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HERPETOFAUNA OF THE ALBERT AHRENS LOCAL FAUNA (PLEISTOCENE:IRVINGTONIAN), NEBRASKA

presented by

Kenneth M. Ford III

has been accepted towards fulfillment of the requirements for

Master's degree in Geology

J. Alan Holman
Major professor

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HERPETOFAUNA OF THE ALBERT AHRENS LOCAL FAUNA
(PLEISTOCENE: IRVINGTONIAN), NEBRASKA

By

Kenneth M. Ford III

A THESIS

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ABSTRACT

HERPETOFAUNA OF THE ALBERT AHRENS LOCAL FAUNA (PLEISTOCENE:IRVINGTONIAN), NEBRASKA

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A fossil herpetofauna from the Albert Ahrens local fauna in south-central Nebraska is the most diverse Irvingtonian herpetofauna known from the Great Plains. The fauna is from deposits thought to be derived from Kansan glaciations and contains a total of thirty-one species, including two salamanders, ten anurans, two turtles, one lizard, and sixteen snakes. _Rana blairi_ is reported for the first time in the fossil record. _Ambystoma laterale_, _Rana sylvatica_, and _Elaphe vulpina_ occured south of their modern ranges, but _Psuedacris clarki_ occurs north of its modern range. These fossil distributions suggest that the Albert Ahrens climate was milder than the modern one and thus support the Pleistocene Climatic Equability Model. The herpetofauna suggests that the site of deposition was a wooded stream with some nearby grassland.

To my grandparents

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I would finally like to thank my parents for their support, understanding, and love.

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INTRODUCTION

The Irvingtonian herpetofauna is known mainly from several cave faunas in the eastern and south-central United States. These assemblages tend to reflect the modern fauna of the locality more closely than do associated mammalian faunas (Holman and Grady, 1989) and suggest that the Irvingtonian climate may have been more equable than originally thought (Holman, 1980). A large, recently discovered Irvingtonian herpetofauna from Nuckolls County in south-central Nebraska provides an opportunity to compare the herpetofauna with the mammalian fauna of the Central Plains and is the subject of this thesis.

The Albert Ahrens local fauna.-The Albert Ahrens fossil locality (University of Nebraska, State Museum site No 104) is located within the E½ SE¼ Sec. 14 T3N R6W on the Oak, Nebraska 7½ minute quadrangle. The site was discovered in a gully by Mr. Albert Ahrens of Angus, Nebraska, after whom the fauna is named. Fossils were collected by crews from the University of Nebraska State Museum during the summers of 1990 and 1991 using standard micro-vertebrate collecting techniques (Hibbard, 1949). Fish, bird, and mammal fossils were recovered as well as the fossil amphibians and reptiles of this report. Mammal fossils are being studied by M.R. Voorhies and R.G. Corner of the University of Nebraska State Museum. Sediment from the skull of a juvenile mammoth provided a pollen sample now being studied by M.R. Bolick, also of the University of Nebraska State Museum.

Most micro-vertebrate fossils were recovered from the base of a white to grayish silt bounded above and below by unfossiliferous red loess deposits. The upper loess/silt contact is conformable, but the lower loess was cut by channels approximately one meter deep. The fossils, yellow, red, and black clay nodules, and carbonate concretions, occurred in lenticular, gravel crossbeds 2-10 cm thick that terminated at or near the base of the channel deposits. Macro-vertebrate fossils were found in the channels as well as higher in the silt.

Pleistocene stratigraphy.-The lower loess overlies a thick volcanic ash deposit which is thought to be the Pearlette type O volcanic ash. The type O ash has been dated at 610 ka by fission track dating (Izett, 1981). The fauna is thus thought to be at about 500 ka (Voorhies, pers. comm.). Preliminary study of the mammalian fauna suggests that the Albert Ahrens local fauna is similar to the Cudahy fauna (Voorhies and Corner, 1991). Hibbard (1970) considered the Cudahy fauna, which occurs below the type O ash, as representing the Kansan glacial stage, but for the reasons discussed below, the traditional Pleistocene stage names will be used only informally.

Differing and inconsistent use of stratigraphic names has caused the traditional North American glacial and interglacial nomenclature to be abandoned (for review see Aber, 1991). Schultz et al. (1978) attempted to divide the Irvingtonian Land Mammal Age into two substages, the Sheridanian and Sappan, and a third Sheridanian and Sap was later added for the medial Irvingtonian (Lundelius et al., 1987). None of these names are in current use. A till stratigraphy has been developed for the lower and middle (pre-Illinoian) Pleistocene of the Central Plains (Hallberg, 1986). Based on relative stratigraphic position to the Pearlette type O, the Albert Ahrens fossil beds are equivalent to the type A1 till which is the classic "Kansas till" of Iowa (Hallberg, 1986). The type "Kansas till" of Kansas is found below the type O (Aber, 1991).

Checklist of the Amphibians and Reptiles.-Species identified in this thesis are listed below. Common names of species follow Collins (1990). The basis for species identifications is given below in the Systematic Paleontology.

Ambystoma cf. A. laterale	Blue-spotted Salamander
Ambystoma tigrinum	Tiger Salamander
Ambystoma sp.	
Scaphiopus bombifrons	Plains Spadefoot
Bufo americanus	American Toad
Bufo cognatus	Great Plains Toad
Bufo woodhousii woodhousii	Woodhouse's Toad
Bufo sp.	
Pseudacris cf. P. clarki	Spotted Chorus Frog
Hyla versicolor or H. crysoscelis	Gray Treefrog
Rana catesbeiana	Bullfrog
Rana clamitans	Green Frog

Rana cf. *R. blari*	Plains Leopard Frog
Rana sylvatica	Wood Frog
Rana sp.	
Chelydra serpentina	Snapping Turtle
Chrysemys picta cf. *C. p. belli*	Western Painted Turtle
Eumeces obsoletus	Great Plains Skink
cf. *Coluber constrictor*	Racer
Elaphe guttata or *E. obsoleta*	Rat or Corn Snake
Elaphe vulpina	Fox Snake
Elaphe sp.	
Lampropeltis triangulum	Milk Snake
Nerodia sipedon	Northern Water Snake
Regina grahami	Graham's Crawfish Snake
Storeria sp.	Brown or Redbelly Snake
Thamnophis proximus	Western Ribbon Snake
Thamnophis radix	Plains Garter Snake
Thamnophis sirtalis	Common Garter Snake
Thamnophis sp. indet.	
Heterodon platirhinos	Eastern Hognose Snake
Heterodon nasicus	Western Hognose Snake
Heterodon sp.	
Agkistrodon sp.	Copperhead or Cottonmouth
Crotalus horridus	Timber Rattlesnake
Crotalus viridis	Western Rattlesnake
Crotalus sp. indet.	
Sistrurus catenatus	Massasauga

SYSTEMATIC PALEONTOLOGY

Fossils collected in the 1990 field season are in the collections of the University of Nebraska State Museum (UNSM). Fossils collected in 1991 are housed at the Michigan State University Museum (MSU VP).

