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HERPETOFAUNAS OF THE BIG SPRINGS AND HORNET'S NEST QUARRIES (NORTHEASTERN NEBRASKA, PLEISTOCENE: LATE BLANCAN)

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Two herpetofaunas of Late Blancan age from northeastern Nebraska were studied, Big Springs Quarry (AP 103) and Hornet's Nest Quarry (KX 127). Big Springs Quarry contains six amphibian species, three of which are extinct, and 25 reptilian species, two of which are extinct. Hornet's Nest Quarry contains seven species of amphibians, two of which are extinct, and 11 reptilian species, none of them extinct. The faunal assemblage is one that would be characteristic of southern Kansas today. The paleoecological interpretation of the two sites indicates that Hornet's Nest Quarry represents a moister and more wooded environment than Big Springs Quarry. Big Springs Quarry was probably deposited in a tall-grass prairie.

† † †

INTRODUCTION

Reptiles and amphibians are excellent ecological indicators for studies of paleoecology. They also can be effectively used to support or refute dating based upon mammalian index fossils because the ratio of extinct to extant species decreases through the Paleogene and Neogene. Also, some reptilian and amphibian species can be used as index fossils.

Species of Big Springs Quarry include one salamander, five anurans, five turtles, two lizards, and 18 snakes. Of these, three toads, one turtle, and possibly one lizard species are extinct. Species of Hornet's Nest Quarry include two salamanders, five anurans, one turtle, one lizard, and nine snakes. Of these, the only extinct species is a toad. These findings are consistent with the Late Blancan age of the assemblage proposed by M. R. Voorhies (personal communication).

The herpetological assemblage at the two localities is one that would be found today in southern Kansas. Ecologically, the two localities differ in that Hornet's Nest Quarry represents a

woodland pond environment with an upland prairie component. Big Springs Quarry apparently represents a lake, river, or prairie marsh with a hilly, rocky, arid or semi-arid component.

GEOLOGIC AND GEOGRAPHIC SETTINGS

The following is quoted from a personal letter from Michael R. Voorhies dated 10 October 1982.

University of Nebraska State Museum (UNSM) Paleontological Locality AP 103, is near Orchard in northwestern Antelope County, northeastern Nebraska. The fossils were recovered by wet-screening lenses of fine gravel overlain and underlain by ashy silt. The ashy silt unit is near the top of a sequence of sand and crystalline gravel correlated with the Long Pine Formation of Skinner and Hibbard (1972). Mammalian fossils from Big Springs Quarry, currently being studied by M. R. Voorhies and R. J. Zakrzewski, indicate a Late Blancan age for the assemblage in terms of the North American land mammal 'ages' (*sensu* Kurten and Anderson, 1980).

UNSM locality KX 127, Hornet's Nest Quarry, is near Center in central Knox County, northeastern Nebraska. The fossils were recovered by wet-screening lenses of fine gravel within a unit of western-source sand and gravel believed to correlate with the Long Pine Formation. The fossiliferous unit at Hornet's Nest Quarry is directly overlain by weathered glacial till of Pleistocene age. Fossil mammals from KX 127, mostly rodents, indicate close time equivalence with Big Springs Quarry (Late Blancan).

SYSTEMATIC PALEONTOLOGY

Class Amphibia

Order Anura

Family Bufonidae

Genus *Bufo**Bufo cognatus* Say

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 1 parasphenoid, 7 right ilia, 7 left ilia, UNSM 52048. KX 127: 1 sacral vertebra, 3 right ilia, 5 left ilia, UNSM 52052.

Remarks. According to Holman (1971), the ilial prominences of *B. cognatus* and its close relative, *B. speciosus*, are higher than those of *B. americanus*, *B. debilis*, *B. punctatus*, and *B. woodhousei*. The fossils are similar to *B. cognatus* and *B. speciosus* in this character.

Holman (1971) separated *B. cognatus* and *B. speciosus* on a character of the sacral vertebrae. In dorsal view the condyles end only slightly posterior to the posterior border of the neural arch in *B. cognatus* and the fossil sacral vertebra, whereas in *B. speciosus* the condyles project well posterior to the posterior border of the neural arch.

Tihen (1962) found that in *B. cognatus* the ilial prominence is 40% to 50% the length of the base and that the supra-acetabular angle is between 115° and 130°. In the fossils the ilial prominence varies between 40% to 51% of the base, and the supra-acetabular angle varies from 119° to 135°. Therefore, the fossils are referred to *B. cognatus*.

Bufo cognatus occurs in Antelope and Knox counties, Nebraska, today and is known as a fossil from the Middle Pliocene to the Recent. This is a primarily nocturnal toad of the Plains and is frequently found near water (Behler and King, 1979; Conant, 1975).

Bufo repentinus Tihen

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 2 right ilia, 7 left ilia, UNSM 52055. KX 127: 1 ilium, UNSM 52062.

Diagnosis. See Tihen (1962).

Remarks. Tihen (1962) separated species of *Bufo* on

the relative height of the ilial prominence, various angles describing the prominence, and the extent of palmation anterior to the sub-acetabular expansion. In *B. repentinus* the height of the prominence is nearly 60% the length of the base, the supra-acetabular angle is nearly 120°, the peak of the prominence is decidedly anterior to the midpoint of the base, and there is extensive palmation anterior to the sub-acetabular expansion. In the fossils the height of the ilial prominence varies between 57% to 77% of the length of the base, the supra-acetabular angle is from 111° to 121°, the peak of the prominence is decidedly anterior to the midpoint of the base, and extensive palmation is present anterior to the sub-acetabular expansion. The fossils are therefore referred to *B. repentinus*.

Bufo repentinus is an extinct species known previously only from the Sangamon, Cragin Quarry, of Meade County, Kansas. Tihen (1962) considered any new species of amphibian from the Pleistocene subject to suspicion. Apparently, *B. repentinus* did not originate in the Pleistocene but, rather, earlier in the Pliocene.

According to Tihen (1962), the close relatives of this species are *B. cognatus*, *B. rexroadensis*, and *B. woodhousei*. Because *B. cognatus* and *B. rexroadensis* are represented in the fauna, possibly *B. repentinus* was the ecological equivalent of *B. woodhousei*. *Bufo woodhousei* inhabits a variety of niches including grasslands, sandy areas near marshes, and temporary rain pools (Behler and King, 1979).

