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REPTILES OF THE EGELHOFF LOCAL FAUNA (UPPER MIOCENE) OF NEBRASKA

BY

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VOLUME 24

REPTILES OF THE EGELHOFF LOCAL FAUNA (UPPER MIOCENE) OF NEBRASKA

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ABSTRACT—The reptile fauna of the Egelhoff local fauna of Keya Paha County, Nebraska, includes two turtles, three lizards, and six snakes. This reptile fauna has three of 11 genera and eight of nine identified species extinct, and contrasts with the amphibian fauna of the site which has none of its seven genera extinct, and six of its nine identified species referred to living forms. The occurrence in the fauna of three archaic snake genera (a natricine, a small colubrine, and a xenodontine) plus an extinct rubber boa strongly suggests an Upper Miocene rather than a Lower Pliocene age for the fauna. The presence of a giant tortoise of the genus *Geochelone* in the fauna indicates a subtropical climate with few if any nights of frost in the winter. The Egelhoff local fauna appears to be temporally equivalent to the Norden Bridge local fauna of Brown County, Nebraska.

INTRODUCTION

THE EGELHOFF LOCAL FAUNA of Keya Paha County, Nebraska, has produced a small but interesting reptile fauna that is particularly well represented by fossil snakes. Since the only documented reptile faunas of similar age in the plains region of North America are the Norden Bridge local fauna of Brown County, Nebraska, and the Kleinfelder Farm local fauna, near Rockglen, Saskatchewan (Estes & Tihen, 1964; Holman, 1970, 1971), the Egelhoff reptile fauna is of considerable importance in the interpretation of the climate of the late Tertiary of the Great Plains, and of the evolution of North American reptiles.

The Egelhoff site was discovered by Morris F. Skinner in 1964. The first collections were made by Skinner and C. W. Hibbard in June, 1967. Additional collections were made by Hibbard and University of Michigan field parties later in 1967 and in 1968. In the summer of 1971, J. A. Holman and a field party from Michigan State University made collections at the Egelhoff site, where they processed thirty-five tons of fossiliferous sand.

The Egelhoff Quarry occurs in an undescribed lithic unit of the lowermost part of the Valentine Formation. Geologically, the Egelhoff site is similar to the Norden Bridge site, which occurs one and one-half miles southeast of the Egelhoff site on the south side of the Niobrara River in Brown County, Nebraska, at an elevation of 2170 feet. The elevation of the Egelhoff site is 2195 feet. The sediments of the Egelhoff local fauna site are very fine grained and contain vertebrates of smaller size than those of the Norden Bridge local fauna site, which has much coarser grained sediments. These sites are here considered to be temporally equivalent and to bear a biofacies relationship to each other (fig. 1). For reasons that will be discussed later, the Egelhoff and Norden Bridge local faunas are considered to represent the uppermost Miocene rather than the lowermost Pliocene. The Egelhoff Quarry is located one mile north of the Niobrara River on the ranch of Franklin H. Egelhoff in the SE corner of the NE¼ SW¼ sec. 29, T 33 N, R 23 W, Keya Paha County, Nebraska (Norden Quadrangle, United States Dept. Interior, Geol. Surv. Map, 1950).

The fossil reptiles reported on in the present paper are either in The University of Michigan Museum of Paleontology (UMMP V) or in the Museum, Michigan State University (MSU-VP).

I would like to take this opportunity to sincerely thank the following persons for their help in the project: Dr. Claude Hibbard for the opportunity to study the Egelhoff reptiles collected by his University of Michigan parties and for the use of field equipment; the Franklin Egelhoff, Loring Kuhre, and Morris Skinner families for their many kindnesses to the Michigan State party; and finally to George Cutts, Christopher King, Daniel and Jane Lyons, and Robert Weigel, members of the 1971 MSU group, for their hard work in the field. Donna Rae Holman made the drawings. The Michigan State field trip to Nebraska in 1971 was financed in part by Grant Number 6034 of the Penrose Fund of the American Philosophical Society and in part by Grant Number 1459-71 of the Geological Society of America.

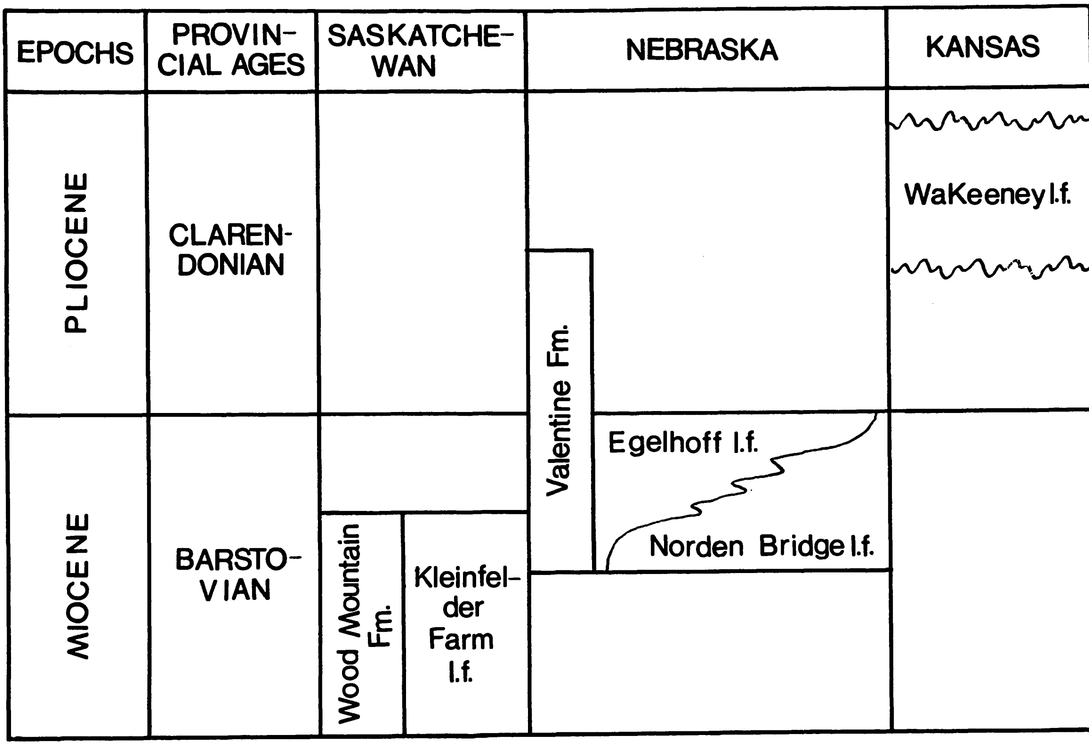

FIG. *1*—Proposed stratigraphic relationships of some late Tertiary North American local faunas containing numerous amphibian and reptile remains.

