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A FOSSIL SNAKE (*ELAPHE VULPINA*) FROM A PLIOCENE ASH BED IN NEBRASKA

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The articulated skeleton of a fossil snake from the late Middle Pliocene of northeastern Nebraska is unique in that it is one of the most complete fossil snakes known; it was preserved by an ash-fall. It is identified as the modern species *Elaphe vulpina*, and it appears to have been trampled by a large ungulate.

† † †

INTRODUCTION

A fossil snake from the Santee local fauna was collected in August 1979 by J. Alan Holman, Raymond A. Holman, and Michael R. Voorhies. The Santee local fauna (University of Nebraska State Museum Locality Kx-111) is exposed in a road cut on the south side of the Lewis and Clark Reservoir of the Missouri River, 17.7 km ENE of the junction of the Niobrara and Missouri rivers, Knox County, Nebraska, at Latitude 42° 49′ N, 97° 50′ W. The matrix of this locality consists of an ash that fell on the area about 4.5 m.y.B.P. during the latter part of the Hemphillian land mammal age.

SYSTEMATIC PALEONTOLOGY

Class Reptilia Laurenti, 1769
Order Squamata Oppel, 1811
Family Colubridae Cope, 1866
Genus *Elaphe* Fitzinger, 1833
Elaphe vulpina (Baird and Girard, 1853), fox snake

Preliminary Remarks

Fossil Material. An articulated skeleton of a fossil snake (Michigan State University Vertebrate Paleontology Number 941) consisting of a partially crushed skull and postcranial skeleton. Recognizable skull-bones: the left frontal, parietal, maxillae, right transpalatine, left palatine, pterygoids, supra-occipital, quadrates, parasphenoid, basisphenoid, splenials, dentaries, angulars, articulars, supra-angulars, and coronoids. The other skull elements crushed beyond recognition. Post-cranial elements: 47 cervical vertebrae, 146 trunk vertebrae, 46 caudal vertebrae, and 155 ribs.

Modern Snake Skeletons Studied. It became obvious early that the fossil skeleton seemed identical to those of the extant species *Elaphe vulpina,* the fox snake. Each fossil bone was compared with a series of *E. vulpina* skeletons and with related species to verify the identification. Modern snake skeletons studied were: *E. guttata emoryi* (2), *E. g. guttata* (6), *E. o. obsoleta* (5), *E. o. quadrivittata* (2), *E. o. rossalleni* (1), *E. subocularis* (1), *E. v. gloydi* (1), *E. v. vulpina* (7), *Lampropeltis c. calligaster* (5), *L. g. getulus* (3), *Pituophis melanoleucus mugitus* (2), and *P. m. sayi* (4).

Comparative Osteology of the Fossil Snake

Frontal. Frontal bones of *Elaphe vulpina* and related species do not appear to be diagnostic at the generic or the specific level. Nevertheless, the fossil is inseparable from modern *E. vulpina.* The fossil has the prominent posterior foramen that occurs in *E. vulpina,* which is often smaller in related species. The internal ventral processes of *E. vulpina* are less robust than in *Lampropeltis getulus.*

Parietal. The parietal is a prominent fused element in *Elaphe vulpina* and related species. Only a small portion of the anterior part of the parietal was present in the fossil.

Maxilla (Fig. 1A). There are strong differences between the maxillae of *Elaphe* and species of related genera, but differences between *E. vulpina* and some other species of *Elaphe* are subtle. *Elaphe vulpina* has fewer maxillary teeth