Class Amphibia

Order Caudata

Family Ambystomatidae

Ambystoma cf. *A. laterale*

Material.-13 vertebrae (UNSM 76400), 1 vertebra (MSU VP 1356).

Remarks.-The vertebrae of the *A. maculatum*-group of *Ambystoma* are the most elongate of the genus (see ratios in Tihen, 1958:19) and have a depressed neural arch (Rogers, 1984). Holman and Grady (1987) and Rogers (1984) separate the *A. jeffersonianum*-complex (*A. jeffersonianum*, *A. laterale*, *A. platineum*, *A. tremblyi*) from *A. maculatum* (the other member of the *A. maculatum*-group) based on two characters: in *A. maculatum* the neural arch often extends past the zygapophyses and the area of the postzygapophyses is wide, while in the *A. jeffersonianum*-complex the neural arch ends anterior to the most posterior extent of the postzygapophyses and the postzygapophyseal area is narrow. Of the species in the *A. jeffersonianum*-complex, vertebrae of seven recent *A. laterale* are identical in size to the Ahrens vertebrae.

None of the members of the *A. jeffersonianum*-complex presently occur in Nebraska. The western border of the ranges of *Ambystoma jeffersonianum* and *A. laterale* runs from central Minnesota through Wisconsin, northern Illinois, and Indiana to north-central Kentucky, with an isolated colony of *A. laterale* in eastern Iowa, about 600 km to the north-east of Nuckolls County (Conant and Collins, 1991).

Ambystoma tigrinum

Material.-1 right dentary, 1 left dentary, 32 vertebrae (UNSM 76401), 4 vertebrae (UNSM 76402), 13 vertebrae (MSU VP 1357), 5 vertebrae (MSU VP 1358).

Remarks.-The dentaries of adults of the subgenus *Ambystoma* have a flange on the lingual edge (Tihen, 1958:33). As the Ahrens dentaries have these flanges and are of similar size to recent dentaries of *A. tigrinum*, they are assigned to *A. tigrinum*. The vertebrae of *A. tigrinum* are distinguished by their short, wide shape, large size, and upswept neural arch extending past the centrum (Tihen, 1958; Holman, 1969).

Nine vertebrae from this locality (UNSM 76402 and MSU VP 1358) have a perforate centrum which Tihen (1942) found characteristic of larvae and recently metamorphosed adults. Some fossil and recent populations of neotenic *A. tigrinum* also fail to develop a septum in the centrum (Holman, 1975; Rogers, 1985). While this appeared to be age independent in a recent sample from Colorado (Rogers, 1985), Tihen (1942, 1958) found this to be an unreliable character in some recent skeletons as older neotenes in his sample had developed septa (Tihen, 1942). These eight vertebrae are similar in size to recent A. tigrinum and to all other A. tigrinum vertebrae thus far collected from the site. Since neotenic vertebrae are usually larger than those of normal adults (Tihen, 1942, 1958; Holman, 1975), it is questionable that neotenic A. tigrinum were present in the Albert Ahrens fauna.

Tiger Salamanders occur throughout Nebraska today as both normal and neotenic adults (Lynch, 1985). Lynch (1985) reports the species in Nuckolls County, and a normal adult was spotted in a pump house at the UNSM campsite in Oak. They are commonly found under rocks or in burrows and may be seen on rainy spring nights during their breeding season (Lynch, 1985).

Ambystoma sp. indet.

Material.-14 vertebrae (UNSM 76403), 12 vertebrae (MSU VP 1359).

Remarks.-This material is too fragmentary to assign to the specific level.

Order Anura

Family Pelobatidae

Scaphiopus bombifrons

Material.-2 left ilia (UNSM 76404), 4 left and 4 right ilia (MSU VP 1360).

Remarks.-The ilia of the subgenus *Spea* can be distinguished from the subgenus *Scaphiopus* by a weak or absent dorsal rim on the acetabulum and a wide ventral acetabular expansion (Chantell, 1971). The Ahrens ilia are similar to *Spea* and especially those of recent *Scaphiopus bombifrons* in that the dorsal prominance is reduced or absent (Holman, 1987c). Lynch (1985) reports *Scaphiopus bombifrons* from Nuckolls County.

Family Bufonidae

Bufo americanus

Material.-6 left and 5 right ilia (UNSM 76405), 8 left and 2 right ilia (MSU VP 1361).

Remarks.-The dorsal protuberence of the ilium of *Bufo americanus* has a long base compared to that of *B. woodhousii fowleri* (Holman, 1967; Wilson, 1975). Both are otherwise similar in having a much lower protuberence than either *B. w. woodhousii* or *B. cognatus* (Tihen, 1962). *Bufo americanus* is today found in Sharpy County, Nebraska approximately 175 km northeast of Nuckolls County (Lynch, 1985). The species tolerates a wide range of habitats but requires moist hiding places and shallow bodies of water for breeding (Conant and Collins, 1991).

Bufo cognatus

Material.-13 left and 9 right ilia, 1 sacrum (UNSM 76406), 19 left and 17 right ilia (MSU VP 1362).

Remarks.-While indistinguishable from each other based on ilial characteristics (Holman, 1964, 1969), Bufo cognatus and B. speciosus can be separated from other members of Bufo on the great height of the dorsal protrbence (Holman, 1969). Holman (1971) found that the sacral condyles of B. cognatus end only slight posterior to the neural arch, whereas those of B. w. woodhousii and B. speciosus extend well past the neural arch. The Ahrens fossils are similar in these respects to B. cognatus. Bufo cognatus is not reported as occurring in Nuckolls County, but its wide range in Nebraska and Kansas suggests that it should be found there (Collins, 1974, Lynch, 1985). Conant and Collins (1991:313) refer to this toad as "...an accomplished burrower...often found... in river bottoms or floodplains."

Bufo woodhousii woodhousii

Material.-2 left and 11 right ilia (UNSM 76407), 22 left and 15 right ilia (MSU VP 1363).

