This is to certify that the

dissertation entitled

HEMPHILLIAN AGE (LATE MIOCENE)
PALEOHERPETOFAUNAS FROM
NEBRASKA

presented by

Dennis Parmley

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Zoology

Major professor

Date August 1989

HEMPHILLIAN AGE (LATE MIOCENE)
PALEOHERPETOFAUNAS FROM
NEBRASKA

By

Dennis Parmley

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1989

ABSTRACT

HEMPHILLIAN AGE (LATE MIOCENE) PALEOHERPETOFAUNAS FROM NEBRASKA

By

Dennis Parmley

Early, middle, and late Hemphillian (late Miocene) herpetofaunas from Nebraska were identified and interpreted. The early Hemphillian (ca. 8 Ma) Potter Quarry of Cheyenne Co. yielded too few fossils for analysis, but at least one salamander, one frog, one lizard, and two colubrid snakes were identified. The mid-Hemphillian (Ca. 7 Ma) Lemoyne Quarry of Keith Co. yielded at least four salamanders, six frogs, one turtle, two lizards, two boid, nineteen colubrid, and two viperid snakes. Collectively, the late Hemphillian (ca. 5 Ma) Devils Nest, Santee, and Mailbox Prospect quarries yielded at least one salamander, seven frogs, seven turtles, two lizards, and twelve colubrid, and one viperid snakes. The mid-Hemphillian fauna lived near a quiet lake cove, while the late Hemphillian faunas lived near a stream or river.

The fossil record of Arikareean through Blancan (Miocene through Pliocene) snake genera from the

midcontinental region of North America suggests erycinine snakes became extinct across the region by late Hemphillian time, and colubrid snakes were modern by late Hemphillian or early Blancan time. Two extinction events may have taken place among late Miocene snakes: one among boids when four genera disappeared between the Barstovian and early Hemphillian, and one among colubrids when five genera disappeared between the mid-Hemphillian and late Hemphillian.

Suggested reasons for this event may reflect any or all of the following dynamics of the Miocene: temporal succession of forest communities to steppe, immigration of modern colubrid genera from Eurasia, radiation of passerine birds and cricetid rodents as a new food supply for large snakes, and competition for all the new environmental and biotic resources among resident boid, archaic colubrid, and modern colubrid genera.

To Julie, Amanda, and Zachary

ACKNOWLEDGMENTS

I am especially grateful to my major professor, Dr. J. Alan Holman, for making available to me necessary literature, fossils, comparative specimens, and artist time. I am grateful to Dr. Holman for the privilege of studying the Hemphillian fossils that form the basis of this report. The fossils were to be the basis of his own study of Hemphillian herpetological life, but knowing my interest in the Hemphillian, "Al" kindly turned the project over to me. Dr. Holman willingly offered encouragement and technical assistance through every phase of my research. Moreover, Dr. Holman's knowledge of fossil and Recent amphibians and reptiles has been an invaluable aid in this study. I also gratefully acknowledge financial support from the Michigan State University Museum.

A special thanks is extended to my doctoral committee members: Drs. Richard Seltin, Grahame Larson, and Richard Snider for valuable advice during the course of my academic career at Michigan State University, for their patience, and for their advice concerning preparation of this work.

I appreciate the extensive discussion with my major advisor and committee members on all of the systematic matters herein, but I take full responsibility for the identification of specimens and naming of new taxa.

Dr. Michael Voorhies and George Corner of the University of Nebraska State Museum are gratefully acknowledged for allowing me to study the Hemphillian fossils under their care, for making funds available for our 1987 field season, and for freely sharing their knowledge of the fossil sites.

Special thanks are due Ron and Pam Adams who kindly provided me with computer equipment. Dr. Christopher Carmichael made additional computer equipment available to me. Drawings are by Lisa Hallock and Irene Rinchetti, Staff Artists of the MSU Museum. Karen Cebra prepared some of the figures. I thank all these people for their patience.

I happily acknowledge my wife, Julie; daughter, Amanada; and son, Zachary for their patience, understanding, and most importantly, total support which made this work possible. Julie always knew when it was time to go camping and collecting for a few days.

Julie and I are indebted to Frank and Alice Lewis, 1987 Camp Hosts at Lake Ogallala State Park, Nebraska, for their friendship and support during our stay in the field.

A special thanks must go to my friends and teachers at Midwestern State University, Texas: Drs. Walter W. Dalquest, Norman Horner, and Fred Stangle. It is their dedication to science and teaching and love of field work that encouraged me to further my training under Dr. Holman.

Last, but certainly not least, I thank my parents, G. W. "Tex" and Marjorie Parmley, for their unrelenting support and faith in me.

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INTRODUCTION

Hemphillian age (late Miocene) herpetofaunas are poorly known in North America, as only two moderately diverse ones have been reported from Texas (Parmley, 1984, 1987, 1988a). Based on these herpetofaunas, I recently suggested (Parmley, 1988a) that the Hemphillian appears to reflect an important modernization of the North American midcontinental snake fauna. The purpose of the present study is to (1) attempt to document this hypothesis by a thorough study of Hemphillian herpetofaunas in midcontinental North America, and (2) if this documentation is substantial, to suggest a reason or reasons for this important evolutionary event.

Field parties from the University of Nebraska State Museum have made collections of vertebrate fossils at the early Hemphillian Potter Quarry (ca. 8 Ma), mid-Hemphillian Lemoyone Quarry (ca. 7 Ma) and late Hemphillian Santee, Devils Next, and Mailbox Prospect quarries (ca. 5 Ma) of Nebraska. Additionally, field parties from the Michigan State University Museum made collections at the Santee and Mailbox Prospect quarries, and my family and I collected at the Lemoyne Quarry during the summer of 1987. All investigators have used conventional screen-washing methods described by Hibbard (1949). These quarries that have yielded the largest Hemphillian herpetological fauna known in North America, form the basis of this report. The fossils provide important information about amphibian and reptilian evolution during this poorly known period. Furthermore, they develop a Miocene-Pliocene biochronology of midcontinental North American snakes.

NORTH AMERICAN LAND MAMMAL AGES

Land Mammal Age terms have largely superseded classic geological time units in modern North American Cenozoic studies (Woodburne, 1987). The concept of land mammal ages is based on wide ranging, but temporally isolated, mammalian taxa, and each age has a type locality and type local fauna or faunas that contain characteristic mammalian species. Land Mammal Ages are basically defined on: (1) first and last occurrences of taxa, (2) taxa restricted to the age, and (3) characteristic taxa of the age. The history and current use of Land Mammal Ages has recently been reviewed by Woodburne (1987).

The Hemphillian Land Mammal Age

The Hemphillian Land Mammal Age was defined by Wood (1941) on the basis of two faunas of the Ogallala Group in the Panhandle of Texas, including the Coffee Ranch local fauna of Hemphill County and the Higgins local fauna of Lipscomb County. Dalquest and Patrick (1989) convincingly argued that definition of the Hemphillian Land Mammal Age be defined solely on the basis of the Coffee Ranch local fauna as follows:

1. Stability demands that a single type locality and type local fauna be the basis of a Land Mammal Age.
2. The "Hemphill Fauna" (Coffee Ranch local fauna) was given a formal name by Matthew and Stirton (1930), but none had been proposed for the Higgins fauna.
3. The Coffee Ranch quarry contains datable volcanic ash, but no datable material is present at the Higgins quarry.
4. There are numerous publications on the Coffee Ranch local fauna, but only a few for the Higgins fauna.
5. The Higgins local fauna is older (early Hemphillian) than the mid-Hemphillian Coffee Ranch.
6. The Higgins quarries are not in Hemphill County, but in Lipscomb County, thus the Higgins would cause confusion as a type local fauna.

Tedford et al. (in Woodburne, 1987) believe that the Hemphillian can be usefully subdivided into two phases: an early phase and a late one. Dalquest (1983), however, argues for an informal three-part division of the Hemphillian: early Hemphillian as conceived by Schultz (1977); mid-Hemphillian to include the Coffee Ranch local fauna and correlatives; and late Hemphillian to include local faunas that have some transitional Blancan forms. Because marked herpetological differences appear to exist between the mid-Hemphillian and late Hemphillian, I chose to follow Dalquest in dividing the Hemphillian into three parts.

The Hemphillian ranges from 9 Ma to 4.5 Ma for a span of 4.5 million years. The Hemphillian age is mostly coeval with the late Miocene, with the late Hemphillian overlapping the Miocene Pliocene boundary (Figure 1). Major mammalian taxa now used to define the age are listed below.

Index Fossils: Agriotherium, Dipoides (also occurs in the Blancan), Ilingoceros, Plesiogulo.

First Appearances: ground sloths, Lutravus, Machairodus, Pliotaxidae.

Last Appearances: Aphelops, Mylaqaulus, Osteoborus (confined to the Hemphillian), Pliauchenia, Pliohippus, Sphenocephalos, Teleoceros.

Characteristic Fossils: Hypolaqus, Megatylopus, Nannippus, Neohipparion.

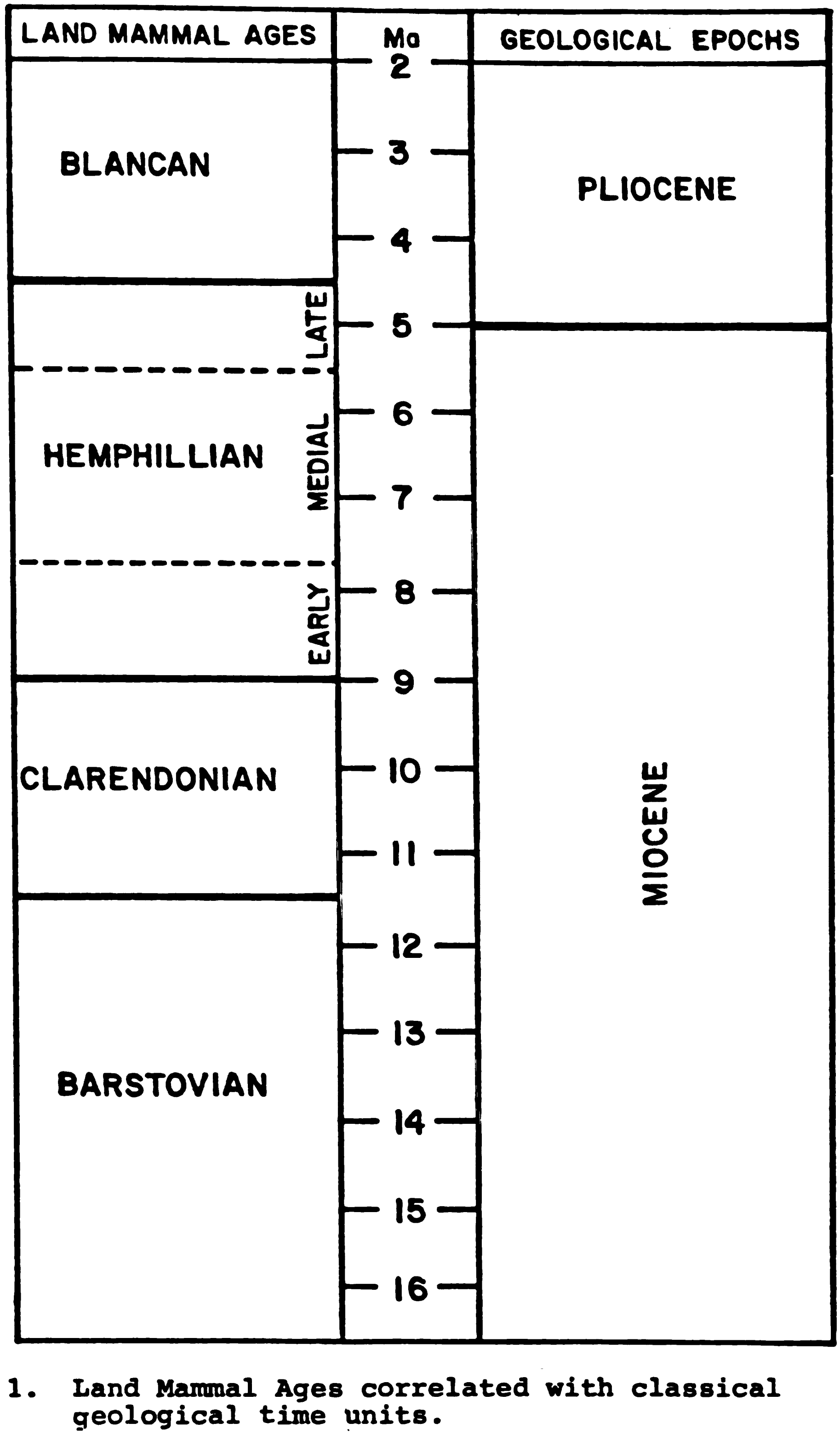

Figure 1. Land Mammal Ages correlated with classical geological time units.

GEOLOGIC SETTING

The fossil faunas detailed here are in the Ogallala Group (Figure 2), and with the possible exception of the Santee and Devils Nest sites, are from the Ash Hollow Formation. The Ash Hollow Formation is separated from the underlying Valentine Formation by a narrow hiatus (Woodburne, 1987, Figure 4 here). Both the Ash Hollow and the Valentine are important fossil bearing formations in Nebraska, and a brief history of them is presented here.

Ogallala Group

The "Ogallala" was named by Darton (1899) as a formation, but was later raised to group status (Lugn, 1938). Today, the Ogallala Group is an extensive complex of alluvial deposits of late Miocene and early Pliocene age, extending from north to south through the Great Plains region for approximately 1280 km and 480 km from east to west (Schultz, 1977; Skinner and Johnson, 1984; see Figure 2 here). In the late Neogene the Ogallala may have been a much larger sheet of sediments, covering 500,000 square miles with a north-south extent of 1600 km or more (King and Beikman, 1978).

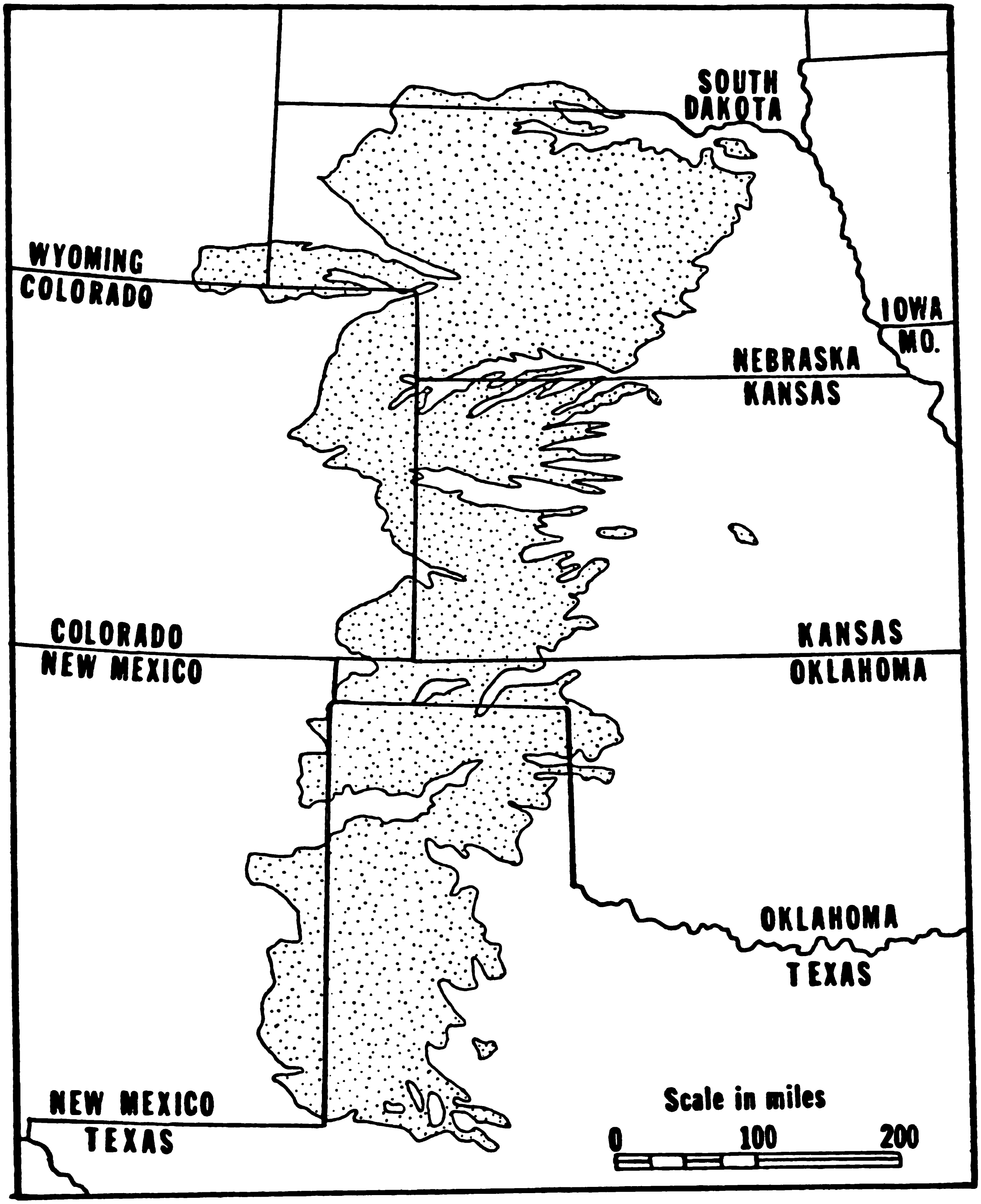

Figure 2. Major distribution of the Ogallala Group (after Frye, 1971).

The depositional history of the Ogallala is complex and has been the subject of many studies for nearly 56 years. A detailed treatment of the vast literature is not possible here, and only a brief overview of major studies is presented. Plummer (1932) suggested that the Ogallala plain formed by merging of numerous alluvial fans spread over a large, flat surface. Frye (1971) summarized the Ogallala depositional history as follows:

> The character of the Ogallala deposits demonstrates that they are primarily the product of stream action, probably locally supplemented by eolian activity and periodically interrupted by widespread soil development. Furthermore, the basal part of the formation consists of a series of fills in the separate valleys that, in general, trended from west to east. Coalescence of the alluvial fills from one valley to another gradually took place as the individual divides were buried in the progressively thickening alluvial fills. The final integration of this extensive plain of alluviation, permitting an essentially unrestricted lateral migration of stream channels, occurred during the last phase of Ogallala deposition. The resultant coalescent plain, marked only by depositional constructional topographic features, maintained an equilibrium sufficiently long to permit the strong development of the "Ogallala-climax soil."

Frye's history is generally accepted, and it is agreed upon that the Ogallala is a series of many braided stream deposits that ended with the completion of the Rocky Mountain orogeny in latest Miocene time.

A Group is composed of two or more stratigraphically contiguous formations that share general geographic and lithogenetic affinities with one another (Savage and Russel, 1983). In Nebraska the Ogallala Group is divided into two formations: the Valentine and Ash Hollow. Both formations are important lithostratigraphic units that have produced important biostratigraphic successions of vertebrate fossils. A brief description of these major fossil bearing formations in Nebraska follows.

Valentine Formation

The Valentine Formation, named for the town of Valentine, Cherry County, Nebraska, is recognized as the lower unit of the Ogallala Group in most of Nebraska (Figure 4). An excellent account of fossil mammals, and to a lesser degree, amphibians and reptiles known from the Valentine Formation of Nebraska is given by Skinner and Johnson (1984).

The Valentine Formation consists of friable cross-bedded channel sand, clay clasts, semiconsolidated argillaceous sandstone, occasional lenses of silicified casts of fossil roots and massive sand and gravel. As it extends eastward, the Valentine becomes more fine-grained (Voorhies, 1969). In Nebraska the formation is divided into four members (Skinner and Johnson, 1984).

Ash Hollow Formation

The upper unit of the Ogallala Group in most of Nebraska is known as the Ash Hollow Formation (Figure 4), which overlies the Valentine formation and is subdivided into at least two members (Skinner and Johnson, 1984). Lugn (1938) designated the type locality of the formation as Ash Hollow Canyon southeast of Lewellen, Garden County, Nebraska, and it now is a widely accepted Ogallala stratigraphic unit (see Skinner and Johnson, 1984:295). The lithology of the Ash Hollow formation is complex and varies geographically, but Skinner and Johnson (1984) provide an excellent review of the lithology of the formation in Nebraska. Basically, the lithology consists of calcereous sandstones, clays, and sandy-silt typically cemented into caliche stones, both of which outcrop across numerous areas in the High Plains. Beds of datable volcanic ash also occur in many areas. Paleochannels that cut into the Ash Hollow often contain vertebrate fossils.

HISTORY OF FOSSIL SITES

Following is a history of each of the five fossil sites that form the basis of this report.

The early Hemphillian Potter Quarry of Cheyenne County and the mid-Hemphillian Lemoyne Quarry of Keith County are located in SW Nebraska, and the three late Hemphillian sites--Mailbox Prospect of Antelope County, Devil's Nest, and Santee quarries of Knox County--are located in the NE section of the state (Figure 3). Figure 4 correlates these sites with other major midcontinental fossil sites that are herpetologically important. The absolute and biochronological ages of the sites (Figure 4), as well as their exact location, history, and stratigraphy are discussed below.

Potter Quarry

Location

The Potter Quarry fossil site is in Cheyenne County, SW Nebraska in sec. 7, T13N, R51W approximately 12 km SE of Scottsbluff. This site is University of Nebraska State Museum locality Cn 106B.

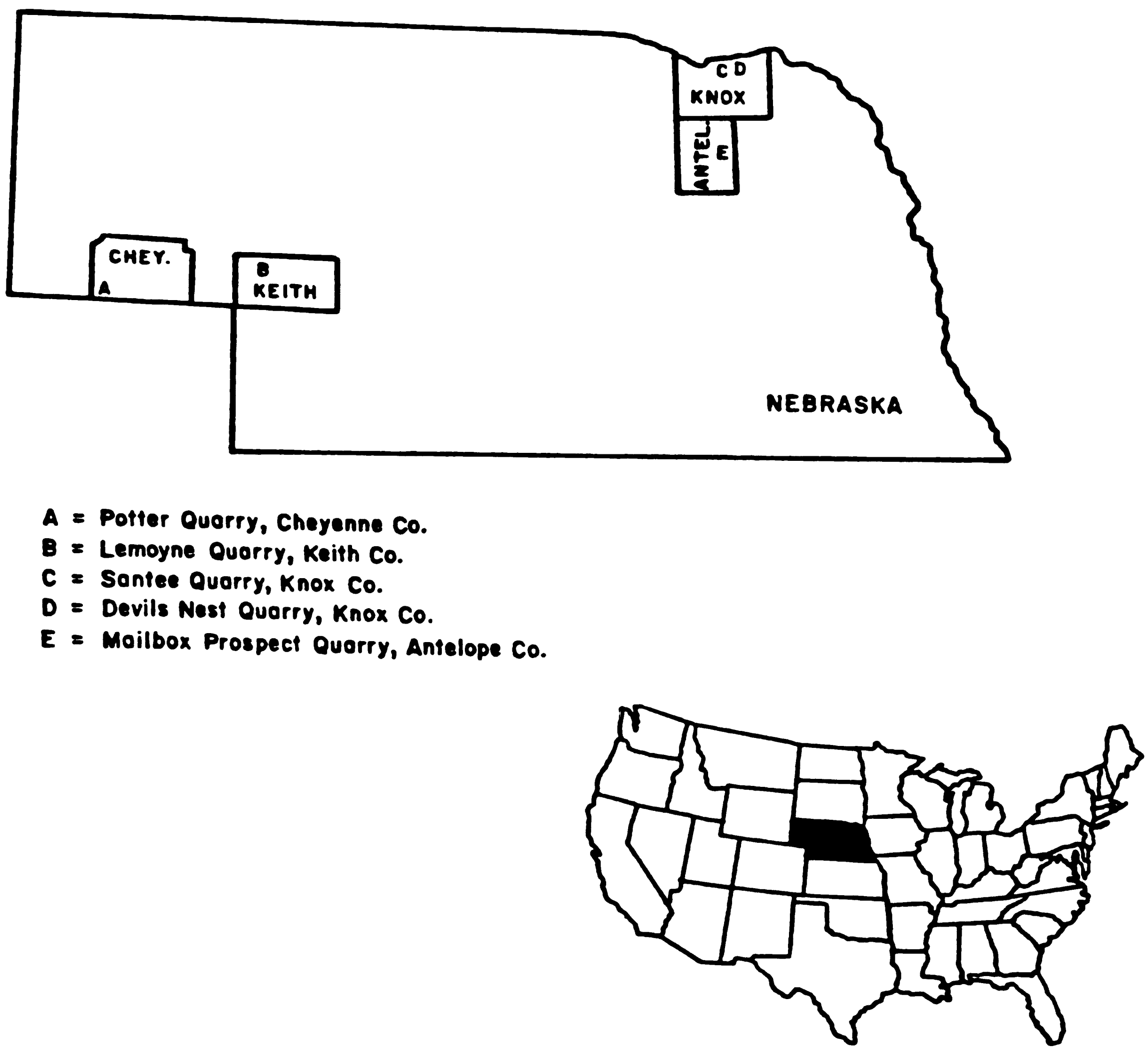

Figure 3. Location of the Early Hemphillian Potter Quarry, mid-Hemphillian Lemoyne Quarry, and Late Hemphillian Santee, Devils Nest, and Mailbox Prospect quarries.

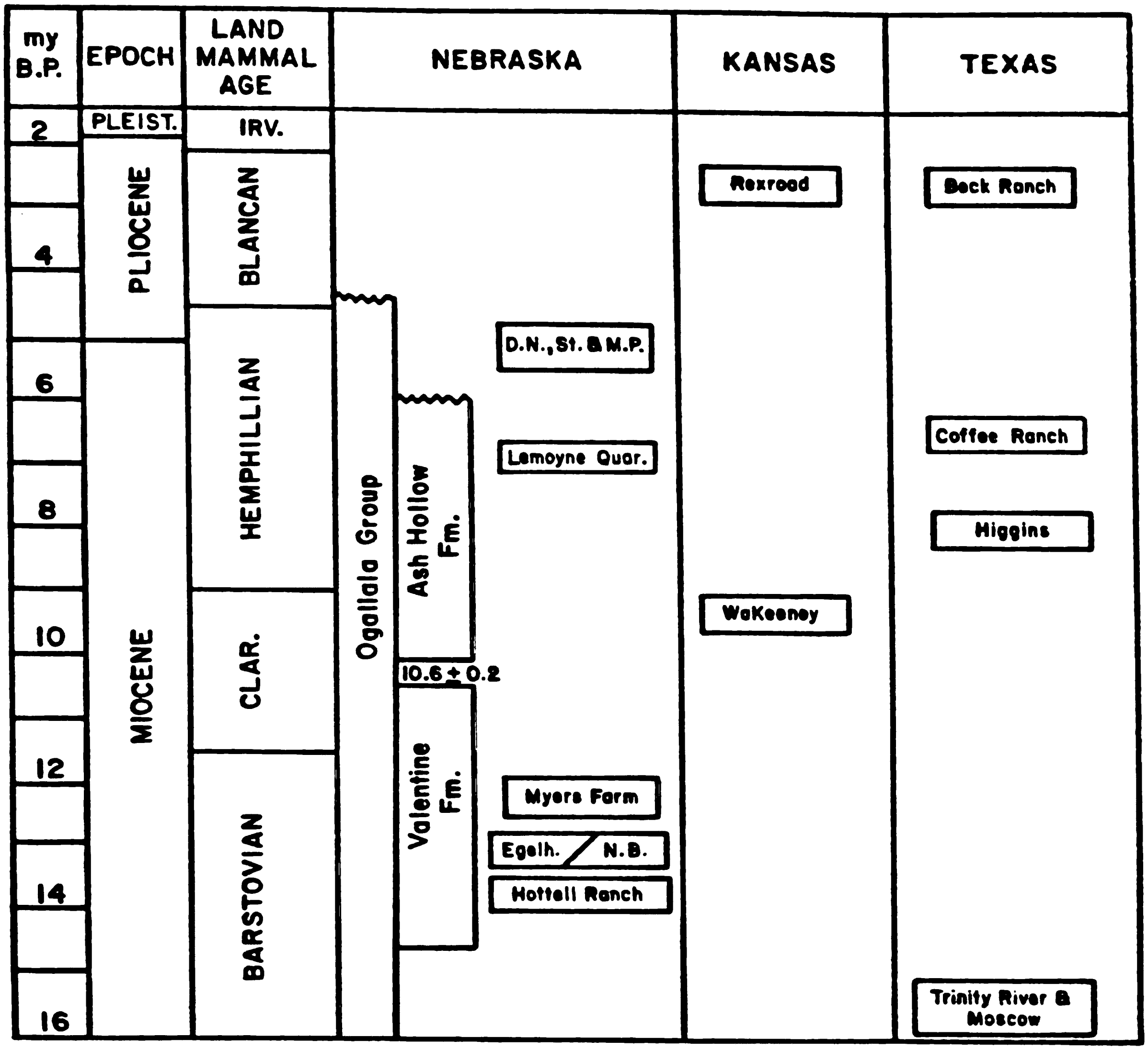

Figure 4. Stratigraphic correlation of Hemphillian faunas in Nebraska with other Great Plains sites with important amphibian and reptile faunas.

History and Previous Investigations

The large mammalian fauna of the Potter Quarry local fauna has been reported by Breyer (1981). There are no reports of amphibians or reptiles from the site.

Age

Breyer (1981) considers the Potter Quarry fauna to be of early Hemphillian age based on the presence of *Pseudoceras*, *Cranioceras* (*Yumaceras*), *Callipus*, *Sthenictis*, *Aelurodon*, *Osteoborus*, *Vulpes*, and *Aelurodon validus*. Of these, *Cranioceras* (*Yumaceras*) is an early Hemphillian genus extending from the chronofauna established by Clarendonian times, and *Osteoborus* and *Vulpes* indicate the beginning of Hemphillian time (Woodburne, 1987).

Stratigraphy

The Potter Quarry fauna is from the middle of a shallow section of the Ogallala Group (Ash Hollow Formation) located on a divide of a major paleovalley (Breyer, 1981). Breyer (1981) figured a measured section of the Ash Hollow rocks that yielded the Potter Quarry fossils.

Lemoyne Quarry

Location

The Lemoyne Quarry site is a north-facing road cut on Nebraska State Highway 92 in the NE1/4, NW1/4, sec. 3, T15N, R40W, approximately 6.4 km west of the townsite of Lemoyne, Keith County, Nebraska. It lies adjacent to the north shore of Lake McConaughy, an artificial reservoir produced by impoundment of the North Platte River. This locality is designated as University of Nebraska State Museum locality Kh-101.

History and Previous Investigations

Lemoyne Quarry was discovered in 1968 during construction of Nebraska Highway 92 by K. A. Rickey of the University of Nebraska State Museum (UNSM). Intensive collecting at the quarry by UNSM parties in 1969 and 1970 (Martin, 1975) yielded thousands of mostly microvertebrate fossils. Field personnel from the University of Wyoming collected at Lemoyne Quarry in 1971 and 1972 (Brown, 1980). Martin (1975) described a new species of microtine rodent (*Paramicrotoscoptes hibbardi*) from the site. Brown (1980) described an extensive insectivore fauna from Lemoyne Quarry, and Leite (1986, 1988) described the stratigraphy and larger mammals from the site. Nonetheless, many of the Lemoyne Quarry mammalian fossils remain unstudied.

Age

The Lemoyne Quarry local fauna has been assigned a mid-Hemphillian age (late Miocene) on the basis of the occurrence of the following mammals (Leite, 1986, 1988): Dipoides, Paramicrotoscoptes hibbardi, Megalonyx, Epicyon validus, Neohipparion eurystyle, Pliohippus nobilis, Megatylopus gigas, Peidomeryx (Yumaceras), and Texoceras. Of these taxa, Dipoides is considered a Hemphillian index fossil, Pliohippus makes its last appearance in the Hemphillian, Megatylopus is considered a Hemphillian characteristic fossil, and Paramicrotoscoptes is confined to the mid-Hemphillian. Woodburne (1987: Figure 8.1) stratigraphically place the Lemoyne Quarry fauna as late mid-Hemphillian.

There is no absolute date for the Lemoyne Quarry fauna, but the Coffee Ranch quarry of Texas, which is younger than Lemoyne Quarry (Leite, 1988), is overlain with a thick bed of volcanic ash dated at ca. 6-6.5 Ma (Izette, 1975), and there is a fission date of 10.6 $\pm$ 0.2 Ma (Figure 4) for the basal unit of the Ash Hollow Formation at the Valentine Formation transitional zone (Boellstorff and Skinner, 1977). Inference from these data and biochronological evidence places the Lemoyne Quarry at approximately 7 Ma.

Stratigraphy

Leite (1986) measured a section of the Lemoyne Quarry and figured the generalized stratigraphy of the quarry. In the summer of 1987, I measured a section of the deposit where the overlying laminated sandstones had previously been removed and found a most productive lens of microvertebrate fossils (Figure 5). The most abundant and complete fossils were taken from sandy, slightly gritty lenses, usually located in the basal area of the greenish-grey claystone (Figure 5).

Santee Fossil Site

Location

The Santee site is in northern Knox County (Voorhies, 1977). The site is designated University of Nebraska State Museum site Kn 111. Voorhies (1977) gives the location of the site as a road cut in the NE1/4, NW1/4, sec. 25, T33N, R5W at an elevation between 450 and 480 meters (Santee Quadrangle, U.S. Geological Survey 71/2 minute Topographic Series, 1978).