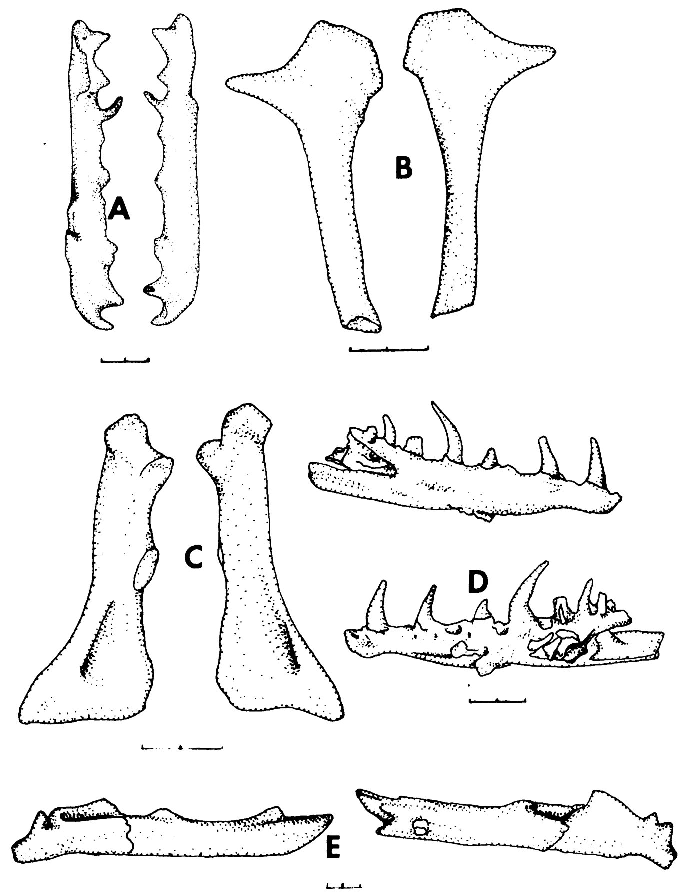

FIGURE 1. Skull bones (all from the right side of the head) of the fossil *Elaphe vulpina*. **A.** Maxilla viewed externally (left); viewed internally (right). **B.** Transpalatine viewed dorsally (left); viewed ventrally (right). **C.** Quadrate viewed externally (left); viewed internally (right). **D.** Dentary viewed externally (upper); viewed internally (lower). **E.** Mandible viewed externally (left); viewed internally (right). Projections equal 2 mm.

and alveolar spaces than do species of *Lampropeltis* and *Pituophis,* and fewer teeth than does *E. subocularis,* but differences in tooth-alveolar counts are not appreciable among *E. vulpina, E. guttata,* and *E. obsoleta* (Table I).

Elaphe vulpina has a less robust maxilla and more gracile teeth than does *Lampropeltis getulus,* and its posterior end is much blunter than that of *L. triangulum.* The maxillary teeth of *E. vulpina* appear to be somewhat shorter and stouter than those of *E. guttata* and *E. obsoleta.* The fossil appears to be indistinguishable from modern *E. vulpina.*

Transpalatine (Fig. 1B). The transpalatine is a specifically diagnostic bone in *Elaphe vulpina* as follows: lateral process narrow and with its tip truncated; medial process directed at nearly a right angle to the shaft, short and not sharply pointed; shaft slightly curved medially; excavation between anterior processes shallow.

TABLE I. Tooth-alveolar counts of maxillae of *Lampropeltis, Pituophis,* and *Elaphe.*

	Number	Mean	Sample Size
Lampropeltis calligaster	12–16	(13.7)	3
Lampropeltis getulus	14	(14.0)	3
Lampropeltis triangulum	12	(12.0)	2
Pituophis melanoleucus	14–16	(15.3)	4
Elaphe guttata	16–19	(17.4)	5
Elaphe obsoleta	16–19	(18.0)	4
Elaphe subocularis	20	(20.0)	1
Elaphe vulpina modern	16–17	(16.8)	4
Elaphe vulpina fossil	17	(17.0)	1

The transpalatine of *Elaphe vulpina* differs from that of *Lampropeltis getulus* in having the medial process directed at nearly a right angle to the shaft and in having the excavation between the anterior processes much shallower. It differs from those of *L. calligaster* and *L. triangulum* in having the anterior processes much shorter and stouter and the excavation between the anterior processes much shallower. It differs from that of *Pituophis melanoleucus* in having its medial process shorter, blunter, and nearly at a right angle to the shaft. It differs also in having its shaft curved.

