HERPETOFAUNA OF THE WAKEENEY LOCAL FAUNA
(LOWER PLIOCENE: CLARENDONIAN)
OF TREGO COUNTY, KANSAS

J. Alan Holman

Abstract.—The WaKeeney local fauna (lower Pliocene: Clarendonian) of Trego County, Kansas, yielded a herpetofauna consisting of at least two salamanders, 15 anurans, five turtles, four lizards, and eight snakes. Almost half (48.2%) of these forms are indistinguishable from species living today, and most genera and families are extant. Some forms are holdovers from earlier times and some forms are unique to the fauna.

Unique forms include a new species of Scaphiopus, a new family of anurans (Tregobatrachidae), a new species of Eumeces, a new genus of Boidae (Tregophis), a new species of Ogmophis, and an extinct species of watersnake (Natrix hillmani). Modern species appearing for the first time in the fossil record include Ambystoma maculatum, A. tigrinum, Bufo cognatus, Sternotherus odoratus, Terrapene cf. T. carolina, Ophisaurus attenuatus and Cnemidophorus cf. C. sexlineatus.

Habitats represented by the herpetofauna include: a basin in a sluggish stream, a marshy area, mesophytic woodlands, and xerophytic woodlands. A subtropical climate with mild winters and temperatures seldom if ever reaching the freezing point and with vegetation similar to that of the Texas Gulf Coastal Plain today is indicated.

Differences between upper Miocene herpetofaunas in Nebraska and Saskatchewan and the lower Pliocene WaKeeney local fauna were many including (1) lack of large cryptobranchid salamanders in the WaKeeney, (2) lack of xenosaurid lizards in the WaKeeney, (3) lack of archaic natricine and colubrine snakes in the WaKeeney, and (4) presence of large numbers (about one-half) of living species.

Taxonomic changes from Wilson (1968) are as follows: Scaphiopus couchi to S. hardeni; Bufo boreas to B. marinus (in part) and B. valentinensis (in part); Ophisaurus ventralis to O. attenuatus; Heterodon sp. to Paleoheterodon sp.; Coluber ? plioagellus to Coluber or Masticophis sp. indet. (in part) and Elaphe sp. (in part); and Ogmophis kansensis and Pituophis sp. to Colubridae (Colubrinae) gen. et sp. indet.

INTRODUCTION

The WaKeeney local fauna of Trego County, Kansas, has yielded the largest lower Pliocene (Clarendonian) herpetofauna known. Almost all of the collecting was done from a single site that represented a small stream-basin filled with fine-grained crossbedded sands. Field parties from Michigan State University removed the matrix from this basin in the summers of 1969, 1970, and 1972; and in 1973 the productive sand gave way to an unfossiliferous clay. One hundred eight and one-fourth tons of these sands were processed by the MSU group. Previous to this work, Wilson (1968) reported some herpetological species based on preliminary collecting at the site. The present paper represents a study of Michigan State material plus a study and re-evaluation of Wilson's material.

History of the Site.—The WaKeeney local fauna was discovered by Lester F. Phillis in about 1941. After the discovery, parties from the University of Michigan and from the University of Kansas collected at the site, but these collections were made at the surface and no detailed excavations were attempted. In 1966 Richard L. and Jan
Wilson removed about 250 "small" sacks of matrix (I interpret this as about two and one-half tons) from the site and wet-screened the material in a nearby spring. The vertebrate fauna from this work was published by Wilson (1968). Shortly after, the Wilsons moved to the west coast, and Claude W. Hibbard of the University of Michigan suggested that I continue excavations at the site in the light of the potentially large and important herpetofauna. Thus, collecting was done in the summers of 1969, 1970, 1972, and 1973. Published references to the site include Hibbard and Phillis (1945), Hubbs and Hibbard (1951), Brodkorb (1962), Feduccia and Wilson (1967), Wilson (1968), Hibbard and Jammot (1971), and Holman (1971).

At present, fishes from the site are being studied by Thomas Kramer of Michigan State University. Dr. Robert Weigel of the Department of Biological Sciences of Illinois State University is studying the birds. Claude W. Hibbard of the Museum of Paleontology of the University of Michigan and D. Jammot described two new shrews from the WaKeeney material collected by Michigan State University (Hibbard and Jammot, 1971); but the remainder of the mammalian material remains unstudied in the Museum at Michigan State University.

**Location and Geology.**—All of the Michigan State material and almost all of Wilson's material came from a single site (UM-K6-59) which is on the Lowell Hillman Ranch 2350-2500 ft S and 75 ft E of the NW corner, Sec. 22, R. 22 W, T. 11 S. The elevation is 2255 ft. The general regional picture of the area is as follows. The Saline River has eroded into the chalky limestone and calcareous shale beds of the Upper Cretaceous Niobrara Formation (upper Smoky Hill Chalk member and lower Fort Hays limestone member). Outcrops of these eroded beds form the so-called "bluffs" that are land marks in the area. The Cretaceous beds are unconformably overlain by the Pliocene Ogallala Formation. These heterogeneous beds are of unconsolidated clastic sediments which vary greatly in particle size; in Trego County, Kansas, they are mainly unfossiliferous. The main site (UM-K6-59) represents a small basin in a stream in the Ogallala Formation. Overlying the Ogallala Formation are Pleistocene sediments of eolian or fluvial origin and overlying the Pleistocene sediments are Recent soils. Wilson (1968) figured a measured section through UM-K6-59.

**Stratigraphic Relationships.**—Based on his analysis of the mammalian remains of the site Wilson (1968) believed that the WaKeeney local fauna was best assigned to the middle or late Clarendonian provincial age.

**History of the Michigan State University Investigations.**—The series of Michigan State University collections began in the summer of 1969 and continued (with the exception of 1971) through the summer of 1973. In 1969 the party sampled matrix from various portions of Wilson's measured section and it was determined that bones were almost entirely confined to a crossbedded sand lens that ranged in thickness from about six inches to about three feet. This lens averaged about two feet thick. This sand lens was quarried laterally into the side of a hill until in 1973 it finally gave way to unfossiliferous bluish clay. Material was collected in burlap sacks, each sack containing about 45 pounds of matrix. A sample of ½ ton would be collected at each visit to the site, and this was then put on special wooden racks (Hibbard, 1949) to dry. The dried concentrate invariably contained small clay balls that had to be re-washed after they were thoroughly dried. Compared to the fauna recovered by the Wilsons from only about 2½ tons of matrix, the bones from the MSU collections were quite scarce. In the summer of 1969 we calculated that about 20 bones, identifiable to the generic level, were present in about 1 ton of raw matrix. In the field seasons to follow these kinds of records were not kept, but if anything, the bones became more scarce each year. The most numerous remains are of fishes and amphibians; the next most numerous remains are those of reptiles; mammals were uncommon; and birds were rare.

Each field season our efficiency in processing matrix increased. In 1969 we processed 13.24 tons of matrix; in 1970, 20 tons; in 1972, 36 tons; and in 1973, 39 tons. In 1972 and 1973 we were greatly aided by use of a small front-end-loader for the removal of overburden.

**CHECKLIST OF AMPHIBIANS AND REPTILES OF THE WAKEENEY LOCAL FAUNA (LOWER PLIOCENE:CLARENDONIAN) OF TREGO COUNTY, KANSAS**

**Class Amphibia**

**Order Urodela**

Family **Ambystomatidae**

*Ambystoma maculatum* (Shaw)

*Ambystoma tigrinum* (Green)

*Ambystoma* sp. indet.

**Order Anura**

Family **Pelobatidae**

*Scaphiopus hardeni* n. sp.

Family **Trogobatrachidae** n. fam.

*Trogobatrachus hibbardi* n. gen. et sp.

Family **Bufonidae**

*Bufo cognatus* Say

*Bufo marinus* (Linnaeus)

*Bufo hibbardi* Taylor

*Bufo plicompaclitis* Wilson

*Bufo valentinensis* Estes and Tihen
Family Hylidae
Acris sp. indet.
Hyla cf. H. cinerea (Schneider)
Hyla cf. H. gratiosa LeConte
Hyla cf. H. squirella Sonnini and Latreille
Hyla sp. indet.
Pseudacris cf. P. clarki (Baird)

Family Ranidae
Rana cf. R. areolata Baird and Girard
Rana cf. R. pipiens Schreber
Rana sp. indet.

Class Reptilia
Order Chelonia
Family Kinosternidae
Sternotherus odoratus (Latreille)

Family Emydidae
Terrapene cf. T. carolina (Linnaeus)

Family Testudinidae
Geochelone orthopygia (Cope)
Geochelone sp.

Family Trionychidae
Trionyx sp. indet.