History and Previous Investigations

Fossils from the Santee area have been collected by UNSM field parties for a number of years. The first report of fossils from the Santee are bones of *Phenacomys parkeri* (Martin) described in 1975. Since then, Voorhies

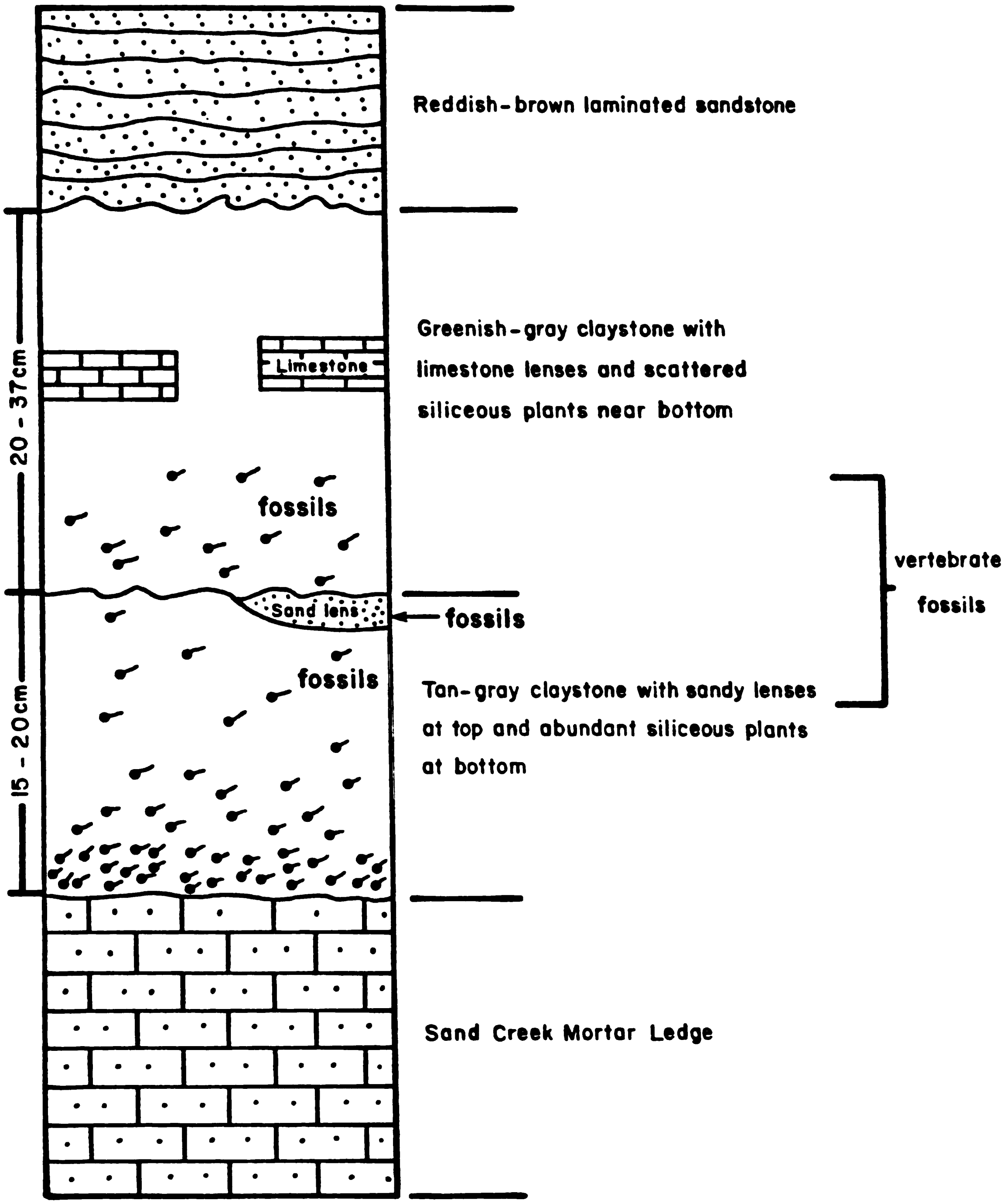

Figure 5. Generalized stratigraphy of Lemoyne Quarry showing most productive areas for microvertebrate fossils.

(1977) has described a new large species of scalopine mole, *Scalopus mcgrewi*, from the Santee and most recently (1988), described a large terrestrial squirrel, *Paenemarmota sawrockensis*, from the site. The only account of an amphibian or a reptile from the Santee is a report by Holman (1982a) of a nearly complete skeleton of the Recent snake *Elaphe vulpina*.

Age

There is a fission-track date of 5.0 ± 0.2 Ma on a white volcanic ash overlying the Santee local fauna (Boellstorff, 1976). Lindsay et al. (1976) briefly commented on the Santee fauna noting that "Fission-track dates on glass are usually younger than other radiometric dates taken on the same volcanic rock, which suggest the Santee fauna might be placed . . . at 5.3 Ma." As pointed out by Voorhies (1988), even if this correction is true, the Santee ash fell within the last million years of the Hemphillian mammal age. The fauna accumulated below the ash and is, thus, at least slightly older than the ash, placing its age at about 5 Ma. Voorhies (1988) firmly believes the mammalian fauna of the Santee, particularly the presence of *Paenemarmota sawrockensis*, supports a late Hemphillian age, and Woodburne (1987: Figure 8.1) places the fauna at 5 Ma.

Stratigraphy

The stratigraphy of the Santee has been discussed by Voorhies (1977), and in a more recent account (1988), he describes the Santee stratigraphy as follows:

> . . . the unit of major interest consists of unconsolidated fluvial clastic sediments deposited in a paleovalley cut into the Pierre Shale (Cretaceous), which forms the pre-Tertiary bedrock throughout Knox County. The basal contact of the fluvial unit (an unnamed, post-Cap Rock channel fill tentatively assigned to the Ogallala Group--undifferentiated) is well exposed at the principal fossiliferous outcrop. . . .

The fossils described here from the Santee local fauna were collected by UNSM field parties from a small area identified as "squirrel lens" (Voorhies, 1977).

Devils Nest Airstrip

Location

The Devils Nest Airstrip is in Knox County approximately 10 km east of the Santee locality. The site is designated as University of Nebraska State Museum site Kx 113. The airstrip is a 1.5 km long, NNW trending dirt landing strip with its north end near the center of SE 1/4, NW 1/4, sec. 24, T33N, R4W and its south end at the center of SW1/4, NE 1/4, SE 1/4, sec. 24, T33N, R4W (Voorhies, 1988). Fossiliferous sediments were well exposed in weathered channels along both sides of the air strip, but are now overgrown with vegetation (Voorhies, *in litt*., 1987).

History and Previous Investigations

There are few accounts of fossil vertebrates from the Devils Nest Airstrip site. White (1987) studied the archaeolagine lagomorphs from the site recognizing two species and a new genus and species. Voorhies (1988) recently listed a diverse mammalian fauna from the Santee. There are no published accounts of amphibians or reptiles from the Devils Nest Airstrip.

Age

Based on the mammals known from the Devils Nest, Voorhies (1988) considers the fauna to be of late Hemphillian age and equivalent to the Santee local fauna. These mammals are rhinocerotids, mylagaulids, dromomerycids, and the genera *Buisnictis*, *Brachyopsigale*, *Sminthosinis*, *Trigonictis*, *Repomys*, and *Paenemarmota* which are considered late Hemphillian arrivals in North America (Lindsay et al., 1976). Woodburne (1987: Figure 8.1) places the fauna at about 5 Ma, but slightly younger than the Santee fauna.

Stratigraphy

The stratigraphy of the Devils Nest Airstrip is similar to the Santee area. Voorhies (1988) described the stratigraphy of the area as follows: "The fossiliferous sequence can be described as a fining-upward paleovalley fill with cobble-gravel and coarse sand at the base, overlain by finer sands and silts." There is no volcanic ash in the upper beds of the Devils Nest Airstrip. The channel fill cuts into remnants of older Pierre Shale and Barstovain sediments. A detailed report on the stratigraphy of the Devils Nest Airstrip is being prepared by Voorhies.

Mailbox Prospect Fossil Site

Location

The Mailbox site lies on the intersection of sections 15, 16, 21, and 22, T28N, R7W in northern Antelope County. This quarry is University of Nebraska State Museum site Ap 125.

History and Previous Investigations

Other than being briefly mentioned in Woodburne (1987), the Mailbox site is unpublished.

Age

On the basis of the microtine rodent *Promimomys*, Repenning (*in* Woodburne, 1987) assigned a late Hemphillian age to the Mailbox fauna. Voorhies (*in litt*., 1988) agrees with this age designation, but believes the Mailbox local fauna is slightly older within the late Hemphillian than the Santee and Devils Nest Airstrip sites. This is in agreement with Woodburne (1987: Figure 8.1), who place the age of the fauna as about 5.4 Ma.

Stratigraphy

The stratigraphy of the Mailbox site is unpublished, but Voorhies (in litt., 1988) describes the fossiliferous unit as unconsolidated sand and gravel overlying the Cap Rock Members of the Ash Hollow Formation. Voorhies regards it as part of the Ogallala Group (undifferentiated), but notes it is lithologically distinct from the units within the Ogallala Group named and described by Skinner and Johnson (1984) in the area lying immediately to the west of the Mailbox area.

SYSTEMATIC PALEONTOLOGY

The classification used here essentially follows Banks et al. (1987). Osteological terminology follows Duellman and Trueb (1985) for salamanders and frogs; Zangerl (1969) for turtles; Estes (1983) for lizards; and Auffenberg (1963a) and Holman (1979) for snakes. All measurements were made with either a dial caliper or an ocularmicrometer and are reported in millimeters unless otherwise noted. Abbreviations used herein are: SV, snout to vent length; Cl, carapace length; TL, total length; P.Q., Potter Quarry; L.Q., Lemoyne Quarry; St., Santee Quarry; D.N., Devils Nest Quarry; M.P., Mailbox Prospect Quarry.

Specimens are deposited in either the Michigan State University Museum, Vertebrate Paleontology Collections (MSUVP) or the University of Nebraska State Museum (UNSM).

Checklist

Following is a checklist of the amphibians and reptiles of the early Hemphillian Potter Quarry local fauna, mid-Hemphillian Lemoyne Quarry local fauna, and late Hemphillian Santee, Devils Nest, and Mailbox

Prospect local faunas. Extinct genera are noted with a double asterisk, extinct species with a single one.

Potter Quarry local fauna

Class Amphibia
Order Caudata
Family Ambystomatidae
Ambystoma maculatum

Order Anura
Family Ranidae
Rana sp. indet.

Class Reptilia
Order Squamata
Family Colubridae
Subfamily Colubrinae
Thamnophis sp. indet.
Subfamily Xenodontinae
*Paleoheterodon tiheni***

Lemoyne Quarry local fauna

Class Amphibia
Order Caudata
Family Plethodontidae
Gen. et sp. indet.
Family Ambystomatidae
Ambystoma maculatum
*Ambystoma minshalli**
Ambystoma tigrinum
Ambystoma sp. indet.

Order Anura
Family Bufonidae
*Bufo pliocompactilis**
*Bufo hibbardi**
*Bufo valentinensis**
Bufo marinus
Bufo sp. indet.

Family Ranidae
Rana cf. *R. pipiens*
Rana sp. indet.

Family Hylidae
Hyla cf. *H. gratiosa*
Hyla sp. indet.

Class Reptilia
Order Testudines
cf. Emydidae

Order Squamata
Family Anguidae
Ophisaurus cf. *O. attenuatus*

Family Scincidae
Eumeces sp. indet.

Family Boidae
Subfamily Erycinae
*Charina prebottae**
Lichanura sp. indet.

Family Colubridae
Subfamily Colubrinae
Arizona sp. indet
Nebraskophis corneri, n. sp.**
*Nebraskophis skinneri***
Paurophis lewisi, n. gen. et sp.**
Paracoluber cf. *P. storeri***
Coluber sp. indet. or
Masticophis sp. indet.
Lampropeltis triangulum
Lampropeltis getulus
*Salvadora paleolineata**
*Elaphe nebraskensis**
Elaphe lemoynensis, n sp. *

Subfamily Natricinae
*Nerodia hillmani**
Nerodia sp. indet.
cf. *Virginia* sp. indet.
Thamnophis cf. *T. proximus* or *T. sauritus*
Thamnophis cf. *T. marcianus* or *T. radix*
Thamnophis sp. indet.
*Neonatrix elongata***

Subfamily Xenodontinae
*Paleoheterodon tiheni***
Heterodon cf. *H. platyrhinos*
Heterodon cf. *H. nasicus*

Family Viperidae
Agkistrodon sp. indet.
Crotalus voorhiesi, n. sp.*
Crotalus sp. indet.

Santee local fauna

Class Amphibia
Order Caudata
Family Ambystomatidae
Ambystoma tigrinum
Ambystoma sp. indet.

Order Anura
Family Bufonidae
Bufo cognatus or
Bufo speciosus
Bufo holmani, n. sp.*
Bufo sp. indet.

Family Pelobatidae
*Scaphiopus wardorum**
Scaphiopus sp. indet.

Family Ranidae
Rana cf. *R. pipiens*
Rana cf. *R. catesbeiana*
Rana sp. indet.

Family Hylidae
Hyla sp. indet.

Class Reptilia
Order Testudines
Family Trionychidae
Trionyx spiniferus
Trionyx sp. indet.

Family Emydidae
Chrysemys picta

Family Kinosternidae
Kinosternon flavescens

Family Testudinidae
Geochelone sp. indet.*

Order Squamata
Family Iguanidae
Crotaphytus cf. *C. collaris*

Family Scincidae
Eumeces sp. indet.

Family Colubridae

Subfamily Colubrinae

Coluber sp. indet. or
Masticophis sp. indet.
Lampropeltis getulus
Lampropeltis sp. indet.
Elaphe obsoleta
Elaphe sp. indet.
Pituophis melanoleucus

Subfamily Natricinae

Thamnophis cf. *T. proximus* or *T. sauritus*
Thamnophis sp. indet.

Subfamily Xenodontinae

Heterodon sp. indet.

Family Viperidae

Crotalus sp. indet.

Devils Nest local fauna

Class Amphibia

Order Caudata

Family Ambystomatidae

Ambystoma tigrinum

Order Anura

Family Bufonidae

Bufo holmani, n. sp.*
Bufo sp. indet.

Family Ranidae

Rana sp. indet.

Class Reptilia

Order Testudines

Family Trionychidae

Trionyx sp. indet.

Family Emydidae

Emydoidea blandingii
Chrysemys picta
Terrapene sp. indet.

Family Chelydridae

Macroclemys temminckii

Family Testudinidae

Geochelone sp. indet.*

Order Squamata
Family Colubridae
Subfamily Colubrinae
Coluber sp. indet. or
Masticophis sp. indet.
Lampropeltis triangulum
Lampropeltis getulus
Elaphe obsoleta
Elaphe cf. *E. guttata*
Elaphe sp. indet.
Pituophis melanoleucus

Subfamily Natricinae
Thamnophis sp. indet.

Family Viperidae
Crotalus sp. indet.

Mailbox Prospect local fauna

Class Amphibia
Order Caudata
Family Ambystomatidae
Ambystoma tigrinum
Ambystoma sp. indet.

Order Anura
Family Bufonidae
Bufo woodhousii

Family Pelobatidae
Scaphiopus sp. indet.

Family Ranidae
Rana cf. *R. pipiens*
Rana cf. *R. catesbeiana*
Rana sp. indet.

Family Hylidae
Hyla sp. indet.

Class Reptilia
Order Testudines
Family Trionychidae
Trionyx sp. indet.

Family Emydidae
Chrysemys picta

Order Squamata

Family Scincidae

Eumeces cf. *E. obsoletus*

Eumeces sp. indet.

Family Colubrinae

Subfamily Colubrinae

Coluber sp. indet. or

Masticophis sp. indet.

Lampropeltis triangulum

Elaphe cf. *E. guttata*

Pituophis melanoleucus

Subfamily Natricinae

Nerodia sp. indet.

Thamnophis cf. *T. proximus* or

T. sauritus

Thamnophis cf. *T. marcianus* or

T. radix

Thamnophis sp. indet.

Subfamily Xenodontinae

*Paleoheterodon tiheni***

Heterodon cf. *H. platyrhinos*

Heterodon cf. *H. nasicus*

Heterodon sp. indet.

Family Viperidae

Crotalus sp. indet.

Class Amphibia Linnaeus, 1758

Order Caudata Oppel, 1811

Family Plethodontidae Gray, 1850

Subfamily Plethodontinae

Gen. et sp. indet.

Material: L.Q.: 23 vertebrae, MSUVP 1238; 56 vertebrae, UNSM 96406.

Remarks: Edwards (1976) reports major groups of salamanders have characteristic arrangements of spinal nerve foramina. Most of the fossil vertebrae have well marked foramina directly posterior to rib bearers as in the family Sirenidae, Salamandridae, Plethodontidae and Ambystomatidae (exclusive of Dicamptodon and Rhyacotriten, Tihen and Wake, 1981). Modern sirenid and salamandrid vertebrae have more complicated neural spines and neural arches than the fossils. Plethodontid vertebrae are similar in structure to those of ambystomatids, but may be separated on the following basis.

Plethodontid vertebrae are small and slender with long, narrow centra, short, centrally located neural spines, and low, thin neural arches. Vertebrae of small ambystomatid species are generally shorter with wider centra, lower and longer neural spines and higher neural arches.

Two subfamilies of Plethodontidae, Desmognathinae and Plethodontinae, are currently recognized. Vertebral differences between the subfamilies have been discussed by Tihen and Wake (1981) and Wake (1966). Important differences between subfamilies are vertebrae opisthocelous in Desmongnathinae, amphicoelous in Plethodontinae, and basapophyses well-developed on posterior central margins in Desmognathinae, absent or weakly developed in Plethodontinae. The fossil vertebrae have no opisthocoely and lack, or have weakly developed basapophyses as in the Plethodontinae. The fossils are similar in size and structural detail to several Recent species of *Plethodon*, and differ from *Eurycea* in having shorter neural spines. But vertebral characters of Recent plethodontids appear to overlap considerably, inter- and intraspecifically, as well as ontogenetically and geographically (Worthington and Wake, 1972) negating identification below the subfamily level.

The Lemoyne Quarry fossils represent only the second Miocene record of a plethodontid salamander east of the rocky mountains. Other Miocene records of plethodontid salamanders are as follow. Peabody (1959) described Miocene trackways of *Batrachoseps* from California. Tihen and Wake (1981) identified *Plethodon* and *Aneides* from the Arikareean (lower Miocene) of Montana and Clark (1975) identified *Aneides* and *Batrachoseps* from the late Hemphillian upper Mehrten Formation of California.

Family Ambystomatidae Hallowell, 1858

Genus *Ambystoma* Tschudi, 1838

Ambystoma maculatum (Shaw, 1802)

Material: P.Q.: 2 vertebrae, UNSM 96445: L.Q.: 5 vertebrae, MSUVP 1235; 10 vertebrae, UNSM 96408.

Remarks: Tihen (1958) divided the genus *Ambystoma* into subgenera and species groups based (in part) on osteological characters. The fossil vertebrae are assigned to the *maculatum* group based on their elongate shape, and on having the postzygapophyses extending further posteriorly than the neural arches, at least in posterior trunk vertebrae (Tihen, 1958). Tihen (1958) further differentiates between _Ambystoma_ groups using ratios based on straight line measurements. The fossils fit the _maculatum_ group in vertebral morphology, measurements and ratios (Table 1). The _maculatum_ group includes the living species _A_. _maculatum_, _A_. _gracile_, _A_. _jeffersonianum_, _A_. _laterale_, _A_. _macrodactylum_, the small extinct Miocene species _A_. _minshalli_ Tihen and Chantell and _A_. _priscum_ recently described by Holman (1987). The fossils represent large adult individuals that agree best in size and in vertebral characters with the living species _A_. _maculatum_. None of the fossils have the posterior ends of their neural arches deeply notched as in _A_. _priscum_ (Holman, 1987).

Ambystoma _maculatum_ presently occurs in the eastern half of the United States (Conant, 1958). It is a moderately large salamander (14-20 cm TL; Conant, 1958) that lives in moist environments, where it usually stays hidden under logs or rocks.

Ambystoma _minshalli_ Tihen and Chantell, 1963

Material: L.Q.: 5 vertebrae, MSUVP 1240; 6 vertebrae, UNSM 96430.

Table 1. Vertebral measurements and ratios of Lemonyne Quarry *Ambystoma maculatum* vertebrae (n=8).

Measurements and Ratios*						
CL	PRZW	PZW	ZL	ACW	CL/NAW	CZW/ZL
3.8	3.9	3.9	5.0	1.5	2.53	1.56
3.4	3.3	3.1	5.0	1.3	2.62	1.01
3.6	3.7	3.6	4.8	1.4	2.57	1.52
3.7	3.6	3.2	5.0	1.5	2.47	1.36
2.9	2.8	2.4	4.2	1.2	2.42	1.24
3.3	3.3	3.4	5.0	1.5	2.20	1.34
2.9	2.9	2.9	4.0	1.0	2.90	1.45
3.7	3.3	3.2	5.0	1.5	2.47	1.30
Ratios for fossils:					2.2-2.62	1.0-1.56
Ratios given by Tihen (1958) for *A. maculatum*					2.2-2.9	1.1-1.4

*Cl = centrum length

PRZW = width through prezygapophyses

PZW = width through postzygapophyses

ZL = length through zygapophyses

ACW = anterior centrum width

Remarks: The small size, elongate, narrow shape and low neural arches of these vertebrae are diagnostic characters of the small extinct salamander *Ambystoma minshalli*. This species belongs to the *maculatum* group of Tihen (1958), whose members today are typically woodland inhabitants.

Ambystoma minshalli is a widespread late Miocene species of the North American Great Plains, and is most common from Barstovian age deposits in Nebraska (Chantell, 1971; Estes and Tihen, 1964; Holman, 1982b, 1987; Holman and Sullivan, 1981; Tihen and Chantell, 1963). It is also known from the late Barstovian of South Dakota (Green and Holman, 1977; Holman, 1978), early Hemphillian of Texas (Parmley, unpublished) and mid-Hemphillian of Texas (Parmley, 1984).

Ambystoma tigrinum (Green, 1825)

(Figures 6-7)

Material: L.Q.: 3 vertebrae, MSUVP 1242; 19 vertebrae, UNSM 96407 & 96409; St.: 3 vertebrae, 1 humerus, UNSM 56949; D.N.: 1 vertebra, UNSM 56900; M.P.: 14 vertebrae, 2 humeri, UNSM 56917.

Remarks: These large fossil vertebrae are assigned to Tihen's (1958) *tigrinum* group based on their short and wide shape. The fossils resemble those of Recent *A. tigrinum* in having the posterior part of the neural

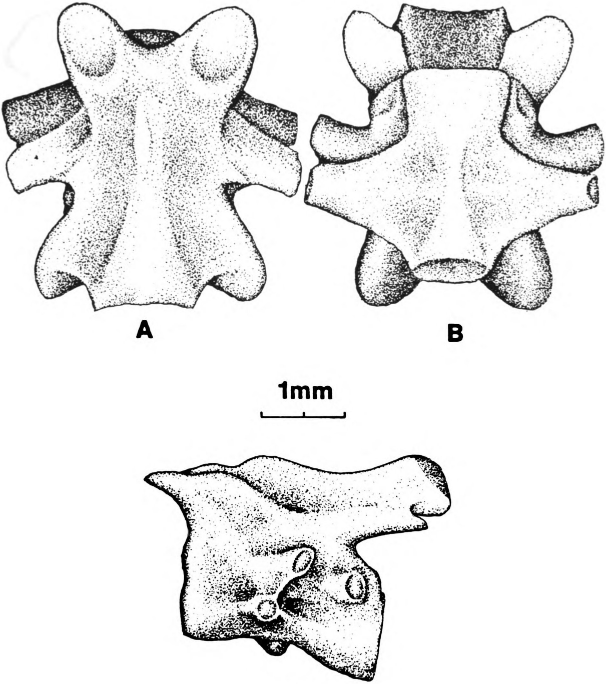

Figure 6. Trunk vertebra of Ambystoma tigrinum (L.Q., UNSM 96407) in dorsal (A), ventral (B), and lateral (C) views.

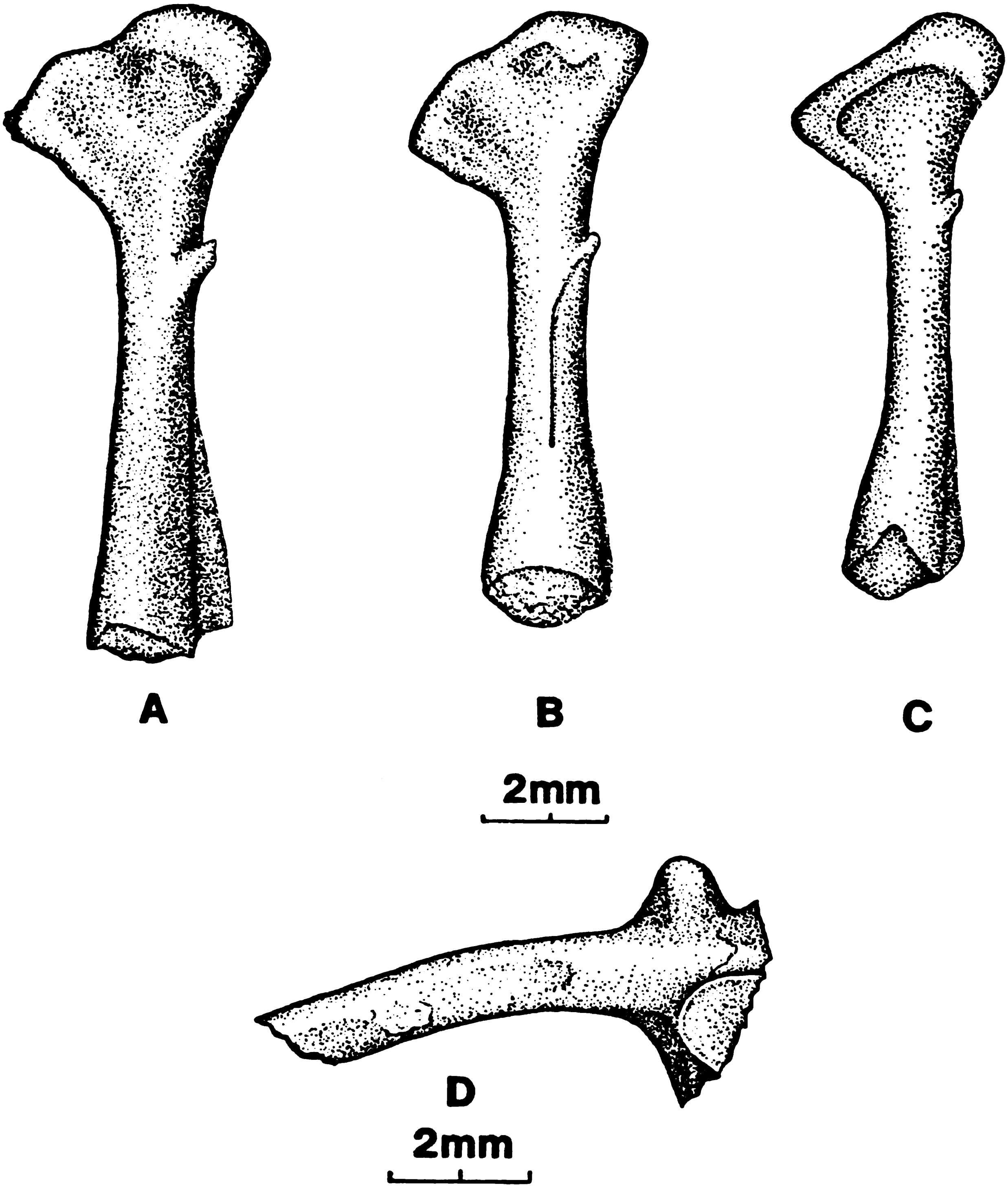

Figure 7. Humerus of *Ambystoma tigrinum* (M.P., UNSM 56916) in ventral view (A) compared with humeri of Recent *A. tigrinum*, (B) and *A. maculatum*, (C) and left ilium of *Bufo pliocompactilis* (L.Q., UNSM 96410) in lateral (D) view.

arches upswept in lateral view (Holman, 1969), and postzygapophyses extending to or only slightly past the ends of the neural arches (Tihen, 1958). Members of the maculatum group usually have longer vertebrae with the postzygapophyses extending beyond the ends of the neural arches.

All of the Mailbox Prospect vertebrae have widely-opened notochordal canals that indicate larval or recently metamorphosed salamanders (Tihen, 1958). In the North American Great Plains region today, larval *Ambystoma tigrinum* most often inhabit shallow, poorly oxygenated playa-type ponds or lakes that do not support large populations of fish (per. obs.). Aquatic habitat of this type must have occurred near the Mailbox Prospect during the time of deposition.

The humerus of *Ambystoma tigrinum* may be distinguished from *A. maculatum* (the only other similar-sized *Ambystoma* species known from the Hemphillian sites) in that the crista ventralis is deep with an uneven lateral edge. *Ambystoma maculatum* has a smaller crista ventralis with an evenly downward sloping lateral edge (Figure 7 A-C). The fossil humeri from the Mailbox Prospect locality are identical to those of *A. tigrinum*. The species occurs throughout Nebraska today (Lynch, 1985).

Ambystoma sp. indet.

Material: L.Q.: 40 vertebrae, UNSM 96411; M.P.: 2 vertebrae, UNSM 56916.

Remarks: These fossils are too fragmentary or too worn to identify past the generic level. Small to large individuals of more than one species appear to be represented.

Order Anura Rafinesque, 1815

Family Bufonidae Gray, 1825

Genus *Bufo* Laurenti, 1768

Bufo pliocompactilis Wilson, 1968

(Figure 7D)

Material: L.Q.: 2 left ilia, UNSM 96410.

Remarks: This small species of extinct toad was originally described by Wilson (1968) on the basis of two frontoparietals and 24 ilia from the Clarendonian WaKeeney local fauna of Kansas. Ilia of this frog are small with high and narrow ilial protuberances (Wilson, 1968). Only the Recent species *Bufo speciosus* and *B. compactilis* and the extinct species *B. rexroadensis* described by Tihen (1962) from the Blancan of Kansas have dorsal prominences with protuberances as high as in *B. pliocompactilis*, but these species are considerably larger with correspondingly larger ilia. The Lemoyne

Quarry ilia are small and seem to be clearly assignable to the distinct species *B. pliocompactilis*.

Bufo pliocompactilis was previously known only form the Clarendoonniaainn of Kansas (Holman, 1975; Wilson, 1968). This small toad was common in the Wakeeney locl fauna of Kansas wherae at least 49 indivdiuals were reported (Holman, 1975; Wilson, 1968). *Bufo pliocompactilis* appears to be rare in the Lemoyne Quarry herpetofauna, but its presence represents the first occurrence of the species in Nebraska, and extends the species temporal range about 3 Ma.

Bufo hibbardi Taylor, 1942

(Figure 8A)

Material: L.Q.: 1 right ilium, MSUVP 1234; 1 right ilium, UNSM 96400.

Remarks: *Bufo hibbardi* is a moderately large toad of the Americanus group (Tihen, 1962). Tihen (1962) described the dorsal prominence of this extinct species as "the posterior slope is not particularly steep, and is a very even slope; the anterior slope is very steep dorsally. . . ." The Lemoyne Quarry ilia are like *B. hibbardi* in size and structure. Previous records of this species include the Clarendonian WaKeeney local fauna of Trego County, Kansas (Holman, 1975) and the Hemphillian (late?) Edson Beds of Sherman County, Kansas (Tihen, 1962).

Bufo valentinensis Estes and Tihen, 1964

Material: L.Q.: 2 left ilia, MSUVP 1231; 3 right ilia, UNSM 96401.

Remarks: This small extinct toad was described on the basis of a frontoparietal and several referred ilia from the Barstovian of Nebraska (Estes and Tihen, 1964). Ilia of *Bufo valentinensis* have low, rounded dorsal prominences with the posterior slopes steeper than the anterior ones (Estes and Tihen, 1964). Ilia of this species are inseparable from those of the poorly known Blancan species *Bufo suspectus* (Estes and Tihen, 1964). The Lemoyne Quarry ilia are like both species, and I have assigned them to *B. valentinensis* on the basis of temporal grounds.

Bufo woodhousii Girard, 1854

Material: M.P.: 5 right and 1 left ilia, UNSM 56920.

Remarks: These fossil ilia have a higher dorsal prominence than *Bufo marinus*, *B. debilis*, *B. valliceps*, *B. hibbardi*, and *B. valentinensis* and a lower prominence than *B. speciosus*, *B. cognatus*, *B. rexroadensis* and *B. spongifrons* as in Recent *B. woodhousii*.

Three extant subspecies of Bufo woodhousii are currently recognized; B. w. woodhousii mainly of the Great Plains region, B. w. fowleri of the eastern half of the United States, and B. w. australis of west Texas, southwest New Mexico, and southeast Arizona (Conant, 1958). One extinct subspecies, B. w. bexarensis, is known from the Rancholabrean (late Pleistocene) of Texas (Mecham, 1959). The Mailbox ilia are much smaller than B. w. bexarensis, which were considerably larger than all Recent subspecies of B. woodhousii. Among the three living subspecies, B. w. woodhousii differs from B. w. fowleri in having higher dorsal prominences (Tihen, 1962). Based on a single specimen of B. w. australis, this subspecies appears to be closest to B. w. woodhousii in dorsal prominence height, but its ilia are smaller. The fossil ilia are from medium-sized individuals with SV lengths between 50-60 (maximum SV length of B. woodhousii 127; Conant, 1958), and have dorsal prominences closest in height to B. w. woodhousii.

Bufo woodhousii was, heretofore, known as a fossil from the Blancan (Rogers, 1976) to the Rancholabrean (Parmley, 1986a). It is a common toad of grasslands throughout most of Nebraska today (Lynch, 1985).

Bufo cognatus Say in James, 1823 or

B. speciosus Girard, 1854

(Figure 8 B-C)

Material: St.: 1 left ilium, UNSM 56945.

Remarks: The dorsal prominence of Bufo cognatus and B. speciosus is higher than in all other similar size extant species of Bufo. Only the extinct species B. spongifrons from the Hemphillian (late?) of Kansas (Tihen, 1962) and B. rexroadensis from the Blancan of Kansas (Tihen, 1962) have a dorsal prominence as high or higher than in B. cognatus and B. speciosus (Tihen, 1962). Ilia of Bufo cognatus and B. speciosus differ from those of B. spongifrons in having the posterior angle of the dorsal prominence into the ilial shaft less steep. The species differ from B. rexroadensis in having the posterior angle of the dorsal prominence distinctly steeper than the anterior angle rather than only slightly steeper as in B. rexroadensis.

Bufo cognatus is widespread in Nebraska today (Conant, 1958), whereas B. speciosus occurs to the south in western Oklahoma and all but about the eastern one-fourth of Texas (Dixon, 1987). Both species are inhabitants of short grass prairies and rarely enter woodlands (Conant, 1958). In the southern Great Plains, B. speciosus inhabits dry mesquite infested prairies (pers. obs.).