Remarks.-The ilia of Bufo woodhousii woodhousii have a dorsal protuberence which is intermediate in height between Bufo cognatus and B. speciosus on one hand and B. americanus and B. w. fowleri on the other (Tihen, 1962; Holman, 1971). Also, the anterior angle of the dorsal protuberence is, in general, steeper than the posterior angle, whereas the two angles of the dorsal protuberence are generally subequal in

B. cognatus (Tihen, 1962). The fossil ilia are identical to B. w. woodhousii in these respects. This toad is found today in Nuckolls county (Lynch, 1985). This species can tolerate many a wide range of conditions, preferring lowlands and sandy habitats (Collins, 1974, Conant and Collins, 1991).

Bufo sp. indet.

Material.-6 left and 5 right ilia (UNSM 76408), 3 left and 5 right ilia (MSU VP 1364).

Remarks.-This material is too fragmentary to assign to the specific level.

Family Hylidae

Pseudacris cf. P. clarki

(Figure 1)

Material.-1 left ilium (MSU VP 1365).

Remark.-This ilium is most similar to P. clarki in having a wide, convex ventral actabular expansion (Chantell, 1968) which meets the ilial shaft at a near right angle. The dorsal protruberence is bulbous (Chantell, 1964) and directed slightly laterally in this fossil. Pseudacris clarki is today found as far north as central Kansas, about 110 km to the south of Nuckolls County, inhabiting open grasslands and the edges of woodlands (Collins, 1974).

Hyla versicolor or H. crysoscelis

Material.-2 right and 1 left ilia (UNSM 76409).

Remarks.-The ilia of both Hyla cinerea and H. versicolor have a low, smooth dorsal prominence and a wide ventral acetabular expansion which forms an obtuse angle with the ilial shaft (Chantell, 1964; Wilson, 1968). The fossils are similar to recent _H_. _versicolor_ in that the dorsal prominence is slightly anterior to the anterior border of the acetabulum, but in _H_. _cinerea_, the dorsal prominence is about even with the acetabulum. _Hyla versicolor_ and _H_. _crysoscelis_ are cryptic species and are distinguished primarily by ploidy and mating call. Both species inhabit trees and low shrubs in woodland areas. _Hyla chrysosocelis_ is found about 45 km east of Nuckolls County today (Lynch, 1985).

Family Ranidae

Rana catesbeiana

Material.-66 left and 67 right ilia (UNSM 76410), 44 left and 28 right ilia (MSU VP 1366).

Remarks.-The ilia of the _Rana catesbeiana_ have a precipitous slope on the posterodorsal border of the ilial crest and a porous area near the acetabular border which is most notable in smaller specimens (Holman, 1965a, 1984). _Rana catesbeiana_ is currently found in Nuckolls County (Lynch, 1985). This species is aquatic with a preference for deep, permanent water.

Rana clamitans

Material.-12 left and 18 right ilia (UNSM 76411), 41 left and 45 right ilia (MSU VP 1367).

Remarks.-The ilia of _R_. _clamitans_ are similar to _R_. _catesbeiana_ in having a preciptious slope to the posterodorsal border of the ilial crest. Rana clamitans can be distinguished by its less rugged vastus prominence, lack of a porous acetabular expansion, and smaller size (Holman, 1967; Holman and Grady, 1987). The upper portion of the vastus prominence is flattened and proximally folded in mature R. clamitans. In small R. catesbeiana, the vastus prominence is flattened but upright. Rana clamitans is currently found about 370 km east of Nuckolls County. It is common in streams and other shallow fresh waters (Conant and Collins, 1991).

Rana cf. R. blairi

Material.-135 left and 158 right ilia (UNSM 76412), 464 left and 443 right ilia (MSU VP 1368).

Remarks.-The ilia of the Rana pipiens-complex have a gentle slope to the posterodorsal border of the ilial crest (Holman, 1965a). Two species from the R. pipiens-complex, Rana blairi and R. pipiens, are currently found in Nebraska with R. blairi reported from Nuckolls County (Lynch, 1985). Though the species in the Rana pipiens-complex are cosmopolitan in habitat, the distribution of modern R. blairi is linked to loess soils in their Nebraska range (Lynch, 1978). As the sediments within and underlying the fossil horizon are silt, it is possible to tentatively refer the fossils to R. blairi. This is the first report of Rana blairi in the fossil record.

Rana sylvatica

(Figure 2)

Material.-42 left and 45 right ilia (UNSM 76413), 20 left and 20 right ilia (MSU VP 1369).

Remarks.-A member of the *Rana pipiens*-group (sensu Holman, 1965a), *Rana sylvatica* can be distinguished by the

dorsal prominence which develops on the lateral surface of the ilium (Holman, 1984). This extralimital frog is found today over a wide range to the north and east of the Albert Ahrens site, about 600 km at it closest. It is principally a frog of moist woodlands and can travel some distance from water (Conant and Collins, 1991).

Rana sp. indet.

Material.-345 left and 460 right ilia (UNSM 76414), (MSU VP 1370).

Remarks.-This material is too fragmentary to assign to the specific level.

Class Reptilia

Order Testudines

Family Chelydridae

Chelydra serpentina

Material.- 1 hyiod, 1 left tibia, 1 left fibula, 1 left femur, and 2 tail vertebra (UNSM 76415), 1 neck vertebra, 1 right humerus, 1 right hypoplastron, and 3 costal fragments (MSU VP 1371).

Remarks.-The skeleton of this species is very distinct (Holman and Schloeder, 1991). The fossils are

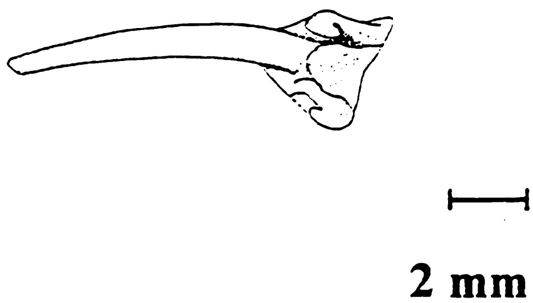

Figure 1 Left ilium of Pseudacris cf. P. clarki (MSU VP 1365) in lateral view.

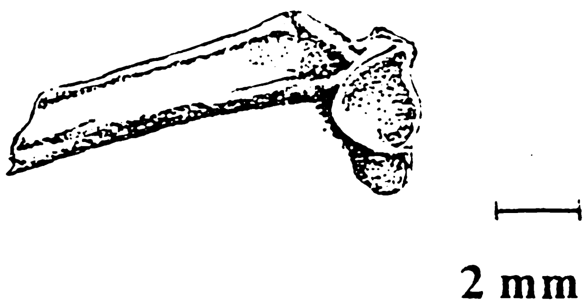

Figure 2 Left ilium of Rana sylvatica (MSU VP 1369) in lateral view.

indistinguishable from recent Chelydra serpentina and are assigned to this species. Chelydra serpentina is known from Nuckolls County and is found throughout Nebraska in most permanent bodies of water (Lynch, 1985).

