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SYSTEMATICS AND FAUNAL ANALYSIS OF A LOWER PLIOCENE
VERTEBRATE ASSEMBLAGE FROM TREGO COUNTY, KANSAS

BY

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SYSTEMATICS AND FAUNAL ANALYSIS OF A LOWER PLIOCENE VERTEBRATE ASSEMBLAGE FROM TREGO COUNTY, KANSAS

RICHARD LELAND WILSON

ABSTRACT—A Lower Pliocene vertebrate assemblage screened from sediments of the Ogallala Formation in Trego County, Kansas, indicates the past environment under which the various vertebrate taxa lived. The WaKeeney local fauna represents the vertebrate community which lived in a river and the environmental areas adjacent to it. Seventy-six vertebrate taxa are discussed: eleven fishes; thirteen amphibians, including a new species of toad; fifteen reptiles, with a new species of gerrhonotine lizard; and three new species of serpents of the genera *Ogmophis*, *Natrix*, and *?Coluber*; three birds, including a teal, cracid, and woodpecker; and 34 mammals. Previously undescribed mammals include a genus of shrew; a species of the mole *Domninoidea*; a species of a small mustelid; a species of the beaver *Eucastor*; and two genera and three species of cricetids.

The past environment of the WaKeeney site is interpreted from geological data, the recovered faunal members, and evidence from other faunas and floras. Stratigraphically the fossiliferous sediments represent the margin of a Lower Pliocene river channel. Sedimentary features such as crossbedding and well-sorted quartzose sand are present. This aggrading river moved laterally, to the south, and cut into its own floodplain.

The fishes indicate a low gradient river with aquatic vegetation, relatively free of suspended clastic material. The amphibians and the semi-aquatic reptiles, by their better preservation and greater numbers, indicate the deposit accumulated near the river margin. The associated faunal assemblage and certain individual members or groups (e.g., the anurans, boid, and cracid) indicate a humid, subtropical climate in the Lower Pliocene of Kansas. These animals suggest general vegetational areas, including trees bordering the river and a savanna and/or grassland some distance from the depositional site.

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INTRODUCTION

AROUND 1941 Lester F. Phillis discovered and reported the occurrence of Lower Pliocene vertebrates from Trego County, Kansas. From that date until the summer of 1966 several small surface collections were made by field parties of the University of Kansas and the University of Michigan.

In the summer of 1966 my wife and I wet-screened a large volume of the productive interval from the Trego County beds. The fine sand and silt matrix was easily disaggregated in a nearby spring. The skeletal remains of the small vertebrates which were screened from the deposit provide the basis for this report. However, the previous surface collections and fossil material obtained from nearby localities greatly augmented the study.

GEOLOGIC SETTING

Trego County, Kansas, is in that area designated by Fenneman (1931) as the Plains Border. The WaKeeney site is on the south side of the Saline River in the northern portion of the county. The rainfall in Trego County is low to moderate and occurs mainly between May and September. Hodson (1965) described the Trego County climate as semiarid and continental.

The Saline River has eroded into the Late Cretaceous Niobrara beds. The Niobrara For-

mation is divided into the upper Smoky Hill Chalk and the lower Fort Hays Limestone members. The Cretaceous Smoky Hill member is unconformably overlain by the Pliocene Ogallala Formation which, in turn, is capped by Pleistocene sediments of eolian and fluvial origin.

Hay (1895) measured and published the sequence of beds of the Ogallala Formation at or near the type locality in Nebraska. The Ogallala was named by Darton (1898) from outcrops in Keith County, Nebraska, but he did not designate a type locality. In 1920, Darton established a type area when he stated (p. 6), "The Ogallala formation is believed to be a stratigraphic unit and to be continuous from the type locality near Ogallala station in western Nebraska . . ."

Elias (1931, p. 135) remeasured the beds outcropping northeast of Ogallala, Nebraska, and gave corrected footages. Hibbard (1933) and Hesse (1935) were first to report the occurrence of vertebrate fossils from the type area in Keith County, Nebraska.

Lugn (1938, 1939) of the Nebraska Geological Survey, classified the Ogallala as a Group with divisions as follows: Kimball (highest), Sidney, Ash Hollow, and Valentine as formations. The Kansas Geological Survey has assigned the Ogallala to the rank of formation and recognized the Kimball (including Sidney),

Ash Hollow, and Valentine as members (Frye *et al.*, 1956). Before the term Ogallala was proposed the terms "tertiary grit," "mortar beds," and "magnesium beds" were used by various workers (Merriam, 1963). The extent of the Ogallala sediments is approximately 800 by 400 miles (Frye *et al.*, 1956). They cover an area from south central South Dakota southward through the Texas Panhandle and from eastern New Mexico, Colorado, and Wyoming east through central Nebraska, western Kansas, Oklahoma, and Texas (text-fig. 1).

The fluvial, unconsolidated Ogallala sediments range in thickness from over 500 feet in some areas of the west to a few feet at the more eastern exposures. The complex problem of regional stratigraphic correlation in this series of deposits where deposition has created a continuous alluvial platform is yet unsolved. Streams flowing to the Gulf of Mexico have continuously deposited sediments in many individual river drainages, thus creating the complex regional patterns of alluvium. Frye *et al.* (1956) utilized nearly all characteristics of the lithologic assemblage in attempting to correlate this sedimentary complex. Although these authors support and further define the original Valentine, Ash Hollow, and Kimball members of the Ogallala Formation, their publication recognizes the difficulty of regional correlation and the need for additional study. It seems misleading to think of these members of the Ogallala as regional when each of the streams carrying sediments from the Rocky Mountains created a local environment with a dispositional history of its own.

GEOGRAPHIC POSITION OF LOCALITIES

The fossil collections described in this report are from two localities in Trego County, Kansas. The major University of Michigan locality, UM-K6-59, is northwest of Ogallala, Kansas (text-fig. 1), on the Lowell Hillman Ranch. Its precise location is 2350–2550 feet south and 75 feet east of the NW corner Sec. 22, R22W, T11S. Elevation is 2255 feet. UM-K6-59 is the locality where *Eucastor* cf. *tortus* was reported by Hibbard & Phillis (1945), *Ictalurus lambda* by Hubbs & Hibbard (1951), and *Nettion ogallalae* by Brodkorb (1962).

The second locality is University of Kansas Museum (Trego County) Loc. 29, 2450 feet south and 10 feet west of the NE corner of Sec. 21, T11S, R22W, (text-fig. 1). *Epigaulus minor* Hibbard & Phillis (1945) is from this locality.

AGE OF THE WAKEENEY LOCAL FAUNA

Stratigraphically, the fauna probably falls into either the lower portion of the Ash Hollow

Member or the upper portion of the Valentine Member of the Ogallala formation. It is older than four of the major Pliocene Ogallala faunas from Kansas and Colorado, namely the Long Island, Edson, Rhinoceros Hill, and Wray (references dealing with these local faunas are reported in Frye *et al.*, 1956, p. 30). Based on beaver and horse specimens, the Valentine faunas of Nebraska (ranging from Norden Bridge to Burge) are older than the WaKeeney local fauna.