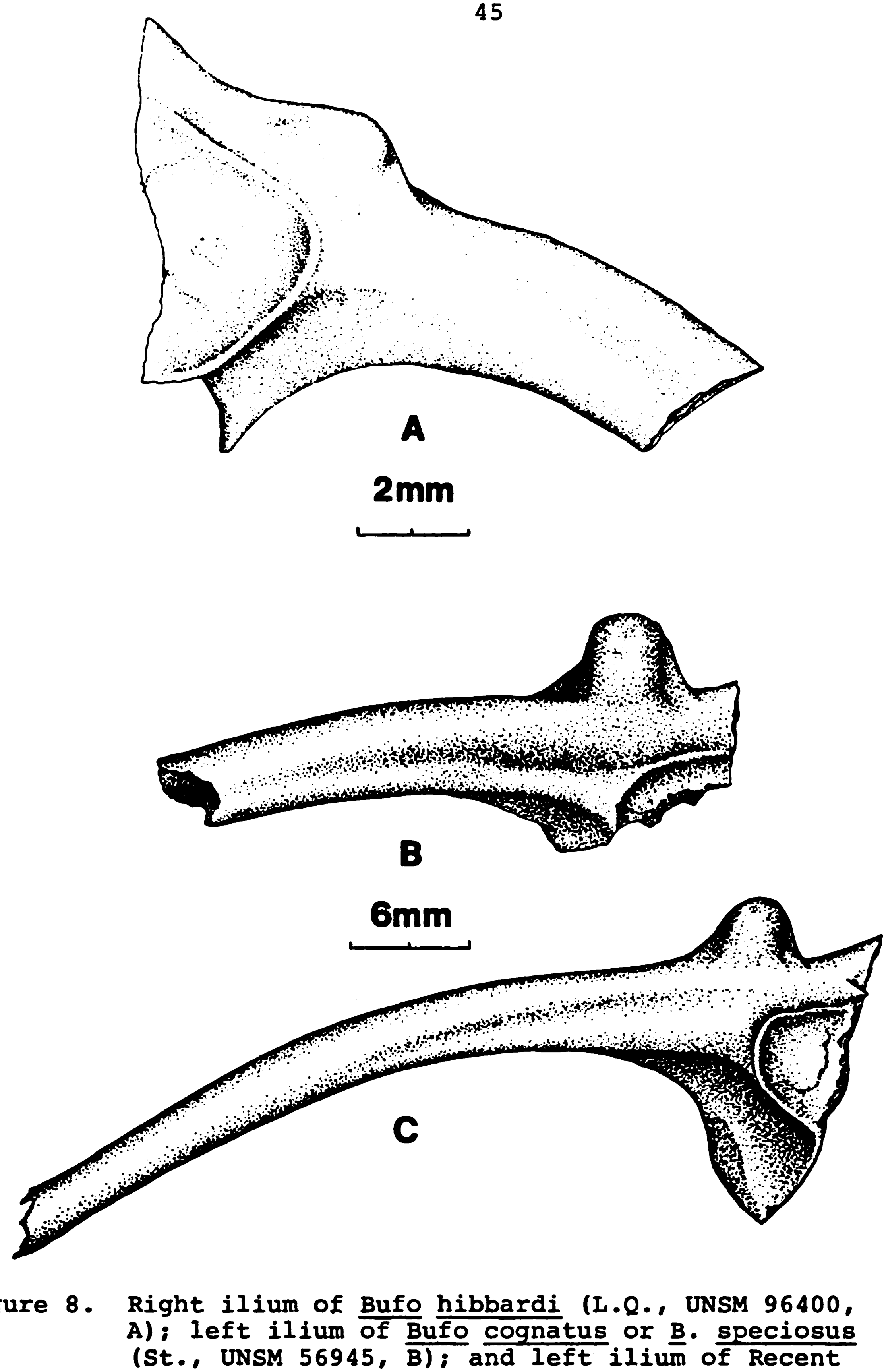

Figure 8. Right ilium of Bufo hibbardi (L.Q., UNSM 96400, A); left ilium of Bufo cognatus or B. speciosus (St., UNSM 56945, B); and left ilium of Recent B. speciosus (C) in lateral view.

Bufo marinus (Linnaeus, 1758)

Material: L.Q.: 1 right ilium, MSUVP 1236; 2 right ilia, UNSM 96402.

Remarks: Ilia of Recent *Bufo marinus* and the fossils have moderately high dorsal prominences that are dorsally produced with rugose, laterally deflected protuberances. The posterior ends of the dorsal prominences lie above the anterior ends of the acetabular cups. The most complete fossil ilium (MSUVP 1236) has a fossa containing a moderately large foramen present on the ilial shaft immediately posterior to the acetabular cup and dorsolateral to the anterior edge of the subacetabular expansion. This foramen is also present on ilia of several Recent *B. marinus*.

Holman (1975) assigned 11 ilia from the Clarendonian WaKeeney local fauna of Kansas to *Bufo marinus*. The Lemoyone Quarry fossils represent individuals slightly larger than the WaKeeney specimens, but they fall within the size range of Recent *B. marinus*.

Bufo marinus occurs no closer to Nebraska than the southern tip of Texas today. This toad lives in many different habitats, but is most common in open grassland situations. Unbroken forest is believed to act as a dispersal barrier (Zug and Zug, 1979).

Bufo holmani, n. sp.

(Figure 9A)

Holotype: UNSM 56902, a right ilium.

Referred Material: Right ilium (UNSM 56943) from the Santee local fauna.

Type Locality: Devils Nest Airstrip, Knox County, Nebraska.

Age: Late Hemphillian (late Miocene).

Diagnosis: A large robust species of Bufo distinct from all extinct and living North American members of the genus in the following characters: (1) large size; (2) thick, robust ilial shaft; (3) large acetabular cup; and (4) high, rounded dorsal prominence.

Etymology: Specific name in honor of J. Alan Holman for his contributions to paleoherpetology.

Description of Holotype: In lateral view: acetabular cup large and moderately shallow with well-defined lip; dorsal acetabular expansion missing; distal end of subacetabular expansion missing, portion ventral to acetabular cup moderately wide; well marked foramen at edge of subacetabular expansion immediately anterior to acetabular cup; dorsal prominence moderately high and rounded with anterior angle steep, posterior angle long and gentle in its descent; ilial shaft wide, flattened along upper two thirds and ridgelike along lower one third.

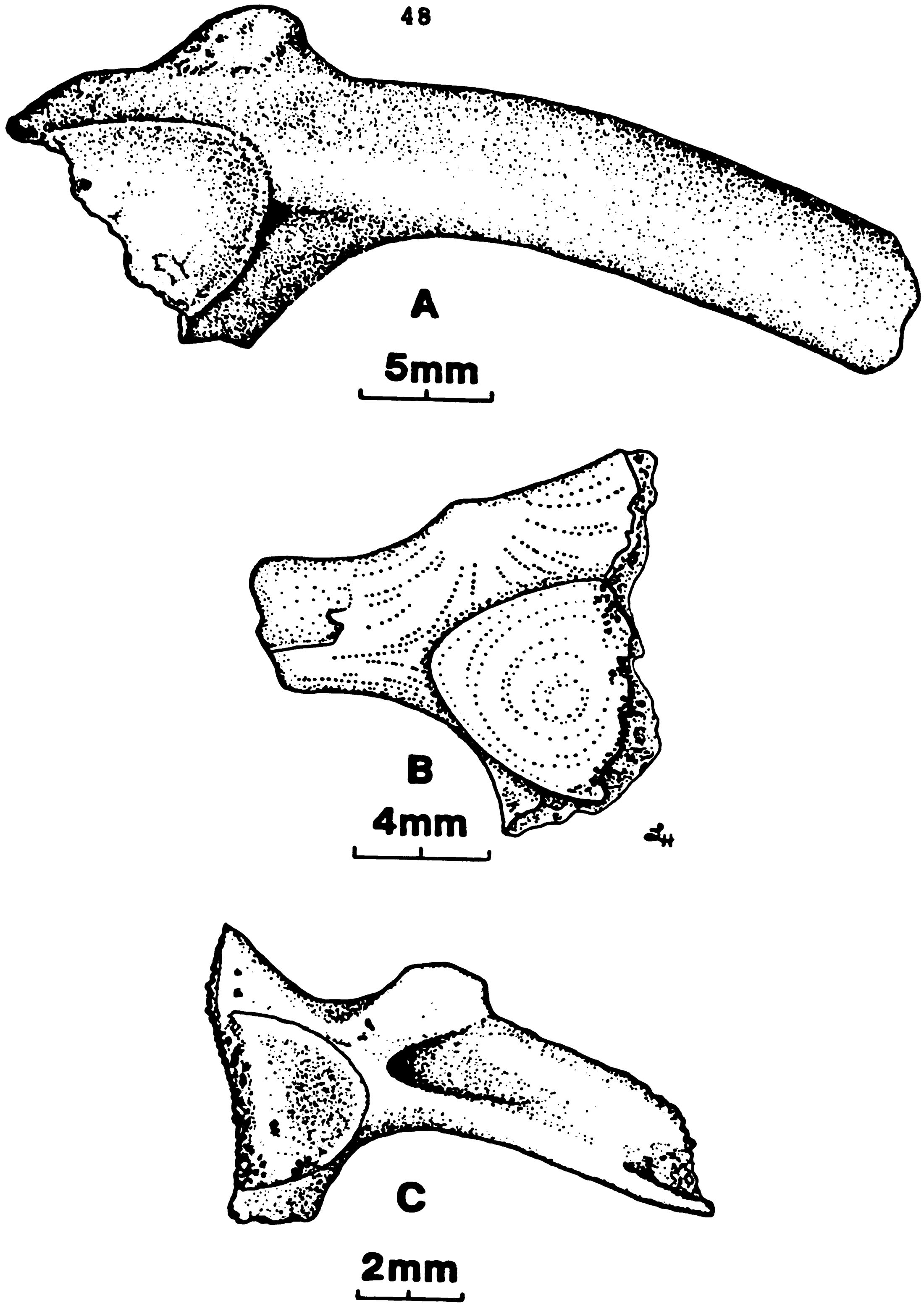

Figure 9. Right ilium of Bufo holmani, n. sp. (D.N., UNSM 56902, A); left ilium of Scaphiopus wardorum (St., UNSM 56946, B); and right ilium of Rana cf. R. pipiens (L.Q., MSUVP 1232, C) in lateral view.

In dorsal view: ilial shaft compressed laterally, dorsal prominence-protuberance complex laterally deflected.

Measurements: Given in Table 2.

Referred Ilium: This ilium is considerably more worn than the holotype, but is similar in having a wide, thick ilial shaft, moderately high dorsal prominence and large, shallow acetabular fossa. It differs from the holotype in having a less steep anterior angle of the dorsal prominence into the ilial shaft. Measurements of the fossil are given in Table 2.

Discussion: Table 2 shows measurements of the type ilia compared with ilia of large Recent individuals of *B. alvarius* and *B. marinus*, the largest toads occurring in North America today. In addition to being larger, thicker, and more robust, ilia of *Bufo holmani* differ from those of other large fossil and Recent species of the genus in the following ways.

Bufo holmani differs from the large Barstovian species *Bufo kuhrei* Holman in having a higher dorsal prominence and a narrower subacetabular expansion.

Bufo holmani differs from large individuals of *Bufo marinus* in having the acetabular cup larger and wider, and in having a longer dorsal prominence.

Table 2. Measurements of *Bufo holmani*, *B. alvarius*, and *B. marinus* ilia

	B. holmani		*B. alvarius* n=6	*B. marinus* n=10
	Type	Referred	Range (Mean)	Range (Mean)
Acetabular fossa height	10.2	10.5	8.0 - 8.6 (8.1)	8.5 - 9.8 (9.0)
Acetabular fossa width	7.5	7.2	6.1 - 6.5 (6.3)	7.0 - 7.8 (7.4)
Dorsal prominence height	7.0	6.9	5.1 - 6.2 (5.7)	5.7 - 6.4 (6.2)
Dorsal prominence length	3.1	2.5	2.1 - 2.6 (2.5)	4.5 - 4.8 (4.3)
Ilial shaft height*	6.3	5.9	3.7 - 4.2 (4.0)	4.5 - 4.8 (4.7)
Ilial shaft width*	3.7	3.6	2.5 - 2.7 (2.5)	2.6 - 3.1 (2.9)

*Measured just anterior to anterior end of ventral acetabular expansion.

Bufo holmani differs from large individuals of the Recent species *Bufo woodhousii* in having a higher dorsal protuberance and a larger acetabular cup.

Bufo holmani differs from the large living southwest species *B. alvarius* in having a shorter dorsal prominence with a steeper posterior angle, and in having the ilial shaft less curved.

It is difficult to suggest a phyletic relationship of *Bufo holmani* to other extinct and living species of the genus, but its large acetabular fossa implies it may have been a primitive form (Holman, 1973b). Based on its moderately high dorsal prominence, the species may be allied with the Americanus group of Tihen (1962).

Bufo sp. indet.

Material: L.Q.: 1 left maxillary fragment, 3 right and 2 left ilia, UNSM 96441; St.: 3 left ilia, UNSM 56950; D.N.: 1 left ilium, UNSM 56901.

Remarks: These fossil ilia are typically *Bufo*-like in lacking ilial blades, and in having well developed dorsal prominence-protuberance complexes. They are either too fragmentary or too badly worn for species identification.

Family Pelobatidae Bonaparte, 1850

Genus _Scaphiopus_ Holbrook, 1836

Scaphiopus wardorum Estes and Tihen, 1964

(Figure 9B)

Material: St.: 1 left ilium, UNSM 56946.

Remarks: _Scaphiopus wardorum_ was described on the basis of an ilium from the Barstovian age Valentine Formation of Nebraska. It is a large extinct _Scaphiopus_ of the subgenus _Scaphiopus_ with ilia that may be distinguished from all living and extinct species of the genus based on their large size, prominent ridge-like dorsal prominences, and in having the portion of the subacetabular expansions anterior to the acetabula very narrow (Estes and Tihen, 1964). Although the dorsal prominence of the Santee ilium is worn, the fossil appears identical to _Scaphiopus wardorum_.

Measurements of the fossil are: greatest height of acetabulum, 7.0; height from ventral border of acetabulum through dorsal acetabular expansion, 11.3; height of ilial shaft just anterior to acetabulum, 4.2; width of ilial shaft just anterior to acetabulum, 4.0.

Scaphiopus wardorum shows similarities to Recent _S. bombifrons_ (Holman, 1987), but it is not known to have given rise to any living species. The Santee ilium represents the youngest species record, extending its temporal range from Barstovian to late Hemphillian.

Scaphiopus (Scaphiopus) sp. indet.

Material: St.: 1 left maxillary fragment, 1 right ilium, UNSM 56947; M.P.: 1 right ilium, UNSM 56940.

Remarks: The labial side of the fossil maxillary fragment is strongly ornamented with vermiform ridges clearly placing it in the subgenus Scaphiopus (Chantel, 1971), but the specimen is fragmentary making further identification difficult.

One of the most important taxonomic characters of the Scaphiopus ilium is dorsal prominence development and shape. The genus is divided into two subgenera partially on the basis of this structure (Zweifel, 1956); Scaphiopus which includes S. holbrooki, S. hurteri, and S. couchi, and Spea that includes S. multiplicatus, S. bombifrons, and S. hammondi. The ilium of the subgenus Spea either lacks a dorsal prominence, or if present, it exists as a small rounded knob. The subgenus is also characterized by a wide subacetabular expansion. In the subgenus Scaphiopus, the dorsal prominence is better developed, often ridge-like, contributes to the height of the dorsal acetabular expansion, and has the subacetabular expansion narrower. The Mailbox specimen has a worn but evident ridge-like dorsal prominence and the remnant of the subacetabular expansion is wide as in Scaphiopus. In fact, structurally the fossil ilium has a dorsal prominence structure very similar to the modern species *S. holbrooki*. The Santee ilium, while smaller and more fragmentary, also appears to represent a member of the subgenus *Scaphiopus*.

Family Ranidae Gray, 1825

Genus *Rana* Linnaeus, 1758

Rana cf. *R. pipiens* Schreber, 1782 Complex

(Figure 9C)

Material: L.Q.: 1 right ilium, MSUVP 1232; 45 right and 35 left ilia, UNSM 96403; St.: 10 right and 5 left ilia, UNSM 56944; M.P.: 2 right and 1 left ilia, UNSM 56919.

Remarks: *Rana* fossils are the most numerous Hemphillian anuran elements. Ranid ilia are easily identified to genus, but species identification is difficult (Chantell, 1971). Nevertheless, certain species or species groups are distinct. The fossil ilia are assigned to the *Rana pipiens* complex (*R. pipiens*, *R. blairi*, *R. berlanderi*, and *R. utricularia*) on the basis of their small size, smooth vastus prominences that lack pronounced tubercles (tubercles present in *R. sylvatica*) and in having the posterodorsal borders of ilial crests sloping gently into the dorsal acetabular expansions (angle of slope much steeper in *R. catesbeiana group*; Holman, 1982c). Within the *R. pipiens* complex, the species R. pipiens and R. blairi occur in Nebraska today (Lynch, 1985).

Rana cf. R. catesbeiana Shaw, 1802

(Figure 10A)

Material: St.: 1 left ilium, UNSM 56948; M.P.: 1 right and 1 left ilium, UNSM 56918.

Remarks: These fossil ilia are provisionally referred to the Rana catesbeiana group based on their large size and in having the posterior part of their ilial blades sloping steeply into the dorsal acetabular expansions (Holman, 1984a).

Based on biochemical evidence (Pytel, 1986), the catesbeiana group, which includes R. catesbeiana, R. clamitans, R. grylio, R. heckscheri, R. septentrionalis, and R. virgatipes, appears to be paraphyletic in that no synapomorphies are shared by any of the members (Pytel, 1986). But the group appears to form a natural group on the basis of immunological distance data (Pytel, 1986). It is interesting to note that these species also appear to form a natural group on the basis of ilial osteology. I have not seen ilia of R. virgatipes, but the remaining species of the group have the slope of the ilial blade into the dorsal acetabular expansion much steeper than in the R. pipiens group.

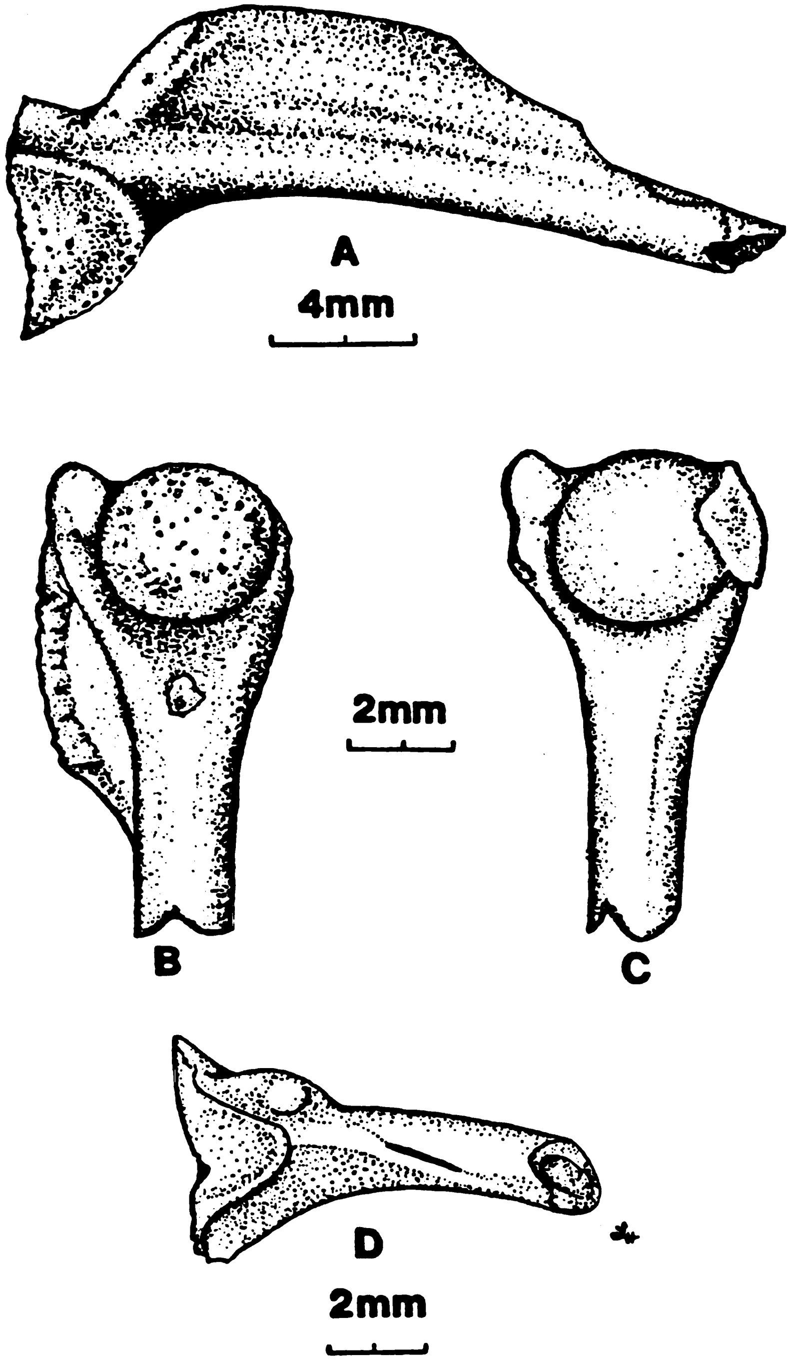

Figure 10. Right ilium of *Rana* cf. *R. catesbeiana* (St., UNSM 56948) in lateral view (A); humerus of male (B) and female (C) *Rana* sp. indet. (St., UNSM 56943); and right ilium of *Hyla* cf. *H. gratiosa* (L.Q., UNSM 96404) in lateral view (D).

Rana catesbeiana occurs throughout Nebraska today, but may do so because of human transplants (Lynch, 1985).

Rana sp. indet.

(Figure 10B-C)

Material: P.Q.: 3 humeri, UNSM 96444, L.Q.: 1 right and 1 left humeri, MSUVP 1302; 13 right and 21 left humeri, 4 right and 2 left scapulae, 78 right and 98 left ilia, UNSM 96404; St.: 1 maxillary fragment, 4 vertebrae, 2 right and 2 left scapulae, 7 right and 17 left humeri, 2 radio-ulnae, 10 right and 9 left ilia, 5 limb bones missing ends, 2 toe bones, UNSM 56943; D.N.: 1 scapula, 2 right and 3 left ilia, MSUVP 1250; 3 humeri, 2 right and 1 left ilia, UNSM 56915; M.P. 4 right and 2 left humeri, 6 right and 6 left ilia, UNSM 56921.

Remarks: The scapula of *Rana* may be separated from those of *Bufo* and *Scaphiopus* chiefly on the basis of coracoid articular process position. In *Rana* this structure lies near the clavicular articular process forming a narrow glenoid opening, whereas in *Bufo* and *Scaphiopus*, it projects laterally from the coracoid process producing a much wider glenoid opening. The remaining skeletal elements appear identical to those of ranid species, but are either too worn or too fragmentary to suggest a species or species group.

Adult male and female individuals were present in the paleopopulations of ranids as indicated by the sexually dimorphic humerus. This bone in male individuals of Rana has the crista lateralis well-developed, long, wide, and often wrinkled along its lateral edge (Figure 10B). In females, this structure is either lacking (Figure 10C), or if present, it is narrower, shorter, and smoother along the lateral edge than in males.

Family Hylidae Gray, 1825

Genus Hyla Laurenti, 1768

Hyla cf. H. gratiosa LeConte, 1856

(Figure 10D)

Material: L.Q.: 2 right ilia, MSUVP 1241; 2 right ilia, UNSM 96405.

Remarks: These fossil ilia are assigned to the genus Hyla on the basis of their wide subacetabular expansions, large and shallow acetabular cups, and rounded and dorsolaterally projected dorsal prominences (Chantell, 1964). Hyla species are difficult to distinguish on the basis of ilial characteristics, but the fossils resemble Hyla gratiosa in size; in having the dorsal protuberances rounded and about one-half anterior to the anterior margin of the acetabular cups; in having a slash-like foremen on the ilial shaft anterior to the anterior edge of the subacetabular expansions; and in having subtriangular acetabular cups. *Hyla* cf. *H. gratiosa* has been reported from the Barstovian age Norden Bridge local fauna of Nebraska (Chantell, 1964) and the Clarendonian WaKeeney local fauna of Kansas (Holman, 1975). This species can be found today throughout the southeastern United States (Conant, 1958). It is known to live in several different habitats and climb as well as burrow (Conant, 1958).

Hyla sp. indet.

Material: L.Q.: 1 right and 2 left ilia, MSUVP 1233; St.: 1 left ilium, UNSM 56951; M.P.: 3 right and 1 left ilia, UNSM 56922.

Remarks: These ilia have the characters of the genus *Hyla* given by Chantell (1964), and they are similar in size and dorsal prominence shape to several living species. But I cannot confidently assign them to species.

Class Reptilia Laurenti, 1768

Order Testudines Batsch, 1788

Family Trionychidae Bell, 1928

Genus *Trionyx* Geoffry St. Hilaire, 1809

Trionyx spiniferus Lesueur, 1827

(Figure 11)

Material: St.: 1 left hypoplastron, UNSM 56967.

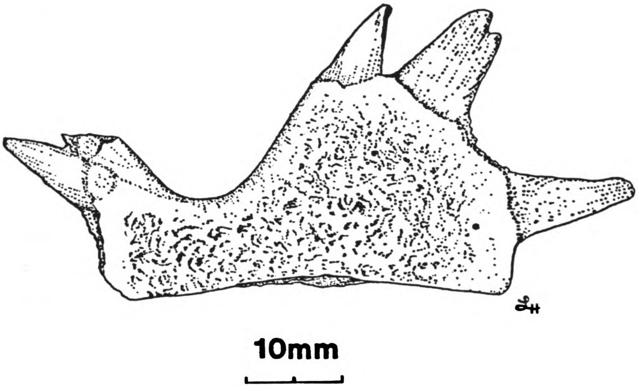

Figure 11. Left hypoplastron of <u>Trionyx</u> <u>spiniferus</u> (St., UNSM 56967) in ventral view.

Remarks: Sculpturing of this fossil plastral bone easily places it in the genus *Trionyx*. Holman (1982b) has shown how the hypoplastron bone of living *Trionyx spiniferus*, *T. ferox*, *T. muticus* and the extinct Barstovian species *T. quinni* Holman can be separated from one another. The diagnostic characters of the hypoplastron bone of *T. spiniferus* and the fossil are posterior margin moderately concave; posteromedial processes long and striated; notch between posteromedial processes encroaches sculptured area; and sculpturing moderately shallow (Holman, 1982b). *Trionyx spiniferus* is a highly aquatic riverine turtle, but it also inhabits lakes and smaller ponds (Conant, 1958). This species occurs along major river drainages in all but the central and western part of Nebraska (Lynch, 1985).

Trionyx sp. indet.

Material. St.: 15 coastal fragments, 8 shell fragments, UNSM 56966; D.N.: 4 shell fragments, MSUVP 1304; 2 neurals, 19 costal fragments, 1 left xipiplastron, 12 shell fragments, UNSM 56912; M.P.: 1 costal, UNSM 56925.

Remarks: The sculpturing of these fossil carapace and plastral elements are typical of the genus *Trionyx*, but they are too fragmentary and undiagnostic to assign to species.

Family Emydidae

Genus _Emydoidea_ Fitzinger, 1826

Emydoidea blandingii (Holbrook), 1838

(Figure 12)

Material: D.N.: 1 right hypoplastron, 1 left xiphiplastron, UNSM 56911.

Remarks: The fossil hyoplastron has the following diagnostic characters of _Emydoidea blandingii_: abdominal-pectoral sulcus joins hyo-hypoplastral suture at midline; humeral-pectoral sulcus placed far anteriorly; angular epi-hyoplastral suture; bridge buttress limited in its anterior extent; and posterior edge of bone lateral to bridge buttress bevelled for hypoplastral hinge attachment.

The fossil xiphiplastron is similar to Recent _Emydoidea blandingii_ in having a relatively short, broad femoral lip; longer, narrower anal lip; and deeply excavated external abdominal oblique muscle scar on its dorsal surface. Only _Clemmys_ has a similarly shaped and structured xiphiplastron, but it is wider relative to its length than in _Emydoidea_ (Preston and McCoy, 1971).

Both fossil elements represent individuals as large, or slightly larger than the maximum size (CL 225) recorded for Recent _Emydoidea blandingii_ (Conant, 1958).

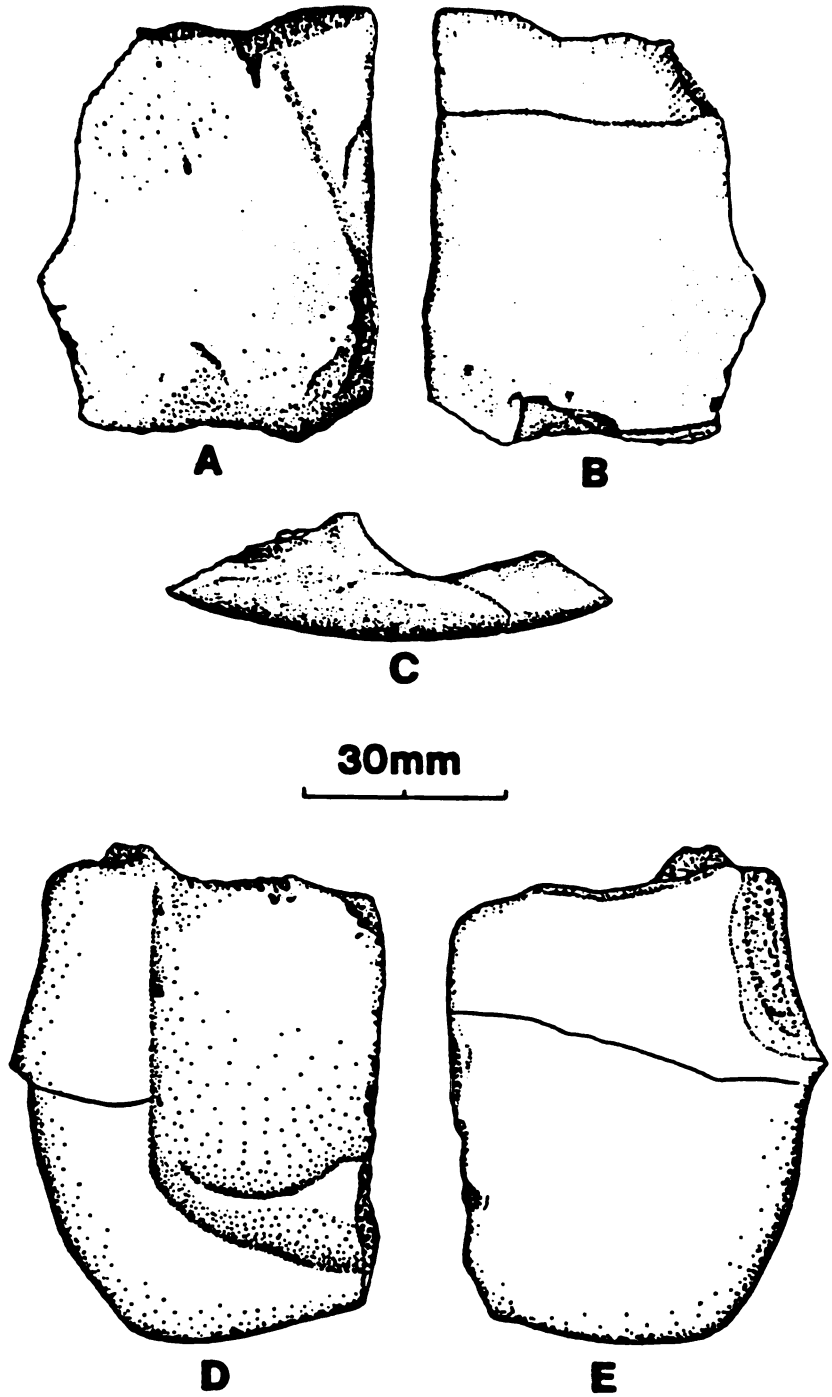

Figure 12. Emydoidea blandingii (D.N. UNSM 56911) right hypoplastron in dorsal (A), ventral (B), and lateral (C) views; left xiphiplastron in dorsal (D) and ventral (E) views.

Emydoidea blandingii mainly occurs in the Great Lakes region at present, but disjunct populations occur along the northern Atlantic Coastal plain as far north as Nova Scotia (Van Devender and King, 1975). The Devils nest record falls within the SW limits of this species present distribution.

Genus *Chrysemys* Gray, 1844

Chrysemys picta (Schneider, 1783)

(Figure 13)

Material: St.: 2 nuchals, 1 epiplastron, 1 right hyoplastron, 1 left xiphiplastron, UNSM 56968; D.N.: 7 peripherals, MSUVP 837, 839, 840, 841, 843, 844, 846; 1 right hyoplastron, MSUVP 852; 1 right xiphiplastron, 9 nuchals, 5 peripherals, 1 hyoplastron, 2 right and 2 left hypoplastra, UNSM 56910; M.P.: 1 epiplastron, UNSM 56927.

Remarks: I choose to recognize the genera *Pseudemys*, *Trachemys*, and *Chrysemys* (Banks et al., 1987) rather than to synonymize *Pseudemys* with *Chrysemys* as suggested by McDowell (1964).

