers

of 1962 and 1963 by J. A. Tihen and Charles J. Chantell, who were assisted in the field by Joseph A. Budek, Peter Morris, and Lawrence Tihen. The site is located on the Ed McCall Ranch, in the SE ¼ of the SW ¼ of Sect. 33, T 33 N, R 23 W, Brown County, Nebraska. The fossil beds are a channel deposit with a maximum width of about 20 yards.

Preceding authors have considered the Valentine formation to represent the lowermost Pliocene (Shultz and Stout 1961) or upper Miocene (Stirton and McGrew 1935, and MacGinitie 1962). Nevertheless, Tihen and Chantell (1963) pointed out that the Valentine beds are essentially transitional between the Miocene and Pliocene series. For a detailed report on the stratigraphy of the deposit, as well as a discussion on previous faunal works on the Valentine formation, the reader is referred to the above paper, which also describes 2 new salamanders of the genera *Cryptobranchus* and *Ambystoma*. Furthermore, Chantell has recently completed a thesis on the hylid frog remains of the Valentine formation.

Since the pioneering work of Gilmore (1938) on the fossil snakes of North America, 2 recent papers have been instrumental in pointing out the diagnostic value of snake vertebrae in fossil studies. Johnson (1955) elaborated the concept that vertebral shape does not correlate with the mode of existence of snakes, and Auffenberg (1963) did a comprehensive study on the fossil snakes of Florida, and identified many vertebrae to the specific level. The anatomical terminology used in the following paragraphs is that of Auffenberg (1963:150–155). Most of the Valentine fossils are fragmentary, but 13 vertebrae are identified to at least the subfamilial level. The families Boidae and Colubridae are represented by at least 3 subfamilies (Boinae, Colubrinae, and Natricinae). The Colubrinae are represented by at least 4 genera and 4 species. The Natricinae and Boinae are each represented by 1 genus and 1 species.

Many thanks are due to Dr. J. A. Tihen of Notre Dame University for allowing me the privilege of studying the fossils. I also wish to extend my appreciation to the following people who have donated snakes used as comparative material: R. S. Simmons, Baltimore, Maryland; H. P. and M. N. Arai, Calgary, Alberta; D. Jenni, Charleston, Illinois; K. Hartz, Chicago, and G. B. Rabb, Brookfield, Illinois; J. H. Hutchison, Eugene, Oregon; W. A. Auffenberg, P. Brodkorb, and A. F. Carr, Gainesville, Florida; C. Meyers, Lawrence, Kansas; H. W. Campbell, Los Angeles, California; F. W. King, Miami, Florida; W. H. Hill, E. Mockford, E. A. Munyer, and R. D. Weigel, Normal, Illinois; and J. D. Lynch and H. M. Smith, Urbana, Illinois.

Donna Rae Holman made the drawings.

Boidae

Subfamily Boinae gen. et sp. indet.

Material.—Caudal vertebra, University of Nebraska No. 61030.

Remarks.—The vertebra represents a small snake of the subfamily Boinae similar to the Recent genus *Charina* Gray, but differs in detail from 2 Recent skeletons of *C. bottae* (Blainville). Because previous descriptions of small fossil boids have been based on precaudal vertebrae, a more definite taxonomic allocation of the fossil is deferred until precaudal vertebrae are recovered.

Description.—The vertebra is relatively short and wide. The neural canal is slightly smaller than the round cotyle. The depressions on either side of the cotyle are deep. The left lymphapophysis is broken, whereas the right one is round, and has only its tip broken. The hemal keel is distinct and moderately wide anteriorly, but bifurcates posteriorly into 2 ventrally produced processes that appear to have their tips broken. The condyle is round, although it is highly eroded. The postzygapophyseal faces are small and ovaloid. The neural arch is massive and vaulted. The neural spine is exceedingly massive and greatly swollen dorsally. It is longer than high. The prezygapophyseal faces are small and ovaloid in shape. The right accessory process is obsolete and projects only slightly beyond the prezygapophysis in dorsal view. The left accessory process is highly eroded. The length of the vertebra through the zygapophyses is 1.9 mm, its greatest height (excluding the lymphapophysis) is 2.8 mm.

The genus *Charina* is first reported from the fossil record as *Charina prebottae* Brattstorm from the upper Miocene of the Barstow formation of San Bernardino County, California, and possibly the Valentine fossil represents this species. *C. prebottae* was described on the basis of 2 "mid-thoracic" (precauda) vertebrae.