Order Sauria
Family Anguidae
Ophisaurus attenuatus Baird
Gerrhonotus mungferum Wilson

Family Teidae
Cnemidophorus cf. C. sexlineatus (Linnaeus)

Family Scincidae
Eumeces hissonorum n. sp.

Order Serpentes
Family Boidae
Tregophis brevirachis n. gen. et sp.
Ogmophis pliocompactus n. sp.

Family Colubridae
Natrix hillmani Wilson
Thamnophis sp. indet.
Paleoheterodon sp. indet.
Coluber or Masticophis
Elaphe sp. indet.
Lampropeltis similis Holman

Following is an annotated list of the WaKeeney local fauna herpetofauna. All measurements are in mm. Specimens are either in the Museum, Michigan State University (MSU-VP) or in the Museum of Paleontology at the University of Michigan (UMMP V). In the figures each line equals 2 mm except in Geochelone the line equals 40 mm.
Measurements of the most complete of the vertebrae are: length through zygapophyses 4.2 – 5.0 (4.70) N4; width through postzygapophyses 2.9 – 3.2 (3.01) N4.

*Ambystoma* sp. indet.

**Material.** – Twenty-six very fragmentary vertebrae, MSU VP 752.

**Remarks.** – These vertebrae are too fragmentary to assign to species. Wilson (1968) listed "*Ambystoma* Form A and Form B" from the WaKeeney fauna. These vertebrae also were too fragmentary for specific identification.

Order ANURA

**Family Pelobatidae**

*Scaphiopus hardeni* n. sp.

**Diagnosis.** – A *Scaphiopus* of the subgenus *Scaphiopus*, intermediate between *Scaphiopus wardorum* Estes and Tihen of the upper Miocene and *Scaphiopus holbrooki* and *Scaphiopus couchi* of the Pleistocene and Recent. Diffsers from *S. wardorum* in being smaller and in having its ilium with the ventral acetabular expansion (sub-acetabular expansion) much wider anterior to the acetabulum. Diffsers from *S. holbrooki* and *S. couchi* in the much more well-developed and rugged dorsal protuberance of the ilium.

**Holotype.** – Right ilium, MSU-VP 753, Fig. 1 C. From lower Pliocene (Clarendonian), Ogallala Formation, locality UM-K6-59 on the Lowell Hillman Ranch 2350-2550 ft S and 75 ft E of the NW corner, Sec. 22, R. 22 W, T. 11 S, elevation 2255 ft. Collected by J.A. Holman and parties 1969-1973.

**Paratypes.** – Six right and six left ilia, MSU-VP 754. From the same locality and collected by the same collector on the same dates.

**Referred Material.** – One sphenethmoid; 10 fragmentary maxillae (Fig. 1 D); one right and one left fragmentary frontoparietal; one right scapula (Fig. 1 D’); and six fragmentary sacrococcyges; MSU-VP 755. From the same locality and collected by the same collectors on the same dates.

**Etymology.** – Named in honor of Warren L. Hardin for his contributions to the knowledge of the history and the paleohistory of Trego County, Kansas.

**Description of the Holotype.** – A comparison of the holotype of *S. hardeni* with that of *S. wardorum* (Fig. 1 C this paper with fig. 2a, p. 458, Estes and Tihen, 1964) shows the differences in the anterior portions of the ventral acetabular expansions (sub-acetabular expansions) in the two forms as well as differences in size. The holotype of *S. hardeni* represents an individual with a snout-vent length of approximately 65 whereas *S. wardorum* represents an individual with a snout-vent length of about 85-90. In lateral view, the holotype of *S. hardeni* has a very well-developed dorsal protuberance that is large and rugged. It is produced dorsally above the dorsal border of the dorsal acetabular expansion and it is also well produced laterally. It has a depression in its lateral surface that divides it into a very well-produced anterior portion and a less produced posterior portion. Behind the dorsal protuberance the dorsal acetabular expansion has another depression. The acetabular fossa is well developed with prominent borders, especially anterograventrally. Anterior to the acetabular fossa the ventral acetabular expansion (sub-acetabular expansion) is well developed, a condition that differs from *S. wardorum*. Just above the ventral acetabular expansion and just anterior to the middle part of the anterior rim of the acetabular fossa is a deep pit. The shaft lacks any kind of a dorsal crest.

Measurements are: greatest height of acetabulum 3.3; height, ventral border of acetabulum through dorsal acetabular expansion 5.4; height of shaft anterior to acetabulum 1.8.

**Paratypes.** – There is very little variation in the paratypes in trenchant characters as all of them represent medium-sized specimens and have the ventral acetabular expansion extending well anterior to the anterior edge of the acetabular fossa and with very well-developed and rugged dorsal protuberances.

Measurements of the paratypes are as follows: greatest height of acetabulum 2.7 – 3.2 (3.00) N6; height, ventral border of acetabulum through dorsal acetabular expansion 4.3 – 5.2 (4.83) N3; height of shaft anterior to acetabulum 1.4 – 1.8 (1.60) N6.

**Referred Material.** – The sphenethmoid represents a *Scaphiopus* with a snout-vent length of about 70. Compared with a Recent *S. holbrooki* and a Recent *S. couchi* of about the same size the WaKeeney fossil is more similar to *S. holbrooki* than *S. couchi* in that in dorsal view the base of its anterior median process is wider than in *S. couchi*. But the sphenethmoid differs from both of these forms in (1) having a stronger posterior median tubercle; (2) lateral process at about right angles to long axis of bone (directed anteriad in *S. holbrooki* and *S. couchi*); (3) posterior part of sphenethmoid much more highly sloping; and (4) lateral processes about twice as high as wide (lateral processes about twice as wide as high in 8.}

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Fig. 1. (A) Trunk vertebra of *Ambystoma maculatum* MSU-VP 750, dorsal view. (B) Trunk vertebrae of *Ambystoma tigrinum* MSU-VP 751, dorsal and lateral views. (C) Holotype right ilium of *Scaphiopus hardeni* n. sp. MSU-VP 753. (D) Bones referred to *Scaphiopus hardeni* n. sp. MSU-VP 755, fragmentary maxilla. (D') Same, right scapula. (E) Holotype left ilium of *Tregobatrachus hibbardi* n. gen. et sp. MSU-VP 766. (F) Ilium of *Bufo hibbardii* MSU-VP 759, right. (F') Same, left. (G) *Bufo valentinensis* MSU-VP 758, left ilium. (H) *Hyla squirella* MSU-VP 763, right ilium.
holbrooki and S. couchi). The sphenethmoid of S. wardorum is unknown.

Measurements of the sphenethmoid are: greatest posterior height 4.8; greatest posterior width 4.5.

I cannot find any characters on the maxillae that hold to separate S. hardeni consistently from S. holbrooki and S. couchi. The largest of the three fossils has the external ornamentation composed of regular tubercles rather than the irregular pits of S. holbrooki and S. couchi, but the two smaller fossil maxillae have the pitted condition.

The fossil right scapula of S. hardeni resembles that of S. holbrooki more closely than it resembles S. couchi. This involves two characters (1) the lateral border of the clavicular articular process is truncated in S. hardeni and S. holbrooki, whereas this process slopes gently into the shaft in S. couchi; and (2) the glenoid opening between the clavicular articular process and the coracoid articular process is more constricted in S. hardeni and S. holbrooki than in S. couchi.

I can find no important characters in the sacrococcygeus or in the partial frontoparietal other than those that indicate the subgenus Scaphiopus (slight webbing on the sacrococcygeus, ornamentation on the dorsal surface of the frontoparietal) rather than the subgenus Spea.

Wilson (1968) listed S. couchi from the WaKeeney local fauna. I have re-studied this material and assign it to S. hardeni.

Tregobatrachidae n. fam.

Tregobatrachus n. gen., type of the fam.

From time to time a totally unexpected and novel fossil amphibian or reptile (Holman, 1973b) turns up in the herpetofauna of the late Tertiary. This is the situation in the case of an ilium of a moderately large anuran recovered by the 1973 MSU field party. This ilium is unlike any previously described fossil or living anuran. To account for its rarity in the fossil record I can only suggest that it might have been an arboreal and perhaps an obstetrical form.

Diagnosis.—A moderately large anuran left ilium separable from other anuran families by the following combination of characters: (1) dorsal acetabular expansion limited in extent, its dorsal border extending straight back from dorsal prominence; (2) no ilial crest or ilial shaft ridge; (3) dorsal prominence well developed and lacking a protuberance, about twice as long as high, one-half anterior to anterior edge of acetabular fossa, with a smoothly rising posterior slope and a more abruptly rising anterior slope, tip of prominence deflected medially; (4) ilial shaft compressed, its medial surface with an anterodorsally directed wide groove, entire shaft abruptly constricted anteriad; (5) large foramen present on shaft just anterior to anterior edge of ventral acetabular expansion; (6) ventral acetabular expansion limited in its extent, its ventral border truncated; (7) acetabular fossa very large, its surface pitted.