Nuchals of *Chrysemys picta* differ from those of species of *Pseudemys* and *Trachemys* in the following ways: longer underlap of nuchal scute than in *P. concinna* and *P. floridana*; longer nuchal scute than in species of *Pseudemys* and *Trachemys*; smoother bone surface than in *Trachemys scripta* complex; and anterior marginal areas

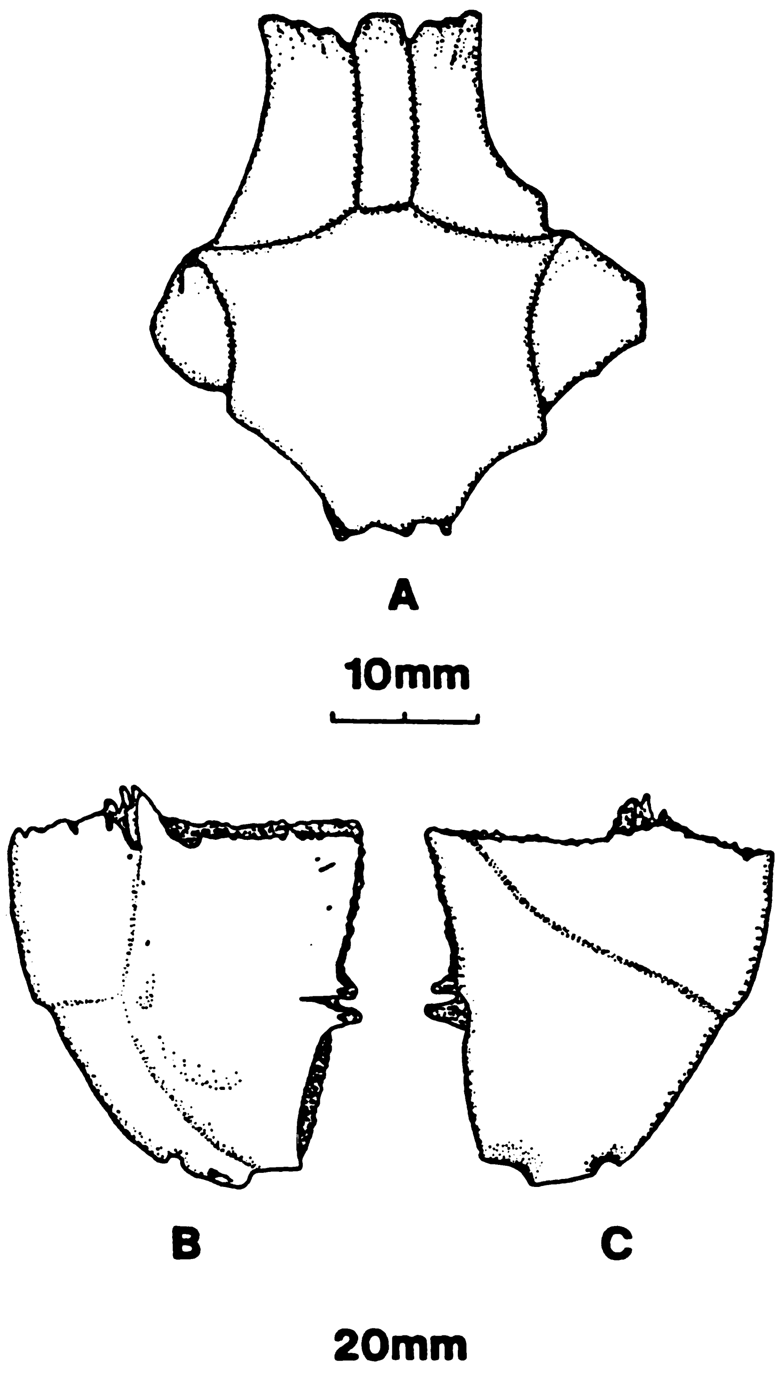

Figure 13. Chrysemys picta nuchal (St., UNSM 56968) in dorsal view (A); and left xiphiplastron (D.N., MSUVP 830) in dorsal (B) and ventral (C) views.

serrated rather than smooth as in most <u>Pseudemys</u> and <u>Trachemys</u> species.

Peripherals of <u>Chrysemys</u> differ from those of <u>Pseudemys</u> and <u>Trachemys</u> in being smooth rather than notched.

The fossil epiplastra resemble <u>Chrysemys</u> <u>picta</u> in having moderately developed epiplastra lips (Preston, 1979).

The fossil xiphiplastra are similar to <u>Chrysemys</u> <u>picta</u> and differ from those of <u>Pseudemys</u> and <u>Trachemys</u> in being wide rather than constricted at the femoranal sulcus (Preston, 1979). One of the fossils (UNSM 56910) represents a large individual with a carapace length of about 225, but this is within the 251 record carapace length given for this species by Conant (1958).

<u>Chrysemys</u> <u>picta</u> is known from the Barstovian (Holman and Sullivan, 1981) to the Recent, but this is the first record of the species from the Hemphillian. It occurs today statewide in Nebraska (Lynch, 1985) where it prefers shallow, vegetated bodies of water (Conant, 1958).

Genus <u>Terrapene</u> Merrem, 1820

<u>Terrapene</u> sp. indet.

<u>Material</u>: D.N.: 2 nuchals and 1 costal, UNSM 56913.

Remarks: These nuchal bones are similar to those of modern Terrapene in having short, wide nuchal and marginal scutes. This genus is known from as early as the Barstovian (Holman, 1987), but this is the first record from the Hemphillian. A single form, Terrapene ornata occurs throughout most all of Nebraska today (Lynch, 1985) and is a very common turtle of plains and prairies.

Family Chelydridae Swainson, 1839

Genus Macroclemys Gray, 1855

Macroclemys temminckii (Troost in Harlan, 1835)

Material: D.N.: 4 posterior peripherals, UNSM 56914.

Remarks: The posterior peripherals of Macroclemys temminckii are deeply notched at and between the interperipheral sutures rather than weakly notched at the interperipheral sutures as in Chelydra serpentina (Preston, 1979). The fossils are from a turtle(s) much smaller than the maximum size of 66 cm obtained by Recent M. temminckii (Conant, 1958).

Macroclemys temminckii does not presently occur in Nebraska (Lynch, 1985). The species may have been a common late Hemphillian turtle of the Great Plains as I have seen several unreported late Hemphillian specimens from Kansas in the University of Michigan paleontological collections.

cf. Emydidae

Material: L.Q.: 1 neural, UNSM 96412.

Remarks: This element is from a very small emydid turtle, but it cannot be further identified. It was the only turtle bone found at Lemoyne Quarry.

Family Kinosternidae (Agassiz, 1857)

Genus *Kinosternon* Spix, 1824

Kinosternon flavescens (Agassiz, 1857)

Material: St.: 1 nuchal, 1 xiphiplastron, UNSM 56969.

Remarks: The nuchal of *Kinosternon flavescens* differs from those of *K. subrubrum*, *K. bauri*, *Sternotherus odoratus* and *Sternotherus minor* in having the vertebral scute wider than long rather than longer than wide. The nuchal bone of *K. flavescens* differs from *K. hirtipes* in being only slightly arched rather than strongly arched as in *K. hirtipes*.

The xiphiplastron resembles *Kinosternon* in being thin and flat with nearly equal anal-femoral scute areas and narrow marginal lips. It is similar to the Recent species *Kinosternon flavescens* in overall size, shape, and thickness, and differs from *K. leucostoum*, *K. hirtipes*, and *K. subrubrum* in having a wider posterior anal scute, and from *K. cruentatum* in having a wider inner anal scute.

This is the first report of *Kinosternon flavescens* from the Hemphillian and the oldest record of the species as a fossil. This species occurs throughout the Republican River drainage and in scattered non-alkaline ponds in the Sand Hills in Nebraska (Lynch, 1985).

Family Testudinidae Gray, 1825

Genus *Geochelone* Fitzinger, 1833

Geochelone sp. indet.

(Figure 14A-B)

Material: St.: 1 nuchal, 1 neural, 9 costal fragments, 6 peripherals, 3 epiplastra, 1 left xiphiplastron, 4 plastral fragments, UNSM 56964 and 56965; D.N.: 4 costal fragments, 8 peripherals, 1 pygal, 1 right and 1 left epiplastron, 3 entoplastra, 1 right hyoplastron, 14 shell fragments, 1 toe bone, 1 osteoderm, UNSM 56908, 56909.

Remarks: Two Neanartic subgenera *Hesperotestudo* and *Caudochelys* are currently recognized. The subgenera are separated (in part) on the basis of different caudal vertebrae and on the presence or absence of ossifications known as supracaudal bucklers (Auffenberg, 1963b). There are no supracaudal bucklers or caudal vertebrae among the late Hemphillian *Geochelone* elements. Nevertheless,

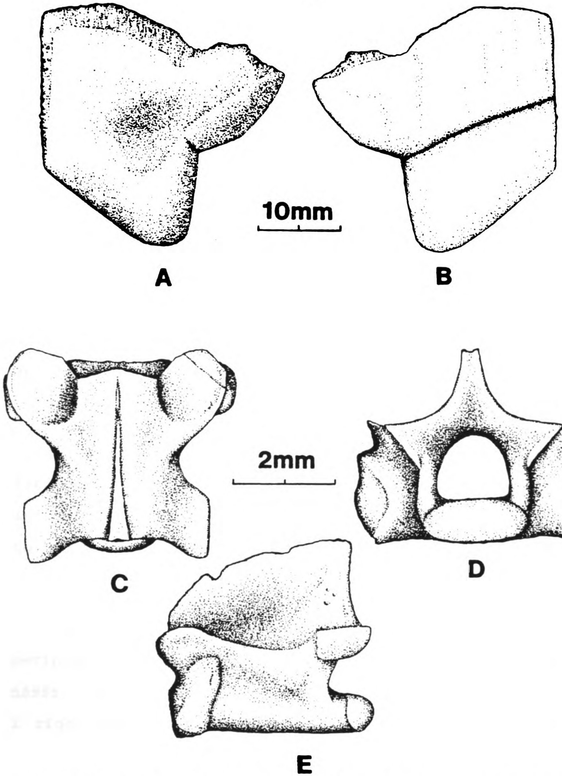

Figure 14. Left xiphiplastron of Geoclelone sp. indet. (St., UNSM 56964) in dorsal (A) and ventral (B) views; trunk vertebra of Ophisaurus cf. O. attenuatus (L.Q., UNSM 96414) in dorsal (C), posterior (D) and lateral (E) views.

members of the subgenus *Hesperotestudo* tend to be small with rugose shells, while those of the subgenus *Caudochelys* tend to be larger with smoother shells. On the basis of these criteria, both subgenera are present.

Geochelone fossils are present only in the late Hemphillian Santee and Devil's Nest local faunas. The fossils are fragmentary and some are badly water worn making specific identification impossible. Nevertheless, at least three species appear to be present; a large-smooth shelled species, a smaller more rugose shelled species, and a very small species.

Geochelone (*Caudochelys*) sp. indet.

D.N.: 1 costal fragment, 1 entoplastron, 2 plastral fragments, 1 osteoderm, UNSM 56908. These fossils indicate a large form of smooth-shelled tortoise similar to *Geochelone* (*Caudochelys*) *rexroadensis* (Oelrich).

Geochelone (*Hesperotestudo*) sp. indet.

Type A: St.: 1 nuchal, 7 costal fragments, 6 peripherals, 3 epiplastra, 2 plastral fragments, UNSM 56965, D.N.: 1 nuchal, 3 costal fragments, 8 peripherals, 1 right and 1 left epiplastron, 2 entoplastra, 1 right hyoplastron, 12 shell fragments, 1 toe bone, UNSM 56909.

These fossils represent a moderately large species of Geochelone with a carapace sculptured with grooves and ridges (growth rings) giving the bone a rugose appearance, as in Hesperotestudo tortoises, possibly of the larger alleni line.

Type B: St.: 1 neural, 2 costal fragments, 1 left xiphiplastron, 2 plastral fragments, UNSM 56964. These elements represent a very small species of tortoise. The xiphiplastron is the best preserved and the most interesting of the fossils. Based on xiphiplastra of Recent Geochelone, the fossil represents a tortoise with a plastron length of about 160 mm, but at least 14 growth rings are evident on its ventral surface suggesting it represents an adult individual.

It is likely that the fossils represents a new small species of Geochelone, but a formal specific description must wait until more complete material is available. Although the subgenus of this material is not certain, the rugosity and size of the bones and deeply notched xiphiplastron suggests a species of the western Geochelone turgida line (Holman, 1972). According to Holman (1972), the western turgida line of the Great Plains region were small, rugose, thick-shelled tortoises with huge epiplastral beaks whose members increased in size and carapace rugosity through time. The lineage began with G. turgida (Cope) of the latest Hemphillian of

Texas, continued with G. riggsi (Hibbard) of the early Blancan of Kansas and terminated with G. oelrichi Holman of the late Blancan of Nebraska. The Santee form fits so neatly into this evolutionary continuum on the basis of its small size, shell thickness (Table 3), degree of rugosity, and early appearance in the geologic record that I suggest it may represent the ancestral morphotype of the turgida line (Figure 15).

Order Squamata Oppel, 1811

Family Anguidae Gray, 1825

Genus Ophisaurus Daudin, 1803

Ophisaurus cf. O. attenuatus (Cope, 1880)

(Figure 14C-E)

Material: L. Q.: 1 trunk vertebra, UNSM 96414.

Remarks: Trunk vertebrae (body vertebrae of some authors) of the anguid genus Ophisaurus are distinct and differ from other similar-sized North American lizards in having the posterior portion of the neural spine thick and triangular in cross-section and extending anteriorly as a think sheet of bone, and in having the ventral surface of the centrum flat and wide with no indication of a hemal keel (Etheridge, 1961). The fossil vertebra is similar in size and structural details to those of Recent O. attenuatus, but I cannot be certain it is this species.

Table 3. Measurements of the Santee Type B *Geochelone* and members of the western *G. turgida* line*

	Santee Type B	*G. turgida*	*G. riggsi*	*G. oelrichi*
Plastron length	160	216	190	235
Xiphiplastron length	30	59	48	75
Xiphiplastron width	31	51	48	64
Xiphiplastron external height	13	--	20	23
Xiphiplastron midline thickness	7.5	--	9	13
Xiphiplastron notch length	15	19	18	24
Xiphiplastron notch width	23	55	41	57
Length of interfemoral sulcus				
Length of internal sulcus	1.49	1.60	1.90	2.80

*Measurements of *G. turgida* group from Holman, 1972:148, Table 3.

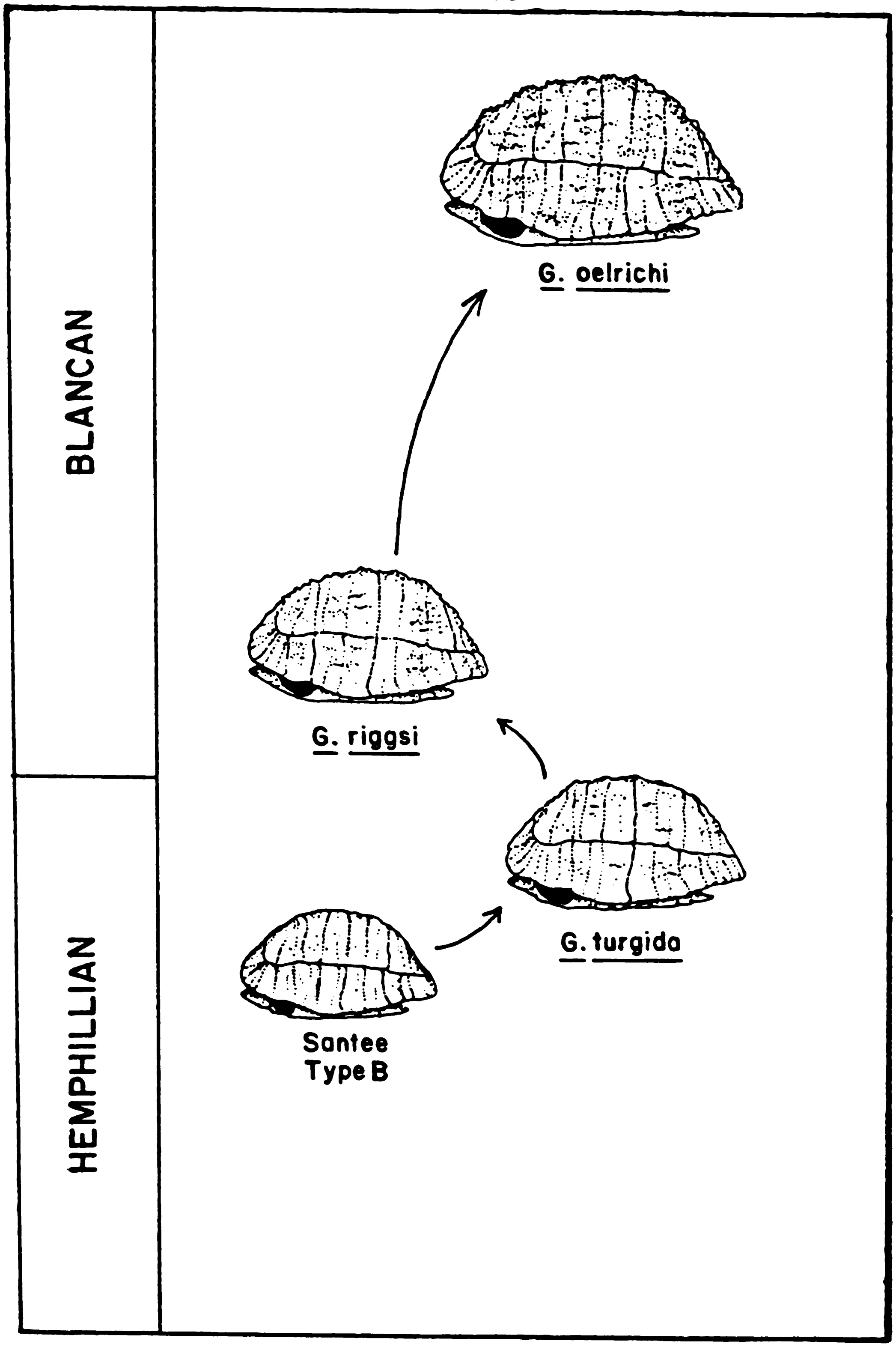

Figure 15. Hypothetical phylogenetic relationships of western Geochelone turgida line.

Ophisaurus attenuatus has previously been reported from the Clarendonian WaKeeney local fauna of Kansas (Holman, 1975), but this is the first report of the genus and species from the Hemphillian. Today, it is a common grassland species over much of the southern Great Plains, but because of habitat destruction, it may be extinct in Nebraska (Lynch, 1985).

Family Iguanidae Gray, 1827

Genus *Crotaphytus* Holbrook, 1843

Crotaphytus cf. *C. collaris* (Say in James, 1823)

Material: St.: 1 partial right dentary, UNSM 56961.

Remarks: This fragmentary dentary is similar in size and tooth morphology to Recent *Crotaphytus collaris* and is thus tentatively assigned to this species. The fossil has six teeth and three open alveoli. In lingual view, the Meckelian groove is widely open proximally and narrowly open distally. The four most anterior teeth are high crowned, slightly bilobed and recurved. The remaining two teeth are more robust, straight, and at least one appears to be weakly trilobed as in living *C. collaris*.

Previously, *Crotaphytus collaris* was known as early as the Blancan of Arizona (Czaplewski, 1987), thus this late Hemphillian record extends the temporal range of the species approximately 2-1.5 Ma. Crotaphytus collaris is presently known in Nebraska by only two records from the southern part of the state, which represent the most northerly records of the species in the Great Plains (Lynch, 1985).

Family Scincidae Gray, 1825

Genus Eumeces Wiegmann, 1834

Eumeces cf. E. obsoletus (Baird and Girard, 1852)

Material: M.P.: 1 right maxilla, UNSM 56924

Remarks: This fossil maxilla has 6 complete teeth, 4 broken teeth, and 6 empty alveoli for a total of 16 teeth. It is placed in the genus Eumeces because the teeth are simple and peg-like with striated crowns (Estes, 1983). The fossil is similar in size to the Barstovian species Eumeces miobsoletus Holman, but differs in having stronger tooth crown striations and a single row of labial or nutrient foramina. Eumeces miobsoletus has a double row of labial foramina (Holman, 1977a). The fossil is provisionally referred to the Recent species E. obsoletus based on its large size and similarity to this species. With the exception of two teeth, the maxillary bone and teeth are uniformly dark, obscuring any evidence of tooth pigmentation. Two lighter teeth appear to have their distal ends strongly pigmented as in Recent _E_. _obsoletus_. _Eumeces obsoletus_ is known from the Blancan to the Recent (Estes, 1983). It is a common lizard of the Great Plains today where it prefers soft soils for burrowing (Conant, 1958). Nebraska records are from the southern border of the state along the Republican River drainage (Lynch, 1985).

Eumeces sp. indet.

Material: L.Q.: 3 right and 2 left dentaries, UNSM 96413; St.: 1 left dentary fragment, UNSM 56962; M.P.: 1 right dentary, UNSM 56923.

Remarks: These fragmentary remains resemble the genus _Eumeces_ in having open meckelian grooves, wide subdental gutters, and simple unicuspid teeth with striated tips. I cannot identify these fossils below the generic level.

Family Boidae Gray, 1825

Subfamily Erycinae Bonaparte, 1831

Status of Hemphillian and Blancan _Ogmophis_, Cope

One mainly Miocene genus, _Ogmophis_, is of special interest regarding the determination of when boid snakes became extinct across midcontinental North America. Thus a brief discussion of important late Miocene and Pliocene records of the genus follows.

The youngest records of <u>Ogmophis</u> in North America are from the Clarendonian of Kansas, mid-Hemphillian of Texas, and Blancan of Texas (Holman, 1975; Parmley, 1984; Rogers, 1976). I reexamined the Coffee Ranch fossils (two vertebrae), and compared them with <u>Ogmophis</u> fossils in the Michigan State University Museum. They are not from a boid, but from a stout-bodied colubrid related to <u>Elaphe</u>. I also examined the Beck Ranch fossils (two vertebrae), and believe they are not from a boid, but rather a small xenodontinine-like colubrid. Thus <u>Ogmophis</u> did not survive into the Hemphillian, but became extinct in the Clarendonian.

Genus <u>Charina</u> Gray, 1825

<u>Charina</u> <u>prebottae</u> Brattstrom, 1958

(Figures 16-18)

<u>Material</u>: L.Q.: 3 trunk vertebrae, MSUVP 1222; 3 trunk vertebrae, UNSM 96416; 1 caudal vertebra, MSUVP 1225; 6 cervical vertebrae, UNSM 96415.

<u>Remarks</u>: Well-preserved <u>Charina</u> vertebrae from the three major regions of the vertebral column (cervical, trunk, and caudal) were taken from Lemoyne Quarry. The trunk vertebrae are separated from those of the similar genus <u>Ogmophis</u> on the basis of their less distinct hemal keels (Holman, 1970) and shorter neural spine (Holman, 1976a). <u>Charina</u> differs from the extinct <u>Calamagras</u> and

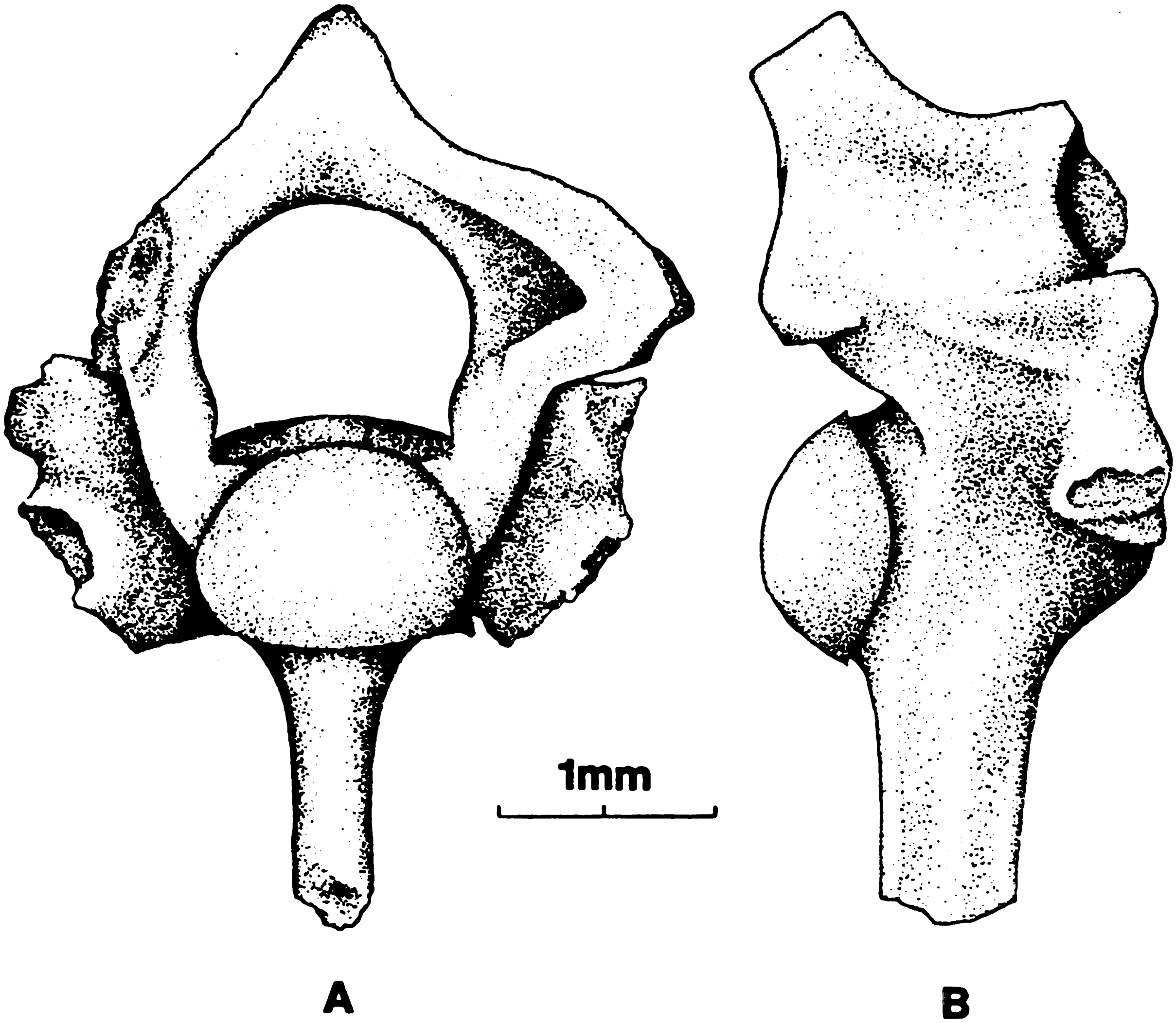

Figure 16. Cervical ventebra of Charina prebottae (L.Q., UNSM 96415) in posterior (A) and lateral (B) views.

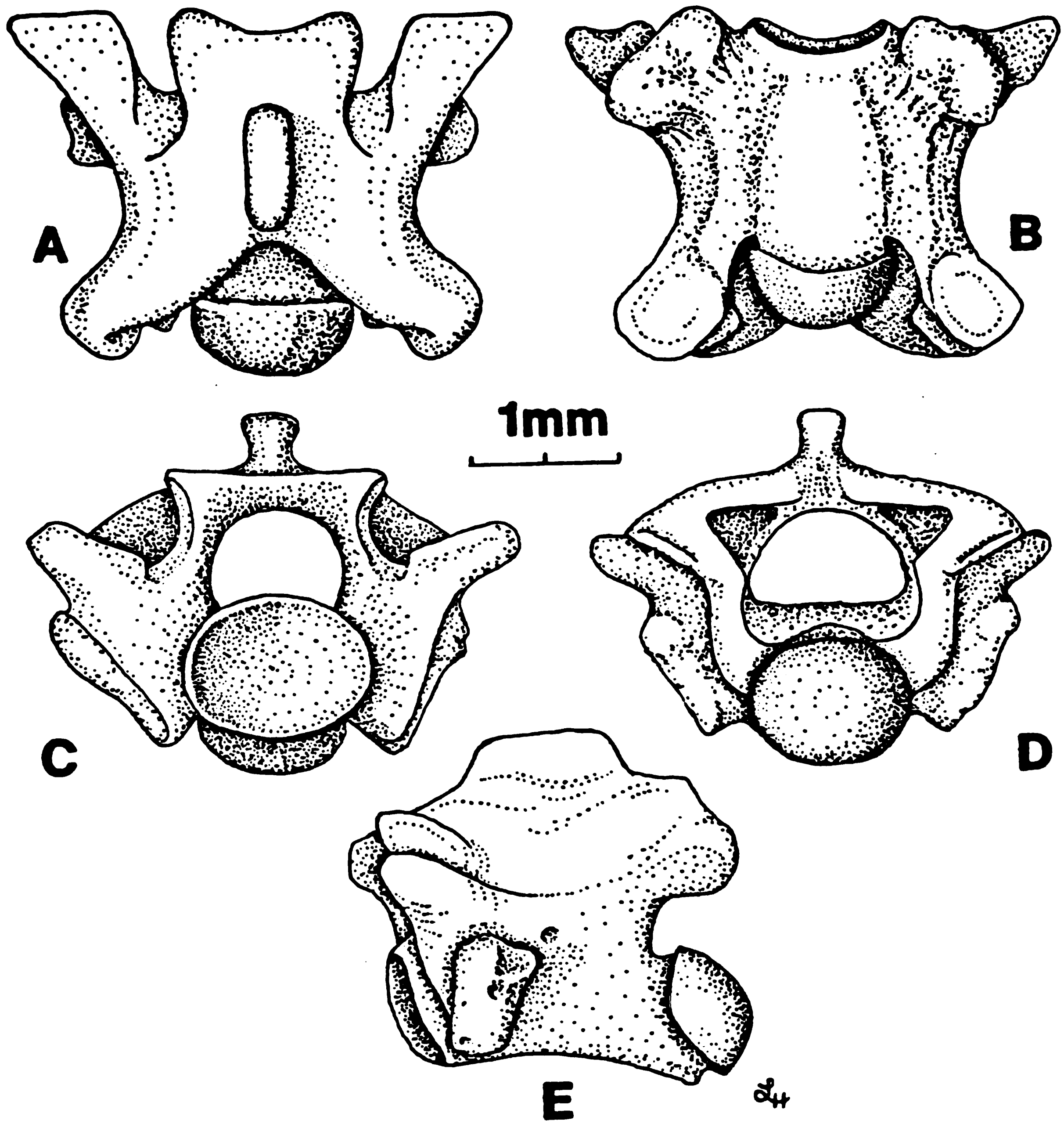

Figure 17. Trunk vertebra of Charina prebottae (L.Q., UNSM 96416) in dorsal (A), ventral (B), anterior (C), posterior (D), and lateral (E) views.

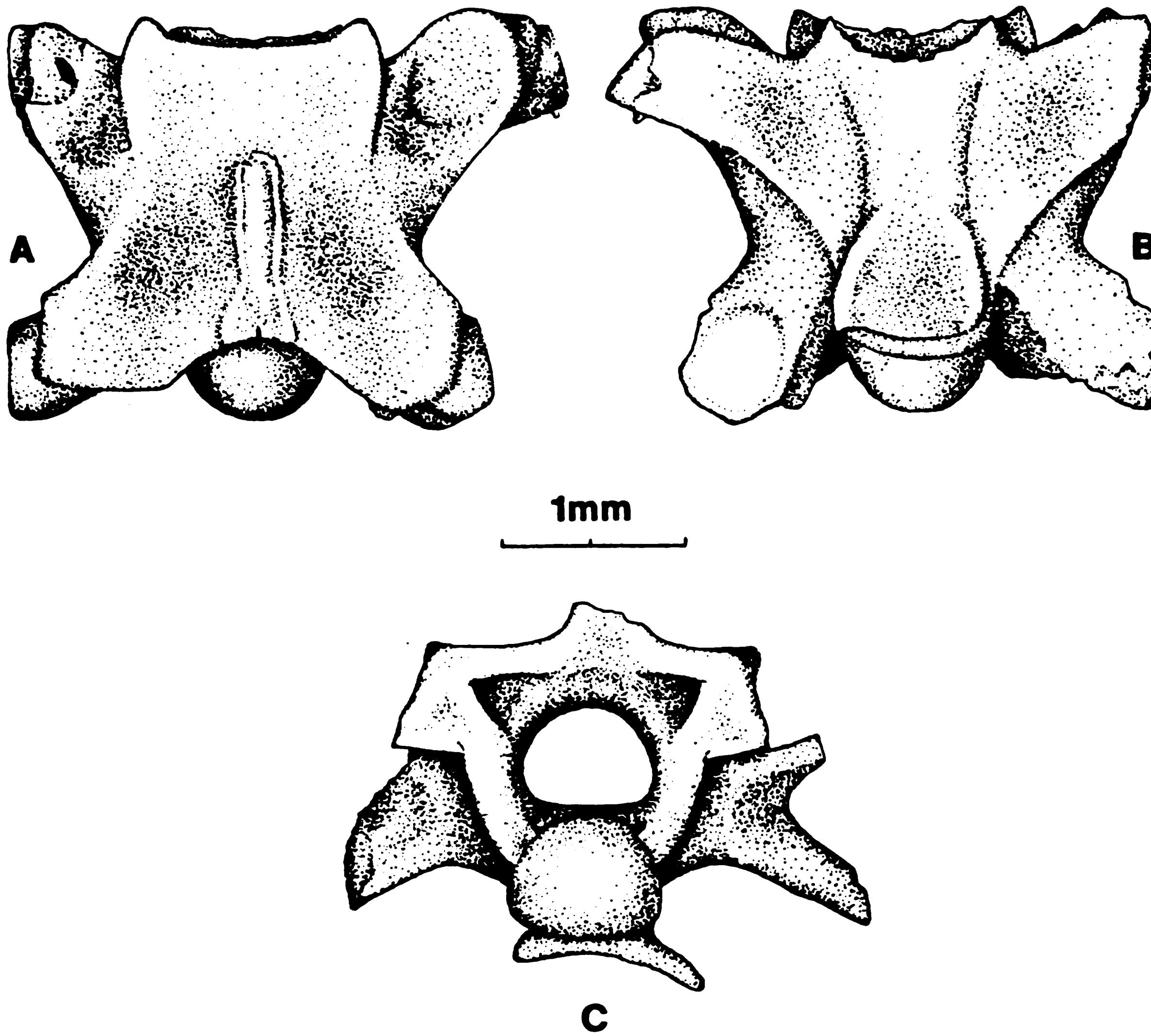

Figure 18. Caudal vertebra of Charina prebottae (L.Q., MSUVP 1225) in dorsal (A), ventral (B), and posterior (C) views.

the living Lichanura in having longer, usually lower and thinner neural spines (Holman, 1976c). Furthermore, trunk vertebrae of Charina are narrower and longer than those of Lichanura as expressed by differing centrum length to neural arch width ratios (cl/naw; see Figure 20 under Lichanura account). The above cervical and caudal vertebrae are inseparable from those of Charina although comparative studies have not been done on these elements. Fossil cervical and caudal vertebrae are heretofore unreported for the genus.