Chantell (1971) identified the amphibians of the Egelhoff local fauna. A checklist of the Egelhoff local fauna amphibians and reptiles follows:

Amphibians

- Family Ambystomatidae
  - *Ambystoma minshalli* Tihen & Chantell
    Extinct Mole Salamander
- Family Pelobatidae
  - *Scaphiopus* cf. *S. bombifrons* (Cope)
    Plains Spadefoot
  - *Scaphiopus* cf. *S. holbrooki* Harlan
    Eastern Spadefoot
- Family Bufonidae
  - *Bufo valentinensis* Estes & Tihen
    Extinct Toad
  - *Bufo* cf. *B. hibbardi* Taylor
    Extinct Toad
- Family Hylidae
  - *Acris* cf. *A. crepitans* Baird
    Cricket Frog
  - *Pseudacris* cf. *P. clarki* Baird
    Spotted Chorus Frog
  - *Hyla* cf. *H. cinerea* Schneider
    Green Frog
  - *Hyla* cf. *H. crucifer* Weid
    Spring Peeper
- Family Ranidae
  - *Rana* sp.
    True Frog

Reptiles

- Family Testudinidae
  - *Geochelone orthopygia* (Cope)
    Extinct Giant Tortoise
- Family Trionychidae
  - *Trionyx* sp.
    Softshell Turtle
- Family Anguidae
  - *Ophisaurus ventralis* (Linnaeus)
    Eastern Glass Lizard
  - *Gerrhonotus* cf. *G. mungerorum* Wilson
    Extinct Alligator Lizard
- Family Scincidae
  - *Eumeces* sp.
    Striped Skink
- Family Boidae
  - *Charina prebottae* Brattstrom
    Extinct Rubber Boa
- Family Colubridae
  - *Neonatrix elongata* n. sp.
    Archaic Natricine Snake
  - *Paleoheterodon tiheni* Holman
    Archaic Hognose Snake
  - *Nebraskophis skinneri* n. sp.
    Archaic Colubrine Snake

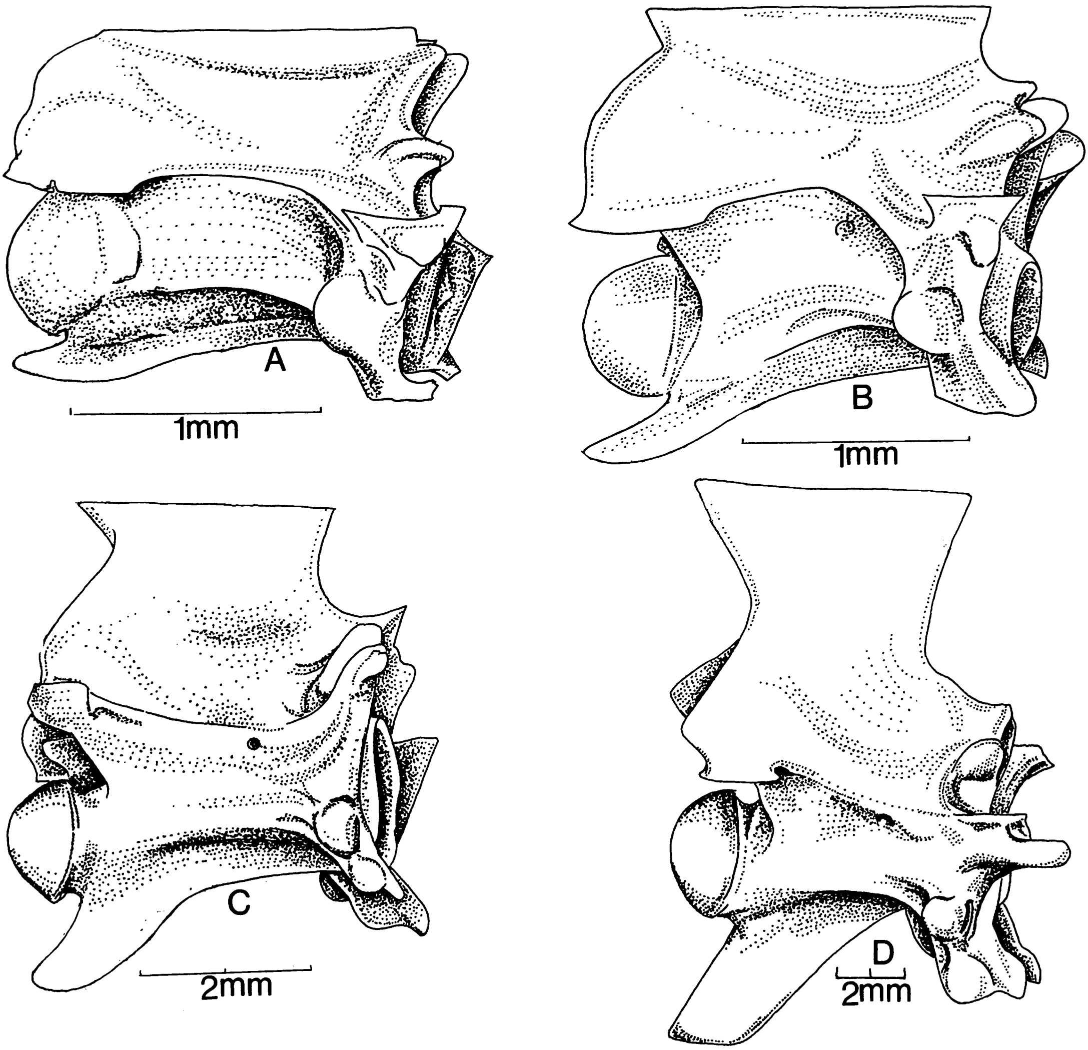

FIG. 2—Lumbar vertebrae of Recent natricine snakes: A, *Tropidoclonion lineatum*; B, *Haldea striatula*; C, *Thamnophis sirtalis*; D, *Natrix cyclopion*.