Bufo rexroadensis Tihen

Locality. Big Springs Quarry, AP 103.

Material. 4 right ilia, 4 left ilia, UNSM 52054.

Diagnosis. See Tihen (1962).

Remarks. The ilium of *B. rexroadensis* has a very high ilial prominence (55% to 60% the length of the base) having subequal anterior and posterior slopes, or with the anterior slightly steeper (resulting in the peak of the prominence being only slightly anterior to the midpoint of the base), and with a supra-acetabular angle of 110° to 115° (Tihen, 1962). The fossil ilia have a prominence height that is 57% to 67% the length of the base, the peaks of the prominences are at the center or slightly anterior to the midpoint of the base and the supra-acetabular angle varies from 112° to 119°. Extensive sub-acetabular palmation is absent. The fossils are therefore referred to *B. rexroadensis*.

Bufo rexroadensis is known as a fossil from the Upper Pliocene of Meade County, Kansas. Its habitat is unknown.

Bufo sp. cf *B. spongifrons* Tihen

Locality. Big Springs Quarry, AP 103.

Material. 1 right ilium, 1 left ilium, UNSM 52057.

Diagnosis. See Tihen (1962).

Remarks. Tihen (1962) characterized this species as having an ilial prominence between 45% and 50% the length of its base, and anterior angle equal to 45°, posterior angle equal to 55° to 65°, and a supra-acetabular angle varying between 95° and 105°. In the fossils the ilial prominence (Fig. 1) is somewhat higher (57% and 63% the length of the base), the anterior angle is about 49°, the posterior angle is about 60°, and the supra-acetabular angles are 91° and 106° making the peak of the prominence decidedly posterior to the midpoint of the base whereas it is at the midpoint or anterior to the midpoint in all other fossils studied.

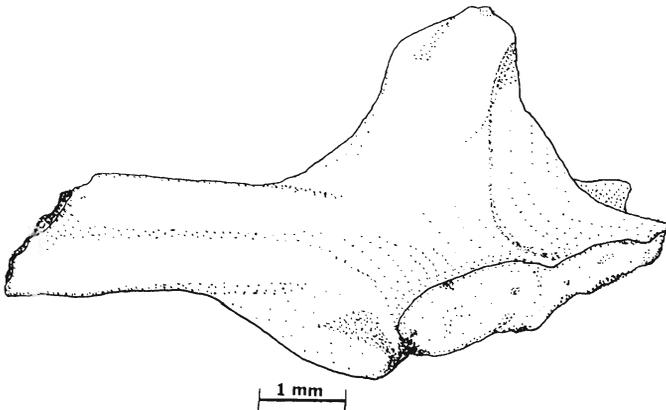


FIGURE 1. *Bufo* cf *Bufo spongifrons* ilium, UNSM 52057, lateral view.

The dorsal border of one ilium posterior to the prominence broke off in the process of remeasuring the supra-acetabular angle so that measurement could not be verified. This is the specimen that most diagnostically shows the *B. spongifrons* characters so the fossils are only tentatively assigned to that species.

Bufo spongifrons is known from the Middle Pliocene of Phillips County, Kansas. Its habitat is unknown.

Bufo sp.

Locality. Big Springs Quarry, AP 103.

Material. 1 prootic, 5 sacral vertebrae, 4 ilia, 1 femur, UNSM 52056.

Remarks. The material is either too fragmentary for identification or is non-diagnostic.

Family Ranidae

Genus *Rana**Rana blairi* or *R. pipiens* or *R. utricularia*

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. KX 127: 27 sacral vertebrae, 95 right ilia, 65 left ilia, UNSM 52050. AP 103: 7 sacral vertebrae, 19 right ilia, 24 left ilia, UNSM 52053.

Remarks. Extant species of *Rana* occurring in or near Nebraska today include *R. areolata*, *R. blairi*, *R. catesbeiana*, *R. palustris*, *R. pipiens*, and *R. utricularia*. According to Holman (1965a), the posterodorsal border of the ilial crest slopes gently into the dorsal acetabular expansion in all of these species except *R. catesbeiana*. *Rana blairi*, *R. pipiens*, and *R. utricularia* can be separated from *R. areolata* and *R. palustris* on characters of the vastus prominence described by Holman (1971). The vastus prominence of *R. areolata* is narrower, more rounded, and less flattened than in *R. blairi*, *R. pipiens*, and *R. utricularia*. *Rana sylvatica* is similar to *R. areolata* in this character. The fossil ilia are comparable to *R. blairi*, *R. pipiens*, and *R. utricularia* in the characters so far discussed.

Bones of *R. blairi*, *R. pipiens*, and *R. utricularia* are extremely similar, and I am unable to separate them. A reliable method of separation is needed, but it is possible that they will not be separable on most elements for paleontological studies. The species are so similar that it is probable that speciation did not occur until after the deposition of the fossils currently under study. If that were the case, then a new species name is needed for the ancestral species.

Members of the leopard frog species are extremely plastic in their habitat preferences so are not good paleoecological indicators. The fossil history of the ancestors of this group is also widespread and of long geologic duration.

Rana catesbeiana Shaw

Locality. Hornet's Nest Quarry, KX 127.

Material. 1 vertebra, 2 sacral vertebrae, 8 right ilia, 8 left ilia, UNSM 52047.

Remarks. These ilia are similar to *R. catesbeiana* in having the posterodorsal border of the ilial crest slope sharply into the dorsal acetabular expansion. No other ranids in or near

Nebraska have this characteristic. The ilia are identical to modern *R. catesbeiana* so have been referred to that species. The sacral vertebrae are shorter and wider than other possible ranid species.

Rana catesbeiana is a widespread frog, both geologically and geographically. It is found throughout Nebraska today, most frequently near permanent bodies of water.

***Rana sylvatica* Le Conte**

Locality. Hornet's Nest Quarry, AP 103.

Material. 2 sacral vertebrae, 2 right ilia, 3 left ilia, UNSM 52049.