Two species of Charina are presently recognized, the extinct species Charina prebottae Brattstrom known from the Hemingfordian of Wyoming (Holman, 1976d) to the early Hemphillian of Texas (Parmley, 1988a), and the living species C. bottae of the northwestern United States and Canada. The trunk vertebrae of C. prebottae are strikingly similar to those of Recent C. bottae in shape and structure (Holman, 1979), but according to Holman (1973c) the hemal keel of C. prebottae is better developed than in C. bottae. Four of the six Lemoyne Quarry Charina trunk vertebrae have better developed hemal keels than in four Recent C. bottae skeletons. A description and figures of each vertebral type follows, and measurements are given in Table 4.

Table 4. Measurements of Lemoyne Quarry _Charina prebottae_ vertebrae

Vertebral type	Centrum length	Neural arch width
Anterior cervical	2.26	2.64
Cervicals	2.02 - 3.20 (mean 2.49)	2.28 - 3.03 (mean 2.60)
Trunk	2.64 - 2.84 (mean 2.71)	2.31 - 2.61 (mean 2.40)
Anterior caudal	2.14	2.13

Cervical vertebrae: These fossils (UNSM 96415) have hypapophyses typical of boid cervical vertebrae (Holman, 1979). One of the fossils (Figure 16) is believed to represent one of the first four or five cervical vertebrae as it differs from more posterior cervicals in having a thinner and more arched zygosphene and a more vaulted neural arch. The fossil is similar to anterior _Charina bottae_ cervicals in being wider than long; with a strongly arched zygosphene; short neural spine that is tubular in cross section; thick hypapophysis; deep, compressed cotyle with cotylar foramen on either side; and in lacking subcentral ridges. Five of the fossils are from a more posterior position along the cervical region, differing from anterior cervicals in having lower neural arches and thicker, flatter zygosphenes viewed anteriorly.

Trunk vertebrae; Six vertebrae (MSUVP 1222; UNSM 96416; Figure 17). These vertebrae are similar to those of living _Charina_ in being robust and about as wide as they are long, with thick, longer than high neural spines. Some of the fossils have a medial concavity extending along the posterodorsal two thirds of their neural spines, while others have this area flat. The prezygapophyseal articular facets are moderately large and ovaloid. The accessory processes are short and slightly oblique to the long axes of the centra. The hemal keels are wide, flat, and only slightly produced from the floors of the centra in two of the fossils, but better developed in the others. Four of the fossils have no subcentral ridges, but two have weakly developed subcentral ridges. The zygosphenes are thick and flat to slightly convex. The neural arches are moderately depressed. The postzygapophyseal articular facets are tilted upward. The paradiapophyses are not distinctly divided.

Anterior caudal: This vertebra (MSUVP 1225) differs from cervical and trunk vertebrae in being smaller and shorter with a thicker neural arch and zygosphene, and in having pleurapophyses and hemapophyses, indicating a post-cloacal position in the anterior part of the caudal region (Figure 18). The fossil is similar to anterior caudal vertebrae of living _Charina_ in having a wide, slightly convex zygosphene; ovaloid prezygapophyseal articular facets; short and rounded accessory processes; and a wide, flattened neural arch.

Lichanura sp. indet.

(Figure 19)

Material: L.Q.: 1 vertebra, UNSM 96417.

Remarks: This vertebra is assigned to the extant genus _Lichanura_ rather than to _Charina_ based (in part) on

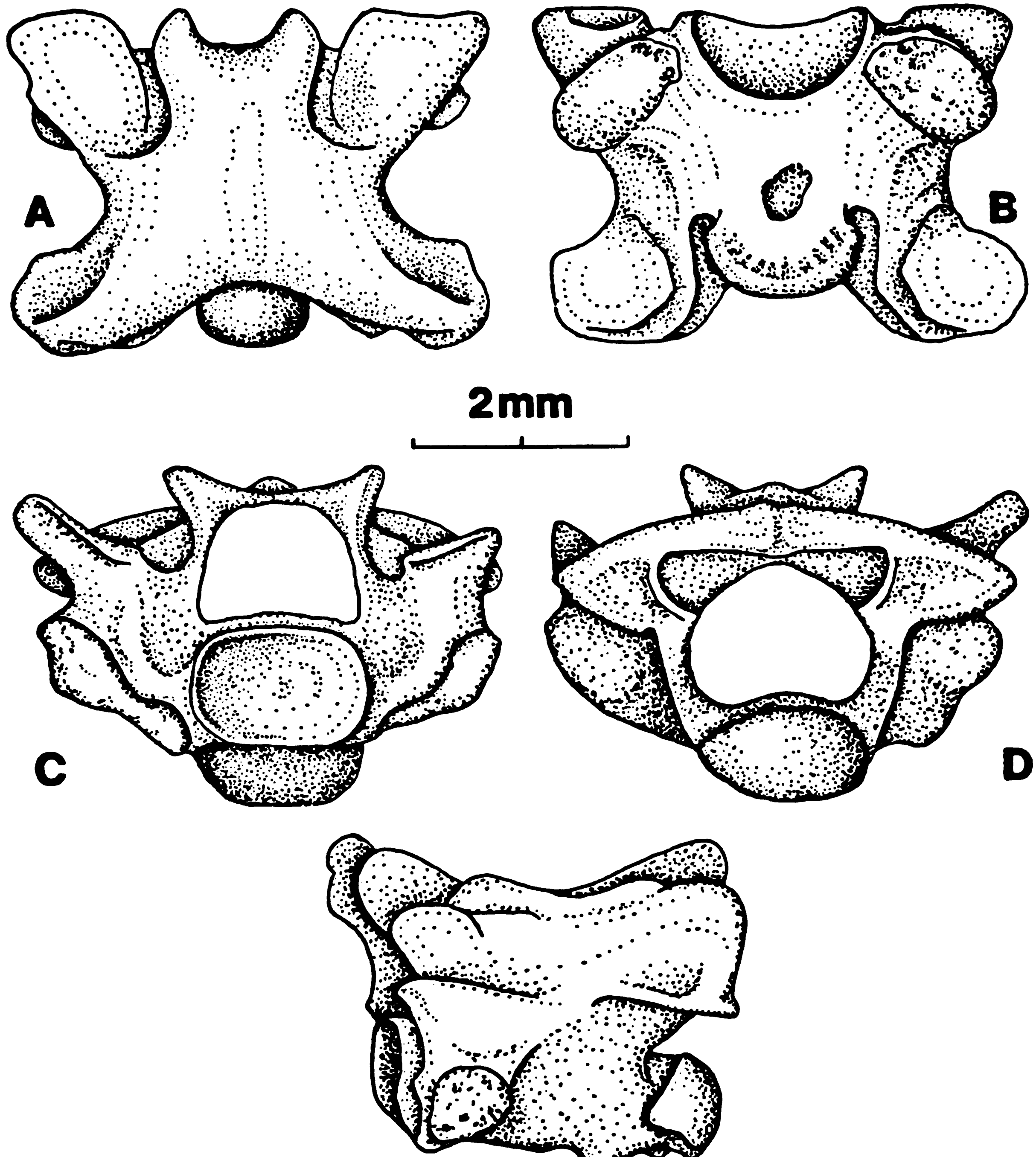

Figure 19. Vertebra of Lichanura sp. indet. (L.Q., UNSM 96417) in dorsal (A), ventral (B), anterior (C), posterior (D), and lateral (E) views.

its shorter, wider shape as expressed by the ratio of centrum length divided by neural arch width (cl/naw). In Charina the ratio ranges from 1.12 to 1.99, while in Lichanura they range from 0.86 to 0.98. The Lemoyne Quarry vertebra had a cl/naw ratio of 0.93 indicating a short, wide vertebral morphology distinctly closer to Lichanura than to Charina (Figure 20). Other important differences between Lichanura and Charina are as follows. The zygosphene of Lichanura viewed dorsally is often strongly U-shaped rather than straight or slightly U-shaped as in Charina. The zygosphene of Lichanura viewed anteriorly is strongly concave rather than flat or moderately concave as in Charina. The neural arch of Lichanura is wider and more depressed than in Charina. Lichanura has the posterior edge of the neural arch more deeply incised than in Charina.

The small size of the vertebra (CL=2.68) is particularly interesting. It is likely the fossil represents a small extinct species of Lichanura directly ancestral to the living species L. trivirgata, but additional and more complete fossils are needed before this can be established.

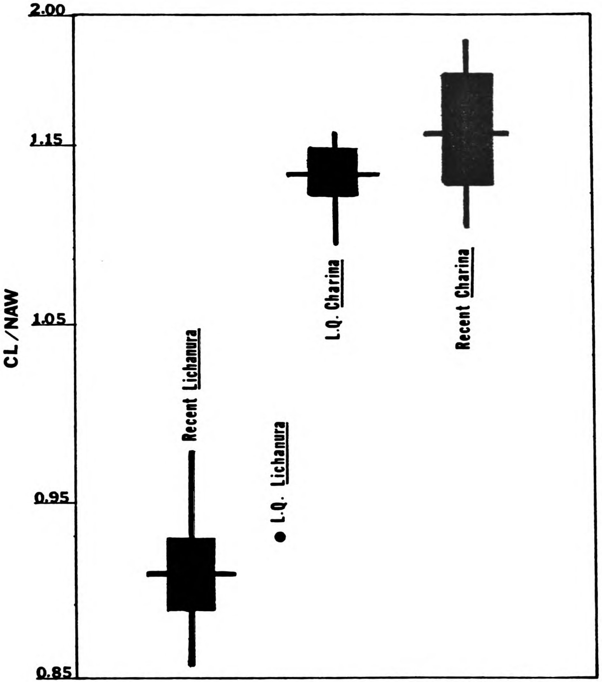

Figure 20. Centrum length divided by neural arch width ratios (cl/naw) of Recent and fossil Charina and Lichanura. Vertical line represents the range, horizonal line and mean, and black, bar 2 standard deviations from the mean.

Family Colubridae Oppel, 1811

Subfamily Colubrinae Cope, 1895

Genus *Arizona* Kennicott in Baird, 1859

Arizona sp. indet.

(Figure 21)

Material: L.Q.: 1 vertebra, MSUVP 1220; 2 vertebrae, UNSM 96432.

Remarks: The trunk vertebrae of *Arizona* are generalized and similar to those of some species of *Elaphe*, particularly *E. guttata*. Recent *Arizona* vertebrae differ from those of modern species of *Elaphe* examined in having longer, more delicate accessory processes, comparatively larger prezygapophyseal articular facets and thinner neural spines. Vertebral characters of *Arizona elegans*, the only living species of the genus, have been discussed by Hill (1971), Holman (1963), and Van Devender and Mead (1978). Characters used to assign the fossils to genus are neural spine high and thin; neural arch vaulted; accessory processes long and gracile; and condyle large. The Lemoyne Quarry vertebrae differ from Recent *A. elegans* in having longer, more robust accessory processes suggesting the fossils represent an extinct species of *Arizona*, but additional fossils are needed before this can be determined.

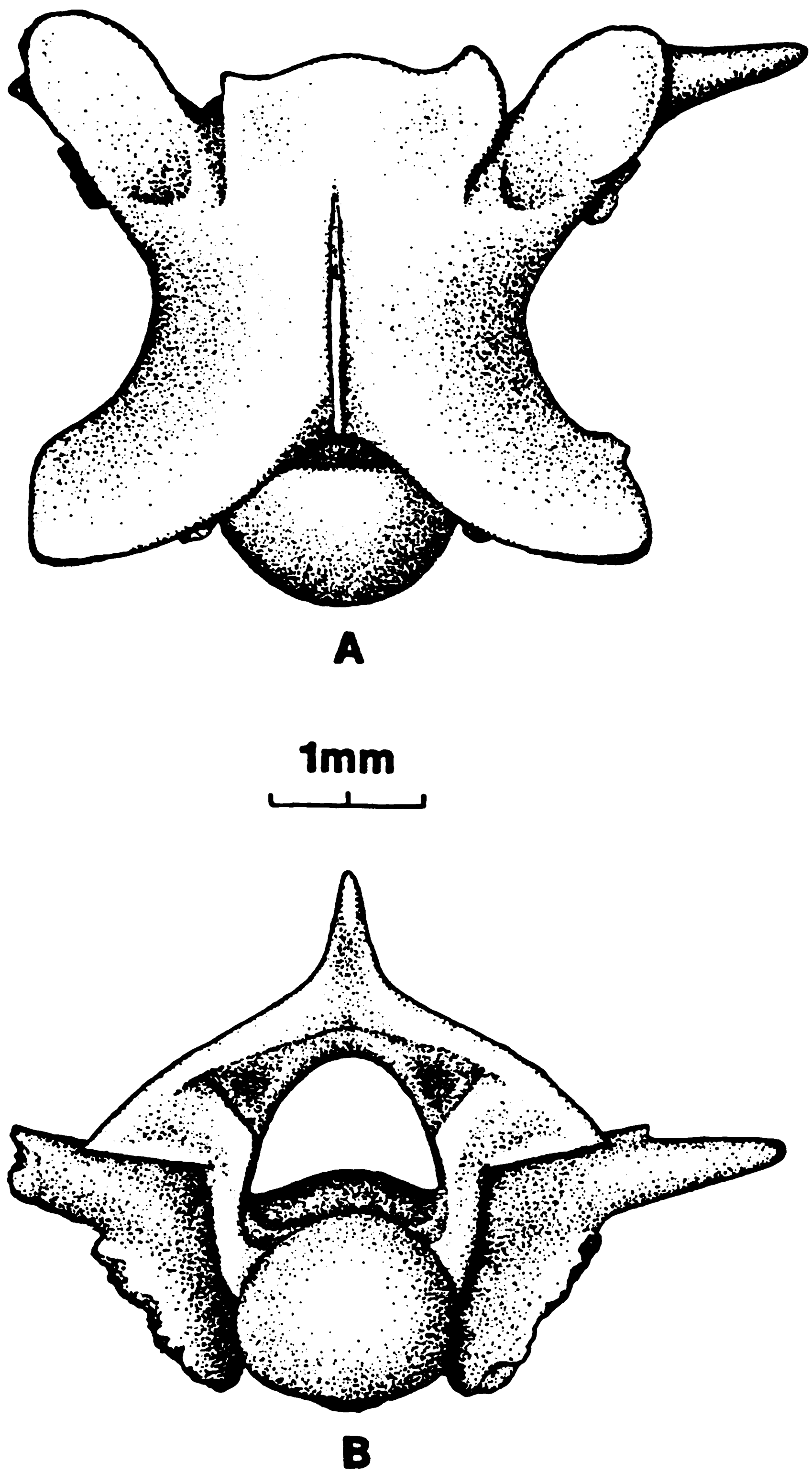

Figure 21. Vertebra of Arizona sp. indet. (L.Q., UNSM 96432) in dorsal (A) and ventral (B) views.

<u>Nebraskophis</u> <u>corneri</u>, n. sp.

(Figure 22)

<u>Holotype</u>: MSUVP 1229, a vertebra.

<u>Type Locality</u>: Lemoyne Quarry, Keith County, Nebraska.

<u>Age</u>: Mid-Hemphillian (late Miocene).

<u>Diagnosis</u>: Vertebra differs form the only other species of the genus, <u>Nebraskophis</u> <u>skinneri</u> Holman, in having a higher neural spine that does not slope into the posterior part of the neural arch, but has a vertical posterior border with a slight posterior overhang; in having a relatively large condyle; in having longer accessory processes; and in being wider through the centrum.

<u>Etymology</u>: Specific name in honor of George Corner of the Nebraska State Museum for his contributions to the vertebrate paleontology of Nebraska.

<u>Description of Holotype</u>: In dorsal view: vertebra longer than wide; prezygapophyseal facets ovaloid; most complete accessory process short, rounded on the end and positioned nearly perpendicular to long axis of centrum; anterior edge of zygosphene slightly convex; neural spine moderately thick with slight posterior overhang, dorsal surface rounded; no epizygapophyseal spines.

In ventral view: centrum long and tapers posteriorly; hemal keel well produced from floor of

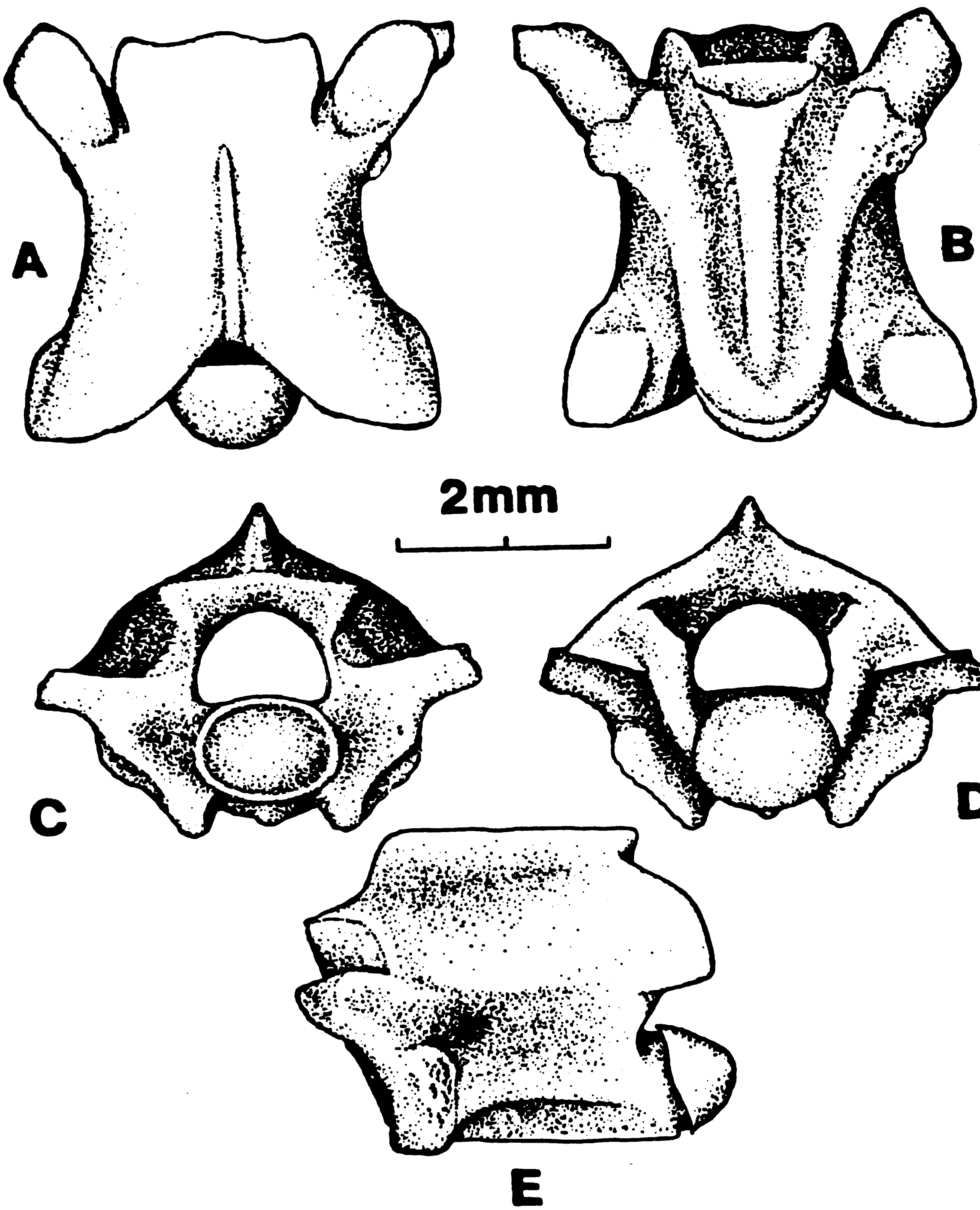

Figure 22. Vertebra of *Nebraskophis corneri*, n. sp. (L.Q., MSUVP 1229) in dorsal (A), ventral (B), anterior (C), posterior (D), and lateral (E) views.

centrum, uniform in width and rounded ventrally; moderately deep concavities between well developed subcentral ridges and hemal keel; postzygapophyseal facets large and ovaloid.

In lateral view: vertebra elongate; neural spine low, long and higher anteriorly than posteriorly; slight posterior overhang; subcentral ridge bowed dorsally; condyle tilted obliquely upward.

In anterior view: zygosphene moderately thick, arched dorsally; cotyle round and about the same size as neural canal; prezygapophyseal facets tilted upward; anterior end of neural spine rounded.

In posterior view; neural arch vaulted; condyle slightly smaller than neural canal; zygantral cavities deep; postzygapophyseal facets tilted upward.

<u>Measurements</u>: Measurements of the Holotype are: centrum length, 3.9; length through the zygapophyses, 4.1; neural arch width, 2.1; zygosphene width, 1.7; height from anterior end of neural spine to top of zygosphene, 0.7.

<u>Discussion</u>: In addition to the previous characters, <u>Nebraskophis</u> <u>corneri</u> differs from <u>N</u>. <u>skinneri</u> in having its neural arch slightly more vaulted; its accessory proceesses more oblique to the long axis of the centrum; and its subcentral ridges better developed.

Nebraskophis skinneri Holman, 1973

(Figure 23)

Material: L.Q.: 1 vertebra, MSUVP 1223; 1 vertebra, UNSM 96422.

Remarks: These fossil vertebrae do not differ from the type vertebrae of Nebraskophis skinneri from the Egelhoff local fauna of Nebraska (MSUVP 708 & 709). Both fossils are well preserved and have the following diagnostic characters: obsolete neural spines with posterior borders sloping gently into the neural arches; short, wide accessory processes; moderately narrow, strong hemal keels; weak subcentral ridges; vaulted neural arches. Measurements of the most complete vertebra are: centrum length, 2.9; neural arch width, 1.6; zygosphene width, 2.1.

Nebraskophis skinneri was previously known only from Barstovian age deposits in Nebraska, thus the Lemoyne Quarry record extends the species temporal range into the mid-Hemphillian. The genus appears to have no living relatives (Holman, 1973c).

Pauropohis, n. gen.

Type Species: Paurophis lewisi, n. sp.

Etymology: Generic name based on pauro, Greek, meaning little or small, in reference to the small size of the vertebra; and ophis, Greek, snake.

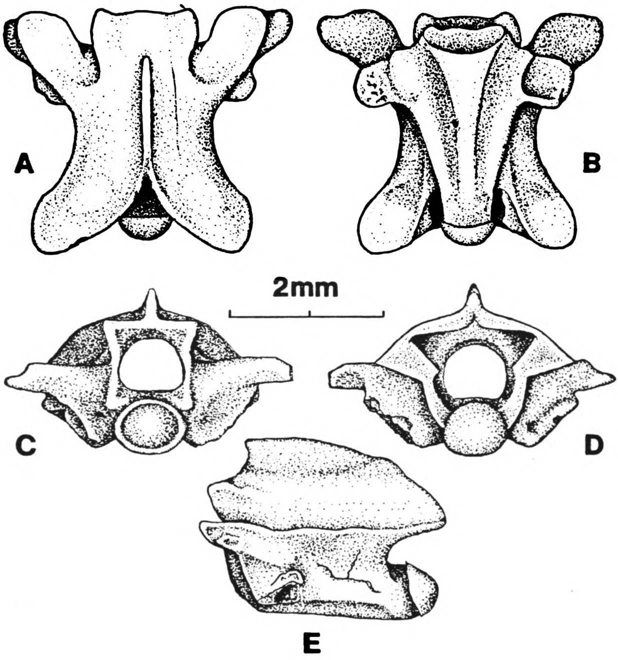

Figure 23. Vertebra of Nebraskophis skinneri (L.Q., UNSM 96422) in dorsal (A), ventral (B), anterior (C), posterior (D), and lateral (E) views.

Diagnosis: A small Colubrinae genus distinguished from all other small fossil and Recent colubrid genera by the following combination of characters: (1) vertebra wide through neural arch; (2) neural spine obsolete; (3) hemal keel thin throughout its length and rounded ventrally; (4) shallow grooves between subcentral ridges and hemal keel; (5) accessory processes very short.

Paurophis lewisi, n. sp.

(Figure 24)

Holotype: MSUVP 1221, a trunk vertebra collected by Julie Parmley in the summer of 1987.

Paratype: MSUVP 1224, a damaged trunk vertebra.

Type Locality: Lemoyne Quarry, Keith County, Nebraska.

Age: Mid-Hemphillian (late Miocene)

Diagnosis: Only known species.

Etymology: Specific name in recognition of Frank and Alice Lewis, 1987 camp hosts of Lake Ogallala State Park.

Description of Holotype: In dorsal view: vertebra wide through the neural arch; prezygapophyseal articular facets large and ovaloid; zygosphene wide with anterior edge moderately convex; neural spine thick without posterior overhang; epizygapophyseal spines lacking; posterior border of neural arch V-shaped; right accessory

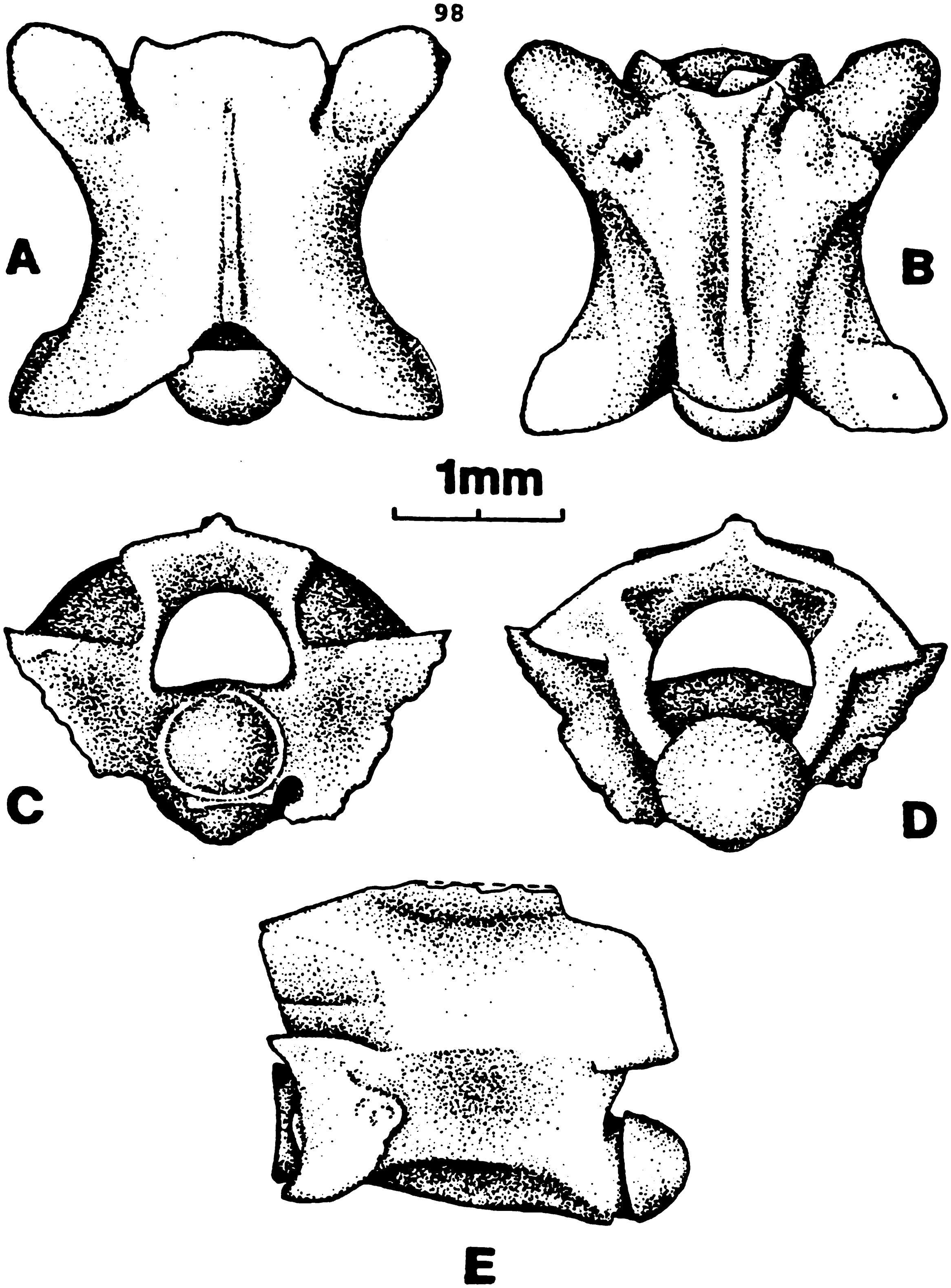

Figure 24. Vertebra of Paurophis lewisi, n. gen. et sp. (L.Q., MSUVP 1221) in dorsal (A), ventral (B), anterior (C), posterior (D), and lateral (E) views.

process missing, left process extending only slightly past prezygapophyseal articular facets.

In lateral view: vertebra elongate; neural spine obsolete, sloping gently from neural arch at anterior end, vertical step at posterior end; subcentral ridges strongly arched upwardly; hemal keel strong, extending nearly to posterior end of condyle; condyle small, tilted upward; paradiapophyses distinctly divided into diapophyseal and parapophyseal sections.

In ventral view: hemal keel uniformly narrow throughout its length, strong and rounded ventrally; subcentral ridges weakly developed with shallow concavities between them and hemal keel; postzygapophyseal facets ovaloid; parapophyseal extending slightly anteriorly; left accessory process short, not extending past prezygapophyses.

In anterior view: neural canal larger than round cotyle; anterior border of zygosphene thin, slightly convex; neural spine obsolete; distinct cotylar foramina present in shallow fossa; prezygapophyses tilted slightly upward.

In posterior view: neural arch moderately vaulted; neural canal larger than small round condyle; neural spine moderately thick.

Measurements: Measurements of the holotype are as follows: centrum length, 2.5; neural arch width, 1.5; length through zygapophyseal articular facets, 3.1; width through prezygapophyseal articular facets, 3.0; width through postzygapophyseal articular facets, 3.0.

Paratype: This vertebra is more fragmentary than the holotype, but has a low, obsolete neural spine and very short accessory process. Measurements of the paratype are as follows: centrum length, 2.7; neural arch width, 1.5; length through the prezygapophyseal articular facets, 2.9.

Discussion: _Paurophis_ may be distinguished from all other small extinct colubrid snakes mainly by its very low, obsolete neural spine and short accessory processes, but it also differs in other details listed in Table 5. The low neural spine of _P_. _lewisi_ compared with this condition in small living colubrid snakes suggest it may have been a secretive fossorial or semifossorial species (pers. obsv.).

Genus _Paracoluber_ Holman, 1976

Paracoluber cf. _P_. _storeri_ Holman, 1970

Material: L.Q.: 2 vertebrae, MSUVP 1237; 11 vertebrae, UNSM 96433.

Remarks: _Paracoluber_ _storeri_ has vertebrae similar to those of the extinct species _Miocoluber_ _dalquesti_

Table 5. Comparison of _Paurophis_ Vertebrae with Those of Other Small Extinct Genera

Taxon	Neural Spine Height	Hemal Keel	Subcentral Ridges	Neural Arch	Accessory Processes	Vertebral Shape
Paurophis	Very low	Strong & narrow	Weak	Vaulted	Very short	Elongate
Texasophis	Higher	Narrower to similar	Stronger to similar	Similar	Longer	Longer & narrower
Dakotaophis	Higher & thinner	Weaker	Similar	Similar	Longer	Similar
Nebraskophis	Higher	Wider	Similar	Similar	Longer & wider	Longer & narrower
Ameiseophis	Higher	Weaker	Similar	More vaulted	Longer	Longer & narrower
Miocoluber	Higher & Shorter	Similar	Similar	Similar	?	Narrower

from the early Hemphillian of Texas (Parmley, 1988a) and species of the living genera Coluber, Masticophis, and Salvadora, but can be distinguished from all four groups. It differs from Salvadora in having longer vertebrae with less distinct hemal keels, less vaulted neural arches, and thicker, lower neural spines. Paracoluber is easily separated from Miocoluber dalquesti based on its larger size and much lower, thicker neural spines. It differs from species of Coluber and Masticophis in having slightly thicker neural spines, less distinct hemal keels, and in lacking epizygapophyseal spines (Holman, 1970). Coluber and Masticophis species usually have very distinct, well-developed epizygapophyseal spines.

The Lemoyne Quarry fossils differ from Paracoluber storeri in individually variable characters (i.e., zygosphene shape, hemal keel development), thus a definite species assignment has not been made.