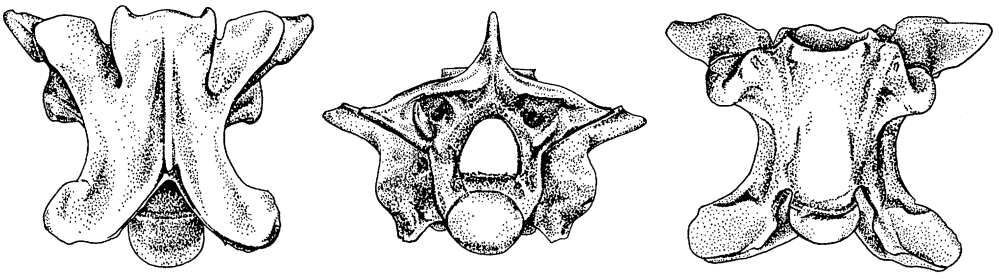

Fig. 1. Holotype (University of Nebraska No. 61031) precaudal vertebra of *Paleoheterodon tiheni* gen. et sp. nov. From left to right, dorsal view, posterior view, ventral view (dorsal view × 5½, others × 6).

COLUBRIDAE

Subfamily Colubrinae

Paleoheterodon gen. nov.

Diagnosis.—A colubrid similar to *Heterodon* Latreille, but differing in having the neural arch vaulted (depressed in *Heterodon*), and in having the accessory processes short (longer in *Heterodon*).

Genotype.—Paleoheterodon tiheni sp. nov.

Paleoheterodon tiheni sp. nov.

Holotype.—Precaudal vertebra, University of Nebraska No. 61031 (Fig. 1).

Paratypes.—Two precaudal vertebrae, University of Nebraska No. 61032.

Type horizon.—Valentinian; Valentine formation; Norden Bridge Quarry.

Type locality.—Near the Norden–Johnstown Road, about 300 yards south of the bridge across the Niobrara River; on the Ed McCall Ranch, SE ¼, SW ¼ of Sect. 33, T 33 N, R 23 W, Brown County, Nebraska.

Diagnosis.—As for the genus.

Etymology.—The species is named in recognition of the paleoherpetological contributions of Dr. J. A. Tihen.

Description of holotype.—The vertebra is relatively short and wide. The neural canal is about equal in size to the oval, depressed cotyle. The pits on either side of the cotyle are moderately excavated. Both the parapophyses and the diapophyses are massive. The anterior edge of the zygosphene is moderately convex from above. The prezygapophyseal faces are subtriangular in shape with their anterior faces slightly rounded. The accessory processes are obsolete; the right process is obtuse, the left process is acute. The top of the neural spine is thick, but part of it is broken. The neural arch is moderately vaulted and it lacks epizygapophyseal spines. The postzygapophyseal faces are subtriangular. The hemal keel is weak, wide, much depressed, and oblong. The condyle is well developed, oval, and depressed. The subcentral ridges are indistinct. The length of the vertebra through the zygapophyses is 5.1 mm, the width through the accessory processes is 6.7 mm, the height from the lower lip of the cotyle through the top of the zygosphene is 3.5 mm.

Additional material.—One paratype is about the same size as the holotype, but is much more fragmentary. The neural arch is a little more vaulted than in the holotype, and the hemal keel is more distinct and more constricted in the region of the parapophyses. The other paratype has the hemal keel similar to that of the holotype.

Remarks.—The vertebrae of *Paleoheterodon* are undoubtedly closer to *Heterodon* than to any other North American genus. The vertebrae of *Heterodon* are quite distinctive (Holman 1962, Auffenberg 1963). The earliest record of *Heterodon* is that of *H. brevis* Auffenberg from the middle Pliocene of Florida. This species is thought to be closely related to Recent *H. platyrhinos* (Auffenberg 1963). The species *H. plionasicus* Peters was described from the upper Pliocene of Kansas on the basis of palatine and maxillary bones. This form is thought to be close to Recent *H. nasicus* (Peters 1953). All of the living species of *Heterodon* are known from various Pleistocene deposits (*H. platyrhinos,* Florida, Holman 1958, 1959, Auffenberg 1963; *H. nasicus,* Texas, Holman 1963; *H. simus,* Florida, Holman 1959, Auffenberg 1963).