The transpalatine of *Elaphe vulpina* differs from that of *E. guttata* in having the medial process shorter, less slender, and directed nearly at a right angle to the shaft, as well as in having the lateral process narrower. It differs from that of *E. obsoleta* in having the medial process shorter, less slender, and directed at nearly a right angle to the shaft, as well as in having the lateral process narrower. It differs from that of *E. subocularis* in having the medial process longer and wider and the lateral process much narrower, as well as in having the excavations between the two processes deeper.

Palatine, Pterygoid, and Supraoccipital. These bones are too damaged to be of diagnostic value, although none of them is separable from *Elaphe vulpina.*

Quadrate (Fig. 1C). The quadrate is a specifically diagnostic bone in *Elaphe vulpina* as follows: proximal end simple, not sharply bevelled, hooked, flared, or with a distinct lateral process; stapedial tubercle short; distal end relatively wide with a lateral flange, not rotated or highly depressed above the trochleae.

The quadrate of *Elaphe vulpina* may be distinguished from those of *Lampropeltis calligaster, L. getulus,* and *L. triangulum* in that its proximal end is simple—not highly bevelled, flared, or hooked—and in that its stapedial tubercle is much shorter. It may further be separated from that of *L. calligaster* in that its distal end is not rotated, and from *L. getulus* in that its articular surfaces are less robust. It may be separated from that of *Pituophis melanoleucus* by its shorter stapedial tubercle and its wider, flange-bearing distal end.

The quadrate of *Elaphe vulpina* may be distinguished from that of *E. guttata* in that the lateral portion of its proximal end is not differentiated into a sharp process. A much less sharp process is present in this area in *E. obsoleta. Elaphe vulpina* may be distinguished from *E. subocularis* in having the quadrate not highly depressed just above the trochleae.

Parasphenoid. The parasphenoid of *Elaphe vulpina* is specifically diagnostic in having a well-produced dorsal tubercle with a narrowly rounded end. *Lampropeltis calligaster, L. getulus,* and *L. triangulum* have this tubercle with its end truncated. This tubercle is not present in *Pituophis melanoleucus* or in *E. guttata* and is only weakly produced or absent in *E. obsoleta.* This tubercle is present only as a tiny, pointed structure in *E. subocularis.*

Dentary (Fig. 1D). The dentary of *Elaphe vulpina* may be separated from those of *Lampropeltis calligaster, L. getulus, L. triangulum,* and *Pituophis melanoleucus* in having more teeth anterior to the notch for the articulation of the angular bone, and also in having more teeth between the angular notch and the mental foramen (Table II).

TABLE II. Tooth-alveolar counts of dentaries of *Lampropeltis, Pituophis,* and *Elaphe.*

	Teeth Anterior to Angular Notch			Teeth between Angular Notch and Mental Foramen		
	No.	Mean	Sample Size	No.	Mean	Sample Size
Lampropeltis calligaster	6–7	(6.5)	2	1–2	(1.5)	2
Lampropeltis getulus	8–9	(8.3)	3	1–2	(1.3)	3
Lampropeltis triangulum	6	(6.0)	2	1	(1.0)	2
Pituophis melanoleucus	8–9	(8.8)	4	1	(1.0)	4
Elaphe guttata	10–11	(10.8)	5	2	(2.0)	5
Elaphe obsoleta	10–12	(11.0)	7	2–4	(2.6)	7
Elaphe subocularis	13	(13.0)	1	4	(4.0)	1
Elaphe vulpina modern	10–11	(10.7)	6	1–3	(2.5)	6
Elaphe vulpina fossil	11	(11.0)	1	3	(3.0)	1

Elaphe vulpina is separable from *E. guttata* in having more teeth between the angular notch and the mental foramen, but is not separable from *E. obsoleta* on these characters (Table II). It is separable from *E. subocularis* in having fewer teeth anterior to the angular notch and also fewer teeth between the angular notch and the mental foramen.