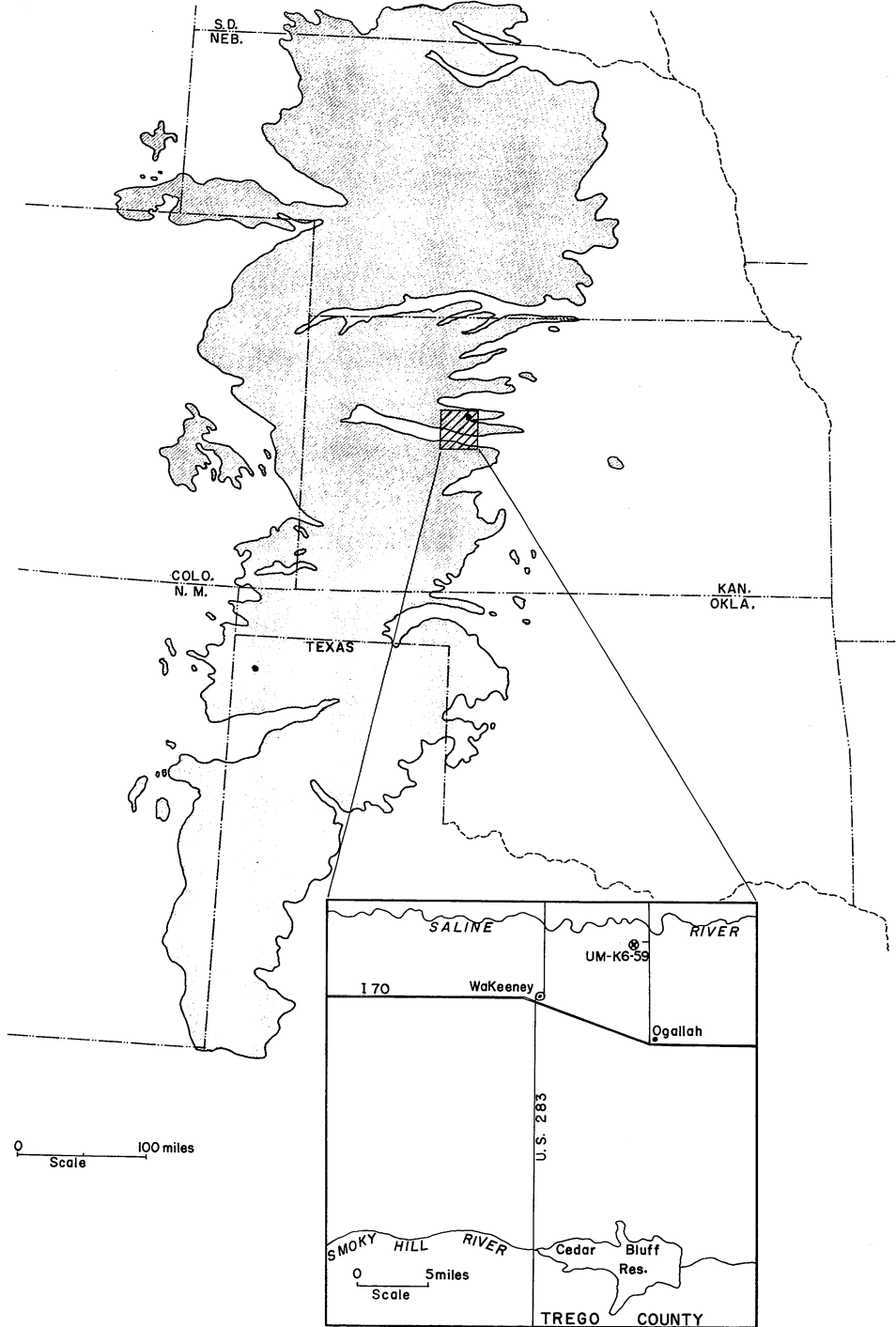
The local faunas of the Plains which are most comparable in age to the WaKeeney are: the Clarendon, Donely County, Texas (Wood *et al.*, 1941); those of the Laverne Formation, Beaver County, Oklahoma (Hesse, 1936; Hibbard, 1951; Woodburne, 1959; and Smith, 1962); the Big Spring Canyon, Bennet County, South Dakota (Gregory, 1942); and the Wolf Creek, Sheridan County, South Dakota (Green, 1956). The Laverne beds seem most equivalent in age to the Trego County strata from which the WaKeeney local fauna was extracted. This conclusion is based on vertebrate similarities (particularly *Eucastor*) and certain molluscan forms (such as *Lymnaea lavernensis* Leonard & Franzen and *Pyrgophorus hibbardi* Leonard & Franzen; Frye *et al.*, 1956, p. 36).

The WaKeeney local fauna is probably older than the Truckee local faunas of Nevada (Macdonald, 1956) and the Juntura faunas described by Shotwell (1963). However, age correlation with many western local faunas is uncertain because of the apparently dissimilar geographic and ecologic conditions (*e.g.*, plains as compared with basin faunas).

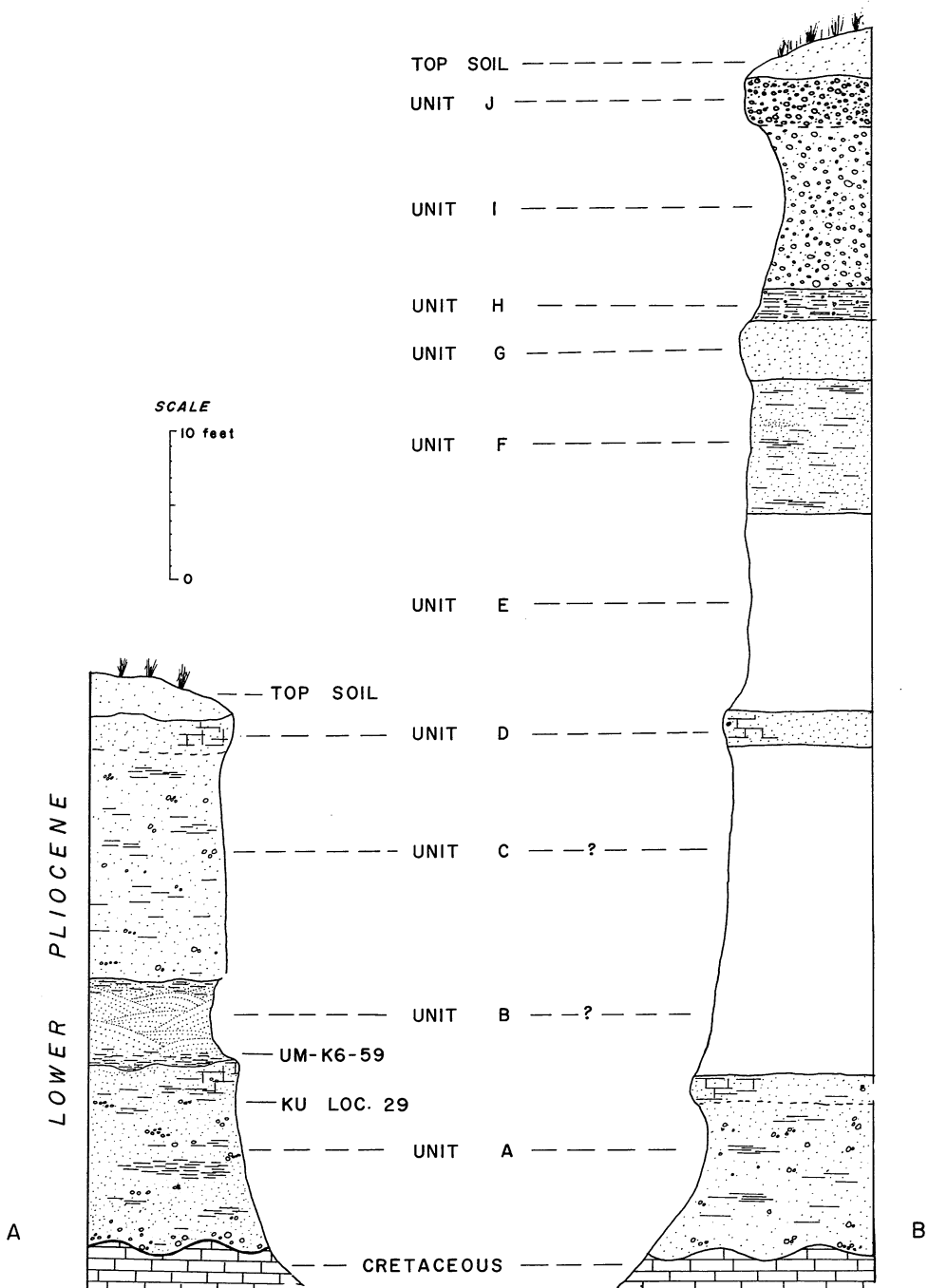
The WaKeeney local fauna from Trego County, Kansas, is best assigned to the Middle or Late Clarendonian provincial age (Wood *et al.*, 1941).