Salvadora paleolineata n. sp.
Extinct Patch-Nosed Snake
Elaphe nebraskensis Holman
Extinct Ratsnake

SYSTEMATIC PALEONTOLOGY

Class REPTILIA

Order CHELONIA

Family TESTUDINIDAE

GEOCHELONE ORTHOPYGIA (Cope)

Material.—Two dermal ossicles, MSU-VP 702.

Remarks.—This species has been reported from the Norden Bridge local fauna by Hibbard (1960) and by Estes & Tihen (1964). These dermal ossicles are referred to this species principally on the basis of their large size. The greatest length of these ossicles is 29.7 and 22.4 mm, the greatest height is 9.9 and 10.7 mm. Hibbard (1960) outlined the climatic significance of large land tortoises of the genus *Geochelone* in fossil faunas. They indicate a climate with very mild winters with temperatures seldom if ever reaching the freezing point.

Family TRIONYCHIDAE

TRIONYX sp. indet.

Material.—Three partial costal plates, MSU-VP 703.

Remarks.—These elements are too fragmentary to assign to species. The softshell

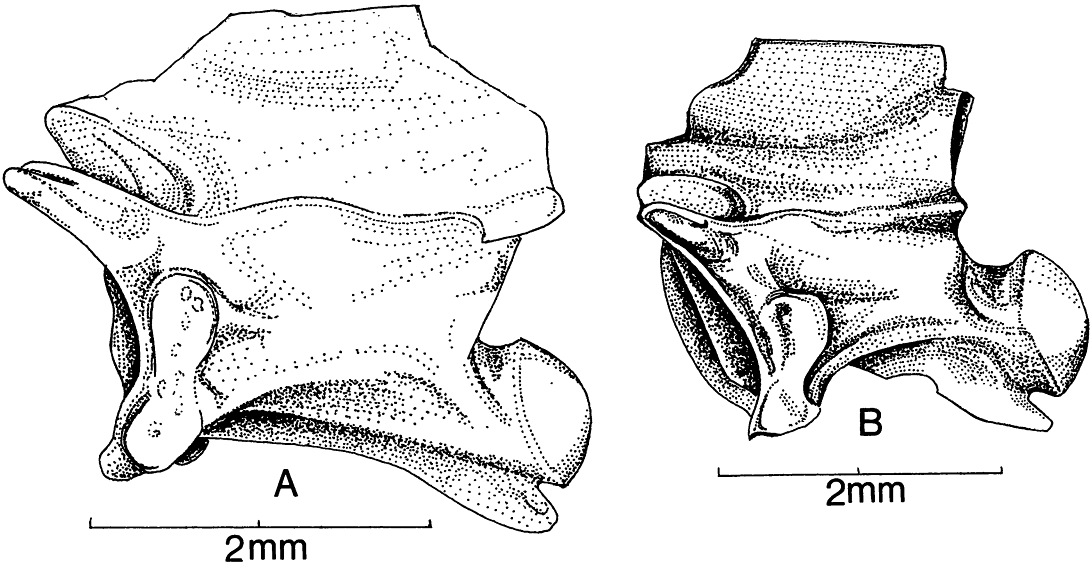

FIG. 3—A, holotype lumbar vertebra of *Neonatrix elongata* n. gen. and sp., MSU-VP 710; B, paratype of *Neonatrix elongata*, MSU-VP 711.

turtle indicates the presence of a permanent aquatic situation. These costals represent at least two small turtles.

Order SQUAMATA

Family ANGUIDAE

OPHISAURUS VENTRALIS (Linnaeus)

Material.—Three body vertebrae, MSU-VP 712, and two body vertebrae, UMMP V57354.

Remarks.—The body vertebrae of *Ophisaurus* may be separated from those of *Barissia* and *Gerrhonotus* on the basis of the wider condyle that lacks a distinct neck region in *Ophisaurus*. In *Barissia* and *Gerrhonotus* the condyle is narrower and it has a distinct neck region. The body vertebrae of *Ophisaurus* may be distinguished from those of *Anguis* in that the neural spine is posteriorly upswept as a high crest in *Ophisaurus*, whereas in *Anguis* the neural spine is uniformly low.

The Egelhoff fossil vertebrae are assigned to the Recent species *Ophisaurus ventralis*. A ratio that has been used to separate Recent species of *Ophisaurus* (Etheridge, 1961) is obtained by dividing the length of the centrum as measured from the greatest depth of the glenoid cavity of the cotyla to the most posterior extent of the condyle by the least width of the neural arch. This ratio in the Egelhoff fossils is 1.33–1.41 (m, 1.37, n, 2). This ratio (data from Etheridge, 1961) is 1.5–2.0 (m, 1.72) in *Ophisaurus compressus*, 1.12–1.55 (m, 1.36) in *O. ventralis*, and 1.10–1.40 (m, 1.23) in *O. attenuatus*. Thus, the Egelhoff vertebrae are most similar to Recent *O. ventralis*. An extinct species of *Ophisaurus*, *O. canadensis*, from the Upper Miocene Kleinfelder Farm local fauna near Rockglen, Saskatchewan, has vertebral proportions that are similar to *O. ventralis*; but in *O. canadensis* there is a unique anterior-directed, narrowly rounded projection of the neural arch that extends to about the level of the anterior edges of the prezygapophyseal faces (Holman, 1970, p. 1319, fig. 1), whereas in *O. ventralis* this edge is broadly rounded and extends only about half-way to the anterior edge of the prezygapophyseal faces. The Egelhoff fossils are similar to Recent *O. ventralis* in this character. This is the earliest fossil record of *O. ventralis* which has previously been reported from the Lower Pliocene WaKeeney local fauna of Trego County, Kansas, by Wilson (1968).