Holotype.—Left ilium, MSU-VP 766, Fig. 1 E. From lower Pliocene (Clarendonian), Ogallala Formation, locality UM-K6-59 on the Lowell Hillman Ranch 2350-2550 ft S and 75 ft E of the NW corner, Sec. 22, R. 22 W, T. 11 S, elevation 2255 ft. Collected by J.A. Holman, R.J. Holman, Richard McArthur, Jason Potter, and Vincent Wilson in August, 1973.

Tregobatrachus hibbardi n. sp.

Diagnosis.—As for the genus.

Etymology.—Named in honor of the many contributions to vertebrate paleontology of Claude W. Hibbard.

Description of the Holotype.—The acetabular fossa is well excavated and its borders are distinct. It is higher than it is long and it is subrounded in shape. Its surface is strongly pitted. The dorsal acetabular expansion is quite limited in its extent and its dorsal border extends straight back from the posterior extent of the dorsal prominence. The dorsal prominence is well developed and it is about twice as long as it is high. The prominence lacks a protuberance. The posterior dorsal border of the prominence rises gently from the shaft, but the anterior dorsal border slopes more precipitously into the shaft. The tip of the prominence is deflected medially and it is about one-half anterior to the anterior edge of the acetabular fossa. There is no dorsal crest or ilial shaft ridge. But the shaft is unique in that it has a distinct wide groove running in an anteroventral direction from the level of the dorsal prominence toward its ventral border. Moreover, the shaft becomes abruptly constricted anteriad so that the shaft-height decreases rapidly in an anterior direction (see measurements). A very large foramen occurs on the shaft just anterior to and partially hidden by the anterior edge of the acetabular border. The ventral acetabular expansion is limited in extent and its ventral border is truncated.

Measurements of the Holotype.—Anterior height of shaft 2.1; height of shaft just anterior to dorsal prominence 3.4; height of shaft through dorsal prominence 4.6; greatest height of acetabular fossa 5.8; greatest length of acetabular fossa 4.5; greatest height through dorsal and ventral acetabular expansion 8.0.

Remarks.—It is extremely difficult to ascertain the relationships of the Tregobatrachidae, but it seems to represent a relatively primitive family. The great encroachment of the acetabular expansion by the acetabular fossa is seen to a degree in the primitive families Ascaphidae, Discoglossidae, and Pipidae, and in some genera of the Leptodactylidae. More advanced families tend to have smaller acetabular fossae and large dorsal and ventral
acetabular expansions. The lack of an ilial blade or an ilial shaft ridge is typical of primitive families as some advanced Leptodactylidae, some Hylidae, and all Ranidae have these structures. But several features are unique to the Tregobatrachidae. These include the large dorsal prominence without a protuberance and with its tip deflected medially; and the abruptly-constricted, widely-grooved ilial shaft. It seems possible that Tregobatrachus is the dead-end of a rather primitive undescribed group of anurans. But why should such a moderately large frog be so rare in the fossil record? Perhaps the reason is that Tregobatrachus was an arboreal form with a breeding strategy (possibly obstetrical habits) that allowed it to stay away from the vicinity of depositional basins.

Family Bufonidae

Bufo cognatus Say

Material.—A right partial frontoparietal (UMMP V554-41) and a left ilium (V55421) were assigned to this species by Wilson (1968).

Remarks.—These elements appear to be indistinguishable from the living form. This is one of the very few faunal elements that is living in the WaKeeney area today.

Bufo marinus (Linnaeus)

Material.—Five left and six right ilia; three distal humeri; one puboischiun, MSU-VP 757.

Remarks.—Wilson (1968) has identified this species previously from the WaKeeney local fauna on the basis of a piece of a left (incorrectly reported as right) frontoparietal, a temporal plate, a right and a left ilium, and two nasal fragments. Wilson based his identification of B. marinus mainly on the characteristics of the fossil frontoparietal. I have studied this frontoparietal, and although it is smaller than in Recent adult B. marinus, it does compare remarkably well with this species, even in minute detail. The ilia (both MSU and UMMP) are identical to B. marinus except that the fossils represent smaller animals. I assign the MSU material to the species B. marinus, but point out that the fossil population from the WaKeeney local fauna represents smaller individuals than in Recent populations.

Measurements of the WaKeeney fossils compared with Recent individuals of B. marinus are as follows. The height from the ventral border of the acetabular cup through the tip of the dorsal prominence of the ilium in 9 fossils is 7.0 – 10.1 (8.47); in 12 Recent B. marinus it is 10.1 – 13.2 (10.98). The width of the fossil frontoparietal is 6.9; in 13 Recent B. marinus it is 8.4 – 10.0 (9.32).

Wilson (1968) assigned a partial right frontoparietal (UMMP V55415) to the extant species Bufo boreas. This identification is in error as the specimen represents a small individual of B. marinus. This element has a distinct pattern of dermal encrustation, whereas in modern B. boreas dermal encrustation is absent except for a very slight pitting in a few individuals. Recent B. boreas skeletons from British Columbia (1), Washington (3), southern California (3), Utah (1), and Colorado (1) were examined and their frontoparietals do not slightly resemble UMMP V55415. Ilia incorrectly identified as B. boreas by Wilson (1968) will be discussed elsewhere in the paper. Bufo boreas is not found in the WaKeeney fauna.

Bufo hibbardi Taylor

Material.—Two left and three right ilia, MSU-VP 759, Fig. 1 F, F'.

Remarks.—Bufo hibbardi ilia are characterized as having an ilial prominence with its height varying from 43 to 48% of the length of its base. Tihen (1962b) states, “the posterior slope of the prominence is not particularly steep, and is a very even slope; the anterior slope is very steep dorsally, with a sharp inflection about halfway between the peak of the prominence and the dorsal edge of the shaft, becoming much less steep at this point, and forming a sort of a web between the ventral half of the prominence and the shaft.” The WaKeeney fossils fit the description so well and are so near the size of B. hibbardi that they are assigned to this species. Bufo hibbardi was described from the middle Pliocene of Sherman County, Kansas. Bufo hibbardi is in the B. americanus group of Tihen (1962a).

Bufo pliocompactilis Wilson

Material.—Forty left and 47 right ilia, MSU-VP 765.

Remarks.—Bufo pliocompactilis was previously described on material from the WaKeeney local fauna (two frontoparietals and 24 ilia) by Wilson (1968, text-figs. 7e, 8a-b) who characterized the ilia “by an anterior angle of from 35-50 degrees (ave. 42), while the posterior angle varies between 41 and 60 degrees (ave. 52). The anterior angle is always less than the posterior on any one specimen. Height of protuberances relative to their base is between 39 and 61% with some of this variation probably a result of stream abrasion.”

The 87 ilia recovered by the MSU groups do not significantly differ from Wilson’s material. The ilia represent a small toad with a very high ilial protuberance. Living B. speciosus and B. compactilis have high ilial protuberances, but both of these species are at least twice as large as B. pliocompactilis. Thus far, B. pliocompactilis has been taken only from lower Pliocene (Clarendonian) deposits and it may be an important stratigraphic marker. Holman (1973a) has reported B. pliocompactilis from the Mission local fauna (lower Pliocene: Clarendonian) of Melette County, South Dakota; and D. Zehr of Fort Hays State College has informed me (pers. comm.,
August, 1973) that he has collected this species from another lower Pliocene fauna in western Kansas.

**Bufo valentinensis** Estes and Tihen

**Material.**—Seven left and four right ilia, MSU-VP 758, Fig. 1 G.

**Remarks.**—Tihen (1962b) described a moderately small *Bufo* ilium with a low, rounded ilial prominence from the Fox Canyon locality of the Blancan Rexroad Formation of Meade County, Kansas, as *Bufo suspectus*. In the same paper he tentatively assigned an ilium from the “lower Pliocene” Valentine Formation of Brown County, Nebraska, to *B. suspectus*. Later, Estes and Tihen (1964) included this ilium as part of a new species, *B. valentinensis*, described on the basis of a right frontoparietal. The above ilia from the WaKeeney local fauna appear to be identical to those of *B. valentinensis* and *B. suspectus* and are assigned to the former species based on temporal reasons. *Bufo valentinensis* is in the *Bufo valliceps* group of Tihen (1962a).

Two ilia (UMMP V55416 and V55420) incorrectly assigned to *B. boreas* by Wilson (1968) are assigned to the species *B. valentinensis*.

**Family Hylidae**

*Acris* sp. indet.