STRATIGRAPHIC HISTORY OF THE WAKEENEY DEPOSIT

The main quarry, UM-K6-59, is here considered as being the basal part of Unit B (text-fig. 2A). The unit includes unconsolidated cross-bedded sand and a few inches of clay-sand on top of a Lower Pliocene flood-plain deposit (Unit A, text-fig. 2A). To the south the lateral lithologic relationship of Unit B is uncertain but along the exposure for a distance of 100 or more feet it varies from a pure sand to a mixture of clay-sand and silty clay. In Unit B the clay is normally lenticular and alternates with the sand. A greenish clay occurs as clay balls deposited within this predominantly sandy layer. The percent of greenish clay decreases from nearly 100% at the base of Unit B to near zero at the center of this unit, where it occurs as



TEXT-FIG. 1.—Distribution of the Ogallala Formation in the Great Plains showing position and detail of Trego County and University of Michigan Locality UM-K6-59. (In part after Merriam, 1963).



TEXT-FIG. 2—Measured sections: A at locality UM-K6-59; B measured 3600 feet west of UM-K6-59.

small rounded nodules. Clay content then increases again toward the top of this unit. The basal contact of Unit B is irregular.

The main river channel was to the north, as indicated by both the lithology and faunal remains. Current velocity, judging from the thin crossbedding of Unit B, was weak and decreased toward the southern margin of the area represented by the outcrop. The current velocity apparently increased from zero or nearly so at the base of Unit B to a rate of flow capable of transporting fine to coarse sand at the middle. Stream direction was apparently to the east or southeast.

The sediments quarried from the base of Unit B reflect a marginal stream environment with certain of the faunal members, such as *Acris*, *Natrix*, small fish, and near-shore terrestrial animals being trapped in these sediments.

The increase in fine clastic material to the south, mainly as clay lenses, correlated directly with the faunal types recovered. The terrestrial forms become more numerous to the south with a corresponding decrease in the small fish.

The remaining section above Unit B (text-fig. 2A and B) represents a typical Ogallala fluvial deposit which varies horizontally and vertically.

Measured Pliocene Section at Locality
UM-K6-59
(Text-fig. 2A)

	Thickness Feet
Unit D. Cemented, calcareous silt and sand; probably the cemented upper portion of Unit C; contains few pebbles; weathers to a hard, white resistant layer, no fossils noted	2.5
Unit C. Argillaceous sand and silt; greenish clay fraction occurring as nodules and lenses; some sand and pebble lenses; coarse to fine sand throughout; slightly fossiliferous; weathers to a buff color; no calcium carbonate	16
Unit B. Fossiliferous unit of fine to coarse, well sorted, unconsolidated, cross-bedded quartzose sand; at base and top, the clay content increases; basal clay greenish with small scattered clay balls and lenses near bottom; Loc. UM-K6-59 at base of this unit	3
Unit A. Gray to tan sandy silt with clay, pebbles, and some basal gravel;	

weathers pink to tan; locally cemented with calcium carbonate decreasing toward Unit B; sand and pebbles predominantly quartz; fossils randomly distributed and rare; KU Trego County Loc. 29 in this unit

Measured Pliocene Section 3600 Feet West
of UM-K6-59
(Text-fig. 2B)

	Thickness Feet
Unit J. Calcareous pebble-sand conglomerate; just below present soil some rounded pebbles present; clastic fraction primarily well rounded quartz	3.5
Unit I. Heterogeneous size pebbles and gravels; primarily quartz; only small amount of sand present; fossiliferous, but specimens rare	11
Unit H. White calcareous clay with scattered sand and pebble grains; very smooth texture	2
Unit G. Coarse to fine grained sand; well sorted and cemented; calcium carbonate present; weathers to a resistant gray-tan layer	4.5
Unit F. Fine-grained silty sand; small pockets of homogeneous sand or clay; calcium carbonate cement..	8
Unit E. Covered interval; sandy silt from slope debris	13
Unit D. Cemented calcareous quartzose sand; well sorted, fine-grained, homogeneous throughout	2.5
Units B-C. Covered interval	23
Unit A. Calcareous, with a silt matrix containing fragments of Cretaceous chalk at base, and gravel, pebbles, and sand throughout; weathers to a reddish buff, upper portion a pink cemented sandstone; fossiliferous	12

Many reports (Frye *et al.*, 1956, for summary) have attempted regional correlations, but at this site the stratigraphic assignment would be tentative. The major portion of the section at the WaKeeney local fauna site most likely represents the Ash Hollow Member of the Ogallala Formation (Frye *et al.*, 1965).

A geologic map, many well core sections and a current résumé of the geologic work in Trego County are found in Hodson's paper (1965). His Trego County sections illustrated there are not correlateable rock units within these Pliocene sediments. There are apparently no Pliocene ash deposits within the northern half of

Trego County (Frye *et al.*, 1956); Hodson, 1965), and no ash deposits were found above the main WaKeeney local fauna site although Hibbard & Phillis (1945, p. 549-550) report one in their section.

The two sites, UM-K6-59 and KU Loc. 29, represent two depositional environments. The lower (KU Loc. 29, Unit A) is a flood-plain deposit typified by a rather heterogeneous clastic lithology alternating from pebble to clay. Unit B, the lateral edge of a stream channel deposit, probably cut into the lower floodplain (Unit A) depositing the near-stream fauna. This stratigraphic unit is typified by sedimentary structures and features indicative of current and transportation (*e.g.*, crossbedding, cut and fill structures, clay lenses, etc.).

METHODS AND MATERIALS

General

The main quarry, UM-K6-59, was worked by wet-screening the sand-clay matrix of the productive interval (text-fig. 2A). The matrix was placed in a screen and immersed in a nearby spring. The fine sand and silt was immediately washed out leaving a residue of disaggregated clay, sand, pebbles and fossils greater than screen mesh size.

After the first screening this residue was allowed to dry so the clay would disaggregate upon the next washing. Similar screening techniques have been described by Hibbard (1949) and McKenna (1962).

When dry, the various size fractions were sorted and all fossil material removed. Bromoform was used to separate the very small specimens from the sand matrix. Although much care was used on each examination, easily identifiable elements would often go unnoticed during the first sortings.