Family Emydidae

Chrysemys picta cf. C.p. belli

(Figure 3)

Material.- 1 entoplastron (UNSM 76416), 1 peripheral (MSU VP 1372).

Remarks.-The fossil turtle shell elements lack sculpturing as in Pseudmys or Trachemys (Holman and Sullivan, 1981; Holman, 1990). The entoplastron (Figure 3) has a bell shape similar to Graptemys, but the pattern of the gular and hemeral scutes run towards the skirt of the bell in Graptemys, whereas the trace of these scutes on the Ahrens fossil extends to the anterior corners. The latter pattern is found in Chrysemys picta.

The smaller subspecies of C. picta have entoplastra that are subtriangular in shape, but the entoplastron of C. p. belli is bell-shaped similar to the fossil. The peripheral is similar to C. picta in having a straight border to the marginal scute with only a slight dimple at its junction with the pleural scute border. Chrysemys picta belli is distributed throughout Nebraska and Kansas (Collins, 1974; Lynch, 1985). They prefer heavily vegetated and shallow waters with muddy bottoms (Conant and Collins, 1991).

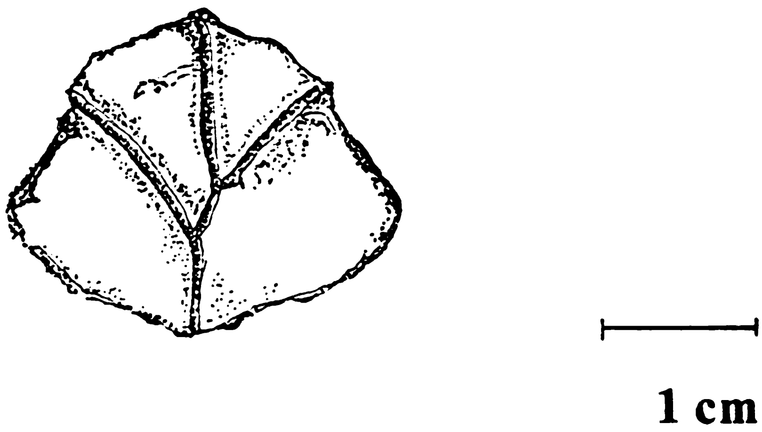

Figure 3 Entoplastron of Chrysemys picta cf. C. p. belli (UNSM 76416) in ventral view.

Order Squamata

Family Scincidae

Eumeces obsoletus

Material.-4 maxilla fragments (UNSM 76417), 2 dentaries (MSU VP 1373).

Remarks.-The teeth of *Eumeces obsoletus* are robust and taper to a pigmented tip (Etheridge, 1958; Holman and Schloeder, 1991). These fossils are similar to *E. obsoletus* in these characters and in size. Nuckolls County is at the northern-most tip of this species' modern range (Lynch, 1985). It inhabits grasslands with fine soils and some rocky cover (Conant and Collins, 1991).

Family Colubridae

Subfamily Colubrinae

cf. *Coluber constrictor*

Material.-10 vertebrae (UNSM 76418), 3 vertebrae (MSU VP 1374).

Remarks.-The vertebrae of *Coluber* and *Masticophis* can be separated from other colubrids based on their more elongate shape and well developed epizygaphophyseal spines (Auffenberg, 1963), but to many authors, they are indistingishable from each other (for discussion see Holman, 1981). *Coluber constrictor* is currently found in Nuckolls County, while the closest any species of *Masticophis* (*Masticophis flagellum*) is found, is about 150 km from the site (Lynch, 1985). Based on these ranges, the fossils are tentatively refered to *C. constrictor*. Diverse in habitat, the various subspecies tend to occur in open areas (Conant and Collins, 1991).

<u>Elaphe guttata</u> or <u>E. obsoleta</u>

Material.-10 vertebrae (UNSM 76419), 9 vertebrae (MSU VP 1375).

Remarks.-Vertebrae from the genus <u>Elaphe</u> have more vaulted neural arches, less developed hemal keels, and straighter subcentral ridges than those of <u>Lampropeltis</u> (Brattstrom, 1955; Auffenberg, 1963; Holman, 1965b). <u>E. obsoleta</u> and <u>E. guttata</u> have higher neural spines than <u>E. vulpina</u> (Holman, 1965b). <u>Elaphe obsoleta</u> inhabits forested regions of southeastern Nebraska and eastern Kansas, about 20 km east of the site (Collins, 1974; Lynch, 1985). <u>Elaphe guttata</u> is at the northern most part of its range in southern Nebraska, including Nuckolls County (Lynch, 1985). Both prefer open woodlands (Collins, 1974).

<u>Elaphe vulpina</u>

(Figure 5)

Material.-7 vertebrae (UNSM 76420), 8 vertebrae (MSU VP 1376).

Remarks.-Characters used to identify <u>E. vulpina</u> are discussed above. <u>Elaphe vulpina</u> is found as far south as Lincoln, Nebraska which is about 85 km north of Nuckolls County (Lynch, 1985), but its prehistoric range was much greater (Holman, 1981). In Nebraksa, <u>E. vulpina</u> inhabits varied habitats, including prairies, stream valleys, woods, and dunes (Conant and Collins, 1991).

Elaphe sp. indet.

Material.-17 vertebrae (UNSM 76421), 17 vertebrae (MSU VP 1377).

Remarks.-This material is too fragmentary to assign to the specific level.

Lampropeltis triangulum

Material.-12 vertebrae (UNSM 76422), 18 vertebrae (MSU VP 1378).

Remarks.-The vertebrae of *Lampropeltis triangulum* can be separated from other species of the genus and *Arizona elegans* by its shorter, laterally-directed accessory processes, depressed neural arches, and rounder prezygapophyseal faces (Holman, 1963; Hill, 1971). Moreover, the neural spine of *L. triangulum* is shorter than other *Lampropeltis* species and the subcentral ridges are straight (Brattstrom, 1955; Parmley, 1986). The wide range of *L. triangulum* in Nebraska and Kansas would suggest that it may occur in Nuckolls County (Collins, 1974; Lynch, 1985). *Lampropeltis triangulum* requires rocky, open hillsides (Collins, 1974).

Subfamily Natricinae

Nerodia sipedon

Material.-102 vertebrae (UNSM 76423), 25 vertebrae (MSU VP 1379).