Remarks. Characters separating *R. areolata* and *R. sylvatica* from other species of *Rana* in or near Nebraska were discussed previously. Tihen (1954) separated the sacral vertebrae of several ranids on the basis of the ratio of the centrum length to the centrum width versus the centrum length. *R. areolata* falls into the short, wide group, and *R. sylvatica* and the fossils fall into the long, narrow group. If associations have been made correctly, these fossils are then assignable to *R. sylvatica*.

The Recent range of *R. sylvatica* is from Labrador to Alaska, south in the east to the southern Appalachians. There are isolated colonies in the Ozarks, Kansas, Colorado, Wyoming, and Idaho (Stebbins, 1966). Thus, its current distribution is 625 km N, 500 km E, 400 km S, and 750 km WSW of the fossil locality. *Rana sylvatica* is known as a fossil from the Late Pleistocene.

According to Stebbins (1966), in the east *R. sylvatica* inhabits damp, shady woods in the vicinity of clear streams and leafy pools, but may move out of the forests when breeding. In the northwest it is found chiefly in open, grassy areas bordered by thickets of willow and aspen, often near spruce or other forest trees.

Order Urodela
Family Ambystomatidae

Genus *Ambystoma*
***Ambystoma maculatum* (Shaw)**

Locality. Hornet's Nest Quarry, KX 127.

Material. 12 vertebrae, UNSM 52045.

Remarks. Tihen (1958) divided the genus *Ambystoma* into subgenera and species groups on the basis of osteological

characters. The *A. maculatum* group has the most elongate vertebrae of all the ambystomatids. *Ambystoma gracile*, *A. jeffersonianum*, *A. laterale*, *A. macrodactylum*, *A. maculatum*, *A. platineum*, and *A. tremblayi* are included in this group (Holman, 1975). Of these, *A. gracile* and *A. macrodactylum* are West Coast species, and the rest are distributed throughout most of the United States east of the Great Plains. According to Tihen (1958), *A. gracile* and *A. maculatum* are large, heavy-bodied forms for the group, but the rest are smaller with more slender bodies and limbs. The fossil vertebrae are elongate, identical in size to Recent *A. maculatum*, and much nearer in Recent range to *A. maculatum* than to *A. gracile*. Diagnostic characters that the fossils share with Recent *A. maculatum* vertebrae are: the neural spine does not extend beyond the postzygapophyses and the arch of the neural spine is low resulting in a low postzygapophyseal area. The fossils (Fig. 2) are therefore referred to *A. maculatum*.

Some of the vertebrae have perforate centra indicating that larval individuals were present, but no indication of neoteny was found using criteria of Tihen (1942 and 1958).

Today, *A. maculatum* occurs 400 km south of Antelope and Knox counties, Nebraska, and is known as a fossil from the Lower Pliocene of Trego County, Kansas (Holman, 1975).

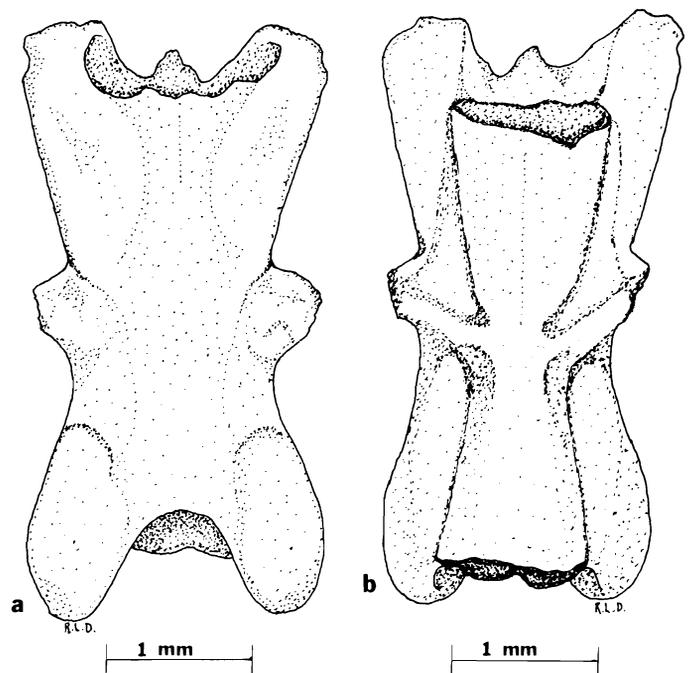


FIGURE 2. *Ambystoma maculatum* vertebra, UNSM 52045. a. Dorsal view. b. Ventral view.

Salamanders of this species spend much of their time underground and inhabit hardwood forest areas near water (Behler and King, 1979).

Ambystoma tigrinum (Green)

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 1 atlas, UNSM 51970; 3 atlases, 25 vertebrae, 9 limb elements, UNSM 52061; 24 vertebrae, UNSM 51399. KX 127: 5 vertebrae, 4 leg elements, UNSM 52046.

Remarks. The vertebrae were identified using characters discussed by Tihen (1958) and Holman (1959 and 1975). The vertebrae are relatively short and wide (Tihen, 1958); the neural arch is upswept and extends well posterior to the ends of the postzygapophyses (Holman, 1975). In other species the vertebrae are longer and narrower, and the posterior part of the neural arch is straighter and does not extend so far posteriorly.

Vertebrae of *A. tigrinum* and the extinct Blaccan species, *A. hibbardi*, are not separable although the species can be distinguished by the degree of ossification of certain bones. Because the necessary elements were not found, the fossils cannot be assigned on that basis. *Ambystoma hibbardi* is a fossil species named from the Upper Pliocene Rexroad Fauna of Meade County, Kansas. According to Tihen (1955), it very closely resembles the extant *A. tigrinum* in size, proportions, and general features. It differs from *A. tigrinum* in having a narrower premaxillary spine, failure of the columellar footplate to fuse with the otic capsule, and the lack of ossification of cartilaginous bones such as the orbitosphenoids, quadrates, and ischia (Tihen, 1955). Because *A. tigrinum* is known in the fossil record from both before (Lower Pliocene) and after the occurrence of *A. hibbardi* in Kansas, possibly *A. hibbardi* should be considered only a local variant of *A. tigrinum*. With this assumption, these fossils are referred to *A. tigrinum*.