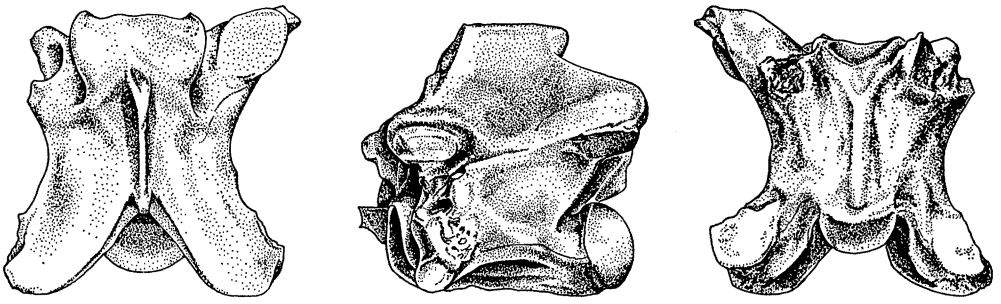

Fig. 2. Holotype (University of Nebraska No. 61033) precaudal vertebra of *Elaphe nebraskensis* sp. nov. From left to right, dorsal view, lateral view, ventral view (all × 5).

It is noteworthy that the holotype of *Paleoheterodon tiheni* more closely resembles Recent *H. nasicus* and *H. simus* than *H. platyrhinos* in having a flatter, less distinct hemal keel, and in the more rounded anterior borders of the prezygapophyseal faces.

Elaphe nebraskensis sp. nov.

Diagnosis.—An *Elaphe* similar to Recent *E. vulpina* (Baird and Girard) in height of neural spine and in size, but differing from this and all other Recent and fossil *Elaphe* species examined in the much more oblique positions of the accessory processes and prezygapophyseal faces to the long axis of the centrum.

Holotype.—Precaudal vertebra, University of Nebraska No. 61033 (Fig. 2).

Paratype.—Precaudal vertebra, University of Nebraska No. 61034.

Referred material.—Anterior vertebra with hypapophysis, University of Nebraska No. 61039.

Type horizon.—Valentinian; Valentine formation; Norden Bridge Quarry.

Type locality.—Near the Norden–Johnstown Road, about 300 yards south of the bridge across the Niobrara River; on the Ed McCall Ranch, SE ¼, SW ¼ of Sect. 33, T 33 N, R 23 W, Brown County, Nebraska.

Description of holotype.—The vertebra is relatively short and wide. The neural canal is about two-thirds the size of the round cotyle. The pits on either side of the cotyle are moderately developed. The anterior edge of the zygosphene is sinuate from above. The prezygapophyseal faces are ovaloid and strongly oblique to the long axis of the centrum. The accessory processes have their ends broken, but these processes are also strongly oblique to the long axis of the centrum. The anterior part of the top of the neural spine is broken, but the spine is only moderately thick, and is much longer than high. The neural arch is moderately vaulted. The right side of the neural arch has a very obsolete epizygapophyseal spine; the left side is without this spine. The postzygapophyseal faces are ovaloid. The hemal keel is strong, but narrow, and roughly oblong. The condyle is well developed and round. The subcentral ridges are distinct, but rather weakly developed. The length of the vertebra through the zygapophyses is 6.5 mm, the height from the condyle through the top of the neural spine is 6.7 mm, the width through the postzygapophyses is 6.9 mm.

Additional material.—The paratype is about the size of the holotype, and although it is more fragmentary than the holotype, the paratype shows no salient differences in characters. The referred anterior vertebra appears to have come from a snake of about the size of the one represented by the holotype.

Remarks.—*Elaphe nebraskensis* is a very distinct member of the genus, and differs from all Recent skeletons of species of *Elaphe* examined (*E. obsoleta*, 9; *E. vulpina*, 7; *E. guttata*, 6; *E. quatuorlineata*, 1; *E. dione*, 1; *E. situla*, 1; and *E. longissima*, 1) and from the fossil *Paleoelaphe kansensis* Gilmore in having much more obliquely placed accessory processes and prezygapophyseal faces. Nevertheless, *E. nebraskensis* appears to be closest to Recent *E. vulpina* in size, and in having a rather low neural spine. Characters for distinguishing the vertebrae of *Elaphe* from those of the closely related

genera *Pituophis* and *Lampropeltis* have been discussed by Brattstrom (1955a), Holman (1959), and Auffenberg (1963).

Auffenberg (1963) suggested that the Pliocene *Paleoelaphe kansensis* should be synonymized with *Elaphe*. Moreover, Auffenberg stated that *P. kansensis* is probably ancestral to Recent *Elaphe obsoleta*. Whether *Elaphe nebraskensis* is ancestral to Recent *E. vulpina* is, of course, speculative at present.

Lampropeltis similis sp. nov.