Remarks.-Vertebrae of the species of *Nerodia* tend to be squarish in shape with long, wide, ventrally directed hypaphyses (Brattstrom, 1967; Parmley, 1988). *Nerodia* sipedon is distinctive from other species in the genus due to its low neural arch (Holman, 1967). Nuckolls County is within the modern range of N. sipedon which occurs along streams, rivers, and marshes (Lynch, 1985).

Regina grahami

(Figure 4)

Material.-15 vertebrae (UNSM 76424), 9 vertebrae (MSU VP 1380).

Remarks.-The vertebrae of Regina grahami are similar in shape to Nerodia, but are distinguished by the concave anterior border of the neural spine and short, trucated hypophyses (Holman, 1972). This snake now occurs about 110 km east of Nuckolls County (Lynch, 1985). Regina grahami frequents ponds, stream margins, and swamps (Conant and Collins, 1991).

Storeria sp. indet.

Material.-157 vertebrae (UNSM 76425), 6 vertebrae (MSU VP 1381).

Remarks.-The vertebrae of both Storeia dekayi and S. occipitomaculata are identical in being small and elongate with very low neural spines which overhang the neural arch (Holman, 1962; Auffenberg, 1963; Holman and Grady, 1987). As both species occur within Nebraska today (Lynch, 1985), the fossils are refered to the genus only. Storeria occipitomaculata is rare, and S. dekayi is found only in the mesic woods in the southeastern corner of the state (Lynch, 1985).

Figure 4 Trunk vertebra of Regina grahami (UNSM 76424) in lateral view.

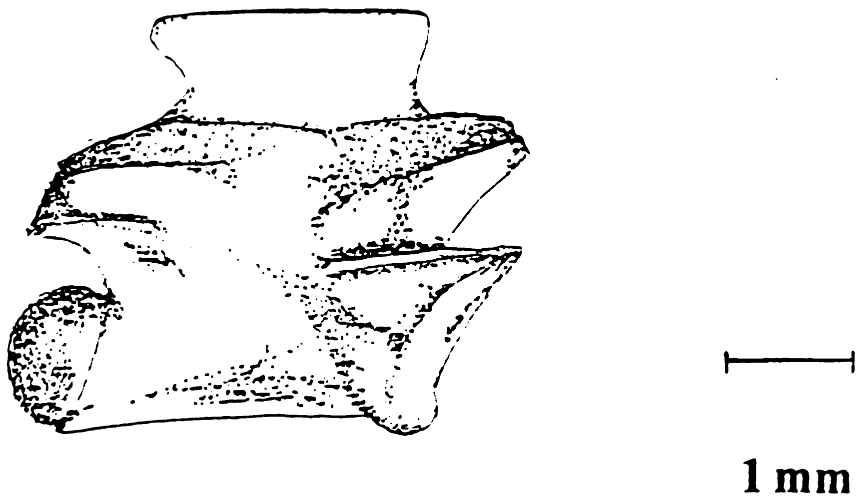

Figure 5 Trunk vertebra of Elaphe vulpina (UNSM 76420) in lateral view.

Thamnophis proximus

Material.-59 vertebrae (UNSM 76426), 10 vertebrae (MSU VP 1382).

Remarks.-Vertebrae of the genus *Thamnophis* are elongate with short hypophyses which are directed posteriorally (Brattstrom, 1967; Parmley, 1988). *Thamnophis proximus* and *T. sirtalis* have higher neural spines with less pronounced overhanging corners and are longer and more gracile than *T. radix* (Holman, 1962, 1984; Rogers, 1982). Large vertebrae of *T. proximus* have less well developed epizygapophyseal spines and straighter anterior borders of the neural spine than *T. sirtalis* (Holman, 1987a). Smaller vertebrae of *T. proximus* have accessory processes which are oblique to the axis of the centrum and oblong prezygapophyses (Holman, 1962; Rogers, 1984). Frequenting most aquatic habitats, *T. proximus* is found in eastern Nebraska about 85 km from Nuckolls County (Lynch, 1985)

Thamnophis radix

Material.-37 vertebrae (UNSM 76427), 12 vertebrae (MSU VP 1383).

Remarks.-Based on the characters discussed above, these fossils are assigned to *Thamnophis radix*. *Thamnophis radix* occurs in Nuckolls County today and is found in wet grassland along marshes and ponds, avoiding rivers where *T. sirtalus* is common (Collins, 1974; Lynch, 1985).

Thamnophis sirtalis

Material.-42 vertebrae (UNSM 76428), 36 vertebrae (MSU VP 1384).

Remarks.-Large fossils are assigned to T. sirtalis based on characters discussed under T. proximus. Smaller vertebrae of T. sirtalis have accessory processes which are nearly perpendicular to the long axis of the centrum and round prezygapophyses (Holman, 1962; Rogers, 1984). Thamnophis sirtalis is common throughout Nebraska and is found in waters associated with streams (Lynch, 1985).

Thamnophis sp. indet.

Material.-131 vertebrae (UNSM 76429), 77 vertebrae (MSU VP 1385)

Remarks.-This material is too fragmentary to assign to the specific level.

Subfamily Xenodontinae

Heterodon platirhinos

Material.-3 vertebrae (UNSM 76430), 8 vertebrae (MSU VP 1386).

Remarks.-Vertebrae of Heterodon have depressed neural arches, extemely flattened or indistinct hemal keels, and are wider through the zygapophyses than long (Auffenberg, 1963; Parmley, 1986). Heterodon platirhinos vertebrae are elongate compared to H. nasicus and have longer prezygapophyseal faces with flattened anterior borders (Auffenberg, 1963; Holman, 1963). Range maps suggest that H. platirhinos should occur in Nuckolls County (Conant and

Collins, 1991). This species has varied habitats (open woodlands, river shores, or dunes) but requires dry, sandy conditions (Holman, 1971).

<u>Heterodon nasicus</u>

Material.-4 vertebrae (UNSM 76431), 13 vertebrae (MSU VP 1387).

Remarks.-Based on the characters discussed above the listed fossils are assigned to <u>Heterodon nasicus</u>. This species prefers dry, sandy prairie or grassland. Range maps suggest that <u>H</u>. <u>nasicus</u> should occur in Nuckolls County (Conant and Collins, 1991).

<u>Heterodon</u> sp. indet.

Material.-3 vertebrae (UNSM 76432).

Remarks.-This material is too fragmentary to assign to the specific level.

Family Viperidae

<u>Agkistrodon</u> sp indet.

Material.-2 vertebrae (UNSM 76433), 1 vertebrae (MSU VP 1388).

Remarks.-Vertebrae of <u>Agkistrodon</u> have a single large foramen within deep pits on either side of the cotyle (Holman, 1963). This material is too fragmentary to identify to species. <u>Agkistrodon contortrix</u> is found 85 km to the east of Nuckolls County (Conant and Collins, 1991).