The fossils are within the size range of Recent *A. tigrinum*. Perforate centra in some vertebrae indicate that larval individuals were present in the population, but no evidence for the presence of neoteny could be found using criteria of Tihen (1942 and 1958).

Ambystoma tigrinum is a widespread species that occurs today in Antelope and Knox counties, Nebraska, and is known as a fossil from the Lower Pliocene to the Recent. Habitat of this species is extremely varied, but larvae require an aquatic environment.

Class Reptilia

Order Chelonia

Family Emydidae

Genus *Chrysemys*

***Chrysemys picta* Schneider**

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 1 nuchal, 3 neurals, 2 marginals, 2 hypoplastra fragments, UNSM 52100. KX 127: 4 pleurals, 1 marginal, 1 epiplastron, UNSM 52101.

Remarks. The elements assigned to *C. picta* were identified using characters described by Weaver and Rose (1967) and Galbraith (1948). The fossils are indistinguishable from Recent *C. picta* except in thickness. All elements measured were about 33% thicker than counterparts of Recent *C. picta*.

Chrysemys picta occurs today in Antelope and Knox counties, Nebraska, and is known as a fossil from the Pliocene and Pleistocene. These turtles live primarily in shallow, slow-moving water, with plenty of emergent vegetation, partially submerged logs, and soft, muddy bottoms (Behler and King, 1979; Conant, 1975).

Genus *Emydoidea*

***Emydoidea blandingi* (Holbrook)**

Locality. Big Springs Quarry, AP 103.

Material. 1 nuchal, UNSM 51381A.

Remarks. This bone represents an adult individual. Identification was based on shape and scute suture lines. This nuchal cannot be separated from Recent *E. blandingi*.

Emydoidea blandingi occurs today in Antelope County, Nebraska, and is known as a fossil from the Pliocene and Pleistocene. This turtle is a semi-aquatic species that occurs in lakes, river sloughs, and prairie marshes (Preston and McCoy, 1971).

Genus *Graptemys*

***Graptemys* sp.**

Locality. Big Springs Quarry, AP 103.

Material. 1 marginal, UNSM 52304.

Remarks. This large, notched marginal undoubtedly represents the genus *Graptemys*, but insufficient comparative material is available to permit specific identification.

Graptemys pseudogeographica occurs today within 25 km of Antelope County, Nebraska. Other species of *Graptemys* range at least within 200 km of the fossil locality. All turtles of this genus are aquatic (Behler and King, 1979).

Emydidae sp.

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 11 carapace and plastron fragments, 1 girdle element, UNSM 52098. KX 127: 5 carapace fragments, UNSM 52102.

Remarks. This material is too fragmentary for specific identification but apparently represents the emydid species described previously.

Family Testudinidae

**Genus *Geochelone*
(*Caudochelys*)**

***Geochelone oelrichi* Holman**

Locality. Big Springs Quarry, AP 103.

Material. 1 marginal, UNSM 51969.

Remarks. This posterior marginal is very thick and rugose so is referred to the *G. turgida* group of Holman (1972a). The fossil material comes from sediments that overlie the Sand Draw faunal sites of Nebraska from which the last member of the *G. turgida* group, *G. oelrichi*, was named. This marginal is therefore referred to *G. oelrichi*.

The fossil marginal is smaller than the type material of *G. oelrichi*, but that material has five growth rings (Holman, 1972a), whereas the present material has only three.

The geological distribution of *G. oelrichi* includes the Long Pine Formation of Nebraska (Holman, 1972a).

The habitat of *G. oelrichi* is unknown, but the structure of the forelimb indicates that the front feet might have been used for digging in sandy banks or for enlarging animal burrows for use by the tortoises (Holman, 1972a).

Family Trionychidae

***Trionyx* sp.**

Locality. Big Springs Quarry, AP 103.

Material. 2 costal fragments, UNSM 51382.

Remarks. Specific identification was not possible. All members of the genus *Trionyx* are thoroughly aquatic, and all species in or near Nebraska are primarily river turtles (Conant, 1975).

Order Squamata: Lacertilia

Family Iguanidae

**Genus *Phrynosoma*
Phrynosoma cornutum (Harlan)**

Locality. Big Springs Quarry, AP 103.

Material. 1 fragmentary dentary, 1 vertebra, UNSM 52097, 2 vertebrae, UNSM 51971.

Remarks. According to Etheridge (1960), the teeth of *P. cornutum* are simple chisel-like cones. The fossil dentary teeth agree with *P. cornutum* in this character. The lateral surface of the dentary is considered diagnostic in *P. cornutum* but is missing in the fossil. However, all areas of the fossil that are present are not distinguishable from Recent *P. cornutum*.

Today, *P. cornutum* occurs 720 km south of Antelope County, Nebraska, and is known as a fossil from the Pliocene and Pleistocene of North America. These are terrestrial lizards that occur on flat, dry land with scanty vegetation (Behler and King, 1979).

Family Scincidae

**Genus *Eumeces*
Eumeces sp. cf *E. striatulus* Taylor**

Locality. Big Springs Quarry, AP 103.

Material. 1 maxilla, UNSM 51302.

Remarks. This fossil is larger than all extant species of scincids at or near the fossil locality. The largest of the extant species has 10 teeth in a space of 4 mm, whereas the fossil and the extinct species, *E. striatulus*, have 6 or 7 teeth in a similar space. Because the fossil is fragmentary, it is only tentatively referred to *E. striatulus*.

Eumeces striatulus was named as a fossil species from the Late Pliocene of Kansas. It is also known from the Early Pleistocene of Kansas. Its habitat is unknown.

Eumeces sp.

Locality. Hornet's Nest Quarry, KX 127.

Material. 1 maxilla, UNSM 52099.

Remarks. This maxilla is too fragmentary for specific identification but undoubtedly represents a species of *Eumeces* comprising moderately small animals.

Order Squamata: Serpentes
Family Colubridae
Subfamily Colubrinae

Genus *Coluber*
Coluber constrictor Linnaeus

Locality. Big Springs Quarry, AP 103.

Material. 36 vertebrae, UNSM 52065.