In most cases the fossil specimens were in excellent condition and very little field and laboratory preparation was needed. Fossil material needing treatment was soaked in thinned glyptal or repaired with a polyvinyl adhesive as described by Wilson (1965).

The crossbedded sand of Unit B (text-fig. 2A) is fossiliferous throughout. However, it is only in the clay-rich base of this unit that the specimens exhibit little or no effects of river transportation.

Illustrations were prepared with the aid of a camera lucida. Measurements of all small specimens were made with a measuring microscope.

SAMPLING PROCEDURE

In the fauna screened from UM-K6-59, the following sampling procedure was used:

1. Each small sack of damp sediment was numbered and its position in the quarry noted. Over 250 sacks were removed from the main quarry.

2. Five to ten sacks constituted a sample.

3. Common window screen and a finer screen with $\frac{1}{2}$ mm mesh were used. In all cases the fine fraction (between the window screen and fine screen sizes) was kept separate from the larger material and labeled according to its particular sack and group.

4. All fossil material, including fragments, was picked from the residue after screening.

5. All bone material was sorted numerous times for identifiable specimens.

6. The fine fraction ($\frac{1}{2}$ -1 mm) was subjected to a bromoform separation process to divide the fossil material from the sand matrix. A check of this method showed that small anuran toe bones and occasionally a limb bone from this group would float with the mineral fraction and thus be removed from the sample, but this was true only for frog remains.

7. The identifiable specimens were then arranged and systematically listed.

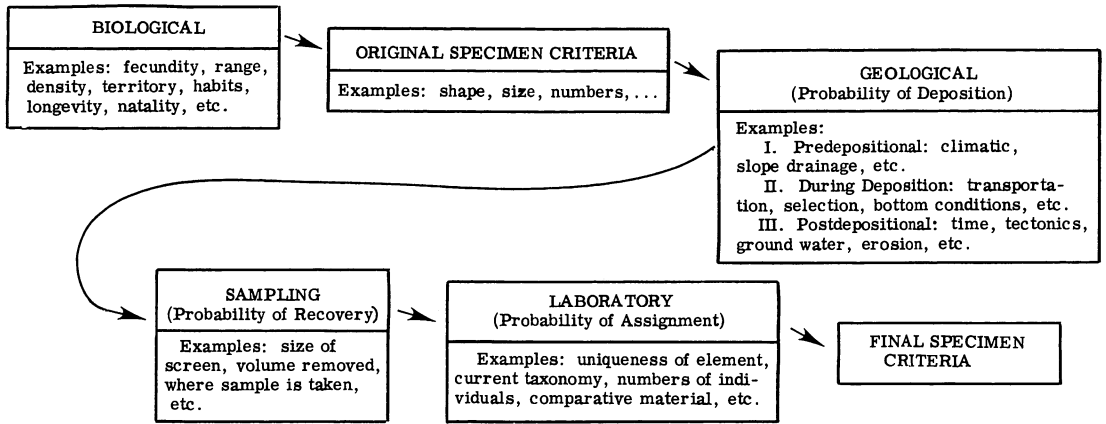
Many other studies deal with methods of sampling a fossil deposit. The procedure used in this study is similar to that described by Shotwell (1963, p. 11). Hibbard (1949), Wilson (1960), and McKenna (1962) also describe sampling procedures that involve screening or volumetric controls.

FAUNAL INTERPRETATION

The paleoecological reconstruction of the fossil community represented by the WaKeeney local fauna was based upon the individual habitat of each taxon. This approach is limited by factors which acted on the animals prior to death and preceding deposition (text-fig. 3). One important bias among the geological effects (text-fig. 3) is river transportation.

River transport differentially affected elements from individual taxa as evidenced by the numbers of identifiable elements recovered. Fossil skeletal remains from the fish assemblage point out the combined effects of river transportation and biological characteristics (table 1).

River transportation selectively acted upon the density and shape of the skeletal elements. The number of pectoral spines (table 1) compared with the dentaries of *Ictalurus* and the number of infrapharyngeals with dentaries in the centrarchids reflect transportation and destruction according to specimen characteristics (table 1). The pectoral spine of the catfish is a dense, resistant element while the dentary is relatively fragile. The infrapharyngeal assigned



TEXT-FIG. 3—Factors in the life, death, recovery, and study of a fossil fauna which affect the final analysis of the community.

TABLE 1—IDENTIFIABLE ELEMENTS COMPARED BETWEEN THE VARIOUS TAXA OF FISHES

Taxa	Dentaries	Scales	Cleithra	Infra-pharyn-geals	Pectoral spines	Pharyn-geal teeth
<i>Lepisosteus</i> cf.						
<i>L. platostomus</i> or <i>L. productus</i>	1, 0*	±100				
<i>Amia calva</i>	3, 2	12	1, 1			
<i>Micropterus</i> cf.						
<i>M. punctulatus</i>	0, 8			0, 1		
<i>Lepomis</i> sp.	0, 5			3, 1		
<i>Pomoxis</i> sp.	2, 4					
<i>Ictalurus</i> sp.	5, 9				40, 43	
<i>Ictalurus lambda</i>					0, 3	
<i>Ictiobus</i> sp.			1, 0			6
cf. <i>Aplodinotus</i> <i>grunniens</i>						1
<i>Fundulus</i> sp.				2, 3		
? <i>Notropis</i>				0, 1		

*Left and right elements separated by comma.

to *Lepomis* is much more massive than those of *Micropterus* and *Pomoxis*.

The size and durability of a particular anuran element largely determine the final number recovered. In this group all forms can be separated on the ilia (table 2). However, the number of ilia does not reflect the true past biological abundance of individuals per taxa from a given size area. Most of the very small (text-fig. 7a) fragile *Acris* ilia are unabraded and often nearly complete. They show little, if any, abrasion. However, the ranid ilia are nearly all abraded and broken. *Rana* has the much larger, more durable ilium and thus this element survived the destructive effects of river transport.

Anuran frontoparietals vary markedly in their size and shape. The bufonids have the

more durable one and from table 2 the number recovered reflects this factor. In *Rana* the frontoparietal is very thin and delicate. This fact is shown by the low number of frontoparietals recovered compared with the number of ilia. The lack of frontoparietals in some groups is again the reflection of size and durability during river transportation.

Other biases are also important in a faunal analysis. Sampling and laboratory procedures largely determine whether a given element is recovered. Taxonomic methods and specimen distinctiveness will determine whether an element is assignable. The anurans, for example, are assigned on only two elements, the ilium and frontoparietal. By contrast, the beaver can be distinguished on limb material, certain vertebrae, and most of the cranial parts.

TABLE 2—NUMERICAL COMPARISON OF THE ANURAN ILIA AND FRONTOPIARIETALS

Taxa	Ilia	Frontoparietals
<i>Scaphiopus couchi</i>	9, 6*	2, 4
<i>Acris</i> sp.	20, 23	
<i>Pseudacris</i> cf. <i>P. clarki</i>	0, 1	
<i>Hyla</i> cf. <i>H. gratiosa</i>	7, 15	
<i>Hyla</i> cf. <i>H. cinerea</i> or <i>versicolor</i>	1, 1	
<i>Bufo boreas</i>	6, 3	0, 1
<i>Bufo cognatus</i>	1, 0	0, 1
<i>Bufo marinus</i>	1, 1	0, 1
<i>Bufo pliocompactilis</i>	15, 9	2, 0
<i>Rana</i> (all)	42, 38	1, 1

*Lefts and rights separated by comma.