Diagnosis.—A small *Lampropeltis* similar to the Recent species group comprising *L. doliata* (Linnaeus), *L. pyromelana* (Cope), and *L. zonata* (Blainville), and to the Pliocene and Pleistocene fossil *L. intermedius* Brattstrom. Closest to *L. intermedius* in having small, narrowly rounded accessory processes (accessory processes usually much larger and more broadly rounded in *L. doliata, L. pyromelana,* and *L. zonata*). Differs from *L. intermedius* in having top of zygosphene gently curved (top of zygosphene with straight, downward-sloping sides in *L. intermedius,* Brattstrom 1955a:153, Fig. 1A), and in having the subcentral ridges slightly convex from below (concave from below in *L. intermedius*).

Holotype.—Precaudal vertebra, University of Nebraska No. 61035 (Fig. 3).

Paratype.—Precaudal vertebra, University of Nebraska No. 61036.

Type horizon.—Valentinian; Valentine formation; Norden Bridge Quarry.

Type locality.—Near the Norden–Johnstown Road, about 300 yards south of the bridge across the Niobrara River; on the Ed McCall Ranch, SE ¼, SW ¼ of Sect. 33, T 33 N, R 23 W, Brown County, Nebraska.

Etymology.—Latin, similis, masculine and feminine, like, resembling, similar, in reference to the similarity of the fossil to the above species of *Lampropeltis.*

Description of holotype.—The vertebra is relatively short and wide. The neural canal is slightly smaller than the cotyle which is oval and depressed. The pits on either side of the cotyle are deeply excavated. The diapophyses and parapophyses on both sides are badly worn. In anterior view, the edge of the zygosphene is gently curved dorsally. The prezygapophyseal faces are ovaloid and about equal in size. The accessory processes are small and narrowly rounded and at about right angles to the long axis of the centrum. The neural spine is much longer than high. The neural arch is moderately vaulted and lacks epizygapophyseal spines. The postzygapophyseal faces are ovaloid, and about equal in size. The hemal keel is moderately strong, narrow, and oblong. The condyle is well developed and slightly eroded. The subcentral ridges are moderately distinct and slightly concave from below. The length through the zygapophyses is 4.0 mm, the width through the prezygapophyses is 4.8 mm, the height from the lower lip of the cotyle through the top of the zygosphene is 3.1 mm.

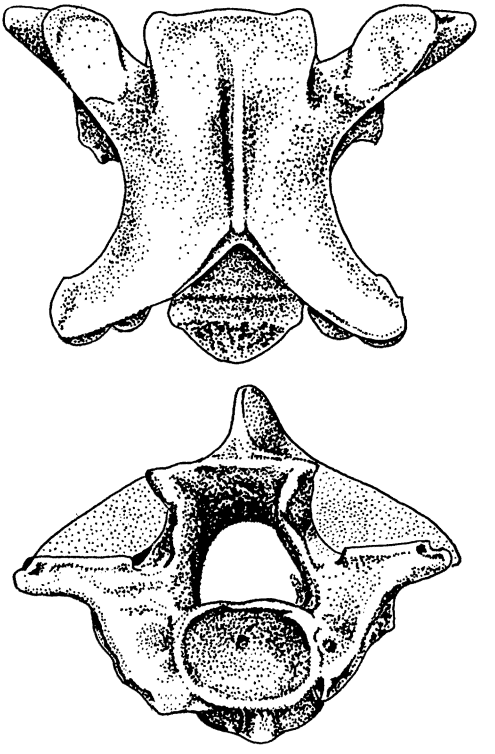

Fig. 3. Holotype (University of Nebraska No. 61035) precaudal vertebra of *Lampropeltis similis* sp. nov. From top to bottom, dorsal view, anterior view (all × 11¼).

Additional material.—The paratype is very close in size to the holotype, but is more fragmentary. It does not differ in important characters from the holotype.

Remarks.—This fossil may be the ancestral form for *L. intermedius,* which is known

from the Pliocene of the Goleta formation, Morelia, Michoacán, México, and from the early Pleistocene of the Curtis Ranch, San Pedro Valley, Cochise County, Arizona (Brattstrom 1955a). Brattstrom indicated the possibility that *L. intermedius* is the stem form for *L. doliata, L. pyromelana,* and *L. zonata. L. doliata* is known from late Pleistocene deposits in Florida (Auffenberg 1963) and Texas (Holman 1963).

Colubrinae gen. et sp. indet.

Material.—Two precaudal vertebrae, University of Nebraska No. 61037.

Remarks.—Two small fragmentary colubrine vertebrae are not particularly close to any Recent or fossil skeletal material available, and may either represent an extinct genus not closely related to living forms or one found in Central or South America today. Because of the fragmentary nature of the fossils, because skeletons of Recent Central and South American genera are not available for study, and because it appears that it will take much time to accumulate such an extensive skeletal collection, further taxonomic allocation of these Valentine fossils is deferred.