Coluber Linnaeus, 1758 or Masticophis Baird and Girard, 1853

(Figure 25)

Material: L.Q.: 5 vertebrae, MSUVP 1226 & 1227; 2 vertebrae, UNSM 96442; St.: 12 vertebrae, UNSM 56956;

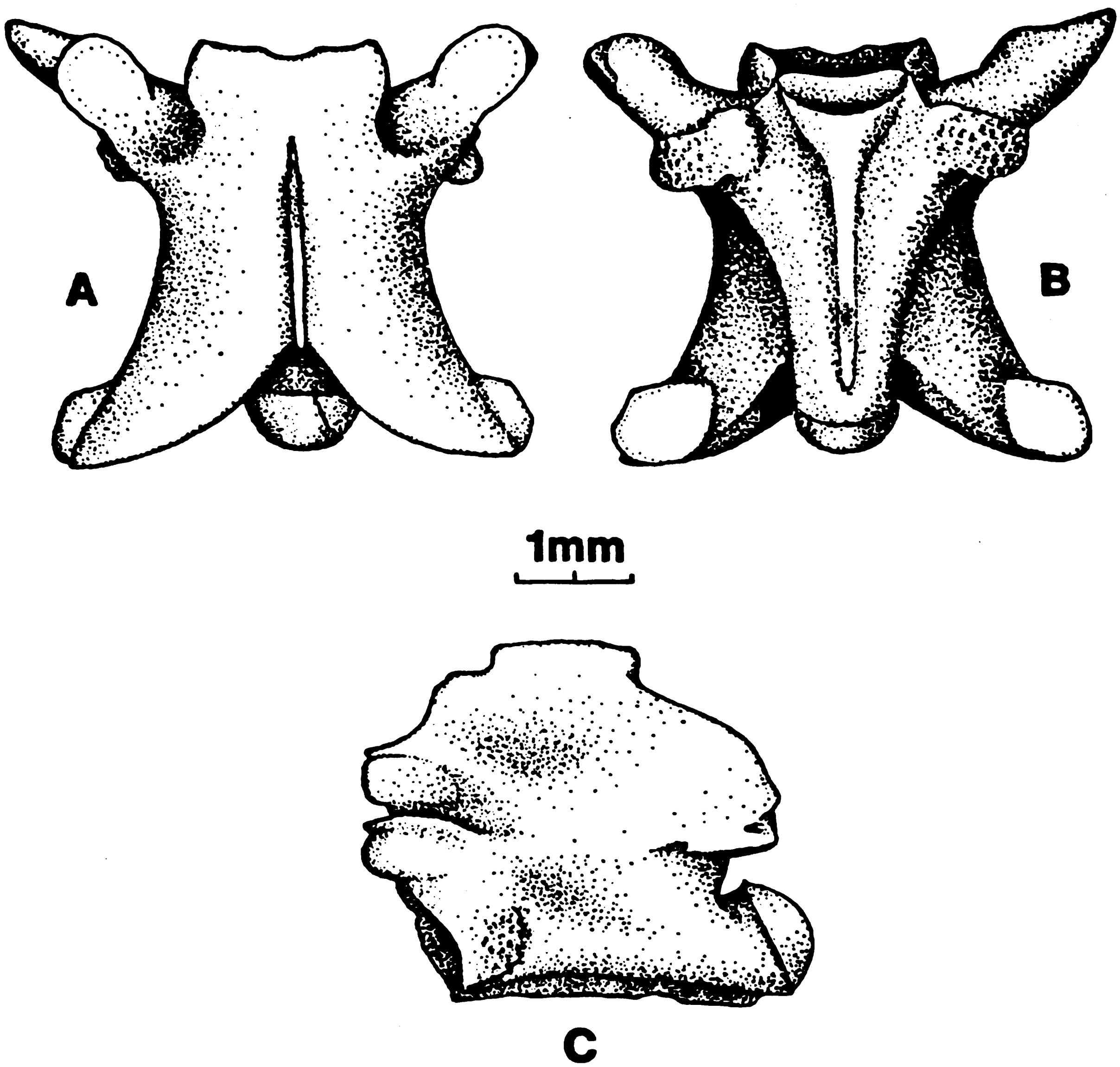

Figure 25. Vertebra of Coluber sp. indet. or Masticophis sp. indet. (L.Q., MSUVP 1226) in dorsal (A), ventral (B), and lateral (C) views.

D.N.: 8 vertebrae, MSUVP 1244; M.P.: 13 vertebrae, UNSM 56934.

Remarks: Coluber vertebrae are inseparable from those of the closely related genus Masticophis (Parmley, 1986a). Trunk vertebrae of the above taxa are similar to those of the extinct genera Paracoluber Holman and Miocoluber Parmley, but differ from both in being more slender with thinner neural spines, more distinct hemal keels, and in having well developed epizygapophyseal spines. Paracoluber and Miocoluber have their epizygapophyseal spines weak or absent. Diagnostic vertebral characters of Coluber-Masticophis are: vertebrae longer than wide with cl/naw values usually greater than 1.50 (cl/naw of the measurable fossils range from 1.67-1.85, mean 1.76); neural spines long and thin; hemal keels uniformly narrow, well defined throughout their length; epizygapophyseal spines well developed; and neural arches vaulted. Some of the fossils lack well defined epizygapophyseal spines.

Genus Lampropeltis Fitzinger, 1843

Lampropeltis triangulum (Lacepede, 1788)

Material: L.Q.: 2 vertebrae, UNSM 96435; D.N.: 2 vertebrae, UNSM 56906; M.P.: 5 vertebrae, UNSM 56931.

Remarks: Trunk vertebrae of Lampropeltis triangulum are distinct and Auffenberg (1963a) and Holman (1963) have discussed vertebral characters of the species. Distinguishing characters are: vertebrae small; neural spines low and short; neural arches depressed; and subcentral ridges weakly developed. _Lampropeltis triangulum_ vertebrae are similar to those of the extinct species _L. similis_ Holman known from the Barstovian (Holman, 1970) to the mid-Hemphillian (Parmley, 1987), differing mainly in having longer and wider accessory processes (Holman, 1964). The fossil vertebrae are referred to _L. triangulum_ because they have long and wide accessory process.

Previously, the earliest occurrence of _Lampropeltis triangulum_ was from the late Hemphillian of Oklahoma (Brattstrom, 1967), thus these mid-Hemphillian fossils represent the earliest geologic record of the species in North America and pose some interesting questions about the phylogenetic history of the species. Some authors have suggested _L. similis_ may be ancestral to _L. intermedius_ Brattstrom from the Blancan of Mexico and Irvingtonian of Arizona, which, in turn, may have given rise to Recent _L. triangulum_ (see Brattstrom, 1955; Holman, 1979; Meylan, 1982; Voorhies et al., 1987). This phylogeny has recently been questioned (Holman, 1981a; Parmley, 1987). The appearance of _L. triangulum_ about 3 Ma earlier than _L. intermedius_ suggests _L. similis_ may be ancestral to _L. triangulum_ rather than to _L. intermedius_.

Lampropeltis getulus (Linnaeus, 1766)

Material: L.Q.: 1 vertebra, MSUVP 1303; 1 vertebra, UNSM 96436; St.: 1 vertebrae, UNSM 56954; D.N.: 1 vertebra, UNSM 56905.

Remarks: Lampropeltis getulus is a medium-sized snake with vertebrae similar to L. calligaster and Elaphe species. Differentiation of L. getulus and L. calligaster presents special problems, but L. getulus usually differs from the later species in having the top of the zygosphene flat in anterior view rather than arched. Lampropeltis getulus differs from Elaphe species in having straighter, better-developed subcentral ridges with deeper valleys between the subcentral ridges and the hemal keel and usually a lower neural arch.

Lampropeltis getulus may have been present as early as the Clarendonian (Webb et al., 1981), but this is the first record of the species from the Hemphillian. The species occurs in southeast Nebraska today (Lynch, 1985). It is a snake with broad ecological tolerances occurring from grasslands to swamp borders (Conant, 1958).

Lampropeltis sp. indet.

Material: St.: 2 vertebrae, UNSM 56970.

Remarks: These vertebrae have depressed neural arches typical of Lampropeltis, but they are too fragmentary for specific identification.

Genus Salvadora Baird and Girard, 1853

Salvadora paleolineata Holman, 1973

Material: L.Q.: 5 vertebrae, UNSM 96418.

Remarks: Salvadora is a living colubrid genus that resembles Coluber and Masticophis in having moderately elongate vertebrae with thin, delicate neural spines and well-developed, uniformly thin hemal keels. But Salvadora differs from both genera in having shorter, wider vertebrae; more delicate neural spines; less developed epizygapophyseal spines (Holman, 1976b); and relatively smaller condyles and cotyles (Van Devender et al., 1985). The extinct species S. paleolineata is similar to the living species S. grahamiae, but differs in lacking epizygapophyseal spines. The Lemoyne Quarry vertebrae are identical to those of S. paleolineata.

Salvadora paleolineata is known from the Hemingfordian (Holman, 1977a) to the mid-Hemphillian (Parmley, 1984).

Genus *Elaphe* Fitzinger, 1833

Elaphe nebraskensis Holman, 1964

Material: L.Q.: 2 vertebrae, UNSM 96419.

Remarks: This large extinct species of *Elaphe* differs from other extinct and Recent species of *Elaphe* in having the accessory processes and prezygapophyseal articular facets more oblique to the long axes of the centra. *Elaphe nebraskensis* has low neural spines which led Holman (1964) to suggest it may be closest to Recent *E. vulpina*. The somewhat fragmentary Lemoyne Quarry vertebrae are assigned to *E. nebraskensis* because they have low neural spines and accessory processes and prezygapophyseal articular facets oblique to the long axes of the centra. *Elaphe nebraskensis* is a common late Miocene snake (Holman, 1979).

Elaphe lemoynensis, n. sp.

(Figure 26)

Holotype: UNSM 96420, a vertebra.

Type locality: Lemoyne Quarry, Keith County, Nebraska.

Age: Mid-Hemphillian (late Miocene).

Diagnosis: The fossil differs from *Lampropeltis* and *Pituophis* and is assigned to the genus *Elaphe* on the basis of its weak subcentral ridges; shallow valleys between the hemal keel and subcentral ridges; and in

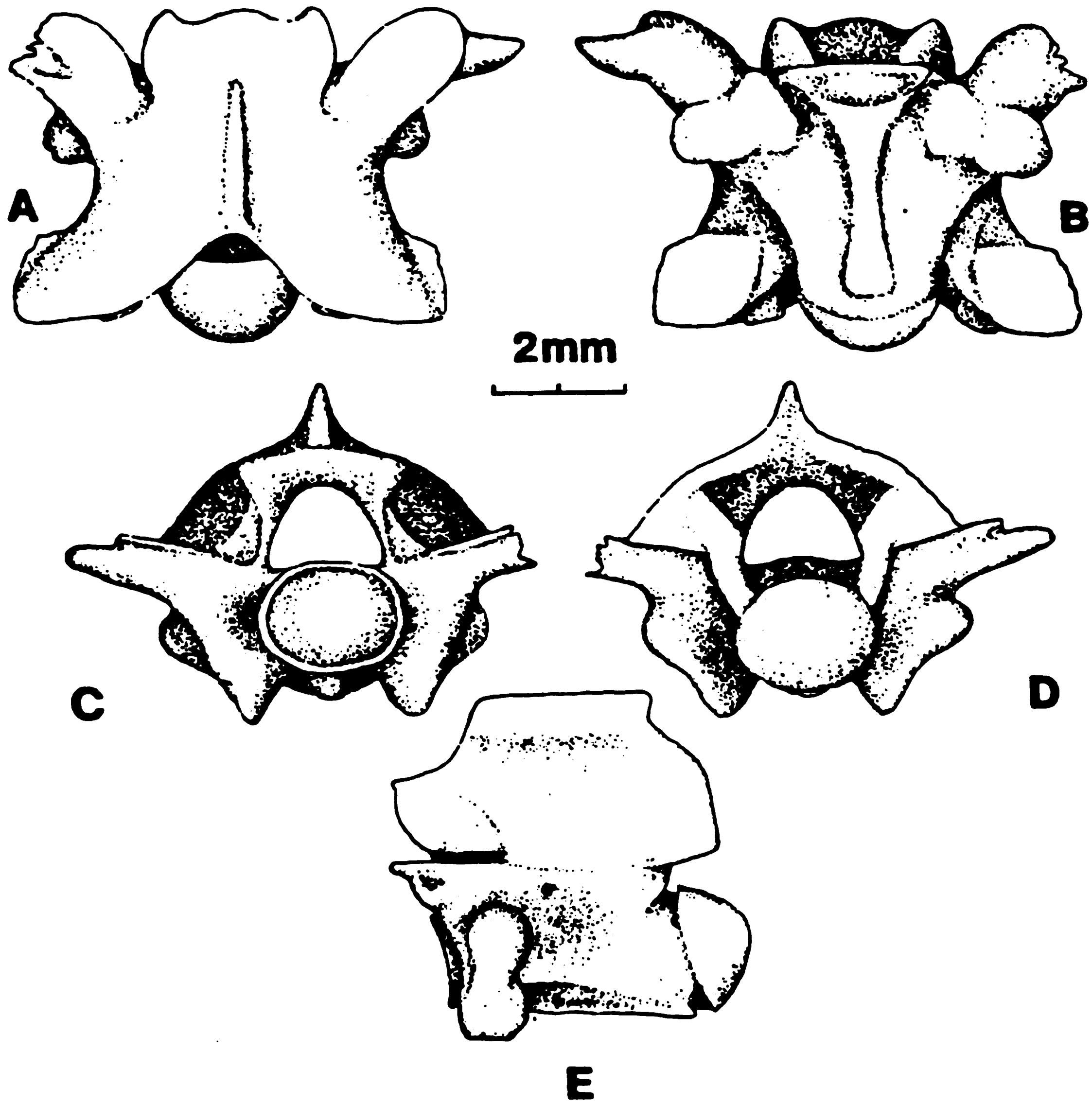

Figure 26. Vertebra of Elaphe lemoynensis, n. sp. (L.Q., UNSM 96420) in dorsal (A), ventral (B), anterior (C), posterior (D), and lateral (E) views.

having a neural arch that is more vaulted than in Lampropeltis but less vaulted than in Pituophis. The species is separated from New World species of Elaphe on the following combination of characters: very low, moderately thick neural spine; accessory processes perpendicular to the long axis of the centrum; a short, wide centrum; and wide neural arch.

Etymology: Species name for the townsite of Lemoyne near the fossil site.

Description of Holotype: In dorsal view: vertebra short and wide; prezygapophyseal accessory processes short and perpendicular to long axis of centrum; prezygapophyseal articular facets large and ovaloid; neural spine moderately thick, bevelled along dorsal edge with slight posterior overhang; zygosphene slightly convex.

In ventral view: subcentral ridges bowed outward and very weakly developed; hemal keel well produced from floor of centrum, wide and nearly uniform in width along its length; postzygapophyseal articular facets round, centrum short and wide.

In anterior view: zygosphene slightly convex dorsally; prezygapophyseal articular facets tilted slightly upward; accessory processes short and thick; cotyle round and larger than neural canal; single foramen in an excavation on either side of cotyle.

In posterior view: neural arch vaulted; condyle round and about as large as neural canal; postzygapophyseal articular facets tiled downward.

In lateral view: vertebra shortened in form; neural spine low, longer than high, with a slight posterior overhang; subcentral ridge bowed upward; hermal keel distinct from centrum with posterior step; condyle tilted dorsally.

Measurements: Measurement of the holotype are as follows: centrum length, 4.6; neural arch width, 3.5; length through prezygapophyseal and postzygapophyseal articular facets, 4.9; width through prezygapophyseal articular facets, 6.2; width through postzygapophyseal facets, 5.7; neural spine height to top of zygosphene, 1.2; neural spine length, 2.5; zygosphene width, 2.5. Based on a skeleton of a Recent Elaphe subocularis with similar-sized vertebrae as the fossil, the holotype represents a snake about 1.2 meters in total length.

Remarks: The phyletic position of Elaphe lemoynensis is difficult to assess because it has a unique combination of vertebral characters not found in any extinct or living species of Elaphe. There are five extant North American species of *Elaphe*: *E. guttata*, *E. obsoleta*, *E. vulpina*, *E. bairdi*, and *E. subocularis*. *Elaphe lemoynensis* differs from *E. guttata*, *E. vulpina*, *E. obsoleta* and *E. bairdi* in having a lower neural spine, accessory processes perpendicular to the long axis of the centrum and a shorter, wider centrum. *Elaphe lemoynensis* is closest to *E. subocularis* in that both species have a short, wide centrum, but *E. lemoynensis* has a wider neural arch in dorsal view and a more vaulted neural arch in posterior view.

Four extinct Miocene and Pliocene species of *Elaphe* are known. These are *Elaphe nebraskensis* from the Barstovian of Nebraska (Holman, 1964), *E. buisi* from the late Hemphillian of Oklahoma (Holman, 1973a), *E. pliocenica* from the Blancan of Idaho (Holman, 1968), and *E. kansensis* from the Blancan (?) of Kansas (Gilmore, 1938). *Elaphe pliocenica* and *E. nebraskensis* have neural spines as low as *E. lemoynensis*, but neither species have accessory processes as perpendicular to the long axes of the centra, or centra as wide as in *E. lemoynensis*. *Elaphe buisi* and *E. kansensis* have higher neural spines and longer accessory processes than in *E. lemoynensis*.

Elaphe obsoleta (Say, 1823)

Material: St.: 1 vertebra, UNSM 56960; D.N.: 1 vertebra, MSUVP 1247.

Remarks: Vertebral characters of *Elaphe obsoleta* have been discussed in detail by Parmley (1986a, b). The vertebrae of this large snake are similar to those of *Pituophis melanoleucus*, but differ in having comparatively lower neural spines; flatter zygosphenes viewed anteriorly; longer accessory processes; and better developed subcentral ridges. *Elaphe obsoleta* has higher neural spines than *E. nebraskensis*, *E. pliocenica*, *E. lemoynensis*, *E. guttata*, *E. vulpina*, *E. bairdi*, and *E. subocularis*.

Elaphe obsoleta is known from the Blancan (Rogers, 1976) to the late Rancholabrean (Parmley, 1986a), but this is the first report of the species from the Hemphillian. *Elaphe obsoleta* occurs in Nebraska today only along the southeast border of the state (Lynch, 1985).

Elaphe cf. *E. guttata* (Linnaeus, 1766)

Material: D. N.: 1 vertebra, UNSM 56907; M.P.: 1 vertebra, UNSM 56936.

Remarks: Parmley (1986a,b) has shown how *Elaphe guttata* vertebrae may be separated from other Recent species of the genus. *Elaphe guttata* differs from the extinct species *E. buisi* and *E. kansensis* in having a lower neural spine, and from *E. lemoynensis* in having longer, less angular accessory processes, a higher neural spine, and a longer, narrower centrum. It differs from *E. pliocenica* and *E. nebraskensis* in having a higher neural spine.

Previously, the earliest fossil record of *Elaphe guttata* was from the Blancan age Beck Ranch local fauna of Scurry County, Texas (Rogers, 1976). This species occurs in Nebraska today along the southern border of the state (Lynch, 1985), thus it had a wider range in Nebraska during Hemphillian time. The species is typically a grassland form, but also occurs in woodlands and swamplands.

Elaphe sp. indet.

Material: St.: 1 vertebra, UNSM 56955; D.N.: 1 vertebra, MSUVP 1248.

Remarks: These vertebrae are similar to *Elaphe* in having vaulted neural arches and moderately developed subcentral ridges, but they are too fragmentary for species identification.

Pituophis melanoleucus (Daudin, 1803)

Material: St.: 1 vertebra, UNSM 56957; D.N.: 2 vertebrae, MSUVP 1245; M.P.: 2 vertebrae, UNSM 56937.

Remarks: Vertebral characters of *Pituophis* have been discussed in detail by Auffenberg (1963a). The most diagnostic characters of *Pituophis* vertebrae are: neural spines high; neural arches vaulted; and subcentral ridges weakly developed. *Pituophis* vertebrae are similar to those of *Elaphe obsoleta*, but differ in details discussed under *E. obsoleta*.

At least some subspecies of Recent *Pituophis* are separable on the basis of vertebral characters (Holman, 1981a). For example, the pine snake, *P. melanoleucus mugitus*, is separable from the bullsnake, *P. m. sayi* in having a higher neural spine. These subspecific differences suggest that the eastern pine snake and bull snake may be distinct species (Lynch, 1985). *Pituophis melanoleucus* occurs from the Blancan (Holman, 1979) to the Holocene (Parmley, 1988b), but these new fossils represent the first Hemphillian occurrence of the species. *Pituophis melanoleucus* is a common snake of all plains and prairies in Nebraska today (Lynch, 1985).

Subfamily Natricinae Bonaparte, 1840

Genus *Nerodia* Baird and Girard, 1853

Nerodia hillmani (Wilson, 1968)

Material: L.Q.: 1 vertebra, UNSM 96428.

Remarks: This small extinct natricine snake was described on the basis of several trunk vertebrae from the Clarendonian age WaKeeney local fauna of Trego County, Kansas. According to Wilson (1968), Nerodia hillmani is separated from all other North American Nerodia species on the basis of its low, dorsally thickened neural spine. Wilson (1968) also stated that well-developed epizygapophyseal spines and a well-developed hypapophysis were diagnostic for N. hillmani, but both conditions occur in many North American natricine snakes. Holman (1975) also referred several vertebrae from the WaKeeney local fauna to this species. Other than having the epizygapophyseal spines mostly worn off, the Lemoyne Quarry vertebra is identical to N. hillmani.

When Wilson (1968) described Nerodia hillmani, he gave no explanation of why he placed it in the genus Nerodia (Natrix) rather than in Thamnophis. Vertebrae of Recent Nerodia are usually shorter with higher neural spines and higher neural arches than those of Thamnophis. The vertebrae of N. hillmani are Thamnophis-like in being small and elongated with low neural spines and comparatively low neural arches.

Nerodia sp. indet.

Material: L.Q.: 1 vertebra, UNSM 96438; M.P.: 3 vertebrae, UNSM 56933.

Remarks: These vertebrae represent a small form, or forms of *Nerodia*, but are too fragmentary to identify to species. The Lemoyne Quarry vertebra is comparable in size to *N. hillmani*, but is missing the top of its neural spine.

cf. *Virginia* Baird and Girard, 1853

Material: L.Q.: 1 vertebra, UNSM 96429.

Remarks: Vertebrae of *Virginia* are easily confused with those of *Storeria* and *Tropidoclonion*. *Virginia* differs from *Tropidoclonion* in having a shorter centrum and shorter, wider accessory processes. It differs from *Storeria* in having a shorter centrum, wider accessory processes that are usually more perpendicular to the long axis of the centrum and in having a lower neural spine (Holman and Winkler, 1987).

Living members of this genus are secretive forms most commonly occurring on rocky hill sides in moist woodlands and woodland edge situations (Collins, 1982).

Genus *Thamnophis* Fitzinger, 1843

Thamnophis cf. *T. proximus* (Say, 1823) or

T. sauritus (Linnaeus, 1766)

Material: L.Q. 2 vertebrae, UNSM 96421; St.: 1 vertebra, UNSM 56959; M.P.: 1 vertebra, UNSM 56930.

Remarks: These fossils are identified as *Thamnophis* rather than *Nerodia*, *Regina*, or the extinct genus

Neonatrix on the basis of their relatively small size, elongate shape (Brattstrom, 1967), and moderately short, posteriorly directed hypapophyses.

The neural spines of *Thamnophis sirtalis*, *T. sauritus*, and *T. proximus* tend to be higher than those of *T. marcianus*, *T. radix* (Holman, 1962) and *T. crytopsis*. Holman (1962) separated most *T. sirtalis* vertebrae from those of *T. sauritus* and *T. proximus* based on the accessory processes tending to be at right angles to the long axes of the centra in *T. sirtalus*, whereas in *T. sauritus* and *T. proximus* they tend to be olique. The fossil vertebrae are most similar to *T. sauritus* and *T. proximus* in the above characters, but I am unable to separate the two species on the basis of vertebrae. One of the fossils is from an exceptionally large individual probably in excess of 100 cm.

Thamnophis sauritus does not occur in Nebraska today, but is confined to about the eastern one-third of the United States (Conant, 1958). *Thamnophis proximus* presently occurs along the eastern and southeastern border of Nebraska (Lynch, 1985). Both occur near marshy areas.

Thamnophis cf. *T. cyrtopsis* (Kennicott, 1860)

Material: L.Q.: 3 vertebrae, UNSM 96427.

<u>Remarks</u>: <u>Thamnophis</u> <u>cyrtopsis</u> is a small garter snake that appears to be readily distinguished from <u>T</u>. <u>proximus</u>, <u>T</u>. <u>sirtalis</u>, <u>T</u>. <u>sauritus</u>, <u>T</u>. <u>marcianus</u>, <u>T</u>. <u>radix</u>, and <u>T</u>. <u>elegans</u> by its lower neural spine and shorter, more robust vertebra. <u>Thamnophis</u> <u>cyrtopsis</u> differs from <u>T</u>. <u>butleri</u> in having the posterior border of the neural spine concave rather than gently curved as in <u>T</u>. <u>butleri</u>. <u>Thamnophis</u> <u>crytopsis</u> is easily separated from <u>T</u>. <u>brachystoma</u> in that it has a much lower neural spine and is more elongate.

<u>Thamnophis</u> <u>cyrtopsis</u> occurs today in the southwestern United States and through much of Mexico (Conant, 1958). The species is usually found near water and inhabits low deserts to high forested mountains (Conant, 1958).

<u>Thamnophis</u> cf. <u>T</u>. <u>marcianus</u>
(Baird and Girard, 1853) or
<u>T</u>. <u>radix</u> (Baird and
Girard, 1853)

<u>Material</u>: L.Q.: 2 vertebrae, MSUVP 1228; 3 vertebrae, UNSM 96437; M.P.: 1 vertebra, UNSM 56929.

<u>Remarks</u>: The neural spines of <u>Thamnophis</u> <u>marcianus</u> and <u>T</u>. <u>radix</u> tend to be lower than those of <u>T</u>. <u>sirtalis</u>, <u>T</u>. <u>sauritus</u>, and <u>T</u>. <u>proximus</u>, but higher than those of <u>T</u>. <u>cyrtopsis</u>. Moreover, <u>T</u>. <u>marcianus</u> and <u>T</u>. <u>radix</u> tend to

have the anterior and posterior neural spine borders strongly concave, whereas in _T_. _sirtalis_, _T_. _sauritus_, and _T_. _proximus_ the neural spine borders are gently curved or nearly straight (Holman, 1972). The fossil vertebrae compare best with _T_. _marcianus_ and _T_. _radix_, but I cannot separate these species on the basis of vertebrae.

Thamnophis _radix_ occurs throughout Nebraska today (Lynch, 1985), and I have collected this species within a few meters of the Lemoyne Quarry fossil site. _Thamnophis marcianus_ occurs south of Nebraska as close as central Kansas (Conant, 1958). Both species are common in dry grasslands near wet areas.

Thamnophis sp. indet.

Material: P.Q.: 12 vertebrae, UNSM 96447; L.Q.: 5 vertebrae, MSUVP 1246; 37 vertebrae, UNSM 96439; St.: 1 vertebra, UNSM 56958; D.N.: 2 vertebrae, MSUVP 1246; M.P.: 23 vertebrae, UNSM 56928.

Remarks: These fragmentary fossil vertebrae are similar in size to several Recent species of _Thamnophis_, but I am unable to identify them to species.

Genus *Neonatrix* Holman, 1973

Neonatrix elongata Holman, 1973

(Figure 27)

Material: L.Q.: 2 vertebrae, UNSM 96424.

Remarks: *Neonatrix elongata* was described on the basis of trunk vertebrae from the Barstovian Egelhoff local fauna of Nebraska. This extinct snake may be separated from living natricines on the basis of its longer than high neural spines and reduced hypapophyses that do not extend past the condyles. The Lemoyne Quarry vertebrae (largest one figured) do not differ from the Egelhoff *Neonatrix elongata* fossils, and are separated from the only other known species of the genus, *N. magna* Holman, on the basis of their smaller size, more elongate shape, and less vaulted neural arches. Important vertebral characteristics and measurements of the most complete vertebra (figured) are vertebral form longer (centrum length 3.6) than wide (neural arch width 1.9); accessory processes moderately long, narrow, and rounded on the ends; no epizygapophyseal spines; neural spine moderately thin and longer (2.5) than high (0.7 to top of zygosphene); hypapophysis short, not extending past the condyle and terminally rounded; subcentral ridges weakly developed; and neural arch vaulted.

There is no evidence to suggest that *Neonatrix elongata* is ancestral to any living form. Its occurrence

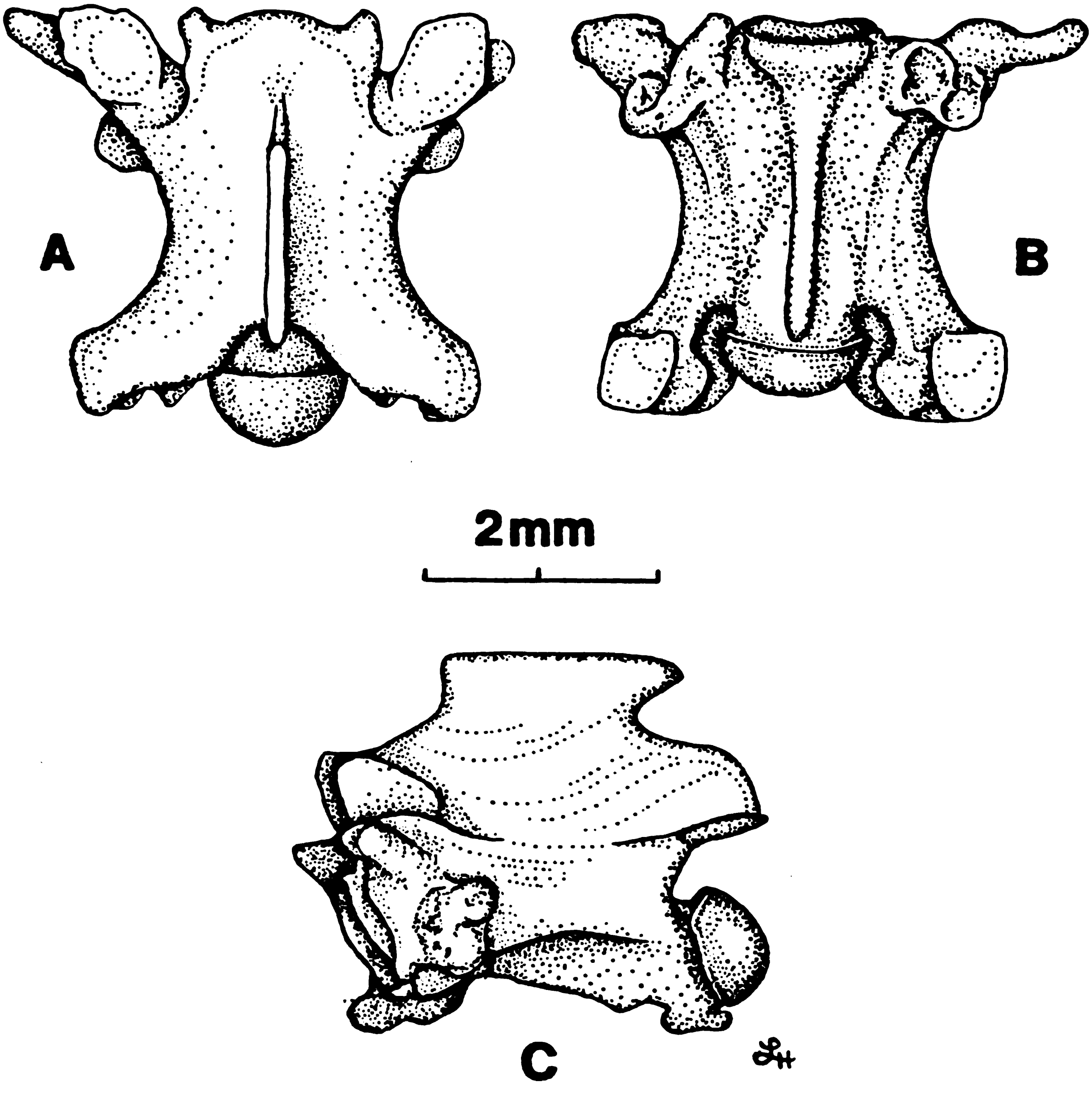

Figure 27. Vertebra of Neonatrix elongata (L.Q., UNSM 96424) in dorsal (A), ventral (B), and lateral (C) views.

in the Lemoyne Quarry herpetofauna represents the latest record of the genus.

Subfamily Xenodontinae Cope, 1893

Genus *Paleoheterodon* Holman, 1964

Paleoheterodon tiheni Holman, 1964

Material: P.Q.: 2 vertebrae, UNSM 96446; L.Q.: 2 vertebrae, MSUVP 1239; 10 vertebrae, UNSM 96440 and 96425; M.P.: 2 vertebrae, UNSM 56926.

Remarks: *Paleoheterodon* is very similar to living *Heterodon* in having short and wide vertebrae with flat, indistinct hemal keels and enlarged blade-like posterior maxillary teeth (Holman, 1977b). *Paleoheterodon* vertebrae differ from those of *Heterodon* in having more vaulted neural arches. I can find no trenchant differences between the fossil vertebrae and those of the only known species of the genus *P*. *tiheni*. *Paleoheterodon tiheni* is a common late Miocene fossil and is known from the Barstovian of Nebraska (Holman, 1964) to the mid-Hemphillian of Texas (Parmley, 1984).

Heterodon cf. *H*. *platyrhinos* Latreille, 1802

Material: L.Q.: 1 vertebra, UNSM 96423; M.P.: 4 vertebrae, UNSM 56938.

Remarks: These vertebrae are separated from *Paleoheterodon* based on their more depressed neural arches. The main difference between *Heterodon* platyrhinos, the two living species H. nasicus and H. simus, and the extinct species H. plionasicus from the Blancan of Kansas (Peters, 1953) is that H. platyrhinos tends to have longer, narrower vertebrae. The fossil vertebrae are long and narrow like those of H. platyrhinos.

It is interesting to note that the Recent genus Heterodon and the extinct genus Paleoheterodon are reported sympatrically here for the first time. Previously, Heterodon was known from the slightly younger Buis Ranch local fauna of Oklahoma (4.5 Ma; Woodburne et al., 1987), although Webb et al. (1981) reported a tentative record of Heterodon from the late Clarendonian of Florida. Their material has not been critically studied, and based on the age of the deposit, may represent Paleoheterodon. Heterodon platyrhinos occurs in Nebraska today mainly along the eastern border of the state, but there are a few records from the southcentral part (Lynch, 1985).

Heterodon cf. H. nasicus

Baird and Girard, 1852

Material: L.Q.: 2 vertebrae, MSUVP 1230; M.P.: 7 vertebrae, UNSM 56932.

Remarks: The vertebrae of Heterodon nasicus and the extinct species H. plionasicus Peters tend to be shorter and broader than those of *H. platyrhinos*. *Heterodon nasicus* is a smaller species than *H. plionasicus* with slightly upturned zygosphenes viewed anteriorly. The zygosphenes of *H. plionasicus* are usually flat (Brattstrom, 1967), but otherwise the species are apparently vertebrally identical. The fossils are most like *H. nasicus*, but it is possible that some of them represent *H. plionasicus*.

Heterodon nasicus prefers moderately dry and sandy habitats that allow it to burrow. This species occurs throughout the western two-thirds of Nebraska today (Lynch, 1985).

Heterodon sp. indet.

Material: St.: 8 vertebrae, UNSM 56953; M.P.: 3 vertebrae, UNSM 56935.

Remarks: These vertebrae are too fragmentary to identify to species and some of them may represent *Paleoheterodon*.

Colubridae gen. indet.

Material: P.Q.: 7 vertebrae, UNSM 96448: L.Q.: 70 vertebrae, MSUVP 1301; 140 vertebrae, UNSM 96443; St. 244 vertebrae, UNSM 56963; D.N.: 56 vertebrae, MSUVP 11249; 44 vertebrae, UNSM 56903; M.P.: 136 vertebrae, UNSM 56939.