Remarks. *Coluber* and *Masticophis* vertebrae are very similar, but according to Hill (1971) the haemal keels of the middle precaudal vertebrae in lateral view are straight in *Masticophis* but slightly curved in *Coluber*. These fossil vertebrae are similar to *C. constrictor* in this character and are otherwise not separable from Recent *C. constrictor*.

Coluber constrictor occurs today in northeastern Nebraska, and it is known as a fossil from the Late Pliocene and Pleistocene. This species has a widespread distribution and occurs in a variety of habitats including grasslands, brushy areas, and woodlands of various types (Behler and King, 1979).

Genus *Elaphe* or *Lampropeltis*
sp. indet.

Locality. Big Springs Quarry, AP 103.

Material. 13 vertebrae, UNSM 52067.

Remarks. These vertebrae are too fragmentary for generic identification although they clearly represent either *Elaphe* or *Lampropeltis*.

Genus *Elaphe*
Elaphe guttata (Linnaeus)

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 8 vertebrae, UNSM 52068. KX 127: 7 vertebrae, UNSM 52069.

Remarks. *Elaphe* vertebrae are very similar to *Arizona*, *Lampropeltis*, and *Pituophis*. *Pituophis* vertebrae can be separated from the other genera in that they have a higher neural spine (Auffenberg, 1963). Compared to *Elaphe*, the accessory processes of *Arizona* are blunter and less delicate (Holman, 1970), and *Lampropeltis* vertebrae have a less vaulted neural arch (Auffenberg, 1963) and straighter sub-central ridges from below (Brattstrom, 1955).

The neural spine of *E. guttata* and the fossils is higher than all other possible extant and extinct species of *Elaphe* except *E. obsoleta* which has a higher neural spine than the fossils. On that basis this material is referred to *E. guttata*. Subspecific assignment is not possible.

Elaphe guttata ranges north to about 550 km south of the fossil localities. It is known as a fossil from the Late Pliocene and Pleistocene. These snakes are primarily nocturnal and frequently burrow or hide beneath stones or logs during the day. They frequent hillsides or rocky draws and often occur near water in arid country (Conant, 1975).

Elaphe vulpina (Baird and Girard)

Locality. Big Springs Quarry, AP 103.

Material. 8 vertebrae, UNSM 52070.

Remarks. The neural spine of *E. vulpina* and the fossils is shorter than other possible species of *Elaphe* except for the fossil species *E. kansensis*, *E. nebraskensis*, and *E. pliocenica*. *Elaphe vulpina* and the fossil vertebrae have a sharper haemal keel and are smaller than *E. kansensis*, have laterally directed accessory processes and prezygapophyseal faces rather than the oblique ones found in *E. nebraskensis*, and compared to *E. pliocenica* have a thinner neural spine and haemal keel (Holman 1964 and 1968). The fossils have therefore been referred to *E. vulpina*.

Elaphe vulpina occurs today in Antelope County, Nebraska, and it has been found as a fossil from the Late Pliocene and Pleistocene. This snake occurs in wooded stream valleys and prairies (Behler and King, 1979).

Genus *Lampropeltis*
Lampropeltis calligaster (Harlan)

Locality. Big Springs Quarry, AP 103.

Material. 11 vertebrae, UNSM 52073.

Remarks. Vertebrae of *Lampropeltis* were distinguished

from those of *Arizona*, *Elaphe*, and *Pituophis* by characters discussed previously for *E. guttata*. Three extant species of *Lampropeltis*, *L. calligaster*, *L. triangulum*, and *L. getulus*, occur at or near the fossil locality. Vertebrae of *L. triangulum* have much lower neural spines than those of *L. calligaster*, *L. getulus*, and the fossil vertebrae Holman (1963). *Lampropeltis getulus* differs from the fossils and *L. calligaster* in that specimens of *L. getulus* are smaller, the vertebrae are more robust with thicker neural spines and neural arches, the haemal keel is stronger (Holman, 1965b), and the subcentral ridges tend to be bent rather than convex, concave, or straight (Auffenberg, 1963). *Lampropeltis calligaster* and the fossil vertebrae also have the top of the zygosphene sloping downwards when viewed anteriorly, whereas it is flat in *L. getulus* and gently curved upward in *L. triangulum*.

Lampropeltis calligaster ranges north today to about 130 km south of Antelope County, Nebraska. This species has been reported previously as a fossil from the Pleistocene. It is a snake of prairies, open woodland, and rocky hillsides (Behler and King, 1979).

***Lampropeltis getulus* (Linnaeus)**

Locality. Big Springs Quarry, AP 103.

Material. 4 vertebrae, UNSM 52074.

Remarks. Characters used to identify this species were discussed for *L. calligaster*.

Lampropeltis getulus ranges north to about 130 km south of the fossil locality, and there is a relict population about 60 km to the west. This species is known as a fossil from the Late Pliocene and Pleistocene. It is found in diverse habitats from the Florida Everglades to desert areas (Behler and King, 1979).

***Lampropeltis triangulum* (Lacepede)**

Locality. Big Springs Quarry, AP 103.

Material. 25 vertebrae, UNSM 52072.

Remarks. Characters used to identify these vertebrae were discussed for *L. calligaster*.

Lampropeltis triangulum occurs today in Antelope County, Nebraska, and is known as a fossil from the Late Pliocene and Pleistocene. The habitats of this species vary from open woodland and rocky hillsides to prairies and high plains (Behler and King, 1979).

***Lampropeltis* sp.**

Locality. Big Springs Quarry, AP 103.

Material. 5 vertebrae, UNSM 52071.

Remarks. Although specific identification was not possible, these vertebrae clearly represent the genus *Lampropeltis*.

**Genus *Masticophis*
Masticophis flagellum Shaw**

Locality. Big Springs Quarry, AP 103.

Material. 11 vertebrae, UNSM 52066.

Remarks. These vertebrae were separated from those of *Coluber* using characters discussed for *C. constrictor*. They could not be distinguished from Recent *M. flagellum*.

Masticophis flagellum ranges to about 900 km south of Antelope and Knox counties, Nebraska, today. This species is known as a fossil from the Late Pliocene and Pleistocene. It occurs in relatively open, dry environments including grasslands, desert scrub, and chaparral (Behler and King, 1979).

**Genus *Rhinocheilus*
Rhinocheilus lecontei Baird and Girard**

Locality. Big Springs Quarry, AP 103.