**Material.**—Four left and six right ilia, MSU-VP 760.

**Remarks.**—The ilia of *Acris* are easily assigned to genus (Chantell, 1964) but they are difficult to assign to the specific level. Wilson (1968) identified 43 ilia as the genus *Acris* (UMMP V55405-V55407).

**Hyla cf. Hyla cinerea** (Schneider)

**Material.**—Six left and six right ilia, MSU-VP 762.

**Remarks.**—These ilia resemble *Hyla cinerea* (and some *H. versicolor*) in having an elongate dorsal ilial protuberance, in having the anterior edge of the protuberance about even with the anterior edge of the acetabular border, and in almost always lacking a slash-like foramen on the ilial shaft just anterior to the anterior edge of the ventral acetabular expansion. Wilson (1968) has reported two ilia (UMMP V55408 and V55409) from the WaKeeney local fauna as representing *H. cinerea* or *H. versicolor*. *Hyla cinerea* is a frog of the southeastern coastal plain today.

**Hyla cf. Hyla gratiosa** Le Conte

**Material.**—Four right ilia, MSU-VP 761.

**Remarks.**—The ilia of this treefrog are tentatively referred to *Hyla gratiosa* on the basis of their large size, on the basis that the dorsal ilial protuberance is rounded and is about one-half anterior to the anterior edge of the acetabular border, and on the basis of the slash-like foramen that is present on the ilial shaft just anterior to the anterior edge of the ventral acetabular expansion. In *Hyla cinerea* and *H. versicolor* skeletons examined, the dorsal ilial protuberance tends to be elongated, its anterior edge tends to be about even with the anterior edge of the acetabular border, and there is usually no slash-like foramen present on the ilial shaft just anterior to the anterior edge of the ventral acetabular expansion. Wilson (1968) listed 15 right and seven left ilia (UMMP V55410, V55412, and V55411) from the WaKeeney site. *Hyla cf. H. gratiosa* has been reported from the upper Miocene of the Norden Bridge fauna of Brown County, Nebraska. But according to the figure of the sole specimen upon which the identification was based (Chantell, 1964, p. 220, fig. 4a) the identification is less than certain. *Hyla gratiosa* is a frog of the southeastern coastal plain today.

**Hyla cf. Hyla squirella** Sonnini and Latreille

**Material.**—Two right ilia, MSU-VP 763, Fig. 1 H.

**Remarks.**—This is the first report of this species from the WaKeeney local fauna. The ilia of *H. squirella* may be separated from *H. crucifer* in that in *H. squirella* the anterior edge of the dorsal protuberance is only slightly anterior to the anterior edge of the acetabular border and the ventral acetabular expansion is relatively wide; whereas in *H. crucifer* the posterior edge of the dorsal protuberance is about even with the anterior edge of the acetabular border and the ventral acetabular expansion is narrower. *Hyla squirella* may be separated from *H. femoralis* in that in *H. squirella* the anterior edge of the ventral acetabular expansion is convex, whereas in *H. femoralis* the anterior edge of the ventral acetabular expansion is concave or straight. *Hyla cf. H. squirella* has previously been reported from the upper Miocene of the Norden Bridge fauna of the Valentine Formation of Brown County, Nebraska (Chantell, 1964).

**Hyla sp. indet.**

**Material.**—Fourteen left and 13 right ilia, MSU-VP 765.

**Remarks.**—These ilia may represent small individuals of *H. cinerea* and/or *H. versicolor* or a moderately small undescribed form.

**Pseudacris cf. Pseudacris clarki** (Baird)

**Material.**—A right ilium (UMMP V55414) identified by Wilson (1968).

**Remarks.**—This form was originally reported by Wilson (1968). The MSU group collected another ilium (MSU-VP 764) that satisfies the criteria of Chantell (1964 and 1966) and Wilson (1968) for the identification of the genus. The MSU ilium is identified as *Pseudacris* sp.
indet. *Pseudacris* cf. *P. clarki* has previously been identified from the upper Miocene of the Norden Bridge local fauna of the Valentine Formation of Brown County, Nebraska (Chantell, 1964).

**Family Ranidae**

*Rana* cf. *Rana areolata* Baird and Girard

**Material.**—Two left and two right ilia, MSU-VP 767.

**Remarks.**—The identification of *Rana* material from the WaKeeney local fauna is quite tentative. Chantell (1971) points out that *Rana* species are very difficult to identify based on skeletal material. Nevertheless, Recent *Rana areolata* tends to have a vastus prominence (Holman, 1965) that is more extensive, flatter, and wider (Holman, 1972b), and a more gentle slope of the posterodorsal border of the ilial crest into the dorsal acetabular expansion than in other Recent species of *Rana*. Wilson (1968) identified *Rana* cf. *R. areolata* from the WaKeeney local fauna on the basis of two frontoparietals (UMMP V55435 and V55436).

*Rana* cf. *Rana pipiens* Schreber

**Material.**—One hundred twelve left and 89 right ilia, MSU-VP 768.

**Remarks.**—These ilia are identical to Recent *Rana pipiens* in the gentle slope of the posterodorsal border of the ilial crest into the dorsal acetabular expansion and in the size and shape of the vastus prominence. This is the first report of this species from the WaKeeney local fauna.

*A Fused Sacral and Presacral Vertebra.*—A ranid sacral vertebra (MSU-VP 769) is fused to the following vertebra. This may have been produced by a developmental error as the left diapophysis of the presacral vertebra resembles a sacral diapophysis and the left diapophysis of the sacral vertebra resembles a presacral diapophysis. Holman (1963) discusses similar fusions in additional fossil and Recent anurans.

*Rana* sp.

**Material.**—Eight left and five right ilia, MSU-VP 770.

**Remarks.**—These ilia have a more precipitous slope of the posterodorsal border of the ilial shaft into the dorsal acetabular expansion than in *Rana areolata* or *Rana pipiens*. These specifically indeterminate fossils may represent forms related to *R. clamitans* or to small individuals of *R. catesbeiana*, *R. grylio*, or *R. heckscheri*.

Class REPTILIA

Order CHELONIA

Family Kinosternidae

*Sternotherus odoratus* (Latreille)

**Material.**—Nuchal bone, left epiplastral bone, MSU-VP 771, Fig. 2 A, A'.

**Remarks.**—The epiplastral bones of *Sternotherus* (*S. carinatus*, *S. depressus*, *S. minor*, *S. odoratus*) may easily be distinguished from those of *Kinosternon* (*K. acutum*, *K. bauri*, *K. cruentatum*, *K. flavescens*, *K. hirtepex*, *K. integrum*, *K. leucostomum*, *K. scorpiodes*, *K. sonoriense* seen only) on the basis of the squarish pectoral shield in *Sternotherus* as opposed to the triangular shield of *Kinosternon*. This is a classical "key" character that may easily be seen on fossil material as the sutures for the epidermal scutes are plainly visible. Another way of expressing differences between the two genera on the basis of the epiplastral bones is that the pectoral-humeral suture of *Sternotherus* intersects the medial edge of the epiplastron at about the middle of its extent, whereas in *Kinosternon* the pectoral-humeral suture intersects the medial edge of the epiplastral bone at the posterior part of its extent. The fossil epiplastral bone from the WaKeeney fauna is readily assigned to the genus *Sternotherus*.

The nuchal bone of *Sternotherus* may be distinguished from *Kinosternon bauri* in that the anterior truncated portion is about three-fourths as wide as the widest part of the bone, whereas in *K. bauri* it is only slightly more than half as wide as the widest part of the bone. The nuchal of *Sternotherus* may be separated from *K. flavescens* in that the area covered by the pleural scute is three times as extensive on the nuchal of *Sternotherus* than it is in *K. flavescens*. The nuchal of *S. odoratus* has much more acutely pointed sides than that of *K. subrubrum*.

Following are characters for distinguishing *Sternotherus odoratus* from *S. minor*. The epiplastron of *S. odoratus* may be separated from that of *S. minor* in that the pectoral-humeral suture extends around to the dorsal surface of the bone and does not appear on the dorsal surface of the bone in *S. minor*. The fossil is identical to *S. odoratus* in this character.

The nuchal bone of *S. odoratus* may be separated from that of *S. minor* on the basis that the sides of *S. odoratus* are more acutely pointed in *S. odoratus* (rounded in *S. minor*) and on the basis that the vertebral scute of *S. odoratus* is much wider anteriorly than in *S. minor*. The fossil resembles *S. odoratus* in this character.