<u>Crotalus horridus</u>

Material.-3 vertebrae (UNSM 76434), 3 vertebrae (MSU VP 1389).

Remarks.-Crotalus vertebrae have indistinct pits on either side of the cotyle which often contain multiple small foramina and have a depressed neural arch (Holman, 1963, 1982). Both C. horridus and C. viridus have relatively low neural spines (Holman, 1967; LaDuke, 1991). Crotalus horridus tends to have a neural spine longer than high whereas C. viridus has a neural spine about as long as high (Holman and Winkler, 1987). Crotalus horridus is now found 110 km from Nuckoll's County in eastern Nebraska (Lynch, 1985).

Crotalus viridis

Material.-2 vertebrae (UNSM 76435).

Remarks.-Based on the characters discussed above, these fossils are assigned to C. viridis. This species occurs 110 km west of Nuckolls County and is found in areas with rocky outcrops or dissected pature land (Lynch, 1985).

Crotalus sp. indet.

Material.-7 vertebrae (UNSM 76436), 7 vertebrae (MSU VP 1390).

Remarks.-This material is too fragmentary to assign to the specific level.

Sistrurus catenatus

Material.-2 vertebrae (UNSM 76437), 3 vertebrae (MSU VP 1391).

Remarks.-These fossils are similar in size to vertebrae of modern Sistrurus catenatus and have a similarly vaulted neural arch (Holman, 1982). This snake prefers wet grassland, bogs, and swamps early in the year and later move to drier woodland in the summer. Once common in eastern Nebraska, *S. catenatus* agricultural development has apperantly resulted in a restriction of it range to isolated occurences in eastern Nebraska (Lynch, 1985).

DISCUSSION

The herpetofauna of the Albert Ahrens local fauna is the most diverse Irvingtonian herpetofauna known from the Great Plains. It contains at least thirty-one species, including two salamanders, ten anurans, two turtles, one lizard, and sixteen snakes. None of these species is extinct.

Only four other herpetofaunas with greater than twenty species have been described from the Irvingtonian. Three of these are from cave deposits in the eastern United States, and the fourth is from a Texas cave deposit (Fyllan Cave: Holman and Winkler, 1987). The eastern cave faunas are all similar to the modern local herpetofauna (Holman and Grady, 1989). Each has between four and five extralimital species (see Table 1), but many of the extralimital species occur relatively near the site. Their absence in the area today may reflect pressures in the recent environment or the difficulty of taking census of modern amphibian and reptile populations (Holman and Grady, 1989). *Cryptobranchus guildayi*, an extinct species from Cumberland Cave described by Holman (1977), may represent the living Hellbender, *C. alleganiensis* (Holman, 1991).

Table 1 Herpetofauna from caves in the eastern United States. Extralimital forms are marked by an X. Possible extinct froms are marked with a ?.

Species	Hamilton Cave West Virginia (Holman and Grady, 1989)	Trout Cave Maryland (Holman, 1982)	New Trout Cave West Virginia (Holman and Grady, 1987)
?Cryptobranchus guildayi	-	X	-
Cryptobranchus sp. indet.	X	-	X
Ambystoma jeffersonianum complex	*	-	*
Ambystoma maculatum	*	-	*
Ambystoma opacum	X	*	*
Ambystoma tigrinum	X	X	-
Desmognathus fuscus	*	-	*
Desmognathus ochrophaeus	*	-	*
Notophthalmus viridescens	*	-	-
Plethodon glutinosus	-	*	-
Gyrinophilus porphyriticus	*	-	-
?Gyrinophilus sp. (neotenic form)	X	-	-
Bufo americanus	*	*	-
Bufo woodhousii fowleri	*	-	-
Bufo sp. indet.	-	-	*
Hyla versicolor or H. chrysoscelis	*	-	-
Hyla crucifer	*	-	-
Rana catesbeiana	*	-	-
Rana clamitans	*	-	-
Rana sylvatica	*	*	-
Rana pipiens-complex	*	*	*
Emydoidea blandingii	-	-	X
Sceloporus undulatus	*	*	*
Eumeces fasiatus	*	*	-
Eumeces laticeps	X	-	*
Coluber constrictor	*	*	*
Elaphe vulpina	-	X	X
Elaphe sp. indet.	*	-	*
Lampropeltis triangulum	*	*	*
Heterodon platirhinos	*	*	*
Carphophis amoenus	*	-	*
Nerodia sipedon	*	-	-
Storeria sp. indet.	*	-	*
Thamnophis sirtalis	-	*	-
Thamnophis brachystoma	-	-	X
Thamnophis sp. indet.	*	*	*
Agkistrodon contortrix	-	*	*
Crotalus horridus	*	*	*
Sistrurus catenatus	-	X	-

In contrast, the mammalian fauna of the Pleistocene was less stable than the herpetofauna both in terms of extinction and in range adjustment (Holman, 1991). Due to the differences between climates indicated by reptilian faunas and models of Pleistocene climates based on boreal mammals, Hibbard (1960) proposed what later became known as the "Pleistocene Climatic Equability Model." Under this model, disharmonious biotas are thought to represent climates with reduced seasonal variability that allowed individual species to adjust according to their own individual climatic tolerances (Lundelius et al., 1983; Graham and Mead, 1987).

Paleoclimatic interpretations.-Based partially on the limited adjustments of some amphibian and reptile species, Holman (1980) found that the Irvingtonian herpetofauna would suggest warmer winters. Minimum mean summer temperatures above those in boreal environments would also be necessary for turtle eggs to successfully develop (Stuart, 1979; Holman, 1987b). Fay (1988:190), however, questioned the use of eastern herpetofaunas to reconstruct climates. He suggested the stability of amphibians and reptiles through the Pleistocene implied either that a proper model had yet to be developed to account for the response of individual herpetological species to climatic change or that the herpetofauna was insensitive to change within the macroclimate.

One explanation for this apparent stability is the lack of a distinctive, identifiable boreal herpetofauna in the eastern United States (Fay, 1988). In other words, northern amphibians and reptiles that would have been displaced into the southern portion of their ranges would be indistinguishable from southern species-complexes (ie. Rana sepetentrionalis). A strictly boreal mammalian fauna, however, is distinguishable from a modern temperate fauna, as a number of mammal species are restricted to boreal habitats.