Material. 2 vertebrae, UNSM 52096.

Remarks. Hill (1971) distinguished *R. lecontei* vertebrae from those of all other North American snake genera by the following combination of characters: zygosphenes flat in anterior view; prezygapophyseal faces obovate to oval; neural spines thick, flat dorsally, overhanging centra posteriorly with indented anterior and posterior edges; centra short; epizygapophyseal spines absent, or if present much reduced; neural arches depressed; cotyla usually round, occasionally slightly compressed; haemal keels and subcentral ridges moderately to strongly developed; accessory processes swollen and flat. The fossil vertebrae agree with *R. lecontei* in these characters and have been referred to that species.

Today, *R. lecontei* ranges to about 1,000 km south of Antelope County, Nebraska, and it is known as a fossil from the Late Pliocene and Pleistocene. This snake hides among rocks or in underground burrows during the day and is active primarily at night. It lives in the dry open prairie and desert brushland, but it also occurs in tropical areas in Mexico (Behler and King, 1979).

Subfamily Natricinae

Natricinae sp.

Locality. Big Springs Quarry, AP 103.

Material. 30 vertebrae, UNSM 52087.

Remarks. These vertebrae are too fragmentary to assign to genus although they clearly represent the subfamily Natricinae.

Genus *Nerodia**Nerodia rhombifera* (Hallowell)

Locality. Hornet's Nest Quarry, KX 127.

Material. 3 vertebrae, UNSM 52082.

Remarks. This is the only species of *Nerodia* near Nebraska that has a neural spine higher than long (Holman, 1968). Because these vertebrae cannot be distinguished from Recent *N. rhombifera*, they are referred to that species.

Nerodia rhombifera ranges to about 700 km southeast of the fossil locality. It was tentatively identified as a fossil from the Late Pliocene of Texas (Rogers, 1976). This is a ubiquitous snake appearing in many types of aquatic habitats and will follow water courses into arid terrain.

Nerodia sipedon (Linnaeus) or *N. hibbardi* (Holman)

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 9 vertebrae, UNSM 52083. KX 127: 8 vertebrae, UNSM 52084.

Remarks. Vertebrae of *Nerodia* can be distinguished from those of *Thamnophis* because of their larger size and higher neural spines (Holman, 1971). Also, the subcentral ridges tend to be more angular in *Thamnophis* than in *Nerodia*.

The only extant species of *Nerodia* that occurs in north-eastern Nebraska today is *N. sipedon*. This is the only extant species of *Nerodia* near Nebraska that has a neural spine that is longer than high. All others have a neural spine as long as high or higher than long (Holman, 1962, 1968, 1970, and 1971).

Nerodia hibbardi was named from the Upper Pliocene of Idaho. Its vertebrae are very similar to *N. sipedon* although there are distinct differences in cranial elements. The vertebrae of the two species differ only in that the accessory

processes of *N. hibbardi* are longer and more robust than those of *N. sipedon*. The two species cannot be distinguished by this character when cranial elements are not available.

Nerodia sipedon occurs today in Antelope and Knox counties, Nebraska, and it is known as a fossil from the Pleistocene. It lives in a variety of aquatic habitats including lakes, swamps, marshes, and rivers and will occur along water courses in otherwise arid country (Behler and King, 1979).

Nerodia hibbardi is known as a fossil species from the Upper Pliocene of Idaho and Texas (Rogers, 1976). Its habitat is unknown.

Nerodia sp.

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 211 vertebrae, UNSM 52080. KX 127: 13 vertebrae, UNSM 52081.

Remarks. Only generic identification of these vertebrae is currently possible. Most probably they represent the previously described species.

Genus *Regina**Regina grahami* Baird and Girard

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 4 vertebrae, UNSM 52085. KX 127: 4 vertebrae, UNSM 52086.

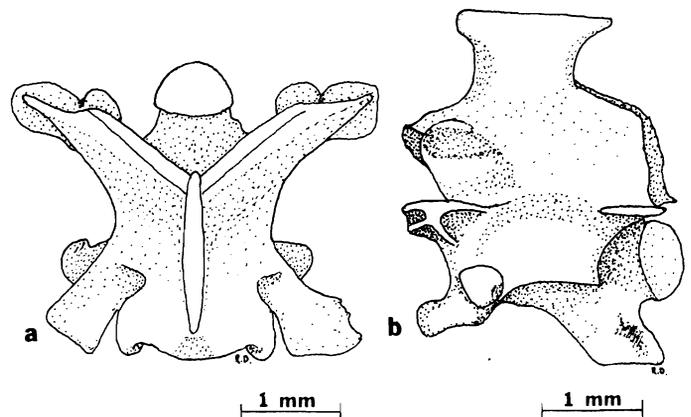


FIGURE 3. *Regina grahami* vertebra, UNSM 52086. a. Dorsal view. b. Lateral view.

Remarks. Holman (1972b) separated vertebrae of *R. grahami* from *Nerodia* and *Thamnophis* by the following combination of characters: vertebrae about as long as wide through the zygapophyses; neural spine longer than high or about as long as high; anterior border of neural spine concave; neural arch vaulted; hypapophysis moderately short with its tip truncated. These fossils (Fig. 3) agree with *R. grahami* in all of these characters and cannot be distinguished from Recent *R. grahami*.

The first fossil of *R. grahami* was reported from the Pleistocene (Yarmouth) of Kansas (Holman, 1972b). These fossils are the earliest known occurrence of this species. *Regina grahami* does not occur today in Antelope or Knox counties, Nebraska, but ranges north to 150 km south of the quarries. These snakes are found in ponds, lakes, ditches, and slow streams where crayfish are abundant (Behler and King, 1979).

Genus *Thamnophis*
***Thamnophis proximus* (Say)**

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 10 vertebrae, UNSM 52090. KX 127: 9 vertebrae, UNSM 52091.