This is the first report of *S. odoratus* from the WaKeeney fauna and it is the earliest record of this species as a fossil.
Family Emydidae

*Terrapene* cf. *Terrapene carolina* (Linnaeus)

**Material.**— Left humerus, MSU-VP 775, Fig. 2 B.

**Remarks.**— The humerus is easily identifiable as that of *Terrapene* in having (1) a compressed rather than a rounded head, (2) a lateral tubercle that is deflected more upward than outward, (3) a deltopectoral crest deflected more upward than inward, (4) a moderately narrow excavation between the lateral tubercle and the deltopectoral crest, and (5) a dorsoventrally bowed shaft.

The humerus is nearer the living species *T. carolina* rather than *T. ornata* based on a strong character. In medial view, the dorsal border of the deltopectoral crest is flat and the posterior portion of this crest is not produced upward as a knob in *T. carolina*, whereas in *T. ornata* the dorsal border of the deltopectoral crest is concave and the posterior portion of this crest is produced upward as a knob. The fossil clearly resembles *T. carolina* in this character, but the fossil does not have the shaft as bowed as in either of the living species, thus more material will have to be obtained before the status of this early box turtle can be more clearly ascertained.

The earliest previously reported *Terrapene* that I am aware of is *Terrapene ornata longinsulae* from the lower middle Pliocene of Long Island, Kansas (Milstead, 1967), thus the WaKeeney fossil appears to be the earliest *Terrapene* known.

Family Testudinidae

*Geochelone orthopygia* (Cope)

**Material.**— Neural bone, one carapacial fragment, and two dermal ossicles of the forelimb, MSU-VP 772, Fig. 2 C.

**Remarks.**— These large bones indicate a land tortoise of giant proportions. Hibbard (1960) outlined the climatic importance of large land tortoises in fossil faunas. They indicate a climate with very mild winters with temperatures seldom if ever reaching the freezing point. *Geochelone* has not previously been reported from the WaKeeney local fauna.

*Geochelone* sp. indet.

**Material.**— Partial peripheral, five plastral and carapacial fragments, and eight dermal ossicles of the forelimb, MSU-VP 773.

**Remarks.**— These smaller bones may indicate a second species of smaller tortoise in the fauna.

Family Trionychidae

*Trionyx* sp. indet.

**Material.**— Four costal fragments and one neural fragment, MSU-VP 744.

**Remarks.**— I am not able to identify these fragments to species. Wilson (1968) identified *Trionyx* sp. from the WaKeeney local fauna.

Other Chelonianns

Wilson (1968) identified *Kinosternon*, *Pseudemys*, and cf. *Chrysemys* from the WaKeeney local fauna, but because of the nature of the bones and the question of the identity of early *Chrysemys* and *Pseudemys* I believe it better to leave these forms off the list.

Order SAURIA

Family Anguidae

*Ophisaurus attenuatus* Baird

**Material.**— Seven caudal and 21 body vertebrae, MSU-VP 776.

**Remarks.**— According to Etheridge (1961) the caudal vertebrae of the three living species (*O. ventralis*, *O. attenuatus*, and *O. compressus*) are diagnostic at the specific level. First, the presence of fracture planes and accessory neural spines are present in *O. ventralis* and *O. attenuatus* and absent in *O. compressus*. The WaKeeney fossils resemble the first two species in this important character. Etheridge further reports that “the angle between the anterior border of the caudal transverse processes and the longitudinal axis of the centrum will diagnose the caudal vertebrae of all three species. These angles are *O. ventralis*, 70 to 75 degrees (mean 73); *O. attenuatus*, 75 to 85 degrees (mean 81); and *O. compressus*, 50 to 65 degrees (mean 55)).” The five measurable caudal vertebrae from the WaKeeney local fauna were 83 to 90 degrees (mean 82.2), thus they most closely resemble *O. attenuatus* in the character. The body vertebrae, although reportedly diagnostic (Etheridge, 1961), are not identified with certainty because important processes were usually broken in the fossils. Wilson (1968) reported *O. ventralis* from the fauna. I have examined this fragmentary material and think that it should tentatively be assigned to *O. attenuatus*. Previously, the earliest record of modern *Ophisaurus* species was that of *O. attenuatus* from the late upper Pliocene of the Rexroad Formation of Meade County, Kansas (Etheridge, 1961).

Fig. 2. (A) *Sternotherus odoratus* MSU-VP 771, nuchal bone. (A') Same, left epiplastral bone. (B) Left humerus of *Terrapene* cf. *T. carolina* MSU-VP 775, anterior and medial views. (C) Neural bone of *Geochelone orthopygia* MSU-VP 772. (D) *Gerrhonotus mungerorum* MSU-VP 788, frontal bone in dorsal view. (D') Same, left maxilla. (E) Holotype left dentary of *Eumeces hixsonorum* n. sp. MSU-VP 779. (F) Holotype lumbar vertebra of *Trogophis braevirachis* n. gen. et sp. MSU-VP 783: (a) dorsal view, (b) posterior view, (c) ventral view, (d) anterior view. (G) Lumbar vertebra of *Ogmophis pliocompactus* MSU-VP 784, dorsal view.
Gerrhonotus mungerorum Wilson

**Material.**—One complete frontal, one left maxilla, two partial right maxillae, two right dentaries, and one partial left dentary, MSU-VP 778, Fig. 2 D, D'.

**Remarks.**—This new species of Gerrhonotus was described by Wilson (1968) on the basis of a single frontal bone (UMMP V55674). The MSU group was fortunate in obtaining considerably more material of this large and interesting lizard. These new bones indicate an animal with different feeding habits than the living form G. multicarinatus.

**Frontal Bone.**—The frontal bone recovered by the MSU group is more complete than the holotype, in fact, the new fossil is complete down to the last detail of structure. The scutellation is the same as that of the holotype and to that of a Recent specimen of G. multicarinatus of the same size (Fig. 2 C this paper and Fig. 9e, p. 98, Wilson, 1968). But two differences are noted between the frontals of G. mungerorum and G. multicarinatus. In G. mungerorum the bone is not as constricted as its middle and is much more heavily sculptured than in G. multicarinatus.

**Dentary.**—The dentary of G. mungerorum was not previously known. In the most complete dentary there is a total of 23 teeth and alveolar spaces. In Recent G. multicarinatus there is a total of 23 teeth and alveolar spaces in the large specimen examined. The anterior four teeth in the most complete fossil are missing, but the anterior four teeth in another specimen are sharply pointed and strongly recurved; the next 13 or so teeth in the complete fossil are bilobed with the posterior lobe being the highest; whereas the remaining posterior teeth are bluntly rounded unicuspids. In the G. multicarinatus specimen the first four teeth are unicuspids, but they are not as sharply pointed as in the fossil and they are not recurved; the next 12 or so are bilobed, and the last few are slightly bilobed, not unicuspids as in the fossil. In other respects the dentaries of the fossil and the Recent animals are very similar.

**Maxilla.**—The maxilla of G. mungerorum has never been previously seen. In the complete fossil maxilla there are a total of 14 teeth and alveolar spaces. In the maxilla of G. multicarinatus there are a total of 18 teeth and alveolar spaces. In the fossil the teeth are thick, unicuspid, sharply pointed and strongly recurved; in G. multicarinatus they are thinner, bilobed, and they are not sharply recurved.

In summary, although the scutellation of the frontal region of the head is similar in G. mungerorum and G. multicarinatus, the dentitional pattern is much different. The strong, unicuspid, sharply pointed, strongly recurved teeth of the dentary of G. mungerorum suggest different feeding habits than do the mainly bilobed teeth of the maxilla and dentary of G. multicarinatus.

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Family Teiidae

Cnemidophorus cf. Cnemidophorus sexlineatus (Linnaeus)

**Material.**—Four left and one right dentaries, one maxillary fragment, MSU-VP 777.

**Remarks.**—This material appears identical in size and characters to the living species Cnemidophorus sexlineatus, thus it is tentatively assigned to this species. Cnemidophorus has not previously been identified from the WaKeeney local fauna.

Family Scincidae

Eumeces hixsonorum n. sp.

**Diagnosis.**—A large Eumeces that may be distinguished from living species of the genus on the basis of the following characters: (1) large size, (2) teeth very low-crowned, (3) teeth closely-spaced, their crowns blunt and unswollen, but a slight neck between the crown and the base of the tooth, (4) lingual shelf thick, and (5) Meckelian groove open.

**Holotype.**—Left dentary, MSU-VP 779, Fig. 2 E. From lower Pliocene (Clarendonian), Ogallala Formation, locality UM-K6-59 on the Lowell Hillman Ranch 2350-2550 ft S and 75 ft E of the NW corner, Sec. 22, T. 11 S, elevation 2255 ft. Collected by J.A. Holman and parties 1969-1973.