The past habits and habitats are delineated through the uniformitarian principle. The methods of defining the past major environmental areas (text-fig. 4) and the habit and habitat of a given taxon, can be divided into two principle lines of evidence: first, the floras and invertebrates of proximate and similar age localities; and second, the animals from the WaKeeney local fauna itself.

OTHER FLORAS AND FAUNAS

MacGinitie (1962) described a large flora (Kilgore) from the Lower Valentine of Nebraska. He recorded (p. 89-92) the genera *Meliosma* and *Cedrela*, two tropical-subtropical plants. He concluded that this Late Mio-Pliocene flora grew in a warm-temperate to subtropical climate. Furthermore, he found no evidence for treeless prairies but rather a savanna with forests along the streams. Although the Kilgore flora is older than the Trego County fauna, there seems to be nothing to indicate any major change in vegetation in the latter occurrence.

Gregory (1942) reported a few seeds and a nutlet of *Lithospermum* from the Lower Pliocene of South Dakota. He inferred a past climate more humid than at present.

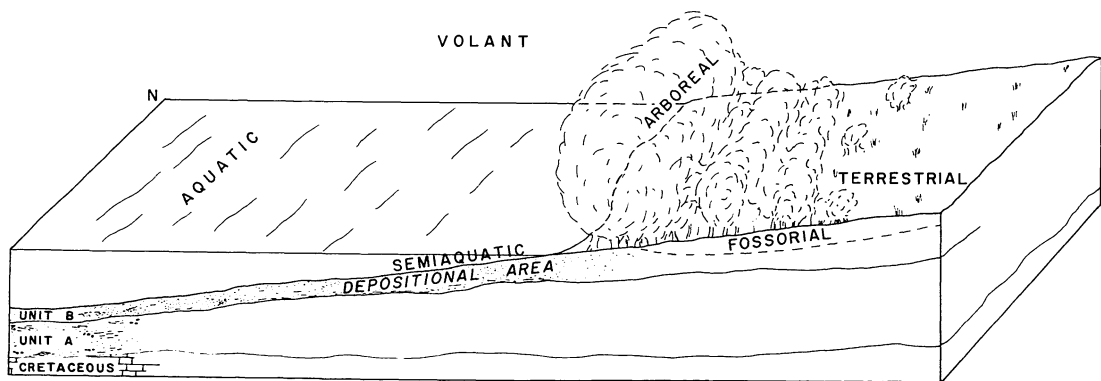
Chaney & Elias (1936, p. 33) interpreted a Lower Pliocene flora from Beaver County, Oklahoma, as being a floodplain assemblage representing a more humid climate than that of the Mio-Pliocene of western Nebraska.

Hibbard (1960), in a discussion of Pliocene climates, reviewed many previous reports and explained the necessity for separating considerations of temperature and moisture in an interpretation of past climates. Regarding the Lower Pliocene in an "area from southern South Dakota to Texas," he stated it was (p. 13) "a moist subhumid, subtropical, savanna with forests and tall grasses along the river valleys, with chiefly shrubs and tall grasses on the valley walls and on the low divides."

Hanna (1932) reported two diatom assemblages from nearby Kansas localities. The majority of his forms were relatively small and he reported that deposition was probably within a lake basin (p. 371). Comparison on a regional basis would place these localities higher in the Ogallala Formation (Middle Pliocene).

The molluscan fauna of the Ogallala Formation from several northern Kansas localities was discussed by Frye *et al.* (1956). In this report (p. 38) they discussed the occurrence of *Lymnaea lavernensis* and *Helisoma valens* Leonard & Franzen, 1944 and *Pyrgophorus* (see Taylor, 1966, p. 214) in Ellis County, Kansas. These molluscs were reported from the Laverne Formation by Leonard & Franzen (1944). The Ellis County locality is approximately 15 miles from the WaKeeney site and probably represents equivalent fluvial deposits. Leonard & Franzen (1944, p. 34) interpreted the deposits laid down during Laverne time as being freshwater, not brackish, concluding that a single large lake or numerous small stream-fed lakes

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TEXT-FIG. 4—The various adaptive areas represented by the WaKeeney local fauna screened from UM-K6-59.

provided the major habitat for the Laverne molluscan assemblage.

WAKEENEY LOCAL FAUNA

The WaKeeney faunal community supports the previous environmental interpretations (text-fig. 4). The following adaptive types are delineated from the fossil vertebrate assemblage: aquatic (river), semi-aquatic, fossorial, arboreal, volant, and terrestrial grassland and/or savanna (text-fig. 4). Where possible, after taxonomy of each vertebrate form, its habitat and habit are given. The habitat determination is based on a combination of the uniformitarian principle and empirical data (Scott, 1963).

The uniformitarian approach is applied to taxa which are judged to be ecologically equivalent to living forms. For example, *Aplodinotus*, *Acris*, *Bufo cognatus* Say, *Ortalis*, and *Myotis* today display a definite set of habits and occupy definite habitats. There is no geological or biological evidence to suggest a present deviation from their past mode of existence. The lower vertebrates are primarily assigned by this principle.

Observational data are also used, such as amount of abrasion, completeness, or functional morphology of the animal as reflected by the fossil element. Empirical data are used to support the habitat placement of extinct forms where ambiguity might exist over the present day equivalent. The amount of abrasion is usually assumed to reflect the distance which an element was transported.

SYSTEMATIC DISCUSSION Class OSTEICHTHYES

In the terminology used in this and the following accounts I shall attempt to conform to accepted usage among each group. If pertinent to the discussion, the author(s) for osteological terminology will be listed under the section used. All numbers preceded by a V refer to specimens of the University of Michigan Museum of Paleontology.

In certain groups in which the help of others is acknowledged, taxonomic placement in this report does not necessarily reflect their determinations, and except when noted all taxonomic decisions are the responsibility of the author.

Smith (1962) listed 20 species of freshwater fishes from the Pliocene deposits of the High Plains. His report, besides forming a summary of work in this geographical area, also indicates the difficulty involved in the taxonomic assignment within many of the groups. A later summary is given by Uyeno & Miller (1963).

Family LEPISOSTEIDAE

LEPISOSTEUS cf. *L. PLATOSTOMUS* Rafinesque
or *L. PRODUCTUS* (Cope)
Text-fig. 5a-b

A broken dentary (V55569), several maxillary fragments (V55571), approximately 100 scales (V55573) and several isolated teeth (V55570 and V55572) are assigned to the gar.

The dentary fragment is 39.8 mm long (text-fig. 5a-b) and appears to be of some taxonomic value by retention of the anterior symphysis. The teeth have been removed by abrasion and only the attachment bases remain. The rounded lateral line pores are probably widened somewhat by abrasion. The type of dentary attachment is similar to that in *L. productus*, *L. platostomus*, and *L. osseus* (Linnaeus), the two dentaries being joined without a curved termination point at the anterior end as in *L. spatula* (Lacépède) and *L. platyrhincus* DeKay. The relatively pronounced attachment position would indicate a more massive jaw than in *L. osseus*. From the face of the symphysis the dentary forms an angle of 12-14 degrees from the midline. This appears to be greater than in *L. osseus* and within the range of *L. productus* and *L. platostomus*.