Remarks. Three species of *Thamnophis* occur in or near the northeastern corner of Nebraska today, *T. proximus*, *T. radix*, and *T. sirtalis*. According to Holman (1962), the neural spine is higher in *T. proximus* and *T. sirtalis* than in *T. radix*. Holman (1962) separated *T. proximus* and *T. sirtalis* on the prezygapophyseal processes. In *T. proximus* the prezygapophyseal processes tend to be oblique to the centrum, but in *T. sirtalis* they tend to be at right angles to the centrum. My observations indicate that prezygapophyses tend to be oblong in *T. proximus* and round in *T. sirtalis*. On the basis of these characters, the fossils have been referred to *T. proximus*.

Antelope and Knox counties, Nebraska, border on the edge of the current range of *T. proximus*. This species is known as a fossil from the Pleistocene of at least four states (Holman, 1981). These snakes live in vegetation along the margins of lakes, ponds, marshes, streams, and rivers (Behler and King, 1979).

***Thamnophis radix* (Baird and Girard)**

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 22 vertebrae, UNSM 52094. KX 127: 6 vertebrae, UNSM 520995.

Remarks. The neural spine of *T. radix* is lower than that of *T. proximus* or *T. sirtalis*. According to Holman (1962), this results in pointed anterior and posterior corners of the neural spine in *T. radix*. The fossils are similar to *T. radix* in these characters and have been referred to that species.

Thamnophis radix occurs in Antelope and Knox counties, Nebraska, today, and it has been tentatively identified as a fossil from the Pleistocene of Texas. This, then, is the earliest fossil occurrence of this species although *Thamnophis* vertebrae are common Pliocene and Pleistocene fossils. This snake is abundant in much of its range and occurs in wet areas and open prairies near water (Behler and King, 1979).

***Thamnophis sirtalis* (Linnaeus)**

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 15 vertebrae, UNSM 52092. KX 127: 33 vertebrae, UNSM 52093.

Remarks. Characters used to identify these vertebrae were discussed previously for *T. radix* and *T. proximus*.

Thamnophis sirtalis occurs today in Antelope and Knox counties, Nebraska, and it is known as a fossil from as early as the Late Pliocene. Snakes of this species are commonly seen in moist vegetation near meadows, marshes, prairie swales, and in woodlands (Behler and King, 1979).

***Thamnophis* sp.**

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 92 vertebrae, UNSM 52089. KX 127: 37 vertebrae, UNSM 52088.

Remarks. Only generic identification of these vertebrae is possible but all could be assigned to the previously described species if they were not fragmentary.

Subfamily Xenodontinae

Genus *Heterodon*

***Heterodon nasicus* Baird and Girard**

Locality. Big Springs Quarry, AP 103.

Material. 2 vertebrae, UNSM 52064.

Remarks. Using the criteria discussed for *H. platyrhinos* (following), these fossil vertebrae are similar to *H. nasicus*

in that they are relatively short and broad, the zygosphere is not convex in posterior view, and the anterior borders of the prezygapophyseal facets are not flat.

Brattstrom (1967) distinguished *H. nasicus* from its ancestral species, *H. plionasicus*, by size (*H. plionasicus* is much larger than *H. nasicus*) and the anterior dorsal edge of the zygosphere that is flat in *H. plionasicus* but slightly upturned at the sides in *H. nasicus*. The fossil vertebrae represent adult individuals but are much smaller than vertebrae of *H. plionasicus*. The largest fossil is 5 mm long. One fossil is similar to *H. plionasicus* in that the anterior dorsal edge of the zygosphere is flat rather than upturned as in *H. nasicus*.

According to Brattstrom (1967), the transition from *H. plionasicus* to *H. nasicus* occurred in the uppermost Pliocene to earliest Pleistocene. These fossils support that idea because they show characteristics of both species.

Heterodon nasicus occurs today in Antelope County, Nebraska, and is known as a fossil from the Pleistocene. These snakes occur in sandy and gravelly-soiled prairie, river flood plains, and scrubland (Behler and King, 1979).

Heterodon platyrhinus Latreille

Locality. Big Springs Quarry, AP 103.

Material. 51 vertebrae, UNSM 52060.

Remarks. Two extant species of *Heterodon*, *H. nasicus* and *H. platyrhinus*, occur today in Nebraska. The vertebrae of *H. platyrhinus* are longer and narrower than those of *H. nasicus*, and the zygosphere tends to be convex in posterior view in *H. platyrhinus* but not in *H. nasicus*. According to Holman (1963), the anterior borders of the prezygapophyseal facets are flatter in *H. platyrhinus* than in *H. nasicus*. The fossils agree with *H. platyrhinus* in these characters and are referred to that species.

Heterodon platyrhinus occurs today in Antelope County, Nebraska, and it is known as a fossil from the Late Pliocene and Pleistocene. These snakes prefer dry, open, sandy areas (Behler and King, 1979).

Family Viperidae

Genus *Agkistrodon*

Agkistrodon sp. cf. *A. contortrix* (Linnaeus)

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 21 vertebrae, UNSM 52076. KX 127: 5 vertebrae, UNSM 52075.

Remarks. Holman (1963 and 1965b) separated vertebrae of *Agkistrodon* from *Crotalus* and *Sistrurus* on the basis of the area next to the cotyle and characteristics of the prezygapophyses. A distinct pit with a moderately large fossa occurs on either side of the cotyle in *Agkistrodon*, but in *Crotalus* the pits are absent and the fossa are tiny. The prezygapophyses of *Sistrurus* are tilted upward much more than those of *Crotalus* and *Agkistrodon*, and a tiny spine is usually present just anterior to the neural spine in *Sistrurus* but absent in the other two genera. The fossils are similar to *Agkistrodon* in all of these characters. They are referred to *A. contortrix* on the basis of range.

Agkistrodon contortrix ranges north to about 400 km south of the fossil localities. It is known as a fossil from the Pliocene and Pleistocene. This is a snake of rocky outcrops on wooded hillsides near ponds and streams (Behler and King, 1979).

Genus *Crotalus* *Crotalus horridus* Linnaeus

Localities. Big Springs Quarry, AP 103; Hornet's Nest Quarry, KX 127.

Material. AP 103: 14 vertebrae, UNSM 52078. KX 127: 1 vertebra, UNSM 52077.

Remarks. *Crotalus* vertebrae were separated from those of *Agkistrodon* and *Sistrurus* by characters discussed for *A. contortrix*.