Posterior Mandible (Fig 1E). This complex consists of the fused articular, angular, supra-angular, and coronoid bones, none of which bears teeth. This element is specifically diagnostic in *Elaphe vulpina* in that it is relatively long and slender and has a low mandibular crest. This element is shorter and has a higher mandibular crest in *Lampropeltis calligaster, L. triangulum, Pituophis melanoleucus, E. guttata, E. obsoleta,* and *E. subocularis. Lampropeltis getulus,* on the other hand, is separable from *E. vulpina* in having this element shorter and stouter and in having an even lower mandibular crest.

Vertebrae and Ribs (Figs. 2 and 3). Usually, the only part of the snake postcranial skeleton that has been used for identification purposes is the trunk section of the vertebral column (Holman, 1979 and 1981). The trunk vertebrae of *Elaphe vulpina* are diagnostic. They may be separated from those of *Lampropeltis calligaster* and *L. getulus* on the basis of their lower neural spines (Table III) and by the more gracile structure of the processes on the bottom of the centrum. They may be separated from those of *L. triangulum* on the basis of their higher neural spine and more vaulted neural arch. Trunk vertebrae of *E. vulpina* may be separated from those of *Pituophis melanoleucus* on the basis of their lower neural spine and smaller condyle, and from those of *E. guttata, E. obsoleta,* and *E. subocularis* on the basis of their lower neural spine. Ribs do not appear to be diagnostic.

Osteological Definition of *Elaphe vulpina*

As a result of the present study the following osteological definition of *Elaphe vulpina* is presented. (1) Maxilla with 16 or 17 teeth and alveolar spaces. (2) Transpalatine with a narrow, terminally truncated lateral process; its medial process directed nearly at a right angle to the shaft, relatively short and not sharply pointed; shaft slightly curved medially; excavation between its anterior processes shallow. (3) Quadrate with its proximal end simple, not sharply bevelled, hooked, flared, or with a distinctly produced lateral process; stapedial tubercle short; distal end relatively wide, not highly depressed above trocleae, and with a lateral flange. (4) Parasphenoid with a well-produced dorsal tubercle with a narrowly rounded anterior end. (5) Dentary with 10 or 11 teeth and alveolar spaces occurring anterior to the notch for the articulation of the angular bone, and with 1 to 3 teeth occurring between the angular notch and the mental foramen. (6) Posterior mandible (fused articular, angular, supra-angular,