Gar scales are very numerous in the fauna. Since they are undoubtedly from different sized individuals and different positions on the body they are of little taxonomic value. However, the absence of any ornamented scales as in the larger individuals of *L. spatula* is noteworthy.

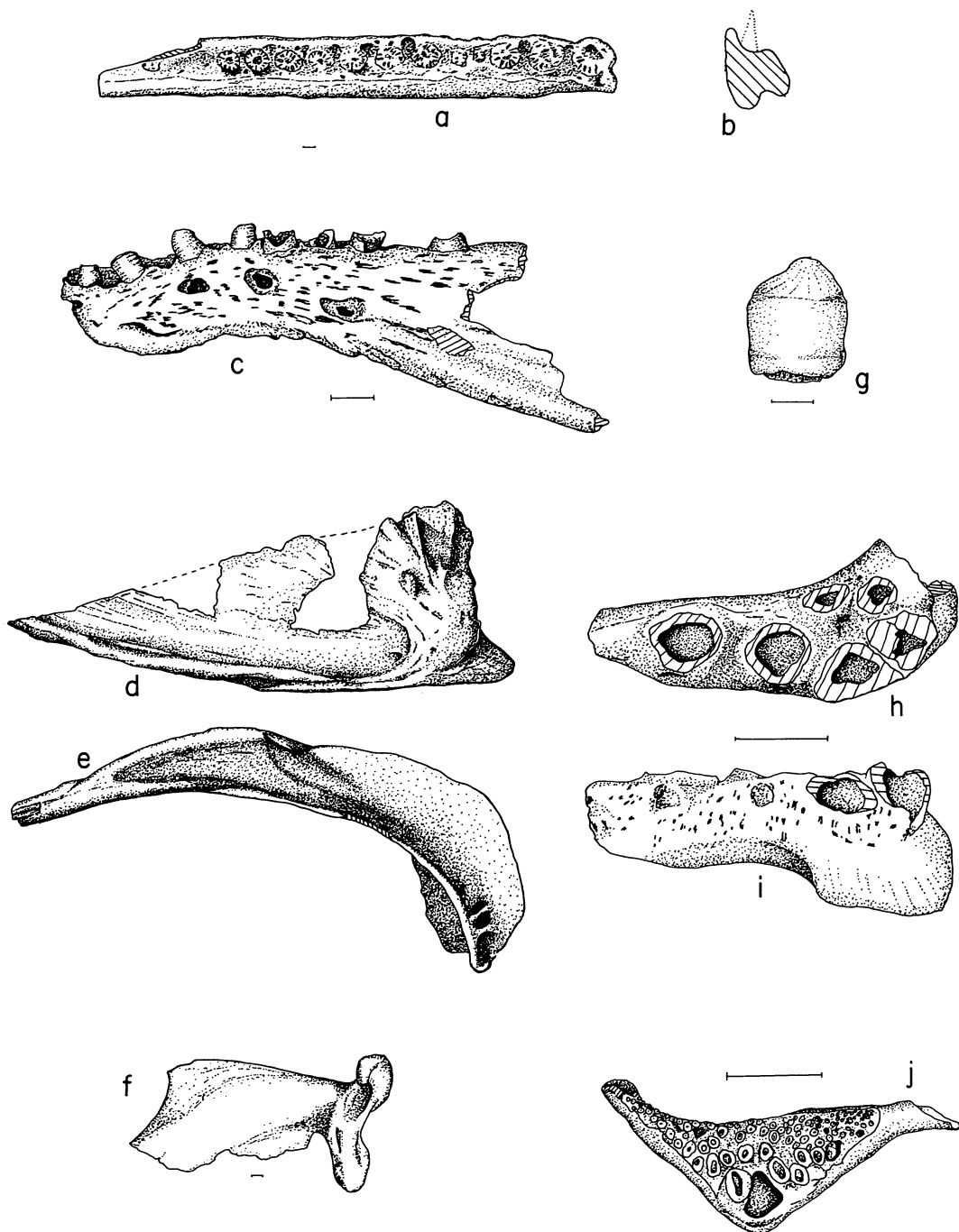
A single tooth (V55570), 12.8 mm in length and 4.81 mm across the base, is similar in size and type of crown to those of *L. spatula*. The tip of this tooth has a flattened triangular blade with sharp edges extending beyond the width of the round shaft. This specimen may represent a second species of gar from that indicated by the dentary.

The maxillary fragments show the evenly spaced lateral teeth to be approximately one-half the size of the larger, medial ones. The lateral teeth and the maxillary fragments match similar elements in *L. productus* and *L. platostomus*.

In North America the genus *Lepisosteus* has a long fossil record extending from Cretaceous to Recent. Smith (1962) reports the genus from the Lower Pliocene of Nebraska and Oklahoma.

Habit and habitat.—Aquatic. Elements of young indicate a shallow water habitat. Larger forms probably were in deeper water. Gar indicates a large, clear, low-gradient stream.

Family AMIIDAE
AMIA CALVA Linnaeus
Text-fig. 5c



TEXT-FIG. 5.—Various elements of fishes from the WaKeeney local fauna. a, *Lepisosteus* cf. *L. platystomus* or *L. productus*, left dentary, V55569, dorsal view. b, cross section of gar dentary, V55569. c, *Amia calva*, left dentary, V55577. d-e, *Ictiobus* sp., left cleithrum, V55589, posterior and lateral views. f, *Ictiobus* sp., left maxilla, V55591, medial view. g, *Aplodinotus* cf. *A. grunniens*, pharyngeal tooth, V55656, lateral view. h-i, ?*Notropis*, right infrapharyngeal, V55594, dorsal and lateral views. j, *Fundulus* sp., infrapharyngeal, V55626, dorsal view. Lines near each element represent one millimeter.

Amia calva, one of the more abundant larger fishes of the WaKeeney local fauna, is based on the following skeletal elements: three right and two left dentaries (V55574 through V55578); a nearly complete right cleithrum (V55579), a right posttemporal (V55583), a right maxilla (V55580); a left premaxilla (V55585); several scales (V55586); and other elements grouped under V55587.

Comparison of these elements with a large series of Recent *A. calva* shows that a range in variation of the latter will include the differences noted in the fossil form. Variations in the cleithrum include a shelf-like muscle attachment on the lateral side of the horizontal ramus and the absence of a foramen dorsad to the mesial wing in the attachment position of the cartilaginous coracoid. Shape of the fossil cleithrum conforms to Recent elements that were compared.

The five dentaries, on the basis of size, probably represent five different individuals of *Amia calva*. The dentaries lack teeth and the larger ones are somewhat abraded, thus opening the lateral line pores and exposing the deeper main canals (text-fig. 5c). The posttemporal bone and other elements assigned to *Amia* are identical to ones in the Recent skeletons examined.

Habit and habitat.—Aquatic, with both large and small individuals occurring near shore. Indicates a low-gradient, clear stream with abundant aquatic vegetation.

Family CATOSTOMIDAE
ICTIOBUS Rafinesque
Text-fig. 5d-f

A nearly complete left palatine (V55590), a left cleithrum (V55589), a partial left dermosphenotic (V55588), a left maxilla (V55591, text-fig. 5f) and several isolated pharyngeal teeth (V55592) are assigned to the genus *Ictiobus*.

The palatine and maxilla compare most closely with *I. bubalus* (Rafinesque), but definite separation from *I. niger* (Rafinesque) is not possible. The cleithrum (text-fig. 5d-e) fits measurements taken for *I. bubalus* and *I. niger* but cannot be differentiated between these two species. All elements differ sufficiently from *I. cyprinellus* (Valenciennes) to exclude the possibility of this form in the fauna.