Two species of *Crotalus*, *C. horridus* and *C. viridis*, are present in northeastern Nebraska today. *Crotalus horridus* vertebrae and the fossil vertebrae are larger than those of *C. viridis*, so the fossils have been referred to *C. horridus*.

Crotalus horridus occurs 300 km south of the area today, and it is known as a fossil from the Pleistocene. Snakes of this species occur in rocky outcrops on wooded hillsides and in swampy areas (Behler and King, 1979).

Genus *Sistrurus* *Sistrurus catenatus* (Rafinesque)

Locality. Big Springs Quarry, AP 103.

Material. 1 vertebra, UNSM 52079.

Remarks. Characters separating the genera of viperids were discussed for *A. contortrix*. The only species of *Sistrurus*

that occurs near the fossil locality is *S. catenatus*, so the fossil has been referred to that species.

Sistrurus catenatus occurs about 400 km south of the fossil locality today. It is known as a fossil from the Late Pliocene and Pleistocene. In the western part of its range, this species occurs on rocky hillsides, grassy wetlands, sagebrush prairie, and desert grasslands (Behler and King, 1979).

CONCLUSIONS

The Big Springs and Hornet's Nest quarry amphibians and reptiles, other than three toads, a turtle, a lizard, and possibly one snake, are indistinguishable from living species, although minor details of osteology may differ. The herpetofauna is not typical of the area today, but is similar to one that might be found in southern Kansas. Two species, *Emydoidea blandingi* and *Elaphe vulpina*, do not occur in southern Kansas today, but both had a much wider distribution in the Late Pliocene/Early Pleistocene (Preston and McCoy, 1971; Holman, 1972a).

According to Dice (1943), southeastern Kansas is an interface between the Carolinian and Illinoian biotic provinces. The southern border of Kansas is an intergradation area between the Illinoian and Texan biotic provinces. The Carolinian is characterized as deciduous forest; the Illinoian by intermingling of prairies with strips of deciduous trees in an area that has about 58 cm to about 102 cm of annual precipitation, hot summers, and cold winters. The Texan is similar to the Illinoian except that the climate is milder. The herpetofauna indicates that northeastern Nebraska was this type of interface area in the Late Blancan.

Holman (1972a) found a similar situation in the Sand Draw Fauna. The Sand Draw Fauna of north-central Nebraska had a herpetofauna characteristic of Recent north-central Kansas. This fauna overlies Sand Draw and has an even more southern influence.

The two sites studied in this fauna, Big Springs Quarry and Hornet's Nest Quarry, indicate different ecological conditions, the latter being moister and more wooded than the former (Table I). The presence of *Ambystoma maculatum* and *Rana sylvatica* at Hornet's Nest Quarry indicates conditions found near a cool woodland stream or pond. The presence of *R. catesbeiana* indicates that at least part of this stream or pond must have been permanent. Other species found at the Hornet's Nest Quarry are widespread and fairly non-specific ecologically or would live in a tall-grass prairie area, either near water or away from it.

Big Springs Quarry species do not indicate such wooded

TABLE I. Summary of species found at the Big Springs Quarry and at the Hornet's Nest Quarry.

Species	Big Springs	Hornet's Nest
Class Amphibia		
Order Anura		
Bufonidae		
<i>Bufo cognatus</i>	*	*
+ <i>B. repentinus</i>	*	*
+ <i>B. rexroadensis</i>	*	-
<i>B. sp. cf +B. spongifrons</i>	*	-
Ranidae		
<i>Rana catesbeiana</i>	-	*
<i>R. pipiens</i> complex	*	*
<i>R. sylvatica</i>	-	*
Order Urodela		
Ambystomatidae		
<i>Ambystoma maculatum</i>	-	*
<i>A. tigrinum</i>	*	*
Class Reptilia		
Order Chelonia		
Emydidae		
<i>Chrysemys picta</i>	*	*
<i>Emydoidea blandingi</i>	*	-
<i>Graptemys</i> sp.	*	-
Testudinidae		
+ <i>Geochelone oelrichi</i>	*	-
Trionychidae		
<i>Trionyx</i> sp.	*	-
Order Squamata		
Colubridae		
<i>Coluber constrictor</i>	*	-
<i>Elaphe guttata</i>	*	*
<i>E. vulpina</i>	*	-
<i>Heterodon nasicus</i>	*	-
<i>H. platyrhinus</i>	*	-
<i>Lampropeltis calligaster</i>	*	-
<i>L. getulus</i>	*	-
<i>L. triangulum</i>	*	-
<i>Masticophis flagellum</i>	*	-
<i>Nerodia rhombifera</i>	-	*
<i>N. sipedon</i> or + <i>N. hibbardi</i>	*	*
<i>Regina grahami</i>	*	*
<i>Rhinocheilus lecontei</i>	*	-
<i>Thamnophis proximus</i>	*	*
<i>T. radix</i>	*	*
<i>T. sirtalis</i>	*	*
Iguanidae		
<i>Phrynosoma cornutum</i>	*	-
Scincidae		
<i>Eumeces</i> sp. cf + <i>E. striatulus</i>	*	-
<i>E. sp.</i>	-	*
Viperidae		
<i>Agkistrodon</i> sp. cf <i>A. contortrix</i>	*	*
<i>Crotalus horridus</i>	*	*
<i>Sistrurus catenatus</i>	*	-

*Species present.

-Species absent.

+Species extinct.

conditions. The presence of *Emydoidea blandingi*, *Graptemys*, and *Trionyx* indicates a permanent river. Many other species from the Big Springs Quarry would be at home in a river valley. The river valley was apparently bordered by tall-grass prairie as evidenced by the number of snakes that prefer that habitat. Other Big Springs Quarry species, including *Heterodon nasicus*, *Phrynosoma cornutum*, and *Rhinocheilus lecontei*, are characteristic of hilly, rocky, arid, or semi-arid areas.

Overall, this fauna supports the idea of an equable climate with cool summers and warm winters in the Blaccan of Nebraska. *Geochelone oelrichi* could live only if the area had mild winters. Other species in the fauna, such as *Rana sylvatica* and *Emydoidea blandingi*, exist in areas that have relatively cool summers. These elements that are ecologically incompatible today therefore suggest a less extreme climate than that currently in the area.

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