**Paratypes.**—Four left and two right dentaries, MSU-VP 780. From the same collection as the holotype.

**Etymology.**—The species is named for Mr. and Mrs. Larry Hixson of WaKeeney, Kansas, who were helpful to the MSU field parties in numerous ways.

**Description of the Holotype.**—The dentary represents a large Eumeces. In lingual view, it has an open Meckelian groove that is widely open posteriorly and more narrowly open anteriorly. The lingual shelf is strong. The teeth are very low-crowned. There is a tooth and alveolar count of 26. The teeth are closely packed. The surfaces of the teeth are blunt and the crowns of the teeth are not swollen, but there is a very slight neck area between the crowns and the bases of the teeth. The crowns are weakly striated. In lateral view, the dentition appears low-crowned. There are four mental foramina. The length of the complete tooth row is 7.0.

**Paratypes.**—The paratypes are very similar to the holotype in size and in characters. In the three paratypes complete enough for a tooth-alveolar count these counts are 25, 25, and 27. The number of mental foramina in the six paratypes are 3–6 (4.0).

**Remarks.**—Tooth counts of Eumeces hixsonorum compared with some Recent Eumeces species are as follows: E. hixsonorum, 25-27 (26.3) N4; E. anthracinus, 21; E. brevilineatus, 24; E. inexpectatus, 24-28 (26.0) N2; E. laticeps, 23-24 (23.5) N2; E. obsoletus, 20-23 (22.3)
**Tregophis** n. gen.

**Diagnosis.**—A genus of small boid with a vertebral form unlike any previously described fossil or Recent snake in that the posterior portion of the neural arch is deeply incised so that the zygantral facets are exposed dorsally; in which the neural spine is very short and thick and triangular in shape from above, and in which the hemal keel is indistinct from the bottom of the centrum.

**Holotype.**—Lumbar vertebra, MSU-VP 783, Fig. 2 F. From lower Pliocene (Clarendonian), Ogallala Formation, locality UM-K6-59 on the Lowell Hillman Ranch 2350-2550 ft S and 75 ft E of the NW corner, Sec. 22, R. 22 W, T. 11 S, elevation 2255 ft. Collected by J.A. Holman and parties 1969-1973.

**Tregophis brevirachis** n. sp.

**Diagnosis.**—As for the genus.

**Etymology.**—From Greek, brevis, short, and rachis, spine, in reference to the very short neural spine.

**Description of the Holotype.**—In dorsal view, the vertebra is very short and wide. The anterior edge of the zygosphene is weakly convex. The prezygapophyseal facets are oval in shape and there are nine annuli visible on the right prezygapophyseal facet. The accessory processes of the postzygapophyses are broken. The neural spine is unique in shape. It is very short, occupying only about one-fourth of the total interzygapophyseal length. Its tip is broken, but it is triangular in shape in dorsal view, and it has two posterior lobes that extend posterior to the posterior edge of the neural arch. The posterior part of the neural arch is also unique in that it is deeply incised exposing the zygantral facets above. There are no epizygaphyseal spines.

In lateral view, the zygaphyseal area of the neural arch is upswept. There is a foramen visible on the neural arch just dorsad and posteriad to the paradiapophyses. The subcentral ridges are strongly arched. The condyle is partially broken. The paradiapophyses are eroded.

In posterior view, the posterior part of the neural spine is massive in appearance. The round condyle is partially eroded and it is about three-fourths as large as the loaf-of-bread-shaped neural canal. There are two symmetrical cavities on either side of the neural arch just posterior to the zygantral facets.

In anterior view, the zygosphenal roof is narrow and thick. The cotyle is depressed and about the same size as the neural canal. The two cavities on either side of the cotyle lack foramina.

In ventral view, the hemal keel is indistinctly marked off from the bottom of the centrum. The postzygapophyseal facets are rounded. Much of the condyle is eroded in this view.

Measurements: width through prezygapophyses 4.6; width through postzygapophyses 4.1; length through zygaphyses 2.8.

**Remarks.**—The combination of characters that leads me to place this strange snake in the family Boidae are as follows. (1) The anterior border of the zygosphene is narrow and thick; (2) the vertebra is much higher than long; (3) the subcentral ridges are arched; (4) the postzygapophyseal part of the neural arch is upswept; (5) foramina are lacking in the cavities on either side of the cotyle; and (6) the neural spine is short and thick.

The small size may or may not indicate a relationship of **Tregophis** to the erycinine boids; at this point it is premature to suggest relationships.

**Ogmophis pliocompactus** n. sp.

**Diagnosis.**—An **Ogmophis** that appears to be most closely related to **Ogmophis compactus** Lambe of the lower Oligocene of the Calf Creek local fauna of Saskatchewan in its wide, very distinct hemal keel, its general proportions, and the constricted anterior portion of its neural spine. But it differs from **O. compactus** in (1) being smaller, (2) having the neural spine ending slightly anterior to the end of the neural arch, (3) neural spine thinner posteriorly, (4) neural spine extending farther anteriad on the zygosphenal roof, and (5) parapophyses visible in dorsal view.

**Holotype.**—Lumbar vertebra, MSU-VP 784, Fig. 2 G. From lower Pliocene (Clarendonian), Ogallala Formation, locality UM-K6-59 on the Lowell Hillman Ranch 2350-2550 ft S and 75 ft E of the NW corner, Sec. 22, R. 22 W, T. 11 S, elevation 2255 ft. Collected by J.A. Holman and parties 1969-1973.

**Description of the Holotype.**—In dorsal view, the vertebra is wider than long. The anterior edge of the...
zygosphene is weakly sinuate. The prezygapophyseal facets are oval. The prezygapophyseal accessory processes are broken. The paradiapophyses are clearly visible and they appear rounded. The posterior part of the neural arch in the postzygapophyseal area is not incised and the zygantral facets are almost completely hidden above. The posterior border of the neural arch is very thick. The condyle is rounded. The neural spine is higher posteriorly than anteriorly. The posterior high part of the neural spine is thicker than the anterior low part. The neural spine extends from just slightly anteriad to the posterior border of the neural arch to about one-fourth of the way onto the roof of the zygosphene.

In lateral view, the neural spine is higher posteriorly than it is anteriorly. The postzygapophyseal part of the neural arch is upswept. The subcentral ridges are arched. The paradiapophyses clearly divided into parapophyseal and diapophyseal segments.

In ventral view, the paradiapophyses are clearly divided into distinct parapophyseal and diapophyseal units. The hemal keel is very wide, but it is distinctly produced from the floor of the centrum. The diapophyses extend onto the floor of the centrum as a ridge, thus a deep groove is produced between the diapophyseal ridges and the hemal keel. The postzygapophyseal facets are oval.

In anterior view, the zygosphene is relatively narrow and it is moderately thick. The round cotyle is about the same size as the neural canal. The prezygapophyseal facets are tilted slightly upward. The cavities on either side of the cotyle lack foramina.

In posterior view, the neural arch is slightly vaulted. The condyle is round and it is slightly smaller than the neural canal. The paradiapophyses are massive.

Measurements: width through prezygapophyses 5.3; width through postzygapophyses 5.1; length through zygaphyses 4.2.

Remarks.—This is another unexpected faunal member. Several features presented in the diagnosis section indicate this fossil is in some ways similar to the larger lower Oligocene form *Ogmophis compactus*. Although the status of the genus *Ogmophis* is unclear, the fossil from the WaKeeney fauna is clearly separable from New World fossil and living boids. *Ogmophis pliocompactus* may be separated from the extinct fossil genus *Calamagras* and the living form *Lichamura* immediately by the much longer neural spine (Holman, 1972a, for a discussion of this). *Ogmophis pliocompactus* may be separated from the living North American genus *Charina* by the following characters. (1) Size large; (2) neural spine thinner and with a constricted anterior portion; (3) posterior edge of neural arch thicker; (4) hemal keel more distinctly produced from the floor of the centrum; and (5) prezygapophyseal processes less strongly tilted upward.

**Family Colubridae**

*Natrix hillmani* Wilson

*Material.*—Twenty-two lumbar vertebrae, MSU-VP 787.

*Remarks.*—These short lumbar vertebrae seem identi- cal to the vertebrae representing the species *Natrix hillmani* described by Wilson (1968). It is interesting to note that both natricine genera from the WaKeeney local fauna (*Natrix* and *Thamnophis*) have well-developed hypapophyses in contrast to the very poorly developed hypapophyses in the natricines from the upper Miocene Egelhoff local fauna of the lower part of the Valentine Formation of Keya Paha County, Nebraska. Wilson assigned several vertebrae (UMMP V55701, holotype, and V55702–V55704, paratypes) as well as several referred vertebrae(V55705, V55706) and a referred right maxilla (V55706) to this small water snake.