GERRHONOTUS cf. G. MUNGERORUM Wilson

Material. — A parietal bone, UMMP V56294.

Remarks.—The parietal appears to be assignable to *Gerrhonotus* in that it bears only three osteoscutes, two lateral ones and one medial one, the medial osteoscute being pierced by the pineal foramen. These osteoscutes occur on about the anterior two-fifths of the dorsal surface of the parietal. The posterior three-fifths of the bone has a rather smoothly polished dorsal surface.

Wilson (1968) described *Gerrhonotus mungerorum* from the Lower Pliocene of Trego County, Kansas, on the basis of a single frontal bone. Wilson reported that *G. mungerorum* had a different scutellation pattern of the frontal bone than in Recent species of the genus and a heavier sculpture pattern. The Egelhoff parietal is identical in scutellation to Recent *Gerrhonotus multicarinatus*, but has a heavier sculpture pattern as in *G. mungerorum*; thus the Egelhoff bone is very tentatively assigned to *G. mungerorum*.

Family Scincidae

Eumeces sp.

Material.—Five right dentaries, two dentary fragments, and two maxillary fragments, MSU-VP 713. Two left and four right dentaries, two dentary fragments, and three maxillary fragments, UMMP V57351.

Remarks.—These elements may be assigned to the genus *Eumeces*, but lack of comparative material makes it impossible to assign them to species.

Family Boidae

Charina prebottae Brattstrom

Material.—Two lumbar and one caudal vertebrae, UMMP V57350.

Remarks.—*Charina prebottae* is a small boid that is very similar to the Recent *Charina bottae* and is evidently directly ancestral to the living form. *Charina prebottae* is previously known from the Upper Miocene of California (Brattstrom, 1958) and from the Upper Miocene of the Kleinfelder Farm local fauna of the Wood Mountain Formation of Saskatchewan (Holman, 1970). Unidentified boid remains, probably representing *Charina prebottae*, have been reported from the Norden Bridge local fauna of Brown County, Nebraska (Holman, 1964). The only difference I can detect between the Egelhoff fossils and two Recent skeletons of *C. bottae* is that the hemal keel appears to be more strongly developed in *C. prebottae* than in *C. bottae*.

Family Colubridae

Subfamily Natricinae

Members of this subfamily have hypapophyses on their lumbar (term of Bullock & Tanner, 1966) vertebrae, a condition that does not obtain in any other subfamilies of the Colubridae. Living natricines have well-developed hypapophyses, but the fossil natricines from the Egelhoff local fauna have very weak hypapophyses. It appears that in many living natricines the habits of the snakes are reflected in their vertebral proportions. In small secretive natricines the vertebrae tend to be long with a very low neural spine and a hypapophysis that tends to be directed more backward than downward such as in *Tropidoclonion lineatum* and *Haldea striatula* (fig. 2A and B). On the other hand, in large, highly aquatic natricines such as *Natrix cyclopion* (fig. 2D) the lumbar vertebrae tend to be short with a high neural spine and a long hypapophysis that tends to be directed more downward than backward. Natricines that are mainly terrestrial and not highly secretive, but that occasionally enter the water, such as *Thamnophis sirtalis* (fig. 2C), tend to be somewhat intermediate in vertebral proportions. In some cases, then, these vertebral proportional similarities in natricines appear to cross taxonomic boundaries. For instance, *Natrix natrix*, a European snake with ubiquitous habits like the American *Thamnophis sirtalis*, has vertebral proportions that are much more like *Thamnophis sirtalis* than the highly aquatic *Natrix cyclopion*, *N. rhombifera*, or *N. taxispilota*.

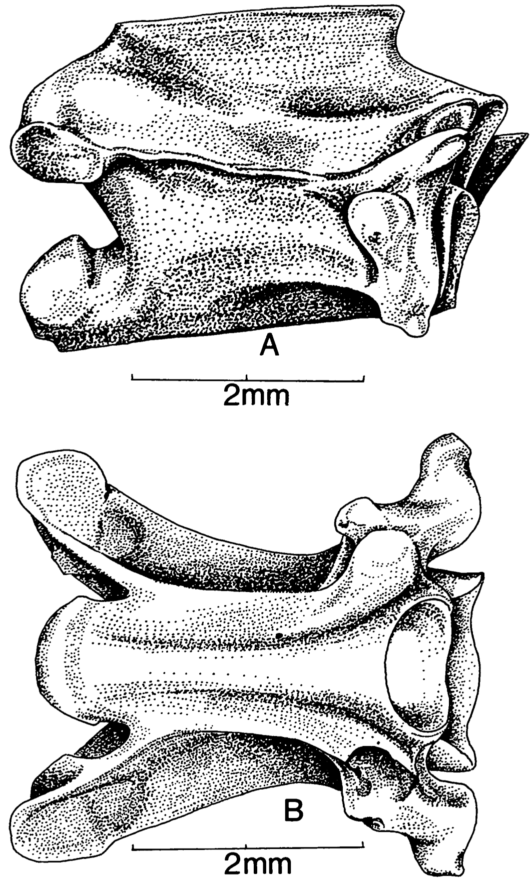

Fig. 4—Holotype lumbar vertebra of *Nebraskophis skinneri* n. gen. and sp., MSU-VP 708; A, lateral view; B, ventral view.

Because the Egelhoff natricine fossils have such small hypapophyses on their lumbar vertebrae it is thought that they represent an archaic extinct natricine genus.

Skeletal specimens examined in the study of the fossil natricine material from the Egelhoff fauna are as follows (numbers of skeletons examined are in parentheses): *Clonophis kirtlandi* (2), *Haldea striatula* (20), *Natrix cyclopion* (14), *N. erythrogaster* (13), *N. fasciata* (24), *N. natrix* (2), *N. sipedon* (12), *N. taxispilota* (6), *N. tesselata* (1), *N. rhombifera* (7), *N. valida* (1), *Regina alleni* (8), *R. grahami* (3), *R. septemvittata* (3), *Seminatrix pygaea* (7), *Storeria dekayi* (15), *S. occipitomaculata* (5), *Thamnophis brachystoma* (1), *T. butleri* (2), *T. cyrtopsis* (1), *T. elegans* (17), *T. macrostemma* (5), *T. marcianus* (8), *T. proximus* (15), *T. radix* (10), *T. sauritus* (13), and *T. sirtalis* (18).