Remarks: These fossil vertebrae are either worn, missing diagnostic structures such as their neural spines, or are from the cervical or caudal region of the vertebral column.

Family Viperidae Gray, 1825

Agkistrodon sp. indet.

Material: L.Q.: 1 vertebra, UNSM 96434.

Remarks: Vertebrae of North American viperids (genera Agkistrodon, Crotalus, and Sistrurus) are relatively easily identified on the basis of their short, wide vertebral shape, long, thick hypapohyses that originate near the condyles and are one-third or more as wide as the condyles (Holman, 1981a) and large condyles. Agkistrodon vertebrae are separated from those of Crotalus in having relatively large cotylar foramina set in deep pits. Crotalus usually has smaller foramina set in shallower pits (Holman, 1965). Meylan (1982) also showed that these characters are useful for separating vertebrae of these closely related genera. Agkistrodon usually differs from Sistrurus in having wider cotyles, larger condyles, and less vaulted neural arches. The Lemoyne Quarry fossil is small and somewhat fragmentary with most of its hypapophysis missing, but is like Agkistrodon in the above characters. The species A. contortrix, A. piscivorous, and A. bilineatus occur in

North America today, but I cannot determine if the fossil represents one of these species or an extinct form.

This mid-Hemphillian record of an Agkistrodon is important because records of North American viperids from Miocene age rocks are rare. The oldest record of the family is a fragmentary viperid vertebra reported from the Arikareean age McCann's Canyon site, Cherry County, Nebraska (Holman, 1981b). Viperid vertebrae are also known from the Barstovian of Texas (Holman, 1977a) and Nebraska (Holman, 1977b). The Lemoyne Quarry Agkistrodon vertebra confirms the occurrence of this genus in midcontinental North America by at least 6-7 million years ago.

Crotalus voorhiesi, n. sp.

(Figure 28)

Holotype: UNSM 96426, a trunk vertebra.

Type Locality: Lemoyne Quarry, Keith County, Nebraska.

Age: Mid-Hemphillian (late Miocene).

Diagnosis: A Crotalus that differs from all Recent North American species of the genus in having a very low neural spine.

Etymology: Specific name honors Michael Voorhies of the Nebraska State Museum for his contributions to vertebrae Paleontology.

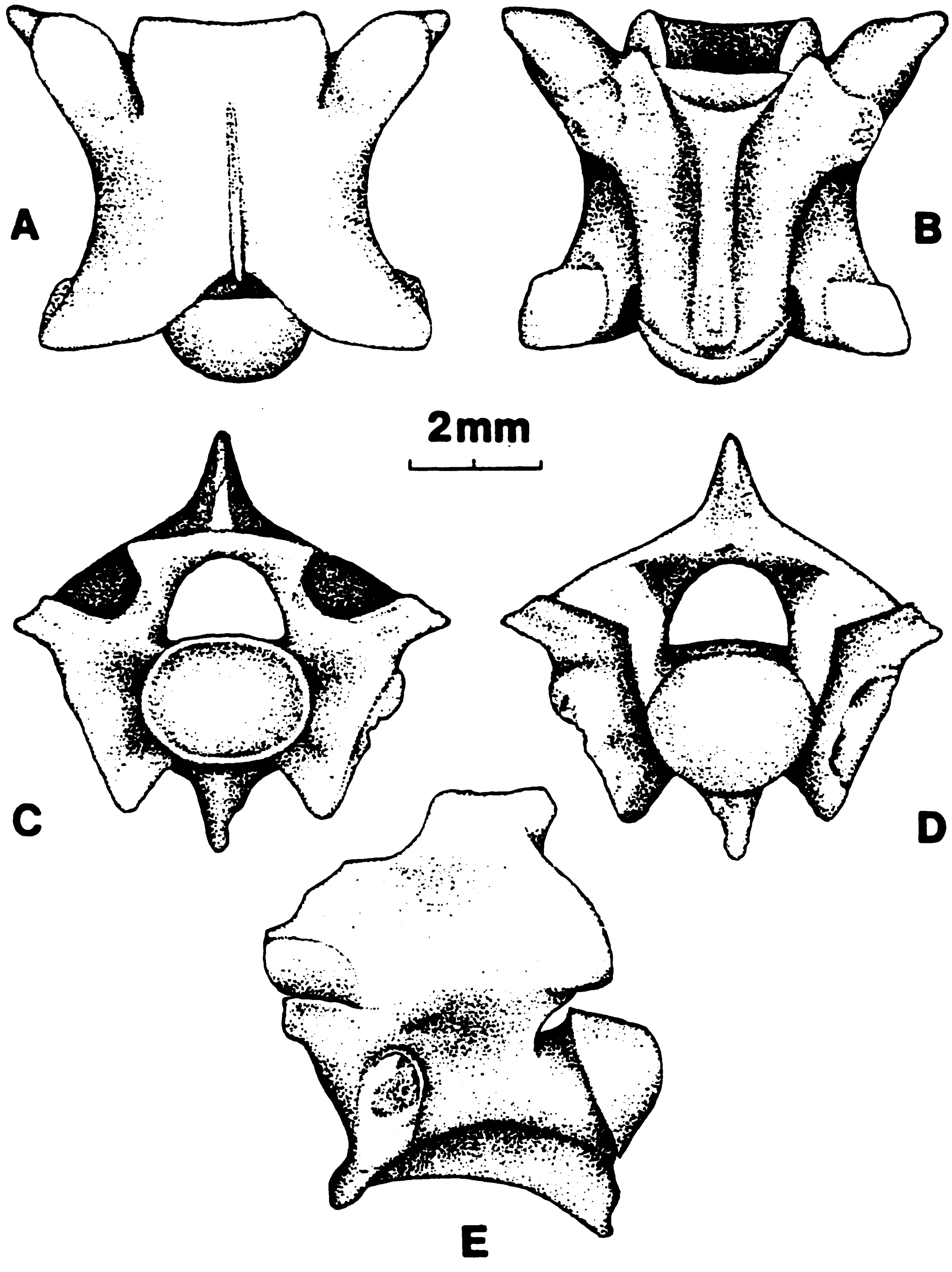

Figure 28. Vertebra of Crotalus voorhiesi, n. sp. (L.Q., UNSM 96426) in dorsal (A), ventral (B), anterior (C), posterior (D), and lateral (E) views.

<u>Description of Holotype</u>: In dorsal view: vertebra about as long through the centrum as it is wide through the articular facets; neural spine moderately thick and rounded on top, slight posterior overhang; condyle large; prezygapophyseal articular facets small; accessory processes short, obtuse, oblique to long axis of centrum; zygosphene wide and slightly convex along anterior margin.

In ventral view: hypapophysis broken, but basal portion thick and posteriorly directed; subcentral ridges indistinct and wide; postzygapophyseal articular facets moderately large and orbicular.

In anterior view: zygosphene thin and convex; two foramina present in shallow concavities on either side of cotyle; prezygapophyseal articular facets tilted upward; cotyle deep and compressed dorsoventrally.

In posterior view: neural arch depressed; neural spine moderately thick; condyle large; basal portion of hypapophysis triangular in cross section.

In lateral view: neural spine low with slight posterior overhang; subcentral ridges arched upward; condyle tilted obliquely upward; hypapophysis projects ventroposteriorly; diapophyseal portion of paradiapophysis damaged, parapophyseal section projects anteriorly.

Remarks: Characters that show the fossil represents a viperid and not a natricine or a colubrid cervical vertebra are: vertebral shape short and wide; hypapophysis thick but narrow laterally and projected ventrally; and condyle large. Moreover, *C. voorhiesi* has a depressed neural arch which further separates it from the natricines and cervical vertebrae of most North American colubrids which usually have arched neural arches. The fossil is assigned to the genus *Crotalus* rather than to *Sistrurus* or *Agkistrodon* based on its large condyle and shallow cotylar concavities that contain relatively small foramina.

Among the 13 currently recognized Recent North American species of *Crotalus*, *C. voorhiesi* differs in having a lower neural spine. The species appears closest to *C. horridus*, but differs in having a lower neural spine with a more pronounced posterior overhang.

Miocene records of *Crotalus* are rare, but living species were present as early as the Clarendonian (Webb et al., 1981).

Crotalus sp. indet.

(Figure 29)

Material: L.Q.: 1 vertebra, UNSM 96431; St.: 2 vertebrae, UNSM 56952; D.N.: 1 vertebra, UNSM 56904; M.P.: 2 vertebrae, UNSM 56941.

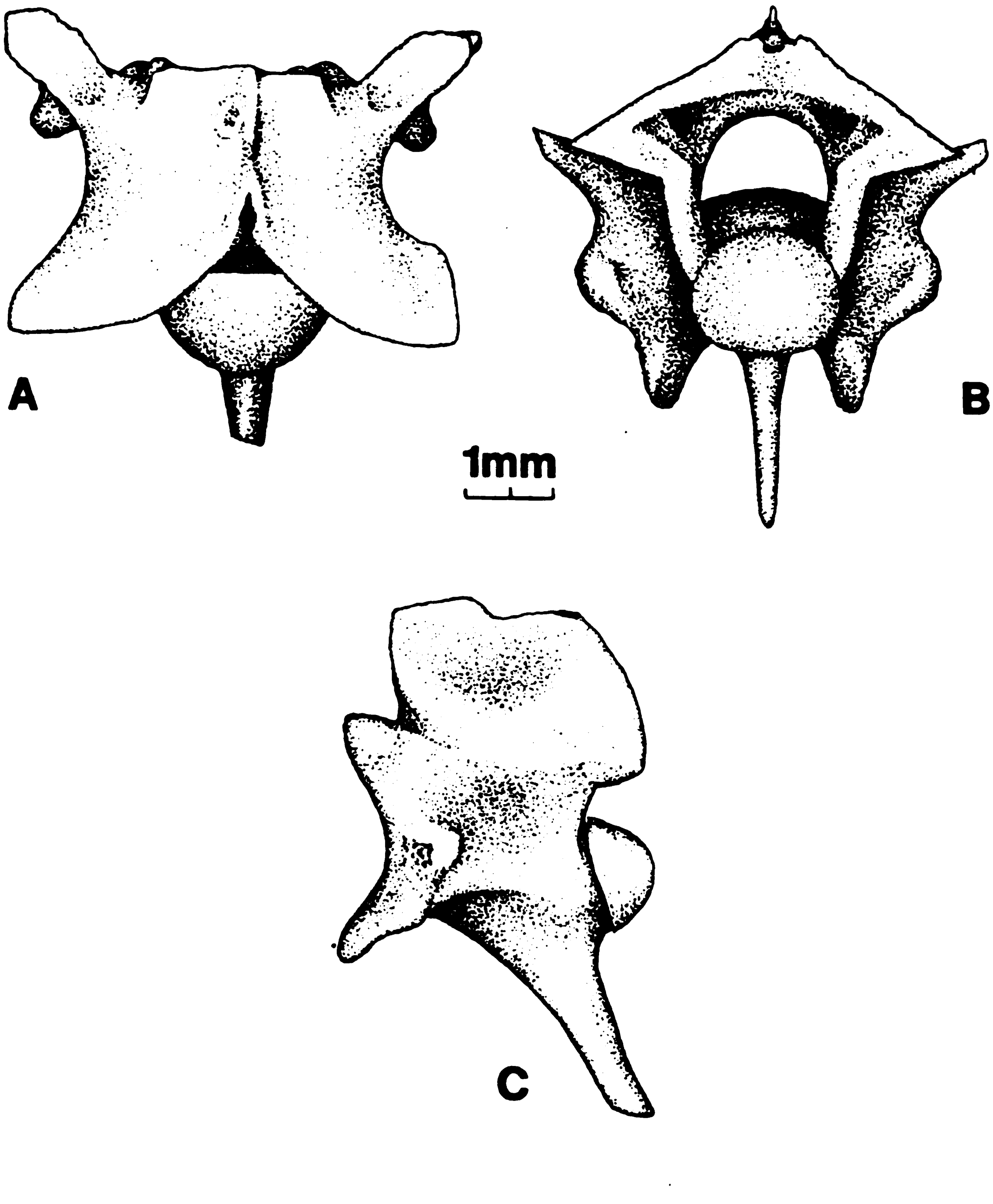

Figure 29. Vertebra of <u>Crotalus</u> sp. indet. (M.P., UNSM 56941) in dorsal (A), posterior (B), and lateral (C) views.

Remarks: These fossils are somewhat fragmentary and most have broken hypapophyses. The most complete specimen (UNSM 56941) is figured. The fossils are assigned to the genus *Crotalus* on the basis of their short and wide shape, large condyles, and relatively small cotylar foramina set in shallow pits (Holman, 1965).

FAUNAL ANALYSES

The early Hemphillian Potter Quarry yielded too few fossils for analysis, but the mid and late Hemphillian quarries were diverse enough for meaningful comparisons. In essence, the mid-Hemphillian herpetofauna is more archaic than the late Hemphillian one, with 44% of its taxa extinct compared with 11% in the late Hemphillian (Table 6). This is more specifically addressed below.

Mid-Hemphillian Fauna

The Lemoyne Quarry herpetofauna is rather modern at the generic level as only 22% of the 23 genera are extinct, but 55% of its 29 species are extinct (Table 6). The living genera _Arizona_, _Heterodon_, _Virginia_, _Lichanura_, and _Agkistrodon_ appear in the fossil record for the first time, and the genus _Paurophis_ may be temporally isolated in the mid-Hemphillian. Seven species appear in the fossil record for the first time. These are: _Heterodon nasicus_, _H. platyrhinos_, _Lampropeltis getulus_, _L. triangulum_, _Thamnophis crytopsis_, _T. marcianus_ or _T. radix_ and _T. proximus_ or _T. sauritus_.

Table 6. Comparison of taxa from the mid-Hemphillian Lemoyne Quarry (L.Q) local fauna and late Hemphillian Santee (St.), Devils Nest (D.N.), and Mailbox Prospect (M.P.) local faunas. Extinct genera are noted by a double aserisk, extinct species by a single one, and + denotes present, - absent.

Taxon	L.Q.	St.	D.N.	M.P.
Salamanders				
Plethodontinae gen. indet.	X	-	-	-
Ambystoma maculatum	X	-	-	-
Ambystoma minshalli*	X	-	-	-
Ambystoma triginum	X	X	X	X
Ambystoma sp. indet.	X	X	-	X
Frogs				
Bufo cognatus or B. speciosus	-	X	-	-
Bufo hibbardi*	X	-	-	-
Bufo holmani*	-	X	X	-
Bufo marinus	X	-	-	-
Bufo pliocompactilis*	X	-	-	-
Bufo valentinensis*	X	-	-	-
Bufo woodhousii	-	-	-	X
Bufo sp. indet.	X	X	X	-
Scaphiopus wardorum*	-	X	-	-
Scaphiopus sp. indet.	-	X	-	X
Rana cf. R. catesbeiana	-	X	-	X
Rana cf. R. pipiens	X	X	-	X

Table 6. Continued

Taxon	L.Q.	St.	D.N.	M.P.
Frogs (Continued)				
Rana sp. indet.	X	X	X	X
Hyla cf. *H. gratiosa*	X	-	-	-
Hyla sp. indet.	X	X	-	X
Turtles				
Trionxy spiniferus	-	X	-	-
Trionyx sp. indet.	-	X	X	X
Chrysemys picta	-	X	X	X
Emydoidea blandingii	-	-	X	-
Terrapene sp. indet.	-	-	X	-
Macroclemys temminckii	-	-	X	-
Kinosternon flavescens	-	X	-	-
Geochelone sp. indet.	-	X	X	-
Lizards				
Crotaphytus cf. *C. collaris*	-	X	-	-
Eumeces cf. *E. obsoletus*	-	-	-	X
Eumeces sp. indet.	X	X	-	X
Ophisaurus cf. *O. attenuatus*	X	-	-	-
Snakes				
*Charina prebottae**	X	-	-	-
Lichanura sp. indet.	X	-	-	-
Arizona sp. indet.	X	-	-	-

Table 6. Continued

Taxon	L.Q.	St.	D.N.	M.P.
Snakes (Continued)				
Coluber sp. indet. or _Masticophis_ sp. indet.	X	X	X	X
Elaphe cf. _E._ _guttata_	-	-	X	X
Elaphe _lemoynensis_*	X	-	-	-
Elaphe _obsoleta_	-	X	X	-
Elaphe _nebraskensis_*	X	-	-	-
Heterodon cf. _H._ _nasicus_	X	-	-	X
Heterodon cf. _H._ _platyrhinos_	X	-	-	X
Heterodon sp. indet.	-	X	-	X
Lampropeltis _getulus_	X	X	X	-
Lampropeltis _triangulum_	X	-	X	X
Lampropeltis sp. indet.	-	X	-	-
Nebraskophis _corneri_**	X	-	-	-
Nebraskophis _skinneri_**	X	-	-	-
Neonatrix _elongata_**	X	-	-	-
Nerodia _hillmani_*	X	-	-	-
Nerodia sp. indet.	X	-	-	X
Paleoheterodon _tiheni_**	X	-	-	X
Paracoluber cf. _P._ _storeri_**	X	-	-	-
Paurophis _lewisi_**	X	-	-	-

Table 6. Continued

Taxon	L.Q.	St.	D.N.	M.P.
Snakes (Continued)				
Pituophis melanoleucus	-	X	X	X
*Salvadora paleolineata**	X	-	-	-
Thamnophis cf. *T. crytopsis*	X	-	-	-
Thamnophis cf. *T. proximus* or *T. sauritus*	X	X	-	X
Thamnophis cf. *T. marcianus* or *T. radix*	X	-	-	X
Thamnophis sp. indet.	X	X	X	X
cf. *Virginia*	X	-	-	-
Agkistrodon sp. indet.	X	-	-	-
*Crotalus voorhiesi**	X	-	-	-
Crotalus sp. indet.	X	X	X	X

Late Hemphillian Faunas

The Santee local fauna has only 6% of its 18 genera and 15% of 13 species extinct (Table 6). The Mailbox fauna has 6% of its 16 genera and 7% of its 14 species extinct (Table 6). The Devils nest fauna has 7% of its 15 general and 10% of its 10 species extinct (Table 6). The toad *Bufo holmani* may be temporally isolated in the late Hemphillian. Five species appear in the fossil record for the first time. These are: *Bufo woodhousii*, *Elaphe guttata*, *E. obsoleta*, *Pituophis melanoleucus*, and *Kinosternon flavescens*.

Amphibian and Reptile Extinctions Compared

No mid or late Hemphillian amphibian genera are extinct. This supports the evidences that the amphibians have been generically stable since at least the Barstovian (Holman, 1987). Twenty-three percent of the mid-Hemphillian salamander species, and 50% of the frog species are extinct; but none of the late Hemphillian salamander species and only 33% of the frog species are extinct.

No turtles were identified from the mid-Hemphillian fauna, but 14% of the late Hemphillian genera are extinct. None of the mid or late Hemphillian lizards are extinct. The greatest differences occur in the snakes. Twenty-nine percent of the mid-Hemphillian genera and

63% of the species are extinct. This contrasts with the late Hemphillian with only 11% of the genera and 10% of the species extinct. This is in agreement with evidence that the midcontinental snake fauna of North America became generically modern in latest Hemphillian or early Blancan time (ca. 4.5-4 Ma; Parmley, 1988a).

PALEOECOLOGICAL IMPLICATIONS

Paleoecological reconstructions were determined by assuming that fossil species and their living representatives have similar requirements and that extinct species have requirements similar to their modern descendants. Certain taxa present difficulties because they represent living forms with broad ecological tolerances, lack living analogs, or were identified only to the generic level.

Lemoyne Quarry Local Fauna

Based on sedimentary structure and abundant diatoms, Leite (1988) believes the site of deposition of the Lemoyne Quarry was a lake with minimal current or wave action. Fish remains, abundant ranid frogs and natricine snakes, and the unabraided condition of the fossils support Leite's interpretation. Moreover, the fact that many of the amphibian and reptile fossils have many delicate processes suggests that they were deposited in a quiet lake cove with little subsequent transport.

The Lemoyne Quarry produced only one small turtle, and it is problematic why such remains are not more common in the lacustrine deposit. The high quantity of silicious plant material in the matrix (Figure 5), as well as numerous diatoms and preserved ungulate footprints (Leite, 1988), suggests the area of the lake that preserved the bones was shallow and probably seasonal and, thus, not good habitat for turtles.

The communities adjacent to the cove indicated by the herpetofauna appear to have been bordering dense grasses, at least some wooded habitat, and more distant upland grasslands (Figure 30).

Members of the lake border community would have included the ranid frogs, *Nerodia hillmani*, *Neonatrix elongata*, and at least occasionally, the *Thamnophis* species. The ranid frogs would have lived in or near the cove, particularly in the surrounding dense vegetation. The habitat preferences of *N. hillmani* are not known, but its *Thamnophis*-like vertebrae suggest it would have been associated with the aquatic element of the site, where it may have been a secretive near-shore form. *Neonatrix elongata* may have had similar habits, as it also has small *Thamnophis*-like vertebrae. The *Thamnophis* species would have entered the water in search of food or to escape a predator. It is likely that the *Thamnophis* species occasionally wandered into wooded and grassland habitats as do modern members of the genus. Several other species would have at least occasionally entered the lake cove to drink or feed. The more terrestrial

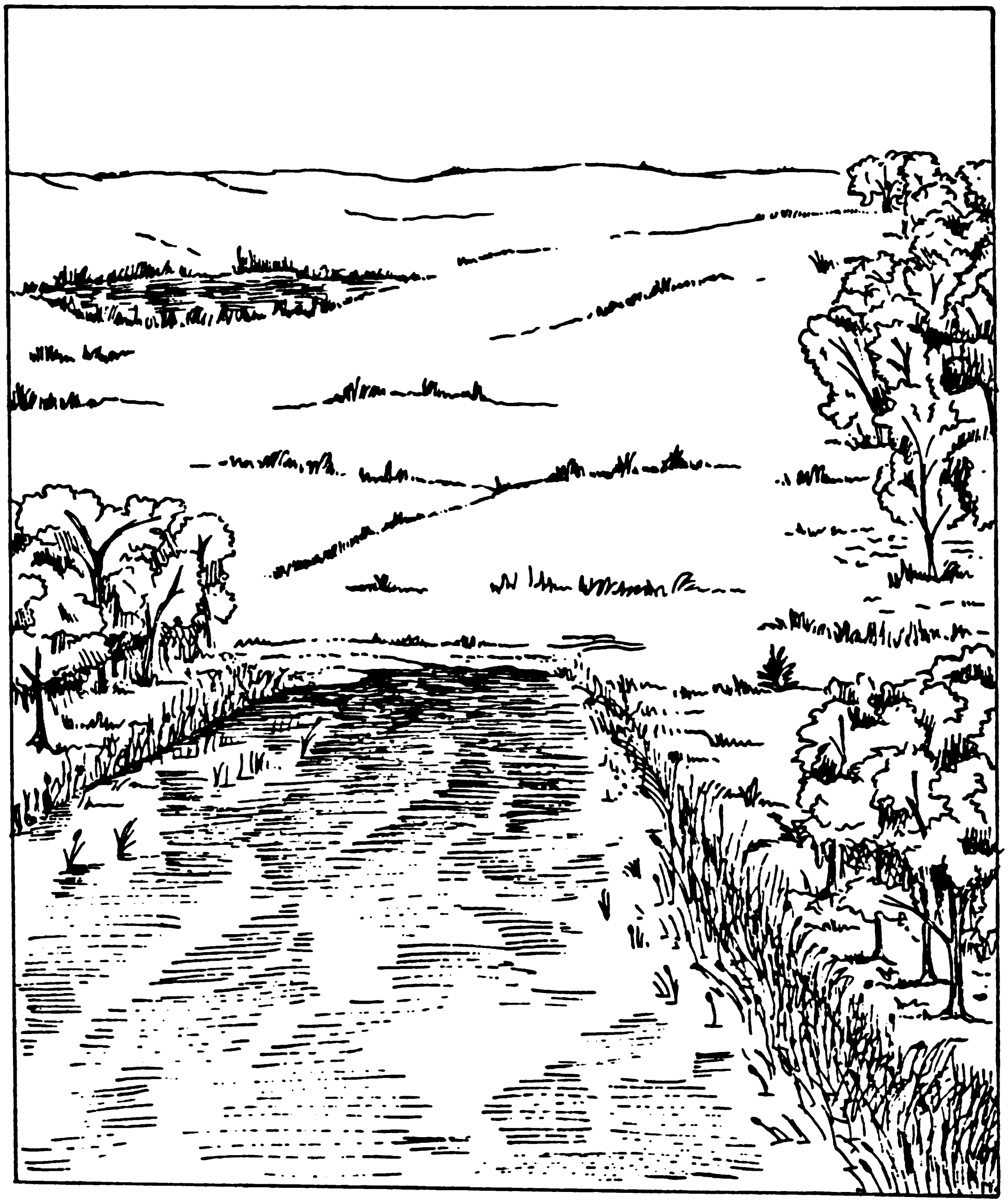

Figure 30. Ecological reconstruction of Lemoyne Quarry fossil locality in mid-Hemphillian time.

amphibians (e.g., *Ambystoma tigrinum*, and *Bufo* species) may have occasionally migrated to the water for breeding purposes.

Forms that would have lived in the wooded habitat include the plethodontid salamander or salamanders, *Ambystoma minshalli* possibly, *A. maculatum*, *Scaphiopus wardorum*, *Bufo hibbardi*, and *B. valentinensis* (Holman, 1987), *Hyla* cf. *H. gratiosa*, and probably the erycinine boid *Charina prebottae* and the colubrid snake *Lampropeltis triangulum*. Living plethodontid salamanders are chiefly inhabitants of moist woodlands (Conant, 1958; Wake, 1966), and it is unlikely their preferences have changed since late Miocene times. The salamanders *Ambystoma minshalli* and *A. maculatum* are members of the *maculatum* group, whose living members are forest-dwelling. *Scaphiopus wardorum* is an extinct toad whose closest relative, *S. holbrooki*, presently lives in woodlands. *Hyla gratiosa* may have lived along the forest edge migrating to the water to breed. *Charina prebottae* is believed to be directly ancestral to living *Charina bottae* (Holman, 1973a), thus it was likely similar to the living form, which lives in open woodlands and forest floors mainly in the Pacific Northwest (Stebbins, 1966). *Lampropeltis triangulum* occurs in many different habiatats today, but in the Plains states it most frequently occurs in wooded areas (personal observation).

It is likely that many of the other herpetofaunal members of the Lemoyne Quarry, particularly the snakes, wandered in and out of the wooded area in search of food. Others may have lived along the woodland ecotone as many snakes do today in the Great Plains region. Holman (1987) believes *Paleoheterodon tiheni* may have been such an ecotonal form.

The upland grassland community would have been inhabited by *Ophisaurus attenuatus*, *Salvadora paleolinata*, *Coluber* or *Masticophis*, *Arizona*, *Elaphe nebraskensis*, and probably *Crotalus voorhiesi*. The glass lizard, *O. attenuatus*, presently lives in grassland and prairies (Conant, 1958). In the plains areas of Kansas, this species frequently occurs near streams and ponds (Collins, 1982), thus the Lemoyne Quarry *O. attenuatus* may have lived in grasslands near the lake. Recent species of *Salvadora* occur in a variety of dry habitats such as prairies and rocky areas (Conant, 1958). The ecological requirements of *S. paleolineata* were probably similar. *Coluber* and *Masticophis* occur in grassland habitats, but *Coluber* also frequents open woodlands throughout the Great Plains region. *Elaphe nebraskensis* may have been either a grassland or a woodland species. *Arizona* is found today in xeric grassland habitat.

Late Hemphillian Local Faunas

Many of the late Hemphillian fossils are badly worn suggesting considerable postmortem transport. Based on biological and sedimentological evidence (Voorhies, 1977, 1988), the sites appear to reflect moderately deep streams or rivers associated with wooded and grassland areas. The biological components of the faunas are similar (i.e., all contain aquatic turtles, etc.), and the faunas are close enough in age (ca. 5 Ma) that a single reconstruction of the paleoenvironmental conditions of late Hemphillian NE Nebraska is appropriate as follows. A moderately large river or stream with some area of deep water was at least partly bordered by trees. Sandy flats probably occurred near the stream. The surrounding country consisted of upland grasslands interspersed with trees, rocky outcrops, and possibly small playa ponds or small creeks (Figure 31).

Aquatic forms were two frogs, five species of turtles, and two snakes as follow: *Rana pipiens*, *R. catesbeiana*, *Trionyx spiniferus*, *Emydoidea blandingii*, *Chrysemys picta*, *Macroclemys temminckii*, *Kinosternon flavescens*, *Nerodia* and *Thamnophis* species. *Rana catesbeiana* would have lived mainly along quiet vegetated areas of the river, while *R. pipiens* would have inhabited its shallow grassy margins. *Trionyx spiniferus*, *E. blandingii*, and C. *picta* live in NE Nebraska today and

Figure 31. Ecological reconstruction of Devils Nest, Santee and Mailbox Prospect quarries in late Hemphillian time.

live near the fossil localities. Two species presently do not occur in NE Nebraska, *M. temminckii* and *K. flavescens*. *Macroclemys temminckii* is the largest freshwater turtle in North America, with a limited range in the SE United States (Conant, 1958). This species would require a climate with milder winters to live in NE Nebraska today, thus its presence suggests less extreme winter temperatures in late Hemphillian times. *Kinosternon flavescens* is widespread in the Great Plains occurring as far north as north central Nebraska, where it prefers nonalkaline ponds and lakes (Lynch, 1985). The species may have been most common in playa ponds during late Hemphillian time. Collectively, the late Hemphillian turtles are characteristic of a river with some deep water areas, quiet coves, and sandy areas near shore for basking and nesting. The *Thamnophis* and *Nerodia* species would have hunted along the river bank, but also would have entered the water for food and protection. The *Thamnophis* species, particularly *T. radix* and *T. marcianus*, would have wandered into the wooded and grassland communities.

Herpetofaunal members of the wooded habitat would have included *Lampropeltis triangulum* possibly, *L. getulus*, and *Elaphe obsoleta*. Both species of *Lampropeltis* utilize a variety of habitats today (Conant, 1958), but prefer woodlands when such habitat is available (personal observation). Elaphe obsoleta prefers riparian woodlands (Parmley, 1986a) where it spends much time in trees, but it also occurs in grasslands.

Grassland species are the most common members of the late Hemphillian herpetofauna. These are: Bufo woodhousii, B. cognatus or B. speciosus, Geochelone sp., Terrapene sp. possibly, Crotaphytus cf. C. collaris, Eumeces cf. E. obsoletus, Elaphe cf. E. guttata, E. obsoleta, Pituophis melanoleucus, Heterodon cf. H. nasicus, H. cf. H. platyrhinos and probably Crotalus sp. All of these tax, particularly the snakes, undoubtedly moved into the other paleoecological communities from time to time in search of food, water, or shelter. Recent members of Geochelone are mainly nonburrowing subtropical turtles, suggesting late Miocene Geochelone would not have been able to survive freezing temperatures. This suggests a relatively frost-free climate in the late Hemphillian. Bufo woodhousii, Eumeces obsoletus, and the Heterodon species would have required soft soil or sandy areas for burrowing. Such habitat may have been available near the aquatic habitat. Crotaphytus collaris would have required rock outcrops.

FAUNAL SUCCESSION OF MIDCONTINENTAL ARIKAREEAN THROUGH BLANCAN SNAKES

The Mio-Pliocene fossil record of midcontinental North America (Figure 32) importantly documents changes that occurred in its snake fauna. Miocene colubrid snakes rapidly radiated and diversified in parallel with near extinction of erycinine boids.

A review of Arikareean (early Miocene; ca. 24 Ma) through Blancan (Pliocene; ca. 2 Ma) midcontinental snakes documents when boid snakes disappeared from midcontinental North America, and suggest when the midcontinental colubrid snake fauna became generically modern. Forty-two biochronologic sites were chosen for this analysis (Appendix A). Although gaps exist in our knowledge of midcontinental Miocene and Pliocene snakes (i.e., Clarendonian snakes are known mainly from the WaKeeney local fauna of Kansas, Holman, 1975), a general history may be attempted. An analysis of midcontinental Arikareean through Blancan snake genera follows.

Arikareean

Our knowledge of midcontinental Arikareean snakes is limited to four extinct genera of erycinine boids

Figure 32. Midcontinental region of North America where Arikareean (Miocene) through Blancan (Pliocene) snake fossils have been studied.

(Table 7) and the extinct boiform incertae sedis genus Goinophis, all extending from earlier Whitneyan and Orellan (Oligocene) time. There are no generic records of colubrids from the Arikareean, but they were certainly present, as this family dates back nearly 35 million years to the middle Oligocene early Orellan of Colorado (Holman, 1984c). There is also an undetermined colubrid vertebra from the Arikareean of Nebraska (Holman, 1976a), but colubrids were apparently not diversified or abundant. A Viperidae appeared in the midcontinental region during this time, but was not generically identified (Holman, 1979). It is unknown whether these colubrids and viperids emigrated from Eurasia or arose in North America. In summary, the known Arikareean snake fauna was dominated by erycinine boids (Figure 33), but at least two extinct colubird genera (Figure 34) and one viperid genus were present (Table 7).

Hemingfordian

The Hemingfordian snake fauna is more diverse than the Arikareean fauna having three erycinine boid and six predominantly archaic colubrid genera (Figures 33 and 34; Table 7). The living erycinine genus Charina appears as do all the colubrid genera (Table 7). The rather diverse colubrid fauna in the Hemingfordian suggests this groups Miocene radiation preceded the Hemingfordian.

Table 7. Snake genera from the Arikareean through Blancan midcontinental region of North America (from Appendix A).