The size difference between these four elements indicates at least three individuals, the smallest approximately 300 mm in total length and the largest around 600 mm.

Habit and habitat.—Aquatic; bottom feeder. Probably fed in the shallow quiet water near river margin.

Family CYPRINIDAE
? NOTROPIS Rafinesque
Text-fig. 5h-i

A broken right infrapharyngeal (V55594) with -4, 2 dentition is questionably referred to the genus *Notropis* (text-fig. 5h-i). The medial-ventral portion, size, and arrangement of the teeth compare favorably with *Notropis*.

Habit and habitat.—Aquatic; bottom feeder. Indicates clear water.

Family ICTALURIDAE

Apparently two species of catfish are present in the fauna. A detailed description is not included here. John Lundberg places the following tentative identifications on the ictalurid material (V55595 through V55625 include the ictalurid elements):

ICTALURUS LAMBDA Hubbs & Hibbard

This species was originally described by Hubbs & Hibbard (1951) from the WaKeeney locality, UM-K6-59. Additional material collected in 1966 is being incorporated to include variations in morphology. Lundberg (per. comm.) tentatively places *I. lambda* in synonymy with *I. furcatus* (LeSueur).

Habit and habitat.—Compared with *I. furcatus*: aquatic, deep water form. Indicates a large stream with sandy bottom and considerable current.

ICTALURUS sp

Abundant remains of a second smaller ictalurid were screened from UM-K6-59. They are tentatively assigned to the species *I. natalis* (LeSueur).

Habit and habitat.—Aquatic, shallow water; primarily bottom feeding form. Indicates a low-gradient, profuse vegetation, and a toleration of a clay or silt bottom.

Family CYPRINODONTIDAE
FUNDULUS Lacépède
Text-fig. 5j

Five infrapharyngeals (V55626 and V55627) are distinct enough to allow identification at the generic level. The different size teeth with strongly curved extremities, and the sharply descending ventral keel of the infrapharyngeal appear unique to the *Fundulus* group (text-fig. 5j).

Habit and habitat.—Aquatic; top feeder. Probably near shore among aquatic vegetation.

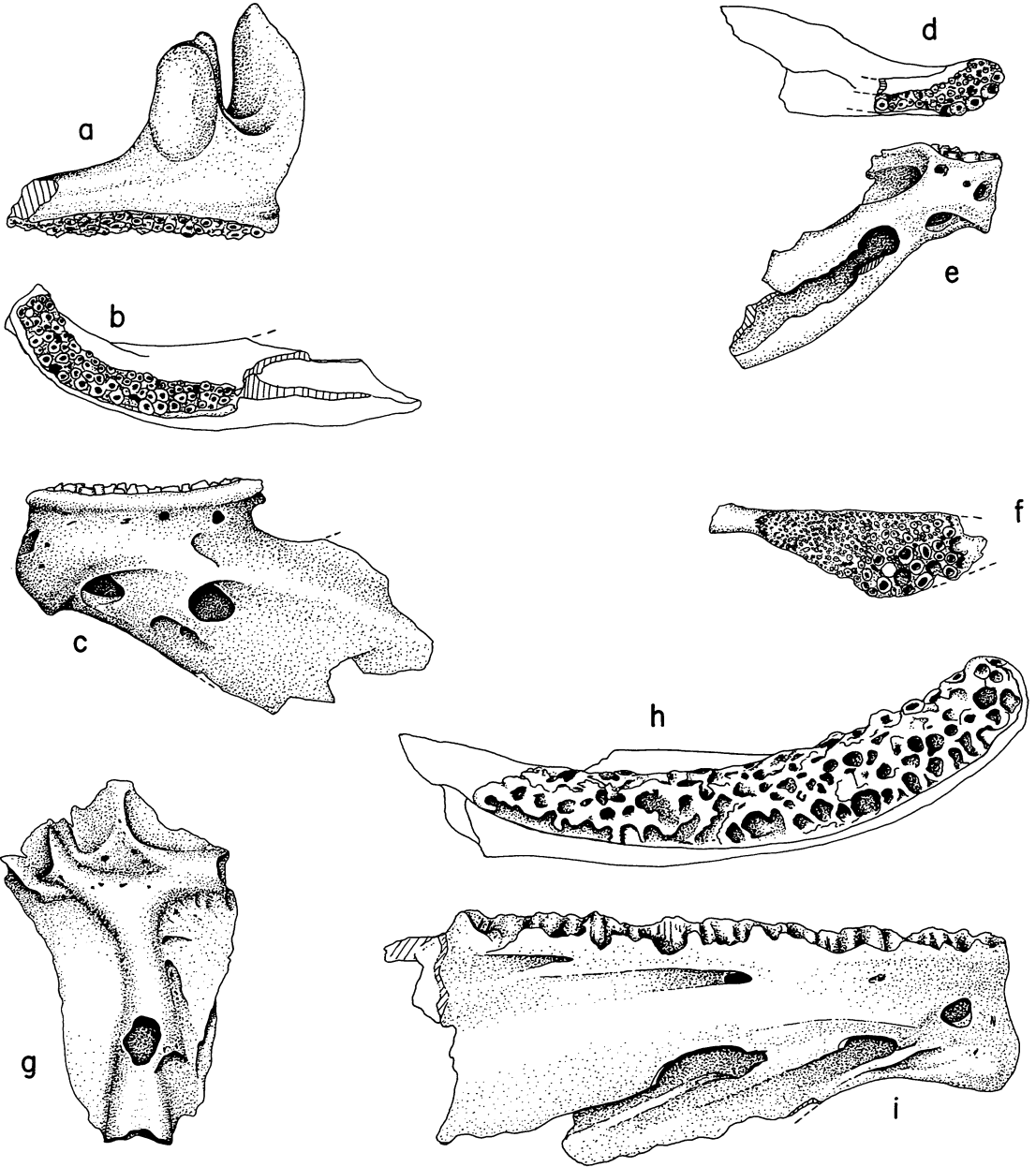
Family CENTRARCHIDAE

The family Centrarchidae, a homogeneous group osteologically, is well represented in the WaKeeney deposit. The fauna contains at least

three different members of this family. The taxonomic assignment is, at best, somewhat artificial because of the extreme variation and possible change in time of this group. The osteological nomenclature follows Dineen & Stokely (1956).

MICROPTERUS cf. *M. PUNCTULATUS*
(Rafinesque)
Text-fig. 6f-i

A frontal (V55628), five dentaries (V55631 through 55635), a premaxilla (V55629), and



TEXT-FIG. 6—Centrarchidae. a-c, *Pomoxis* sp., a, right premaxilla, V55651, lateral view; b-c, left dentary, V55647, dorsal and lateral views. d-e, *Lepomis* sp., right dentary, V55638, dorsal and lateral views. f-i, *Micropterus* cf. *M. punctulatus*; f, infrapharyngeal, V55630, dorsal view; g, right frontal, V55628, dorsal view; h-i, right dentary, V55631, dorsal and lateral views. All specimens drawn to same scale. Line represents one millimeter.

an infrapharyngeal (V55630) are assigned to the genus *Micropterus*. The frontal and infrapharyngeal compare best with those of the extant species *M. punctulatus*.