NEONATRIX n. gen.

Diagnosis.—A natricine genus with distinctly smaller hypapophyses of the lumbar vertebrae than any known natricine genus.

Remarks.—The very small, weak hypapophyses of the lumbar vertebrae are unique among natricine genera I have observed. It may be that this genus is basal to many of our modern North American natricine genera.

Type species.—*Neonatrix elongata* n. sp.

NEONATRIX ELONGATA n. sp.

Diagnosis.—A *Neonatrix* with a neural spine much longer than high.

Holotype.—Lumbar vertebra, Michigan State University, Vertebrate Paleontology Number 710 (fig. 3A).

Paratypes.—Two lumber vertebrae, MSU-VP 711 (one paratype illustrated, fig. 3B).

Type locality.—Upper Miocene, lower Valentine Formation, Egelhoff local fauna, one mile north of the Niobrara River on the Ranch of Franklin H. Egelhoff in the SE corner of the NE¼ SW¼ sec. 29, T 33 N, R 23 W, Keya Paha County, Nebraska (Norden Quadrangle, United States Dept. Interior Geol. Surv. Map, 1950).

Etymology.—The species name, from the Latin *elongata*, refers to the long, low neural spine of this species.

Description of the holotype.—In anterior view, the cotyla is round and slightly wider than the loaf-of-bread-shaped neural canal. The zygosphene is very slightly convex dorsally and the sides of the neural canal are very slightly convex medially. The prezygapophyses are slightly tilted upward. Moderately excavated concavities occur on either side of the cotyla. Foramina cannot be discerned on either side of the cotyla, but this may be because they are

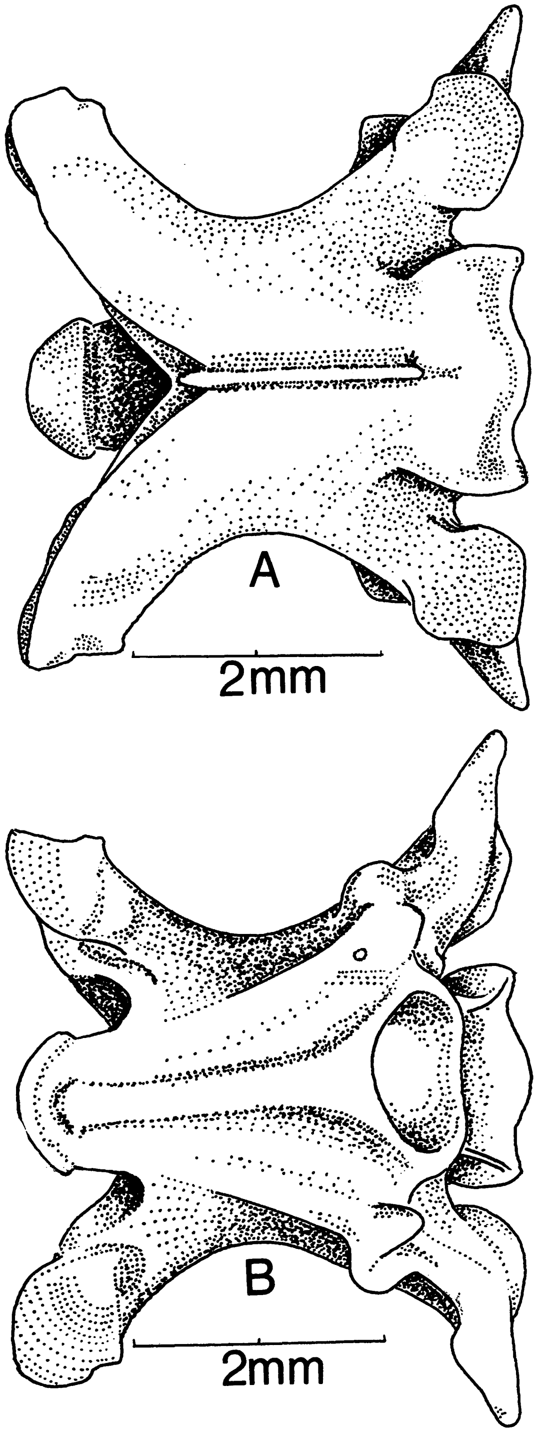

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FIG. 5—Holotype lumbar vertebra of *Salvadora paleolineata* n. sp., UMMP V56292; A, dorsal view; B, ventral view.

filled with matrix. The left paradiapophyses are badly damaged. The right paradiapophyses are moderately well developed.

In dorsal view, the centrum is longer than wide. The prezygapophyseal faces are ovaloid in shape. A prezygapophyseal process (accessory process) is present only on the left side as the right process is broken off. This process is moderately long with a moderately pointed end. The anterior edge of the zygosphene is moderately convex. The neural spine is moderately thick and partially broken so that it is not known whether a posterior overhang is present or not. The diapophyses are only slightly produced laterally. There are no epizygapophyseal spines.

In posterior view, the neural arch is vaulted. The neural arch is well excavated by the zygantral facets. The postzygapophyses are tilted slightly upward. The oval condyle is slightly depressed and appears to be just about the same size as the neural canal. The hypapophysis projects only slightly below the condyle.

In ventral view, the centrum is long and narrow. The subcentral ridges are weak. The hypapophysis is narrow and ends well anterior to the posteriormost extent of the condyle.

In lateral view, the vertebra is moderately elongate. The neural spine is partly broken, but it is much longer than high. The subcentral ridge is very slightly convex dorsally. The hypapophysis is very short and weak and has a narrowly rounded tip; it ends anterior to the posteriormost extent of the condyle.

The length of the vertebra through the zygapophyses is 3.7 mm.

Paratypes.—The paratypes do not show salient differences from the holotype. The neural spine of one of the paratypes is somewhat more complete than in the holotype. This complete paratype neural spine is about three times as long as high. This same vertebra (fig. 3B) has the hypapophysis slightly stronger and more pointed than in the holotype.