The Albert Ahrens herpetofauna provides an opportunity to examine the adjustment of amphibians and reptiles to early Pleistocene glaciations. Much of the modern herpetofauna of the Great Plains occurs in grasslands, thus amphibians and reptiles from intruding boreal woodland would be easily recognizable in a Great Plains locality. In particular, the three modern species that occur a great distance north of the Great Plains (Ambystoma laterale, Bufo hemiophrys, and Rana sylvatica) are of considerable interpretive importance. These factors allow Great Plains amphibians and reptiles to better reflect Pleistocene climatic changes than those in the east where woodlands dominate.

In a preliminary report on the mammalian fauna (Voorhies and Corner, 1991), small mammals showed a strong boreal trend. Initial pollen analysis, which mainly indicated boreal conifers, substantiated this assessment

(Bolick, 1991). This initial data suggested to Voorhies and Corner (1991) that the fauna may represent the last of the Kansan glaciations in southern Nebraska. Voorhies (pers. comm.) felt that the deposit might have been concurrent with the maximum glacial advance into the Great Plains, as the mammals indicated a climate similar to the area around The Lake of the Woods in Ontario and Minnesota.

In the herpetofauna, at least eleven species are extralimital in the Albert Ahrens local fauna (based on range maps in Conant and Collins, 1991). Sistrurus catenatus appears to be locally extirpated due to human activity and is therefore excluded as extralimital. These species are broken down into geographic groups in Table 2. While no single area of sympatry for the complete Albert Ahrens herpetofauna exists, twenty-six species (all species now found in Nuckolls County and seven extralimital species) can be found 220 km to the east in the northeastern corner of Missouri near the Nebraska border (Figure 6).

Several species outside of this area of sympatry are within 200 km of Nuckolls County. Ambystoma laterale and Rana sylvatica, however, have suffered a much more dramatic range adjustment of at least 600 km. The occurrences of R. sylvatica and Elaphe vulpina in Illinoian deposits in Kansas suggested to Holman (1984, 1987a) a cooler, wetter climate than Recent. While a full boreal climate is not indicated by the Albert Ahrens herpetofauna, the presence of the boreal A. laterale as well as R. sylvatica and E. vulpina

Table 2 Geographic breakdown of extralimital amphibian and reptile species in the Albert Ahrens local fauna. Species extralimital to the area of sympatry in Figure 6 are marked by an asterisk (*).

Northern and Northeastern

*_Ambystoma laterale_
*_Rana sylvatica_
Elaphe vulpina

Western

*_Crotalus viridus_

Eastern

Bufo americanus
Hyla versicolor/H. chysoscelis
*_Rana clamitans_
Thamnophis proximus
Crotalus horridus

Southern and Southeastern

*_Pseudacris_ cf. _P. clarki_
Regina grahami
Agkistrodon sp.

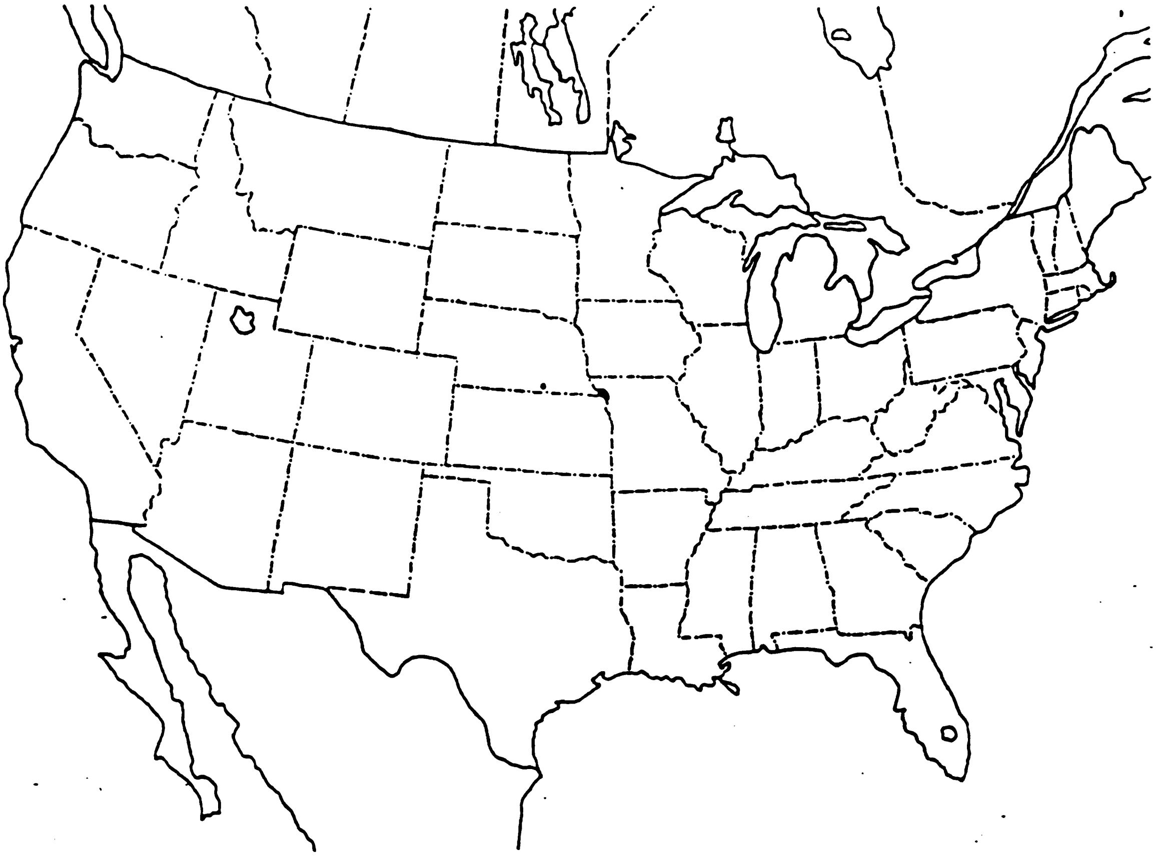

Figure 6 Area of sympatry for the Albert Ahrens herpetofauna. The black dot is the location of the Albert Ahrens fauna. The oval, black mark indicates the area of sympatry.

would suggest at least a cooler summer climate during the time of deposition of the fossils. The absence of turtles other than Chyrysemys picta and Chelydra serpentina may also indicate cooler summer temperatures (Holman and Richards, 1993). These "boreal" species contrast with the presence of Psuedacris clarki, a southern extralimital species. An equable climate may have been capable of supporting temperate species (such as Psuedacris clarki) and boreal species (such as Ambystoma laterale and Rana sylvatica) in what would have been a mosaic community (Holman, 1976).