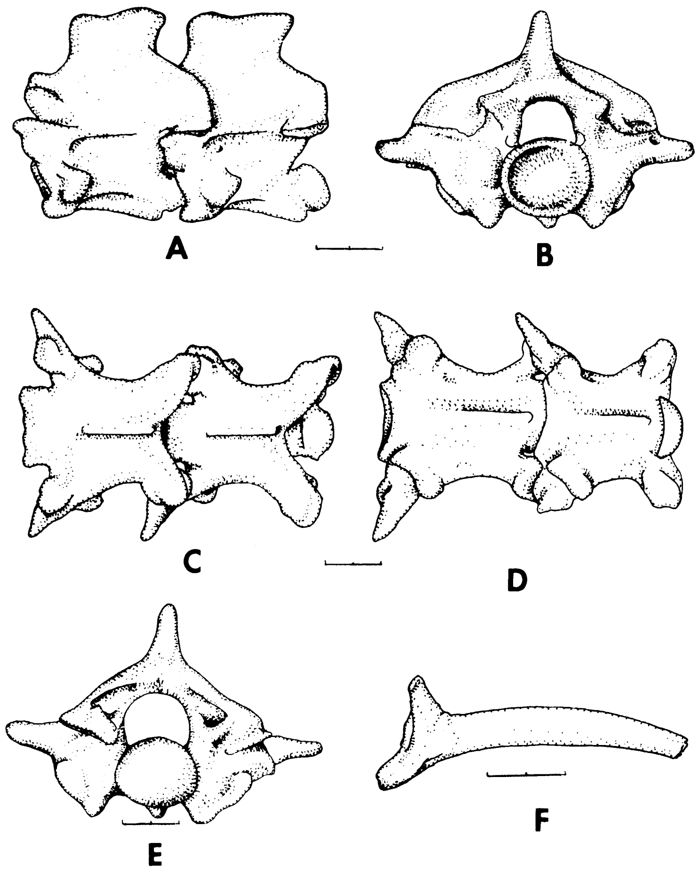

FIGURE 2. Two articulated vertebrae, A-E, and a single rib, F, of the fossil *Elaphe vulpina*. **A.** Lateral. **B.** Posterior. **C.** Dorsal. **D.** Ventral. **E.** Posterior. **F.** Ventral. The vertebrae are undamaged; the rib has its distal end broken. Projections equal 2 mm; that between A and B applies equally to A and B; that between C and D applies equally to C and D.

and coronoid) long and low and with a low mandibular crest. (7) Trunk vertebrae with a low neural spine (longer than high), but not an obsolete one; neural arch vaulted; condyle not enlarged; ventral processes of the centrum gracile.

PRESENT DISTRIBUTION AND FOSSIL RECORD OF *ELAPHE VULPINA*

Today *Elaphe vulpina*, called the fox snake throughout most of its range, occurs from southern Ontario to eastern Nebraska and the upper peninsula of Michigan to central Illinois and northern Missouri; in other words, the main part of its range is in the so-called Great Lakes Region. In Michigan it has a disjunct distribution, the subspecies *E. v. gloydi* occurring in southeastern Michigan where it is found in the marshy areas bordering Lake Huron. The subspecies *E. v. vulpina* occurs in the western part of the upper peninsula where it is often locally called "pine snake."

TABLE III. Height of neural spines of subspecies of *Lampropeltis, Pituophis,* and *Elaphe.*

	Number Higher than Long	Number as Long as High	Number Longer than High
Lampropeltis c. calligaster	0	4	0
Lampropeltis g. getulus	2	1	0
Lampropeltis t. triangulum	0	0	2
Pituophis melanoleucus mugitus	2	0	0
Pituophis melanoleucus sayi	0	2	0
Elaphe guttata emoryi	0	2	0
Elaphe g. guttata	3	1	0
Elaphe o. obsoleta	4	0	0
Elaphe o. quadrivittata	2	1	0
Elaphe o. rossalleni	1	0	0
Elaphe subocularis	0	1	0
Elaphe v. gloydi modern	0	0	1
Elaphe v. vulpina modern	0	0	7
Elaphe vulpina fossil	0	0	1

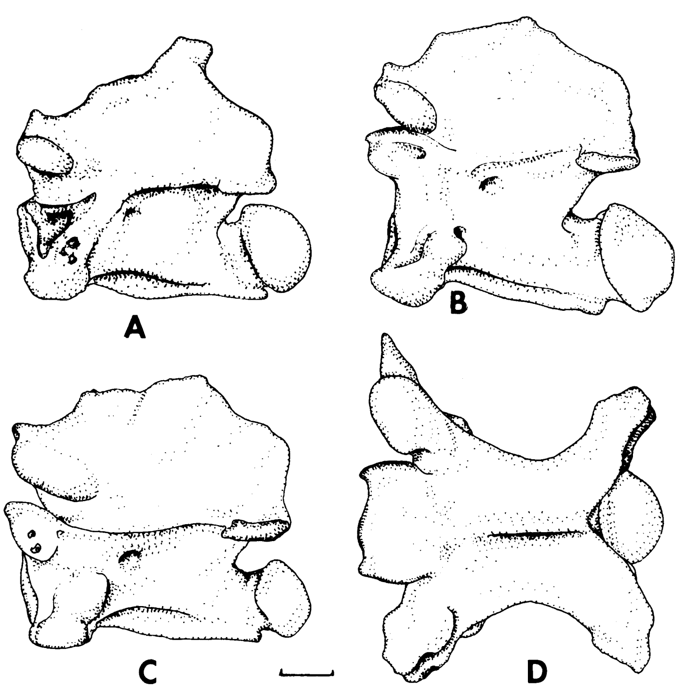

FIGURE 3. Three vertebrae of the fossil *Elaphe vulpina*. **A-C.** Lateral views showing degrees of damage to the neural spine. **D.** Dorsal view showing a broken left prezygapophysis. Projection equals 1 mm and applies equally to A-D.