*Thamnophis* sp.

*Material.*—Twenty-eight lumbar vertebrae, MSU-VP 788.

*Remarks.*—These elongate natricine vertebrae belong to the genus *Thamnophis*, but I am unable to make specific designations. Wilson (1968) recorded four *Thamnophis* vertebrae (UMMP V55707–V55710) from the WaKeeney local fauna.

*Paleoheterodon* sp. indet.

*Material.*—Seventeen lumbar vertebrae, MSU-VP 786.

*Remarks.*—The material resembles *Paleoheterodon thi eni* vertebrae from the upper Miocene of the Norden Bridge local fauna of the lower part of the Valentine Formation in Brown County, Nebraska, and differs from *Heterodon* in having a more vaulted neural arch (Holman, 1964, p. 633). It differs from *Xenodon* in having a wider, flatter, hemal keel. All of the material assigned to *Heterodon* (UMMP V55691–V55693) and to cf. *Paleo- heterodon* (UMMP V55694–V55697) by Wilson (1968) should be re-assigned to *Paleoheterodon*.

*Coluber* or *Masticophis*

*Material.*—Five lumbar vertebrae, MSU-VP 781.

*Remarks.*—I have been unable to find consistent differences in the lumbar vertebrae of *Coluber* and *Masticophis*. Nevertheless, it seems that the WaKeeney fossils represent the first New World records of *Coluber-Masticophis*-type vertebrae. This type of vertebra may be characterized as being long and narrow; as having a flattened subcentral area, with a straight, thin, hemal keel; a long, thin, neural spine; and with well-developed epizygapophyseal spines. The MSU WaKeeney fossils are very similar to several species of Recent *Coluber* and
Masticophis and may be related to Coluber constrictor and/or Masticophis flagellum.

Wilson (1968) described a form he named "Coluber ?plioagellus" on the basis of six lumbar vertebrae. I have re-studied this material and find that two of the paratypes of this form (UMMP V55616 and V44714) are not of the Coluber-Masticophis type and they are re-assigned to Elaphe in the present paper. The other vertebrae (UMMP V55711, holotype, and V55712, V55713, and V55715, paratypes) are better regarded as "Coluber or Masticophis" as none of the characters listed by Wilson (1968) sufficiently separate this form from living species of Coluber or Masticophis.

Elaphe sp. indet.

Material.—Thirteen lumbar vertebrae, MSU-VP 782.

Remarks.—These vertebrae are similar to Recent species of Elaphe and differ from the extinct species, Elaphe nebraskensis, from the Norden Bridge local fauna of the lower part of the Valentine Formation of Brown County, Nebraska, in having the accessory processes of the prezygapophyses almost at right angles to the long axis of the centrum, not at a strongly oblique angle to the long axis of the centrum as in E. nebraskensis. But the WaKeeney Elaphe vertebrae are too fragmentary to assign to species.

Two precaudal vertebrae, formerly assigned to "Coluber ?plioagellus" by Wilson (1968), UMMP V55714 and V55616, are re-assigned here to Elaphe sp. They all lack the characters of the Coluber-Masticophis type of vertebra and are very similar to the Recent genus Elaphe.

Lampropeltis similis Holman

Material.—Four lumbar vertebrae, MSU-VP 785.

Remarks.—These small colubrid vertebrae with low neural spines and a depressed neural arch seem identical to the extinct species Lampropeltis similis from the upper Miocene of the Norden Bridge local fauna of the lower part of the Valentine Formation of Brown County, Nebraska. These vertebrae may be separated from L. triangulum, L. pyromelana, and L. zonata in that they have smaller accessory processes of the prezygapophyses. They may be separated from the closely related L. intermedius Brattstrom of the Pliocene and Pleistocene in that they have the top of the zygosphene curved rather than straight.

Indeterminate Colubrid Vertebrae

In 1968 Wilson described a new species of the boid genus Ogmophis as O. kansensis on the basis of four fragmentary lumbar vertebrae (UMMP V55687, holotype, and V55688–V55690, paratypes). I have re-studied these vertebrae and I find that they represent a subadult individual of a rather large colubrid and should be placed in the family Colubridae and removed from the Boidae.

Characters that show that "Ogmophis kansensis" is a colubrid rather than a boid are as follows. (1) In anterior view, the zygosphenal border of O. kansensis is wide and quite thin as in many subadult colubrids. In boids the zygosphenal border is much narrower and very much thicker. (2) In lateral view, the entire vertebral shape is typically colubrid in O. kansensis, as the vertebra is about as high as long, the subcentral ridges are straight, and the entire postzygapophyseal area is downswept. In the Boidae the vertebrae are higher than long, even in the low-spined species, the subcentral ridges are arched, and the postzygapophyseal area is very typically upswept. (3) There are large foramina in the depressions on either side of the cotyle in O. kansensis and in many colubrids. Boids appear to lack these foramina. (4) The neural spine is very thin as in most colubrids. I have seen no boids with a spine this thin. Even Eryx conicus, the boid with the thinnest neural spine I have observed, has a much thicker neural spine than O. kansensis.

The type material of O. kansensis is fragmentary and it is difficult to assign it to any living colubrid genus with certainty. Therefore, I suggest that Ogmophis kansensis Wilson be re-assigned as Colubridae (Colubrinae) genus and species indeterminate.

Vertebrae assigned to Pituophis by Wilson (1968) should also be referred to as Colubridae (Colubrinae) genus and species indeterminate. These vertebrae (UMMP V55717–V55719) are too long; they have the neural spine too low; the subcentral area is differently shaped; and the central foramina are much smaller in the fossils than in Recent Pituophis.

DISCUSSION AND SUMMARY

The WaKeeney local fauna may be said to be very modern as 93.3% of 15 families, 83.3% of 24 genera, and 48.2% of 27 species are living today. There are some forms that are carryovers from earlier times and there are some forms that are not represented elsewhere in the fossil or Recent record. Sometime in the future, when more complete herpetofaunal lists are available from Cenozoic deposits in North America, it could be instructive to compare extinction percentages between faunas. But at present it seems too early to attempt these comparisons.

Temporal Faunal Elements.—From a temporal standpoint the WaKeeney herpetofauna is divisible into four faunal elements. (I) Elements that are holdovers from earlier Tertiary times. (II) Distinctive forms reported from no other fossil or Recent localities. (III) Extinct Pliocene forms known from other sites. (IV) Species living today.
Group I forms are listed as follows. (1) Bufo valentinensis has been reported from upper Miocene localities in Saskatchewan (Holman, 1970) and Nebraska (Estes and Tihen, 1964; Chantell, 1971). (2) Gerrhonotus mungorum has been reported (cf.) from the upper Miocene of Nebraska (Holman, 1973c). (3) Paleoheterodon was described from the upper Miocene of Nebraska (Holman, 1964). (4) Geochelone orthopygia has been reported from the upper Miocene of Nebraska (Holman, 1973a). (5) Lampropeltis similis was described from the upper Miocene of Nebraska (Holman, 1964).

Group II forms are listed below. (1) Scaphiopus hardeni n. sp. (2) Tregobatrachus hibbardi n. fam. gen. et sp. (3) Eumeces hixsonorum n. sp. (4) Tregophis breviroachis n. gen. et sp. (5) Ogmophis pliocompactus n. sp. (6) Matrix hillmani an extinct species described by Wilson (1968).

Group III forms are as follows: (1) Bufo hibbardi, (2) Bufo pliocompactus, and (3) Geochelone orthopygia. Bufo pliocompactus, thus far, has been reported only from lower Pliocene localities.


Phylogenetic Relationships.— Many of the WaKeeney local fauna amphibians and reptiles appear to be temporal equivalents of species living today. These forms are listed in the preceding paragraph. Other forms are discussed below.

Scaphiopus hardeni is intermediate in characters between Scaphiopus wardorum Estes and Tihen of the upper Miocene of Nebraska (Estes and Tihen, 1964) and the modern forms of the subgenus Scaphiopus, S. holbrooki and S. couchi. It seems possible that S. hardeni could have been ancestral to both modern forms.

The phylogenetic relationships of the Tregobatrachidae (n. fam.) represented by Tregobatrachus hibbardi (n. gen. et sp.) are difficult to ascertain as Tregobatrachus is not really similar to any known living or fossil anuran family. Tregobatrachus has, at once, primitive and unique ilial characters, thus it seems possible that it is a specialized dead-end of a rather primitive group of anurans. One might question why this family has such an isolated position in the fossil record. A similar situation exists in the case of an extinct and temporally isolated lizard subfamily, the Nordenosaurinae (Holman, 1973b). It was suggested that this lizard was rare in the fossil record because of its arboreal habits. Possibly the rarity of Tregobatrachus is due to its arboreal habits, perhaps coupled with some type of obstetrical breeding strategy.