Other Irvingtonian herpetofaunas from the Great Plains have produced species which would be ecologically incompatible today. In particular, Bufo hemiophyrs has been found in three faunas, the Cudahy, Courtland Canal, and Hall Ash (Tihen, 1962; Rogers, 1982). Of these, only Courtland Canal has greater than ten species with a total of twelve. This fauna also has the species Pseudemys scripta and Agkistrodon contortrix which caused Rogers (1982) to suggest that the Courtland Canal climate was more equitable. This and the occurrence of Bufo hemiophrys in the other faunas agree with the reconstruction proposed for the Albert Ahrens herpetofauna.

Ranid Taphonomy.-Gravel appearing to be continuous with the stream deposits was found in a deep depression along one channel. This gravel pocket contained mostly disarticulated anuran fossils including cranial elements. Anuran cranial elements are not typically found as fossils (Holman, 1965a).

Ilia from this pocket belonged almost entirely to *Rana pipiens*-complex (referred to *R. blairi*; see remarks on page 12). This depression is thought here to represent a quiet area along the bank of the stream where these frogs may have been living.

Freezing of the latter pond may have caused mass death of frogs hibernating within the mud along the margins. This mechanism may have also caused the concentration discussed above and/or other concentrations (Holman, pers. comm.). The presence of an as yet unidentified articulated anuran (UNSM uncatalogued) from the upper silt could also be interpreted in this manner. It should be noted that Fay (1984) attributed high numbers of the species *Bufo americanus* in the St. Elzear l.f. to hibernaculum mortality.

Depositional Environment.-Sedimentary evidence suggests that micro-vertebrates from the lower gray silt were deposited on point bars within a system of small, shallow streams. Fossils, along with gravel, would have accumulated during periods of rapid run off. The clay nodules appear to be soil which fell into the streams at cut banks during these periods. Otherwise, the stream appears to have had a weak current.

As dicussed above, ranids are by far the most common fossils in the entire Albert Ahrens herpetofauna and are found as scapulae, humeri, and sacra as well as ilia (see individual species accounts). Numerous indeterminate anuran elements are most likely ranid, as well. The amount and variety of ranid fossils suggests that very little transport occurred prior to their deposition as Rana species shun rapid flowing water; the in situ or near in situ deposition of these fossils suggest a low energy environment.

The upper portion of the gray silt appears to be paludal in origin. This deposit is thought to indicate the presence of a beaver dam which blocked the flow of the Albert Ahrens stream system (Voorhies, pers. comm.). It is undoubtedly aquatic as a humerus from Chelydra serpentina was recovered from the lower portions of the deposit. Other aquatic species are also suggestive of pond or marsh habitats. In particular, Thamnophis radix may be associated with the marshland (see remarks on page 22).

A breakdown of the habitat preferences of the entire Albert Ahrens herpetofauna is given in Table 3. The most common fossils in terms of minimum number of individuals appear to be those associated with woodland edge or open woodlands. Thirteen species belong to a group which Holman (1992) considered conifer woodland tolerant. Remaining woodland species belong to a group more adapted for mixed conifer-deciduous woodland. Almost all appear to be at least semi-aquatic. Grassland species are much less numerous. Fossils of grassland species that are not seasonally dependent on aquatic habitats tend to show more wear than those of aquatic, woodland species, most likely due to a greater amount of transport to the site.

Table 3 Habitat preferences and abundances of amphibian and reptile species in the Albert Ahrens local fauna. Infered habitats are from Collins (1974) and Lynch (1985). Forest preferences from Holman (1992). Number of salamander and snake vertebrae are in parathesis. Abbreviations are as follows: S-seasonal, F-frequent, I-infrequent, (C)-conifer tolerant, (D)-mixed forest, (B)-species or subspecies in both grous.

Species	Pond or stream	Pond or stream edge	Grassland	Open woodland	Woodland	Minimum number of individuals
Ambystoma laterale	S	S	-	F	F(C)	1(14)
Ambystoma tigrinum						
adult	S	S	F	F	F(C)	1(45)
larva	F	-	-	-	-	1(9)
Scaphiopus bombifrons	-	S	F	-	-	6
Bufo americanus	S	S	-	F(C)	-	15
Bufo cognatus	-	F	F	I	-	31
Bufo w. woodhousii	S	F	F	-	-	36
Pseudacris clarki	S	S	F	F	-	1
Hyla versicolor and H. crysoscelis	S	F	-	F	F(B)	2
Rana catesbeiana	F	F	-	-	(C)	110
Rana clamitans	S	F	-	-	(C)	63
Rana blari	S	S	I	-	-	601
Rana sylvatica	-	-	-	-	I(C)	65
Chelydra serpentina	F	S	-	-	(C)	1
Chrysemys picta belli	F	S	-	-	(C)	1
Eumeces obsoletus	-	-	F	-	-	1
Coluber constrictor	-	-	F	F(D)	I	1(13)
Elaphe guttata and E. obsoleta	-	-	F	F	-	1(19)
Elaphe vulpina	-	-	I	F(B)	-	1(15)
Lampropeltis triangulum	-	-	F	F	F	1(30)
Nerodia sipedon	F	F	-	-	(C)	1(127)
Regina grahami	F	F	-	-	-	1(24)
Storeria sp.	-	-	-	F	F(B)	1(163)
Thamnophis proximus	-	F	-	-	-	1(69)
Thamnophis radix	-	F	F	-	-	1(49)
Thamnophis sirtalis	-	F	-	F	F(C)	1(78)
Heterodon platirhinos	-	I	F	F(D)	-	1(15)
Heterodon nasicus	-	-	F	-	-	1(17)
Agkistrodon sp.	-	F	-	-	F	1(3)
Crotalus horridus	-	-	-	F	-	1(6)
Crotalus viridis	-	-	F	-	-	1(2)
Sistrurus catenatus	-	-	F	-	-	1(5)

CONCLUSION

The Albert Ahrens local fauna has produced a large herpetofauna of thirty-one species. Like many eastern cave faunas from the Irvingtonian, the majority of the Albert Ahrens herpetofauna is similar to the modern fauna; however two distinct northeastern species, Ambystoma laterale and Rana sylvatica, as well as Elaphe vulpina show that there was some amount of range adjustment to possible Irvingtonian glaciation. In contrast to Fay's (1988) comments based on eastern Rancholabren cave faunas, the Great Plains herpetofauna from the Irvingtonian appears consistent with the "Pleistocene Climatic Equability Model."

The depositional environment appears to have been a slow stream system bordered by a mixed conifer-deciduous forest. Later blockage of the streams resulted in a pond which developed into a marsh. Some amount of grassland was present within the drainage basin. Grassland species appear to be a mix of amphibian species which would have made seasonal use of the stream system and of remains washed into the depositional site from varying distances.

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