The ancestor of *Elaphe vulpina* is thought to be the fossil *E. nebraskensis* that ranges from the Middle Miocene of Texas to the Late Miocene of Saskatchewan, South Dakota, and Nebraska (Holman, 1979). The present paper reports the earliest known occurrence of *Elaphe vulpina* (the late Middle Pliocene of southeastern Nebraska). The next earliest known occurrence of *E. vulpina* is from the Late Pliocene of Twin Falls County, Idaho (Holman, 1968). *Elaphe vulpina* is known from Early, Middle, and Late Pleistocene sites and it had a wider distribution in the Pleistocene than it has today (Holman, 1981: Fig. 2) occurring in Virginia, the Ozark Region, and the Great Plains states. The restriction of the range of *E. vulpina* from the Late Pliocene to the present is not completely understood.

TAPHONOMY

The fact that this is possibly the most complete fossil snake skeleton known from the North American Cenozoic is noteworthy. The fossil was discovered in August 1979 when a portion of its vertebral column was noticed weathering out of the Santee ash deposit. It was put in a plaster cast and taken to the Vertebrate Paleontology Laboratory at the Museum, Michigan State University. After the cast was removed, the specimen was prepared by gently dripping water over the skeleton to float away the soft ash matrix. The snake was mainly in a right-side-up position, but folds of the body were randomly overlapped rather than being neatly coiled. The skull was crushed. Unfortunately, before the specimen could be figured or photographed, a jet of water dissassociated the skeleton except for a few very short sections of vertebral column. At this point, the individual bones and sections were cleaned and hardened to avoid further damage.

Breakage of individual snake bones was studied and the results are summarized in Table IV. It is apparent that something crushed the snake either before or during the time it was being covered by the ash-fall that preserved it. I hypothesize that some large ungulate or group of ungulates trampled the snake. Perhaps the ash storm that produced the Santee deposit caused herds of ungulates to move or stampede in terror, and these trampled to death the fox snake that became buried by the ash and ultimately fossilized. Two giant ungulates that occurred in northeastern Nebraska during the late Middle Pliocene were the mastodon, *Serridentinus*, and the rhinoceros, *Teleoceras*. Perhaps one or the other of these animals formed part of the taphonomic process that produced this unique snake fossil.

TABLE IV. Breakage analysis of Santee fossil *Elaphe vulpina*.

Bone	Number Present	Number Present	Type of Breakage
Frontal (L)	1	1	Ventral processes broken
Parietal	1	1	Crushed
Maxilla (L, R)	2	2	L, proximal end broken; R, prefrontal process broken off
Transpalatine (R)	1	1	Proximal end broken off
Palatine (L)	1	1	Badly crushed
Pterygoid (L, R)	2	2	Both crushed
Supraoccipital	1	1	Crests broken off
Quadrate (L, R)	2	1	R, proximal end broken
Parasphenoid	1	1	Lateral wings missing
Basisphenoid	1	1	Badly crushed
Dentary (L, R)	2	2	Teeth broken in both
Mandible (L, R)	2	2	Both broken in middle
Cervical vertebrae	47	33	33 neural spine breaks as well as 1 broken prezygapophysis, 1 broken postzygapophysis, 17 broken hypapophyses
Trunk vertebrae	146	88	88 neural spine breaks as well as 1 broken prezygapophysis, 2 broken postzygapophyses, 1 broken zygosphene
Caudal vertebrae	46	46	46 lateral process breaks as well as 27 neural spine breaks
Ribs	155	151	151 shaft breaks

ACKNOWLEDGMENTS

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