A description of the more complete of the 2 vertebrae follows. The vertebra is relatively long and narrow. The neural canal is slightly smaller than the oval, slightly depressed cotyle. The depressions on either side of the cotyle are shallowly excavated. The parapophyses and diapophyses are strongly developed, with the diapophyses much produced beyond the lateral edges of the prezygapophyses. The anterior edge of the zygosphene is crenate from above. The prezygapophyseal faces are ovaloid. The accessory processes are broken. The neural spine is complete and is much longer than high. The neural arch is moderately vaulted and has its posterior edge very strongly beveled. Epizygapophyseal spines are lacking. The right postzygapophyseal face is broken, the left one is partially broken, but appears to be subtriangular in shape. The condyle is complete, well developed, oval, but only slightly depressed. The hemal keel is well developed, moderately wide, and spatulate. The subcentral ridges are distinct and straight from below. The length through the zygapophyses is 3.6 mm, the width through the prezygapophyses is 3.6 mm. There is no significant variation in the other specimen, which is more fragmentary, but possibly came from the same snake.

Subfamily Natricinae gen. et sp. indet.

Material.—Two vertebrae, University of Nebraska No. 61038.

Remarks.—The above vertebrae show the characteristics of the subfamily (Auffenberg 1963), but are not identified to genus because of their fragmentary nature. In size they represent a rather small natricine snake, but not one of the diminutive forms.

Discussion

The Valentine formation fossils represent the earliest essentially modern snake fauna from the New World based on living colubrid genera present, and the number of colubrid forms present as opposed to aniliids and boids. The status of the Valentine snake fauna may be reflected by a brief examination of the few North American Tertiary terrestrial snake faunas that have produced more than 1 or 2 forms.

Hecht (1959) listed a fauna from the middle Eocene of the Bridger formation of Wyoming which consists of Aniliidae (1 genus, 2 species), Boidae (3 genera, 3 species), and an *incertae sedis* genus and species that is thought to be related to the Boidae. No colubrids are present.

I have recently examined an early Oligocene fauna from the Cypress Hills formation of Saskatchewan, Canada. This fauna consists entirely of aniliid and/or boid forms.

Auffenberg (1963) listed a fauna from the early Miocene of the Thomas Farm of Florida. This fauna consists of Aniliidae (1 genus, 1 species), Boidae (3 genera, 3 species), and Colubridae (2 genera, 2 species). Both of Auffenberg's colubrid genera are extinct. One of these (*Pseudocemophora*) may be ancestral to both *Lampropeltis* and *Cemophora,* whereas the other (*Paraoxybelis*) is thought to be unrelated to any North American genus, and may be close to one of several Central and South American forms.

The Valentine formation snakes from beds thought to be transitional between the Miocene and Pliocene series consists of Boidae (1 genus, 1 species) and Colubridae (5 genera, 5 species). One of the 3 named colubrid genera is extinct, and 2, *Elaphe* and *Lampro-*

peltis, are living today. The extinct genus (*Paleoheterodon*) appears closely related to the North American genus *Heterodon*, whereas vertebrae identified only as Colubrinae may represent an extinct genus not closely related to any living forms. The natricine vertebrae appear to represent a single form although the bones are too fragmentary for generic identification. No aniliids are present.

A middle Pliocene fauna from Alachua County, Florida (Auffenberg 1963), consists of all living genera, but all named forms are considered extinct species. Colubrid forms described as new species include *Heterodon, Stilosoma,* and *Diadophis,* and *Crotalus* ? and *Micrurus* ? represent the Viperidae and Elapidae. No aniliids or boids are present.

Pleistocene snake faunas from Florida and Texas have no aniliids or boids, and the colubrids, viperids, and elapids consist almost entirely of living species (Auffenberg 1963; Holman 1962, 1963).

Thus far, the fragmentary fossil record of North American Tertiary terrestrial snakes indicates (1) only aniliids and boids from the early Tertiary, (2) mainly aniliids and boids in early Miocene, but appearance of extinct colubrid genera, (3) appearance of living colubrid genera (extinct species) and lack of most aniliid and boid forms by the transition period between late Miocene and early Pliocene, (4) appearance of more living colubrid genera (extinct species) as well as viperid and elapid genera that seem close to living genera by middle Pliocene, and (5) appearance of living species of Colubridae, Elapidae, and Viperidae in the Pleistocene.

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Department of Biological Sciences, Illinois State University, Normal, Illinois.