Remarks.—Based on criteria of vertebral shape as discussed in the section on the subfamily Natricinae and illustrated in figure 2, I would guess that *Neonatrix elongata* was a rather secretive terrestrial snake, perhaps similar in habits to some of the smaller *Thamnophis* species today such as *Thamnophis butleri.*

Subfamily Colubrinae

The lumbar vertebrae of the subfamily Colubrinae are quite diverse in their proportions and in the shape of various structures; nevertheless they never bear hypapophyses as in the subfamily Natricinae, and they lack the combination of the depressed neural arch and the very wide hemal keel of the Xenodontinae.

Nebraskophis n. gen.

Diagnosis.—A distinctive colubrine genus that may easily be distinguished from other colubrine genera on the basis of characters of the lumbar vertebrae. These characters are: vertebrae elongate; neural arch vaulted; neural spine obsolete, its posterior border sloping gently into neural arch; hemal keel moderately narrow and moderately strong. I can find no other living or fossil colubrine genus with this combination of characters.

Type species.—*Nebraskophis skinneri* n. sp.

Nebraskophis skinneri n. sp.

Holotype.—Lumbar vertebra, Michigan State University, Vertebrate Paleontology Number 708 (fig. 4).

Paratype.—A fragmentary lumbar vertebra, MSU-VP 709.

Type locality.—Upper Miocene, lower Valentine Formation. Egelhoff local fauna, one mile north of the Niobrara River on the Ranch of Franklin H. Egelhoff in the SE corner of the NE¼ SW¼ sec. 29, T 33 N, R 23 W, Keya Paha County, Nebraska (Norden Quadrangle, United States Dept. Interior Geol. Surv. Map, 1950).

Etymology.—The species is named after Morris F. Skinner, who discovered the Egelhoff locality in 1964.

Description of holotype.—In anterior view, the cotyla is oval and slightly depressed and slightly larger than the loaf-of-bread-shaped neural canal. The zygosphene is very slightly convex dorsally, the sides of the neural canal are slightly convex medially. The prezygapophyses are slightly tilted upward. Moderately large foramina occur on either side of the cotyla. The paradiapophyses are partially broken on the left side and have a beveled-off appearance on the right side.

In dorsal view, the centrum is longer than wide. The prezygapophyseal faces are ovaloid in shape. The prezygapophyseal processes (accessory processes) are short with rounded ends. The anterior edge of the zygosphene is very slightly convex. The neural spine is moderately thick with no posterior overhang. The diapophyses are moderately produced laterally. There are no epizygapophyseal spines.

In posterior view, the neural arch is vaulted. The neural arch is well excavated by the zygantral facets. The postzygapophyses are tilted slightly upward. The round condyle is slightly smaller than the round neural canal.

In ventral view, the centrum is long and narrow. The subcentral ridges are weak. The hemal keel is moderately narrow and moderately strong.

In lateral view, the vertebra is elongate; the neural spine is obsolete and its posterior end slopes gently into the neural arch. The anterior edge of the neural spine has a slight overhang. The subcentral ridge is weak and slightly convex dorsally.

The length of the vertebra through the zygapophyses is 3.7 mm; the width of the vertebra through the prezygapophyseal processes is 4.1 mm.

Paratype.—The paratype is more fragmentary than the holotype, but it does not show any salient differences.

Remarks.—It is difficult to suggest relationships of *Nebraskophis* to any known colubrine genera. A vertebra, UMMP V56556, unidentified to genus and species, but possibly representing a larger individual of *Nebraskophis*, has a duplicate left side similar to the condition discussed and figured for *Natrix natrix* by King (1959, p. 88, fig. 1). This vertebral duplication was found in the Recent genera *Coluber*, *Diadophis*, *Elaphe*, *Lampropeltis*, *Natrix*, *Rhadinaea*, and *Thamnophis* by King. The presence of a duplicated vertebra indicates the presence of an extra rib and an extra "half-ventral" scute in living snakes. This appears to be the first time this condition has been reported in fossil snakes.

SALVADORA PALEOLINEATA n. sp.

Diagnosis.—A *Salvadora* with the lumbar vertebrae similar to those of Recent *S. lineata* Schmidt, but differing in lacking epizygapophyseal spines.

Holotype.—Lumbar vertebra, University of Michigan Museum of Paleontology No. V56292 (fig. 5).

Paratypes.—Five lumbar vertebrae, UMMP V56293, and 11 lumbar vertebrae, MSU-VP 706.

Type locality.—Upper Miocene, lower Valentine Formation. Egelhoff local fauna, one mile north of the Niobrara River on the Ranch of Franklin H. Egelhoff in the SE corner of the NE¼ SW¼ sec. 29, T 33 N, R 23 W, Keya Paha County, Nebraska (Norden Quadrangle, United States Dept. Interior Geol. Surv. Map, 1950).

Description of holotype.—In anterior view, the neural canal is about the size of the cotyla. The cotyla is oval and is slightly depressed. The neural canal is loaf-of-bread-shaped. The zygosphene is convex dorsally. The sides of the neural arch are convex medially. A large foramen occurs on either side of the cotyla. The prezygapophyses are tilted slightly upward and the prezygapophyseal processes are well developed.

In dorsal view, the vertebra is about as wide as it is long. The zygosphene has its anterior edge slightly convex. The prezygapophyseal faces are subrounded. The prezygapophyseal processes (accessory processes) are well developed and moderately pointed. They are about two-thirds as long as the width of the prezygapophyseal faces. The diapophyses are only moderately produced laterally. The neural spine is thin and delicate and slightly overhangs the posterior part of the neural arch.

In posterior view, the postzygapophyseal faces are subrounded. The hemal keel is strong, but it is thin and uniformly very narrow. The subcentral ridges are also strong and narrow.

In lateral view, the neural spine is low, about four times as long as high, and it has a slight anterior and a slight posterior overhang. The subcentral ridge is convex dorsally. The condyle tilts obliquely upward.