Taxon	Land Mammal Age						
	Ar.	He.	Ba.	Cl.	EMH.	LH.	B.
Erycinine genera							
Clamagras	X	X	X				
Geringophis	X		X				
Anilioides	X						
Ogmophis	X	X	X	X			
Charina		X	X		X		
Pterygoboa			X				
Tregophis				X			
Lichanura					X		
Extinct colubrid genera							
Ameiseophis		X	X				
Dakotaophis		X	X				
Paracoluber		X	X		X		
Pseudocemorphora		X					
Neonatrix		X	X		X		
Paleoheterodon			X	X	X	X	
Nebraskophis			X		X		
Texasophis			X	X			
Dryinoides			X				
Miocoluber					X		
Paurophis					X		
Living colubrid genera							
Salvadora		X	X		X		
Elaphe		X	X	X	X	X	X
Lampropeltis		X	X	X	X	X	X
Nerodia		X	X	X	X	X	X
Thamnophis		X	X	X	X	X	X
Coluber							
Masticophis				X	X	X	X
Heterodon					X	X	X

Table 7. Continued

	Land Mammal Age						
Taxon	Ar.	He.	Ba.	Cl.	EMH.	LH.	B.
Pituophis						X	X
Rhinocheilus							X
Arizona					X		
cf. *Virginia*					X		
Viperidae							
Agkistrodon					X		X
Crotalus					X	X	X
Sistrurus							X
Elapidae							
Micrurus			X				

*Ar., Arikareean; He., Hemingfordian; Ba., Barstovian; Cl., Clarendonian; EMH., early & middle Hemphillian; LH., late Hemphillian; B., Blancan.

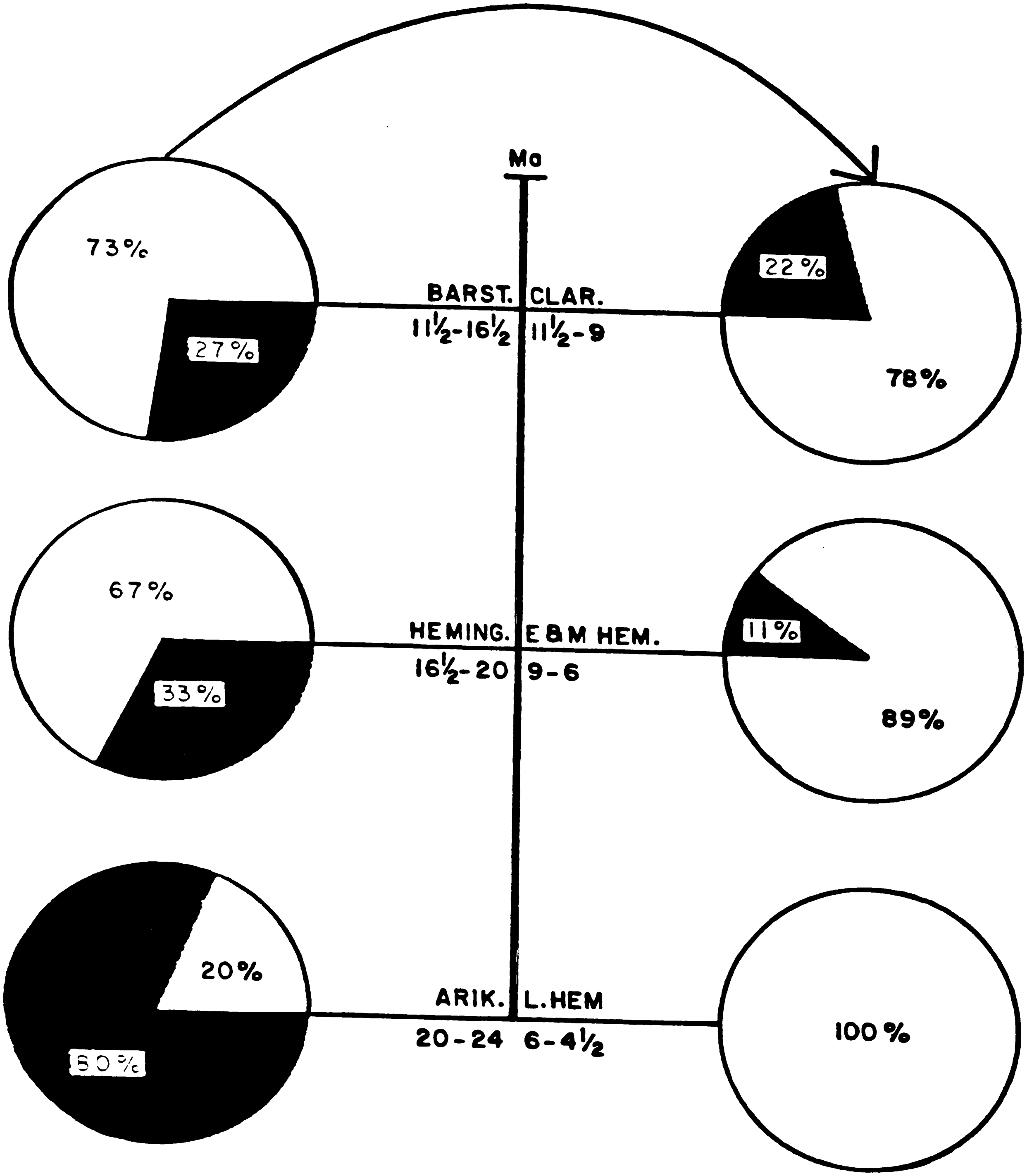

Figure 33. Percentages of boid (black) to colubrid (white) genera from Arikareean to late Hemphillian time.

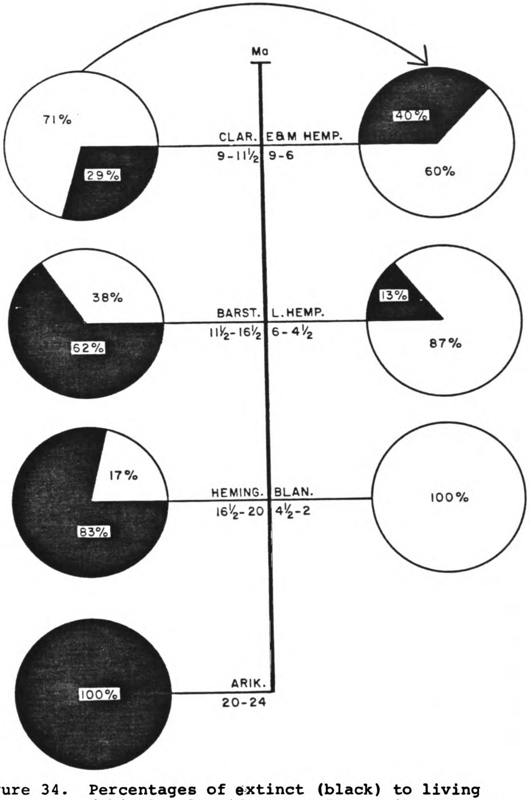

Figure 34. Percentages of extinct (black) to living (white) colubrid genera from Arikareean to Blancan time.

Barstovian

The Barstovian snake fauna is better documented than the Hemingfordian. Five erycinine boid genera, 13 colubrid genera, a generically unidentified viperid and a living elapid genus (Micrurus; Table 7) were present. Xenodontinae (Paleoheterodon), living natricines (Thamnophis and Nerodia), the living Colubrinae genera Lampropeltis and Elaphe, and the Elapidae genus Micrurus appear for the first time. Boids were still prominent in the midcontinental snake fauna and eight of the 13 colubrid genera were extinct. The greatest change from the Hemingfordian snake fauna was the continued expansion of colubrids over boids (Figure 33), and a trend towards generic modernization of colubrids, but archaic genera still outnumber living colubrid genera (Figure 34).

Clarendonian

The midcontinental Clarendonian snake fauna comes mainly from the WaKeeney local fauna of Kansas (Holman, 1975) which has to extinct erycinine boid genera (Ogmophis and Tregophis which appear to be temporally isolated) and seven genera of colubrids (Table 7). Of the colubrid genera, only Paleoheterodon and Texasophis are from earlier times. There were almost certainly more boids in the Clarendonian than is suggested by the fossil record because at least one genus, Charina, is known to occur before and after this age (Holman, 1976b; Parmley, 1988a). The only previously unreported colubrid genus is Coluber or Masticophis. Thus the trend in the Clarendonian is for a decline in boid genera, continued expansion of colubrids over boids (Figure 33), and a continued modernization of the colubrid fauna, with living genera outnumbering extinct ones (Figure 34). The relatively high percentage of modern colubrid genera in the Clarendonian may be due to the poor fossil record of this period.

Early-to-Mid-Hemphillian

The midcontinental early and mid-Hemphillian snake faunas are so similar that I have combined them. The only genus that occurs in the early Hemphillian, but not the mid-Hemphillian, is Miocoluber, known only from the Higgins local fauna of Texas (Parmley, 1988a). Conversely, Paurophis (described here) occurs in the mid-Hemphillian, but is not known from the early Hemphillian. Further study of snakes from both units of the Hemphillian may show that more differences exist. As in the Clarendonian, two erycinine boid genera are known from the Hemphillian. But unlike the Clarendonian, both are living genera, Charina and Lichanura, of which the later appears for the first time (Table 7). This suggests that four genera of archaic boids became extinct some time between Barstovian and early Hemphillian time. Six of the total 15 Hemphillian colubrid genera are extinct forms (Table 7), of which Neonatrix, Nebraskophis, Paleoheterodon, and Paracoluber are from earlier times. The extinct genera Paurophis and Miocolubr may be isolated to this period. The living genera Arizona, Heterodon, and cf. Virginia appear for the first time. The New World viperine genera Crotalus and Agkistrodon are present with the latter possibly for the first time. Thus, early-to-mid-Hemphillian time shows a small modern erycinine fauna that is almost entirely dominated by colubrids (Figure 33), and a colubrid fauna dominated by living genera (Figure 34).

Late Hemphillian

The late Hemphillian snake fauna of midcontinental North America consists of colubrids and viperids, which, except for one colubrid genus, are all living (Table 7). No boids are known from this time suggesting that by five million years ago, this family of snakes had become extinct in the region, and that surviving forms Charina and Lichanura were already restricted to their present northwest and southwest distributions. Eight genera of colubrids are known from the late Hemphillian, of which Paleoheterodon is the only extinct form (Table 7). Pituophis appears for the first time and the Recent viperid genus Crotalus is present. Thus the late Hemphillian snake fauna differs from the early-to-mid-Hemphillian fauna in lacking erycinine boids (Figure 33), and in having a markedly modern colubrid fauna (Figure 34). Five archaic colubrid genera of early-to-mid-Hemphillian time do not appear to have survived into the late Hemphillian, suggesting that an episode of extinction occurred between 6 to 5 million years ago.

Blancan

The midcontinental Blancan snake fauna is comprised of nine living colubrid genera and three living viperid genera (Table 7) Thus by approximately 4.5 to 4 million years ago, the midcontinental snake fauna was entirely modern at the generic level (Figure 34).

Summary

The Arikareean (early Miocene) in midcontinental North America was dominated by erycinine boids. Soon after the Arikareean boids were dominated by rapidly radiating colubrids. By mid-Hemphillian time only two living erycinine genera remained, and by the late Hemphillian (cf. 5 Ma), these were extinct.

Colubrids probably began their Miocene radiation in the Arikareean. The generic diversity of archaic and living genera quickly and steadily increased into the mid-Hemphillian. By latest Hemphillian or early Blancan time, the midcontinental colubrid fauna was entirely modern at the generic level.

Two especially marked generic extinction events appear to have occurred. One took place among erycinine boids between Barstovian and early Hemphillian time when four genera became extinct. Another took place among colubrid snakes when five archaic genera became extinct between mid and late Hemphillian time.

CONCLUSIONS

This study substantiates the hypothesis by Parmley (1988a) that the Hemphillian was the critical age for the modernization of the North American snake fauna. In this evolutionary event, boid genera became dominated by colubrid genera, boids became extinct, and finally archaic colubrid genera were dominated by modern ones.

Suggested reasons for this event may reflect any or all of the following dynamics of the Miocene: (1) temporal succession of forest communities to grasslands and steppe, (2) immigration of modern colubrid genera from Eurasia, (3) radiation of passerine birds and cricetid rodents as a new food supply for large snakes, and (4) competition for all of the new environmental and biotic resources among resident boid, archaic colubrid, and modern colubrid genera. A brief discussion of each of these points follows, but refinement and interpretation of these points await further studies.

The uplift of the Rocky Mountains in early Miocene time disrupted upper atmosphere circulation patterns resulting in major changes of vegetational communities across midcontinental North America (Webb, 1983).

Temporal succession of forest communities to grassland and finally steppe was paralleled by the demise of boids and rapid radiation and modernization of colubrids (Figures 33 and 34). Thus a correlation between Miocene snake evolution and widespread vegetational changes might be suggested.

Presence of modern colubrid genera in the Oligocene of Europe (Rage, 1984) as well as modern finds of Miocene colubrid genera common to both Europe and North America (Rage and Holman, 1984; Szyndlar, 1987) suggests the rapid Miocene radiation of colubrids in North America may have followed a widespread immigration of modern colubrid genera from Eurasia. Such an invasion in the early Miocene would account for the diverse colubrid fauna of the Hemingfordian.

Interestingly, the rapid Miocene radiation of passerine birds and cricetid rodents is roughly coeval with the Miocene radiation of colubrid snakes (Stanley, 1979). Small birds and rodents would have provided large colubrid snakes with a new and probably abundant food supply. Early Miocene colubrids were small snakes only large enough to have preyed upon invertebrates or very small vertebrates. It is not until the radiation of small passerine birds and small rodents that colubrids large enough to eat large prey appear in the fossil record.

With the appearance of grasslands across midcontinental North America, competition for new environmental and biotic resources among Miocene snakes likely helped determine the composition of the modern fauna. The apparent adaptive ability of colubrids to invade this new biome may have contributed to the ultimate demise of boids.

SUMMARY

Herpetofaunas of the early Hemphillian Potter Quarry, mid-Hemphillian Lemoyne Quarry, and late Hemphillian Santee, Devils Nest and Mailbox Prospect quarries are identified. The faunas are from the Ogallala Group, and are referred to the Ash Hollow Formation. The Potter Quarry local fauna, a ca. 8 million year old stream deposit in SW Nebraska, yielded too few fossils for a meaningful comparison with the others. But the mid- and late Hemphillian faunas are diverse enough for a comparison which shows the mid-Hemphillian fauna has four times as many extinct taxa as the late one (44% versus 11%).

The mid-Hemphillian Lemoyne Quarry local fauna is a ca. 7 million year old lake deposit in SW Nebraska. The ecological setting was a quiet, shallow lake cove with bordering dense grasses, some woodlands, and distant upland grasslands. The fauna has 22% of its 23 genera and 55% of its 29 species extinct. One genus and three species are new (*Paurophis*, *Elaphe lemoynensis*, *Nebraskophis corneri*, *Crotalus voorhiesi*).

The late Hemphillian Santee, Devils Nest, and Mailbox Prospect local faunas are ca. 5 million year old

stream deposits. The ecological setting for the fauna was a moderately large river or stream which was at least partly bordered by trees and upland grasslands. Nine percent of the 23 genera and 8% of the 24 species are extinct. The toad Bufo holmani is new.

The Arikareean (early Miocene) through Blancan (Pliocene) record of midcontinental North America snake genera is reviewed. The Arikareean (ca. 24 Ma) is dominated by erycinine boids, but by Clarendonian time (ca. 11 Ma) colubrid snakes dominated the region. By late Hemphillian time (ca. 5 Ma) boids were extinct, and by the Blancan (ca. 4 1/2 Ma) colubrids were modern at the generic level. Extinction events took place among erycinine boids between Barstovian (ca. 16 Ma) and early Hemphillian time (ca. 9 Ma) when four genera became extinct, and among colubrid snakes between mid-Hemphillian (ca. 7 Ma) and late Hemphillian time (ca. 6 Ma) when five genera became extinct.

The hypothesis by Parmley (1988a) that the Hemphillian was the critical age for modernization of the North American snake fauna is substantiated. Suggested reasons for this evolutionary event may reflect the following dynamics of the Miocene: (1) temporal succession of forest communities to steppe, (2) immigration of colubrid genera from Eurasia, (3) radiation of passerine birds and cricetid rodents as new food supply, and (4) competition for new environmental and biotic resources.

APPENDIX

APPENDIX A

FAUNAL LISTINGS OF MIDCONTINENTAL ARIKAREEAN THROUGH BLANCAN SNAKES

Arikareean

1. Snakes from the Gering Formation (lower Miocene) of Nebraska. (J. A. Holman. 1976c. Herpetologica 32:88-94).

Erycinae:
Calamagras platyspondyla
Calamagras angulatus
Geringophis depressus
Anilioides nebraskensis
Family Incertae Sedis
Goinophis minusculus

2. A boid and a colubrid from the Harrison Formation (lower Miocene: Arikareean) of Sioux County, Nebraska. (J. A. Holman. 1976a. Herpetologica 32:387-389).

Erycinae:
Boid indet.
Colubridae:
Colubrid indet.

3. Additional snakes from the Miocene of Western Nebraska. (J. A. Holman, 1977c. Herpetologica 33:443-446).

Erycinae:
Geringophis yatkolae
Ogmophis cf. *O. miocompactus*
Calamagras cf. *C. platyspondyla*
Colubrid:
Colubrinae indet.

4. Snakes of the Monroe Creek Formation (lower Miocene: Arikareean) of Wyoming. (J. A. Holman. 1977d. Copeia 1977:193-194).

Erycinae:
Calamagras cf. C. angulatus
Anilioides nebraskensis
Family Incertae Sedis:
? Geringophis depressus

5. A herpetofauna from an eastern extension of the Harrison Formation (early Miocene: Arikareean), Cherry County, Nebraska. (J. A. Holman. 1981b. J. Vert. Paleont. 1:49-56).

Erycinae:
Calamagras angulatus
Calamagras platyspondyla
Ogmophis miocompactus
Geringophis depressus
Anilioides nebraskensis

Viperidae:
Viperid gen. et sp. indet.

Hemingfordian

1. Snakes of the Split Rock Formation (Middle Miocene), central Wyoming. (J. A. Holman, 1977d. Herpetologica 32:419-426).

Erycinae:
Calamagras weigeli
Ogmophis cf. O. miocompactus
Charina prebottae
Extinct colubrid genera:
Ameiseophis robinsoni
Dakotaophis greeni
Paracoluber storeri
Pseudocemophora cf. P. antiqua
Living colubrid genera:
Salvadora paleolineata
Viperidae:
cf. Crotalinae indet.

2. Snakes from the Rosebud Formation (Middle Miocene) of South Dakota. (J. A. Holman. 1976b. Herpetologica 32:41-58).

Erycinae:
Ogmophis miocompactus
Calamagras weigeli
Charina prebottae
Pterygoboa miocenica
Extinct colubrid genera:
Neonatraix elongata
Dakotaophis greeni
Living colubrid genus:
Salvadora paleolineata

3. Additional snakes from the Miocene of western Nebraska. (J. A. Holman. 1977c. Herpetologica 33:443-446). (Marsland Fm.)

Erycinae:
Charina prebottae
Extinct colubrid genus:
Dakotaophis greeni
Living colubrid genus:
Salvadora paleolineata

Barstovian

1. Fossil snakes form the Valentine Formation of Nebraska. (J. A. Holman, 1964. Copeia 4:631-637).

Extinct colubrid genus:
Paleoheterodon tiheni
Living colubrid genera:
Elaphe nebraskensis
Lampropeltis similis

2. Herpetofauna of the Wood Mountain Formation (upper Miocene) of Saskatchewan. (J. A. Holman. 1970. Canadian J. Earth Sci. 7:1317-1325).

Erycinae:
Charina prebottae
Extinct colubrid genus:
Paracoluber storeri
Living colubrid genera:
Elaphe nebraskensis
Lampropeltis similis

3. Reptiles of the Egelhoff local fauna (upper Miocene) of Nebraska. (J. A. Holman, 1973c. Univ. Michigan. Cont. Mus. Paleont. 24:125-134).

Erycinae:
Charina prebottae
Extinct colubrid genera:
Neonatrix elongata
Nebraskophis skinneri
Living colubrid genera:
Salvadora paleolineata
Elaphe nebraskensis

4. Amphibians and reptiles from the Gulf Coast Miocene of Texas. (J. A. Holman. 1977a. Herpetologica 33:391-403).

Boinae:
Boinae genus indet.
Erycinae:
Ogmophis miocompactus
Calamagras weigeli
Extinct colubrid genera:
Dakotaophis greeni
Texasophis fossilis
Neonatrix elongata
Living colubrid genera:
Elaphe nebraskensis
Salvadora paleolineata
Viperidae:
Viperidae sp. indet.

5. Upper Miocene snakes (Reptilia, Serpentes), from southeastern Nebraska. (J. A. Holman. 1977b. J. Herpetol. 11:323-335).

Erycinae:
Geringophis depressus
Pterygoboa miocenica
Extinct colubrid genera:
Paleoheterodon tiheni
Neonatrix elongata
Nebraskophis skinneri
Living colubrid genera:
cf. *Nerodia*
cf. *Thamnophis*
Salvadora paleolineata
Elaphe nebraskensis

Viperidae:
? Crotalinae indet.
Elapidae:
Micrurus sp. indet.

6. A late Tertiary stream channel fauna from South Bijou Hill, South Dakota. (M. Green and J. A. Holman. 1977. J. Paleont. 51:543-547).

Erycinae:
Charina prebottae
Living colubrid genera:
Salvadora sp. indet.
Elaphe nebraskensis
Lampropeltis similis

7. Herpetofauna of the Bijou Hills local fauna (Late Miocene: Barstovian) of South Dakota. (J. A. Holman. 1978. Herpetologica 34:253-257).

Erycinae:
Ogmophis miocompactus
Charina prebottae
Extinct colubrid genera:
Paleoheterodon tiheni
Neonatrix elongata
Dakotaophis greeni
Ameiseophis robinsoni
Living colubrid genus:
Salvadora paleolineata

8. A small herpetofauna from the type section of the Valentine Formation (Miocene: Barstovian), Cherry County, Nebraska. (J. A. Holman and R. M. Sullivan. 1981. J. Paleont. 55:138-144).

Extinct colubrid genus:
Neonatarix elongata
Living colubrid genus:
Salvadora paleolineata

9. New herpetological species and records from the Norden Bridge (Miocene: late Barstovian) of Nebraska. (J. A. Holman. 1982b. Trans. Nebraska Acad. Sci. 10:31-36).

Erycinae:
Geringophis depressus

Extinct colubrid genera:
Ameiseophis cf. _A_. _robinsoni_
Nebraskophis skinneri
Neonatrix elongata
Neonatrix magna
Living colubrid genus:
Salvadora paleolineata
Viperidae:
Viperid indet.

10. The Hottell Ranch rhino quarries (basal Ogallala: Medial Barstovian), Banner County, Nebraska Part I: geologic setting, faunal lists, lower vertebrates. (M. L. Voorhies, J. A. Holman, and X. Xiang-Xu. 1987. Univ. Wyoming Contrib. Geo. 25:55-69).

Extinct colubrid genera:
Paleoheterodon tiheni
Dakotaophis greeni
Living colubrid genera:
Elaphe nebraskensis
Lampropeltis similis
Salvadora paleolineata
Nerodia sp. _indet_.
Thamnophis sp. indet.

11. Herpetofauna of the Egelhoff site (Miocene: Barstovian) of north-central Nebraska. (J. A. Holman. 1987. J. Vert. Paleont. 7:109-120).

Erycinae:
Charina prebottae
Extinct colubrid genera:
Paleoheterodon tiheni
Ameiseophis cf. _A_. _robinsoni_
Nebraskophis skinneri
Neonatrix elongata
Neonatrix magna
Living colubrid genera:
Elaphe nebraskensis
Lampropeltis similis
Salvadora paleolineata
Nerodia sp. _indet_.
Thamnophis sp. indet.

12. A new genus of colubrid snake from the Upper Miocene of North America. (W. Auffenberg. 1958. Amer. Mus. Nat. Hist. Novitates 1874:1-16). (Montana)

Extinct colubrid genus:
Dryinoides oxyrhachis

Clarendonian

1. Herpetofauna of the WaKeeney local fauna (Lower Pliocene: Clarendonian) of Trego County, Kansas. (J. A. Holman, 1975. Univ. Michigan Paps. Paleont. 12:49-66).

Erycinae:
Tregophis brevirachis
Ogmophis pliocompactus
Extinct colubrid genera:
Paleoheterodon sp. indet.
Living colubrid genera:
Natrix hillmani
Thamnophis sp. indet.
Coluber or Masticophis
Elaphe sp. indet.
Lampropeltis similis

2. A Pliocene colubrid snake (Reptilia: Colubridae) from west-central Nevada. (J. Ruben. 1971. Paleo Bios 13:1-19).

Living colubird genus:
Coluber sp. indet. (partial skeleton in matrix)

3. Texasophis (Reptilia: Colubridae), an addition to the Miocene (Clarendonian) of North America. (J. A. Holman. 1984b. Copeia 1984: 660-661.)

Extinct colubrid genus:
Texasophis wilsoni

4. Herpetofauna of the Mission local fauna (Lower Pliocene) of South Dakota. (J. A. Holman. 1973b. J. Paleont. 47:462-464).

Living colubrid genus:
Lampropeltis similis

Early Hemphillian

1. Early Hemphillian (late Miocene) snakes from the Higgins local fauna of Lipscomb County, Texas. (D. Parmley. 1988a. J. Vert. Paleont. 23:322-327.)

Erycinae:
Charina prebottae
Extinct colubrid genera:
Paleoheterodon tiheni
Miocoluber dalquesti
Living colubrid genera:
Coluber or Masticophis
Thamnophis cf. T. sirtalis or T. proximus

2. Potter Quarry local fauna, Cheyenne Co., Nebraska (reported here).

Extinct colubrid genus:
Paleoheterodon tiheni
Living colubrid genus:
Thamnophis sp. indet.

Mid-Hemphillian

1. Herpetofauna of the Coffee Ranch local fauna (Hemphillian Land Mammal Age) of Texas. (D. Parmley, 1984. pp. 97-106 in N. V. Horner (ed.), Festschrift for Walter W. Dalquest. Midwestern State Univ. Press, Wichita Falls, Texas).

Erycinae:
Ogmophis pliocompactus
Extinct colubrid genera:
Paleoheterodon tiheni
Paracoluber storeri
Living colubrid genera:
Salvadora paleolineata
Elaphe nebraskensis

2. Lampropeltis similis from the Coffee Ranch local fauna (Hemphillian Land Mammal Age) of Texas. (D. Parmley. 1987. Texas J. Sci. 39:123-128).

Living colubrid genus:
Lampropeltis similis

3. Lemoyne Quarry, Keith Co., Nebraska (reported here).

Erycinae:
Charina prebottae
Lichanura sp indet.
Extinct colubrid genera:
Nebraskophis corneri
Nebraskophis skinneri
Paurophis lewisi

Paracoluber cf. P. storeri
Neonatarix elongata
Paleoheterodon tiheni
Living colubrid genera:
Arizona sp. indet.
Coluber or Masticophis
Lampropeltis getulus
Lampropeltis triangulum
Lampropeltis sp. indet.
Salvadora paleolineata
Elaphe nebraskensis
Elaphe lemoynensis
Elaphe sp. indet.
Nerodia hillmani
Nerodia sp. indet.
Thamnophis cf. T. proximus or T. sauritus
Thamnophis cf. T. cyrtopsis
Thamnophis cf. T. marcianus or T. radix
Thamnophis sp. indet.
cf. Virginia
Heterodon cf. H. platyrhinos
Heterodon cf. H. nasicus
Heterodon sp. indet.
Viperidae:
Agkistrodon sp. indet.
Crotalus voorhiesi
Crotalus sp. indet.

Late Hemphillian

1. A fossil snake (Elaphe vulpina) from a Pliocene ash bed in Nebraska. (J. A. Holman. 1982a. Trans. Nebraska Acad. Sci. 10:37-42).

Living colubrid genus:
Elaphe vulpina

2. Devils Nest Airstrip local fauna, Knox County, Nebraska. (reported here).

Living colubrid genera:
Coluber or Masticophis
Lampropeltis triangulum
Lampropeltis getulus
Elaphe obsoleta
Elaphe cf. E. guttata

<u>Pituophis</u> <u>melanoleucus</u>
<u>Thamnophis</u> sp. indet.
Viperidae:
<u>Crotalus</u> sp. indet.

3. Mailbox Prospect, Antelope Co., Nebraska (reported here).

Extinct colubrid genus:
<u>Paleoheterodon</u> <u>tiheni</u>
Living colubrid genera:
<u>Coluber</u> or <u>Masticophis</u>
<u>Lampropeltis</u> <u>triangulum</u>
<u>Elaphe</u> cf. <u>E</u>. <u>guttata</u>
<u>Pituophis</u> <u>melanoleucus</u>
<u>Nerodia</u> sp. indet.
<u>Thamnophis</u> cf. <u>T</u>. <u>proximus</u> or <u>sauritus</u>
<u>Thamnophis</u> cf. <u>T</u>. <u>marcianus</u> or <u>T</u>. <u>radix</u>
<u>Thamnophis</u> sp. indet.
<u>Heterodon</u> cf. <u>H</u>. <u>platyrhinos</u>
<u>Heterodon</u> cf. <u>H</u>. <u>nasicus</u>
<u>Heterodon</u> sp. indet.
Viperidae:
<u>Crotalus</u> sp. indet.

4. Santee local fauna, Knox Co., Nebraska (reported here).

Living colubrid genera:
<u>Coluber</u> or <u>Masticophis</u>
<u>Lampropeltis</u> <u>getulus</u>
<u>Elaphe</u> sp. indet.
<u>Pituophis</u> cf. <u>P</u>. <u>melanoleucus</u>
<u>Thamnophis</u> cf. <u>T</u>. <u>proximus</u> or <u>T</u>. <u>sauritus</u>
<u>Thamnophis</u> sp. indet.
<u>Heterodon</u> sp. indet.
Viperidae;
<u>Crotalus</u> sp. indet.

<u>Blancan</u>

1. Blancan age faunas listed in: B. H. Brattstrom. 1967. A succession of Pliocene and Pleistocene snake faunas from the High Plains of the United States. Copeia 1967:188-202.

a. Buis Ranch local fauna, Beaver Co., Oklahoma.

Living colubrid genera:
<u>Thamnophis</u> sp. indet.

Heterodon plionasicus
Coluber constrictor
Elaphe nr. E. obsoleta
Lampropeltis triangulum
Viperidae:
Crotalus cf. C. viridis

b. Fox Canyon, Meade Co., Kansas.

Living colubrid genera:
Nerodia sp. indet.
Thamnophis sp indet.
Elaphe obsoleta
Heterodon plionasicus
Heterodon platyrhinos
Lampropeltis getulus
Lampropeltis triangulum
Pituophis melanoleucus
Coluber constrictor
Viperidae:
Agkistrodon contortrix
Crotalus viridis
Sistrurus catenatus

c. Rexroad local faunas: location no. 3, Meade Co., Kansas.

Living colubrid genera:
Nerodia sp. indet.
Thamnophis sp. indet.
Coluber constrictor
Lampropeltis getulus
Elaphe obsoleta
Heterodon plionasicus
Heterodon platyrhinos
Viperidae
Agkistrodon contortrix
Crotalus viridis
Sistrurus catenatus

d. Saw Rock local fauna: Seward Co., Kansas

Living colubrid genera:
Nerodia sp indet.
Thamnophis sp. indet.
Elaphe obsoleta
Coluber constictor
Viperidae:
Agkistrodon contortrix

2. Upper Pliocene snakes from Idaho. (J. A. Holman. 1968. Copeia 1968:152-158).

Living Colubrid genera:
Nerodia hibbardi
Thamnophis sp. indet.
Elaphe pliocenica
Elaphe vulpina
Lampropeltis sp. indet.

3. A fossil snake of the genus *Heterodon* from the Pliocene of Kansas. (J. A. Peters. 1953. J. Paleont. 27:328-331).

Living colubrid genus:
Heterodon plionasicus

4. Herpetofauna of the Beck Ranch local fauna (upper Pliocene: Blancan) of Texas. (K. Rogers. 1976. Publ. Mus. Michigan State Univ. Paleont. Ser. 1:167-200).

Erycinae:
Ogmophis parvus
Living colubrid genera:
Heterodon platyrhinos
Heterodon plionasicus
Coluber constrictor
Masticophis flagellum
Nerodia sp. indet.
Nerodia erythrogaster
Nerodia cf. *N. hibbardi*
Nerodia cyclopion or
Nerodia rhombifera
Thamnophis sp. indet.
Thamnophis sirtalis
Thamnophis marcianus
Elaphe guttata
Elaphe obsoleta
Elaphe vulpina
Pituophis melanoleucus
Rhinocheilus lecontei
Lampropeltis getulus
Lampropeltis triangulum
Viperidae:
Akgistrodon contortrix
Crotalus atrox
Crotalus viridis
Sistrurus catenatus

5. A new Pliocene snake, genus _Elaphe_, from Oklahoma. (J. A. Holman. 1973a. Copeia 1973:574-584).

Living colubrid genus:
Elaphe buisi

6. Herpertofaunas of the Big Springs and Hornet's Nest Quarries (northeastern Nebraska, Pleistocene: late Blancan). (K. Rogers. 1984. Trans. Nebraska Acad. Sci. 12:81-94).

Living colubrid genera:
Coluber constrictor
Elaphe guttata
Elaphe vulpina
Lampropeltis calligaster
Lampropeltis getulus
Rhinocheilus lecontei
Nerodia rhombifera
Nerodia sipedon or
Nerodia hibbardi
Nerodia sp. indet.
Regina grahamii
Thamnophis proximus
Thamnophis radix
Thamnophis sirtalis
Thamnophis sp. indet.
Heterodon nasicus
Heterodon platyrhinos
Viperidae:
Agkistrodon cf. _A_. _contortrix_
Crotalus horridus
Sistrurus catenatus

7. Amphibians and reptiles of the Sand Draw local fauna (J. A. Holman. 1972. _in_ Skinner, M. F. et al. Early Pleistocene preglacial and glacial rocks and faunas of north-central Nebraska. Bull. Amer. Mus. Nat. Hist. 148:55-71).

Living colubrid genera:
Nerodia sipedon
Thamnophis sp. indet.
Heterodon platyrhinos
Coluber sp indet. or _Masticophis_ sp. indet.
Elaphe vulpina

8. Geology and paleontology of the Early Pleistocene (late Blancan) White Rock fauna from north-central Kansas. (R. E. Eshelman. 1975. Univ. Michigan Paps. Paleont. 13:1-56).

Living colubrid genera:
Nerodia sipedon
Heterodon cf. *H. platyrhinos*
Elaphe cf. *E. vulpina*
? *Pituophis* sp indet.
Viperidae:
Viperid gen. et sp. indet.

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