Tihen (1962a) has discussed the relationships of Bufo hibbardi. Bufo pliocompactus is a unique little toad that has been reported only from the WaKeeney fauna and from the lower Pliocene Mission local fauna of South Dakota (Holman, 1973). Its relationships are not well known, but I imagine it was a dead-end species. I picture it being quite abundant and having habits something like the little Oak Toad, Bufo quercicus, that lives in the Southeastern Coastal Plain today. The relationships of Bufo valentinensis were discussed by Tihen (1962b).

Geochelone orthopygia, a giant tortoise, is a relatively thin-shelled species of the upper Miocene and lower and middle Pliocene. Geochelone orthopygia may have given rise to or have been replaced by a thick-shelled species, Geochelone rexroadensis Hibbard (1960).

The relationships of Gerrhonotus mungorum are somewhat in doubt. The scutellation of the frontal region of the head is the same as in Recent G. multicarinatus, but the presence of sharply recurved teeth in both the maxillary and the dentary bones suggests a different diet than in the modern form.

Eumeces hixsonorum may be most closely related to Eumeces inexpectatus, a Recent species of the Southeast Coastal Plain, but this is a tentative suggestion.

The relationships of the bizarre boid genus Tregophis are not well understood as there have been no similar snake vertebrae described previously. Possibly Tregophis is a dead-end form with no living relatives. I can offer no guess as to why Tregophis occupies such an isolated spot in the fossil record.

Ogmophis pliocompactus appears closely related to the early Oligocene form O. compactus. It seems possible that O. pliocompactus might represent the last survivor of this evolutionary line.

The relationships of Matrix hillmani were discussed by Wilson (1968). Paleoheterodon probably gave rise to Heterodon by middle Pliocene times (Auffenberg, 1963). Lampropeltis similis probably gave rise to L. intermedius Brattstrom later in the Pliocene. Lampropeltis intermedius is probably ancestral to L. triangulum, a modern species.

Paleoecology.— Based on ecological preferences of living forms related to the WaKeeney fossil amphibians and reptiles the following habitats were represented during the time of the deposition of the WaKeeney bones: (I) a basin in a sluggish stream; (2) a nearby marshy area; (III) mesophytic woodlands at the lower elevations; and (IV) xerophytic open woodlands in the higher elevations. The most abundant animals appeared to have lived in the region including the edge of the basin and the marshy area. This probably reflects the proximity of these animals to the depositional site.

Animals that lived in the stream-basin include Sternothrus odoratus and Trionyx. Animals that lived in the zone between the edge of the basin and the marshy area

Animals of the mesophytic woods which may have ventured into habitats at higher and lower elevations at times include: *Ambystoma maculatum*, *A. tigrinum*, *Scaphiopus hardeni*, *Bufo marinus*, *B. hibbardii*, *B. valentiniensis*, *Hyla* cf. *H. cinerea*, *H. cf. gratiosa*, *H. cf. squirella*, *Rana* cf. *R. areolata*, *Terrapene* cf. *T. carolina*, and *Lampropeltis similis*.

Animals of the xerophytic woods include the following forms, some of which may also have moved into lower habitats from time to time: *Bufo cognatus*, *Ophisaurus attenuatus*, *Gerrhonotus mungerorum*, *Cnemidophorus c. sexlineatus*, *Eumeces hixsonorum*, *Paleoheterodon* sp., and *Coluber* or *Masticophis*.

The presence of the large, thin-shelled tortoise, *Geochelone orthopygia* is of climatic importance. Hibbard (1960) outlined the climatic significance of large land tortoises of the genus *Geochelone* in fossil faunas. They indicate a climate with very mild winters with temperatures seldom if ever reaching the freezing point.

There is no single spot on the map where all of the WaKeeney local fauna amphibians and reptiles with close relationships to living animals could be found living together today. Nevertheless, the majority of forms in the fauna with close relationships to living animals could be found in southeastern Texas in the vicinity of the LaVaca Bay area. These forms are: *Ambystoma maculatum*, *A. tigrinum*, *Acris* sp., *Hyla* cf. *H. cinerea*, *Hyla* cf. *squirella*, *Pseudacris* cf. *P. clarki*, *Rana* cf. *R. areolata*, *Rana* cf. *p. pipiens*, *Sternotherus odoratus*, *Terrapene* cf. *T. carolina*, *Trionyx* sp., *Ophisaurus* attenuatus, *Cnemidophorus c. sexlineatus*, *Thamnophis* sp., *Coluber* or *Masticophis*, and *Elaphe* sp.

Other forms with different spatial relationships today are present in the fauna. The closest relatives of *Scaphiopus hardeni* are *S. couchi*, which occurs in southwestern United States and Mexico, and *S. holbrooki*, which occurs in southeastern United States. The toad, *Bufo cognatus*, occurs in the Plains Region of the United States, Canada, and Mexico. *Bufo marinus* is essentially a tropical form today, reaching the Rio Grande Valley in the southern tip of Texas. The treefrog, *Hyla* cf. *gratiosa*, is a southeastern species, mainly confined to Florida and adjacent states. Finally, *Gerrhonotus* is presently a form with its species distribution mainly in the western United States.

The climate and the vegetation of the WaKeeney, Kansas, area must have been much different than today, with much warmer winters with few if any frosts and a vegetation that must have been much like that found in southeastern Texas along the coastal regions today.

Correlation.—In an earlier paper (Holman, 1973c) herpetofaunal changes between upper Miocene (Barstovian) and lower Pliocene (Clarendonian) times were discussed. These comments were based on three upper Miocene herpetofaunas (Egelhoff and Norden Bridge faunas of Nebraska, Kleinfelder Farm fauna of Saskatchewan) and the lower WaKeeney local fauna. It was stated that the amphibian, turtle, and lizard fauna was rather stable from upper Miocene to lower Pliocene times, but that at least in the Plains Region of North America, there appears to have been a definite change in the snake fauna. It was reported that upper Miocene boids and archaic colubrid genera that are not closely related to any living colubrid forms are present, whereas in the WaKeeney fauna there were no boids or archaic colubrids present. Since that time, two vertebrates representing two distinctive boid snakes have turned up in the WaKeeney fauna. On the other hand, a new faunule from the upper Miocene Norden Bridge site in Nebraska yielded three unexpected new forms that are thus far absent from Clarendonian sites.

In the following paragraphs faunal differences between upper Miocene herpetofaunas (Egelhoff and Norden Bridge faunas of Nebraska, Kleinfelder Farm fauna of Saskatchewan) and the lower Pliocene WaKeeney fauna will be summarized.

Extinct herpetofaunal elements reported from the upper Miocene and thus far not reported from the lower Pliocene include the following forms: (amphibians) *Andrias matthewi*, a large cryptobranchid salamander (Estes and Tihen, 1964); *Ambystoma minshalli*, a small ambystomatid salamander (Estes and Tihen, 1964); *Scaphiopus wardorum*, a large spadefoot (Estes and Tihen, 1964); *Scaphiopus* cf. *S. alexanderi*, a smaller spadefoot (Estes and Tihen, 1964); *Bufo kuhrei*, a large toad (Holman, 1973); and *Pseudacris nordensis*, a large chorus frog (Chantell, 1964); (reptiles) *Geochelone nordensis*, a small, smooth-shelled land tortoise (Holman, 1973d); *Nordenosaurus magnus*, a large xenosaurid lizard (Holman, 1973b); *Charina prebottae*, a rubber boa (Holman, 1973c); *Neonatrix elongata*, a natricine with a very small hypopla- physsis (Holman, 1973c); *Nebraskophis skinneri*, a small, archaic colubrine snake (Holman, 1973c); *Paracoluber storeri*, an extinct racerlike snake (Holman, 1970); *Salvadora paleolineata*, an extinct patchnosed snake (Holman, 1973c); and *Ophisaurus canadensis*, an extinct glass lizard (Holman, 1970).

Animals of the WaKeeney local fauna that differ from those of the above upper Miocene sites include (I) modern species of animals making their first appearance in the fossil record, and (II) extinct animals unique to the WaKeeney local fauna or nearby lower Pliocene sites.

Group I animals are *Ambystoma maculatum*, *A. tigrinum*, *Bufo cognatus*, *Sternotherus odoratus*, *Terrapene* cf. *T. carolina*, *Ophisaurus* attenuatus, and *Cnemidophorus c. sexlineatus*. 
Group II animals are *Scaphiopus hardeni*, *Tregobatrachus hibbardi*, *Bufo plicompaclis*, *Tregosps brevirachis*, and *Ogmopis plicompaclis*.

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LITERATURE CITED