The holotype was chosen because of its almost perfect preservation, but, based on Recent *Salvadora* skeletons, it appears quite possible that the holotype was from a posterior part of the lumbar series of the vertebral column, thus accounting for the low neural spine.

Paratypes.—None of the paratypes are preserved as well as the holotype although some are remarkably well preserved compared to most fossil snake vertebrae I have examined. One of the paratype vertebrae has a higher neural spine than in the holotype, but this may be due to a more anterior location of this vertebra in the lumbar series. None of the paratypes have even an obsolete epizygapophyseal spine.

Remarks.—The genus *Salvadora* is relatively easy to distinguish on the basis of vertebral form from other colubrine genera. *Salvadora* is most similar to *Alsophis*, *Coluber*, and *Masticophis* in having a thin, delicate neural spine, and in having a strong but uniformly thin hemal keel. But Recent *Salvadora* may be distinguished from *Alsophis*, *Coluber*, and *Masticophis* on the basis of (1) its shorter vertebra which is about as wide as long, (2) its obsolete epizygapophyseal spines, (3) its lower neural spines, and (4) the more dorsally convex subcentral ridges as seen in lateral view. The fossil *Salvadora* is similar to *S. lineata* and differs from *S. hexalepis* in having a much less long and narrow diapophysis as seen in dorsal view. The fossil differs from *S. lineata* in lacking epizygapophyseal spines. Very small epizygapophyseal spines are present in *S. lineata*.

ELAPHE NEBRASKENSIS Holman

Material.—Four lumbar vertebrae and a parietal bone, UMMP V56290. Ten lumbar vertebrae, MSU-VP 707.

Remarks.—*Elaphe nebraskensis* was described from the Norden Bridge Quarry of the lower Valentine Formation of Brown County, Nebraska, based on three vertebrae. The vertebrae of *E. nebraskensis* are similar to Recent *E. vulpina* in having a low neural spine, but they may be distinguished from this and all other Recent and fossil *Elaphe* species examined on the basis of the much more oblique positions of the prezygapophyseal (accessory) processes and prezygapophyseal faces to the long axis of the centrum (Holman, 1964, p. 634, fig. 2). The Egelhoff material appears to be identical to the Norden Bridge vertebrae. The only other locality from which the species has been reported is from the Kleinfelder Farm locality of the Wood Mountain Formation (Upper Miocene) of Saskatchewan (Holman, 1970). *Elaphe nebraskensis* is the largest of the Upper Miocene North American snakes.

Parietal bones of colubrine snakes are very difficult to work with because of a great deal of individual variation. The above parietal is similar to some specimens of Recent *Elaphe vulpina*, thus it is tentatively assigned to the species *E. nebraskensis*.

Subfamily Xenodontinae

Members of this subfamily lack hypapophyses of their lumbar vertebrae and have depressed vertebral neural arches and wide vertebral hemal keels. They are also characterized by having very large, solid fangs on the posterior end of the maxilla. Underwood (1967) includes three genera *Xenodon*, *Heterodon*, and *Lystrophis* in the Xenodontinae. All of these genera have upturned snouts and thick bodies and feed to a great extent upon toads and in some cases upon frogs. The upturned snouts are used to root the toads out of the sand and the long saber-like fangs are used to deflate the bodies of the toads as they are being eaten by the snakes. The fossil genus *Paleoheterodon* is similar to *Heterodon* and differs from *Xenodon* in having a wider hemal keel, but *Paleoheterodon* has a less depressed neural arch than *Heterodon*.

Paleoheterodon tiheni Holman

Material.—Twelve lumbar vertebrae, MSU-VP 705; six lumbar vertebrae, UMMP V56291.

Remarks.—This species was described on the basis of three vertebrae from the Norden Bridge local fauna of Brown County, Nebraska, by Holman (1964, p. 633, fig. 1). The diagnostic character that was used to separate the fossil genus *Paleoheterodon* from the genus *Heterodon* was "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*)."

In the light of additional fossil and Recent material of *Paleoheterodon* and *Heterodon* it appears that the "neural arch" character is a valid one and that the "accessory process" character is not a diagnostic one for separating the two genera. In the seventeen Egelhoff vertebrae that could be examined for the character, all but one had the neural arch more vaulted than in 17 skeletons of Recent *H. platyrhinos*, 3 skeletons of Recent *H. simus*, and 3 skeletons of Recent *H. nasicus*. The length of the accessory processes appears to be an individually variable character in both the fossil and the Recent material.

DISCUSSION

The reptile fauna of the Egelhoff local fauna contrasts sharply with the amphibian fauna. The reptile fauna has three of eleven genera and eight of its nine identified species extinct. The amphibian fauna has none of its seven genera extinct, and six of its nine identified species are referred to living forms.

Phylogenetic relationships.—The giant tortoise *Geochelone orthopygia* is shown to be on a dead-end evolutionary line that is terminated in early Pliocene times (Auffenberg, 1963, fig. 32). The affinities of the softshell turtle, *Trionyx*, are unknown. The *Ophisaurus* from the Egelhoff local fauna is so similar to the Recent form *O. ventralis* that it is tentatively assigned to that species. The relationships of the alligator lizard, *Gerrhonotus* cf. *G. mungerorum*, are not well known as the type species was based on a frontal bone; and although Wilson (1968) assigned the frontal bone to the genus *Gerrhonotus*, he used the genus ". . . in a broad sense to include the genera *Barissia*, *Gerrhonotus*, *Elgaria*, and *Coloptychon*." The Egelhoff fossil parietal has identical scutellation to *Gerrhonotus multicarinatus* although the fossil has heavier sculpturing, thus it may be possible that the Egelhoff form may be ancestral to this Recent species. The affinities of the fossil striped skink, *Eumeces*, are unknown.

Charina prebottae, the extinct rubber boa, seems to be unquestionably ancestral to the living rubber boa, *Charina bottae*. The phylogenetic relationships of the archaic natricine genus, *Neonatrix*, are obscure. The weakly developed hypapophyses of the lumbar vertebrae separates the genus from all living natricines. *Nebraskophis skinneri* is a unique little colubrine snake that as far as is known has no living relatives. *Salvadora paleolineata* may have evolved into the living species *S. lineata*.

Finally, *Elaphe nebraskensis* is thought to be ancestral to the living species *Elaphe vulpina.*

Climatic implications.—As in the Upper Miocene Kleinfelder Farm herpetofauna of Saskatchewan, the Egelhoff local fauna has (I) forms with living relatives that occur well south of the fossil locality, and (II) forms that have living relatives with the center of their distribution either in eastern North America or in western North America. Group I forms include *Hyla* cf. *cinerea, Geochelone orthopygia, Ophisaurus ventralis,* and *Salvadora paleolineata.* Group II forms include *Scaphiopus* cf. *holbrooki* (eastern), *Acris* cf. *crepitans* (eastern), *Hyla* cf. *cinerea* (eastern), *Hyla crucifer* (eastern), *Trionyx* sp. (eastern), *Ophisaurus ventralis* (eastern), *Gerrhonotus* cf. *mungerorum* (western), *Charina prebottae* (western), and *Elaphe nebraskensis* (eastern). It appears that eastern elements dominate the fauna. The occurrence of the southern forms, and especially of *Geochelone orthopygia* in the fauna, suggests a mild subtropical climate with the temperature seldom if ever reaching the freezing point (see Hibbard, 1960; Holman, 1971). The predominance of eastern forms and the diverse anuran fauna suggests to me a more mesophytic vegetation than at present for the area.

Paleoecology.—The fine-grained, weakly cross-bedded sands that form the matrix that contains the Egelhoff local fauna indicates a depositional environment of a relatively slow-moving body of water, probably a sluggish section of a stream. A relatively diverse fossil fish fauna as well as a softshell turtle (*Trionyx*) indicates a rather permanent aquatic situation. The spadefoots (*Scaphiopus*) and the true toads (*Bufo*) may have lived in sandy areas near the stream. The hylid and ranid frogs (*Acris, Pseudacris, Hyla,* and *Rana*) probably lived in vegetation near the edge of the stream. The lizards (*Ophisaurus, Gerrhonotus,* and *Eumeces*) as well as the snakes (*Charina, Neonatrix, Nebraskophis, Salvadora, Elaphe,* and *Paleoheterodon*) were probably terrestrial forms, with *Neonatrix* possibly spending some of the time near the water.

Correlation. — Amphibians, turtles, and lizards do not appear to have changed much from Barstovian (Upper Miocene) to Clarendonian (Lower Pliocene) times, but at least in the Plains Region of North America there appears to be a definite change in the snake fauna. In the Barstovian Kleinfelder Farm fauna of Saskatchewan boids and archaic colubrid genera that are not closely related to any living colubrid forms are present. But in the Clarendonian WaKeeney local fauna of Kansas, where over 70 tons of fossiliferous matrix has been processed for small vertebrate fossils, there are no boids present (boids were incorrectly reported by Wilson, 1968) and all of the colubrid genera appear to be living ones. Both the Egelhoff local fauna and the Norden Bridge local fauna have boids and archaic colubrid genera, and for this reason I am suggesting a Barstovian rather than a Clarendonian age for both the Egelhoff and the Norden Bridge faunas (fig. 1). It also appears that the Egelhoff and Norden Bridge faunas are closely temporally equivalent and bear a biofacies relationship to one another. The Egelhoff fauna consists mainly of small animals; the Norden Bridge fauna has many large animals, including rhinoceri. The Norden Bridge fauna (El. 2170) which occurs only one and one-half miles away from the Egelhoff fauna (El. 2195) comes from much coarser grained sediments than the Egelhoff fauna, and I suggest a higher energy aquatic environment in the same sedimentary sequence for the Norden Bridge fauna.

LITERATURE CITED

AUFFENBERG, W., 1963, Fossil testudinine turtles of Florida genera *Geochelone* and *Floridemys*: Bull. Florida State Mus., v. 7, no. 2, p. 53–97.

BRATTSTROM, B. H., 1958, New records of Cenozoic amphibians and reptiles from California: Bull. Southern Calif. Acad. Sci., v. 57, pt. 1, p. 5–12.

BULLOCK, R. E., & W. W. TANNER, 1966, A comparative osteological study of two species of Colubridae (*Pituophis* and *Thamnophis*): Brigham Young Univ. Sci. Bull., v. 8, no. 3, p. 1–29.

CHANTELL, C. J., 1971, Fossil amphibians from the Egelhoff local fauna in North-Central Nebraska: Contrib. Mus. Paleontology Univ. Mich., v. 23, no. 15, p. 239–246.

ESTES, R., & J. A. TIHEN, 1964, Lower vertebrates from the Valentine Formation of Nebraska: Am. Midl. Naturalist, v. 72, no. 2, p. 453–472.

ETHERIDGE, R., 1961, Late Cenozoic glass lizards (*Ophisaurus*) from the southern Great Plains: Herpetologica, v. 17, no. 3, p. 179–186.

HIBBARD, C. W., 1960, An interpretation of Pliocene and Pleistocene climates in North America: 62nd Mich. Acad. Rept., 1959–1960, p. 5–30.

HOLMAN, J. A., 1964, Fossil snakes from the Valentine Formation of Nebraska: Copeia, 1964, no. 4, p. 631–637.

———, 1970, Herpetofauna of the Wood Mountain Formation (Upper Miocene) of Saskatchewan: Canadian Jour. Earth Sci., v. 7, no. 5, p. 1317–1325.

———, 1971, Climatic significance of giant tortoises from the Wood Mountain Formation (Upper Miocene) of Saskatchewan: *Ibid.*, v. 8, no. 9, p. 1148–1151.

KING, W., 1959, Vertebra duplication, an osteological anomaly widespread in snakes: Herpetologica, v. 15, pt. 2, p. 87–88.

UNDERWOOD, G., 1967, A contribution to the classification of snakes: British Mus. Nat. History Publ. 651, 179 p.

WILSON, R. L., 1968, Systematics and faunal analysis of a Lower Pliocene vertebrate assemblage from Trego County, Kansas: Contrib. Mus. Paleontology Univ. Mich., v. 22, no. 7, p. 75–126.