The dentary (text-fig. 6h-i) assigned to the genus *Micropterus* is distinct by having a widened tooth row at the anterior portion which descends medioventrally to the inner side. This increases the number of tooth bases. The teeth, judging from the size of the bases, are nearly equal in size; they are enlarged slightly at the external margin. In *Chaenobryttus* and *Lepomis* the teeth are greatly enlarged in this area. Curvature of the dentary, positions of the mandibular lateral line openings, relative proportions, and the angle of the inward sloping ventral portion are identical to those of *Micropterus*.

The premaxilla, by exhibiting the extremely wide tooth attachment area at the anterior extreme, is similar to species of *Micropterus*.

A nearly complete right frontal from a young individual (text-fig. 6g) allows comparison at the specific level within the genus *Micropterus*. It measured 7.8 mm anteroposteriorly and 5.1 mm across the widest portion. The relative proportions, curvature of the sensory canal and its openings, and the three posterior keels which connect to the same structures in the parietal, are most similar to those in *M. punctulatus*.

Only one right infrapharyngeal (text-fig. 6d) is assigned to *Micropterus*. The external margin is straight and the teeth at the antero-external margin are minute but increase in size at the middle of the internal margin similar to *M. punctulatus*. The internal shelf of the pharyngeal is very thin and porous and the entire element is quite fragile.

Definite assignment to *M. punctulatus* is not possible owing to the osteological similarity with other species of *Micropterus*, particularly *M. treculi* (Vaillant & Bocourt) and *M. salmoides* (Lacépède). The two elements used in the specific reference were from small individuals with an estimated length of 80 mm. These two elements are fragile and suggest little if any transportation. The two larger dentaries are from individuals estimated at 140 and 190 mm. It is also possible that both *M. punctulatus* and another bass such as *M. salmoides* were in the fauna.

Habit and habitat.—Aquatic. Probably an active predator covering many stream habitats from near shore to deep water. *M. punctulatus* prefers large streams with low gradients and deep pools.

Five dentaries (V55636 through V55638),

LEPOMIS Rafinesque
Text-fig. 6d-e

five infrapharyngeals (V55639 through V55643), a suprapharyngeal (V55644), and two premaxillae (V55645 and V55646) are assigned to the genus *Lepomis*. These elements define a rather short-jawed form of this genus with pharyngeals of moderate width and blunt teeth.

The dentary (text-fig. 6d-e) is distinctly of the *Lepomis* type with sockets for five enlarged anteromarginal teeth and an extreme ventral projection to the ventral portion of the dentary. The two anterior openings of the sensory canal are nearly equidistant from the symphysis.

The larger infrapharyngeals, if correctly associated with the dentaries assigned to *Lepomis*, represent a form approximately 200 mm in standard length. They are characterized by a straight external border, slight horizontal curvature, moderate width, and teeth variable in size ranging from the smaller external ones to the largest at the medial edge near the area of greatest width. The pharyngeals (text-fig. 6j) are similar to those of *L. macrochirus* Rafinesque, *L. auritus* (Linnaeus), *L. punctatus* (Valenciennes) and *L. megalotis* (Rafinesque). However, it is quite possible that more than one form is present.

Habit and habitat.—Aquatic. Probably was a quiet, shallow water form.

POMOXIS Rafinesque
Text-fig. 6a-c

The genus *Pomoxis* is assigned from 6 dentaries (V55647 through V55650), and four premaxillae (V55651 through V55654).

The largest dentary (text-fig. 6b-c) is 8.62 mm long and 2.72 mm deep at the anterior border. The tooth row is narrow and the jaw is extremely curved as is typical of *Pomoxis*. The nearly uniform teeth are small with slightly larger ones at the antero-buccal margin. The teeth are set on a shelf which is wider than the dentary directly beneath.

A large right premaxilla (V55651, text-fig. 6a) assigned to this genus is 4.8 mm wide at the anterior margin. The premaxillary teeth are uniform and set on a distinct shelf. The medial ascending process is flared anteromedially and the straight medial ascending process contains a large oval condyle for articulation of the maxilla.

Other bones of this form in the fauna cannot be differentiated from the other Centrarchidae with certainty. The dentaries and premaxillae used in the generic assignment cannot be distinguished from or assigned to either of the two living forms or the extinct form *P. lanei* Hibbard (1936).

Habit and habitat.—Aquatic. Probably tolerated a variety of available habitats from deep to shallow water.

cf. Family SCIAENIDAE

APLODINOTUS cf. A. GRUNNIENS Rafinesque
Text-fig. 5g

A single pharyngeal tooth (V55656) was recovered and compared with genera characterized by massive barrel-shaped pharyngeal teeth (text-fig. 5g). It is identical to those on the arches of *Aplodinotus*. The cylindrical shape with a slight broadening of the base and the blunt off-center crown seem typical of drums.

Habit and habitat.—Aquatic; bottom feeder. Probably fed exclusively in the deep river pools.

Class AMPHIBIA

Family AMBYSTOMIDAE

AMBYSTOMA Tschudi
Form A

The smaller of two ambystomatids in the fauna is assigned on six trunk and cervical vertebrae (V55657 through V55660). These vertebrae have a large circular neural canal, the transverse processes (= parapophyses and diapophyses) are short and nearly separate, with the pre- and postzygapophyses horizontal and extended beyond the margin of the centrum.

Form B

Six larger, laterally compressed caudal and trunk vertebrae (V55661 through V55667) are also placed in the Ambystomidae. Distinct from Form A, these vertebrae show a definite webbing on the ventral surface of the centrum at the connection of the parapophyses. The centrum is open, indicating the persistence of a notochord. As in extant neotenic ambystomatids, the caudal vertebrae have a double neural process directed posteriad with a thin hemal arch. The relatively long transverse processes are directed posterolaterally about 60° from the axes of the vertebrae. Lengths of centra of the three complete trunk vertebrae range from 3.0 to 3.5 mm with the widths of the anterior centra between 1.4 and 1.6 mm.

There are two possible explanations for the presence of these two forms in the fauna. First, by using a direct comparison with the present day situation in the species *A. tigrinum* (Green), a neotenic and terrestrial form of the same species were deposited at this site. This would infer that Form A is the terrestrial equivalent of Form B. The morphological differences between the two fossil forms and the

two different living forms of *A. tigrinum* appear to parallel one another. Secondly, the possibility that two species of ambystomatids are present must not be ruled out.

Habit and habitat(s).—Semi-aquatic, fossorial, shallow water or near-stream forms. May bridge two major habitats, the fully aquatic and semi-aquatic.

Family PELOBATIDAE

SCAPHIOPUS COUCHI Baird

Text-fig. 7f, o, p, s-v

The identification of this species is based on three partial maxillae (V55390, V55391 and V55395), six frontoparietal fragments (V55399 through V55404), two sacrococcyges (V55397 and V55398), a nearly complete right otic capsule (V55396), and nine left and six right ilia (V55392, V55393 and V55394).

The six frontoparietals are broken near the foramen for the occipital artery but retain the anterior suture in the nasal region. One frontoparietal (V55399, Text-fig. 7u) has extensive dermal ornamentation extending to the midline of the roofing bones. The dermal encrustation is high (nearly twice the thickness of the underlying bone) and in the form of vermiculate ridges running to the medial half of the element. The other frontoparietals differ only in the degree of dermal encrustation in the medial region. In Recent specimens the dermal encrustation appears to vary ontogenetically with the older individuals having greater ornamentation near the center of the frontoparietal.

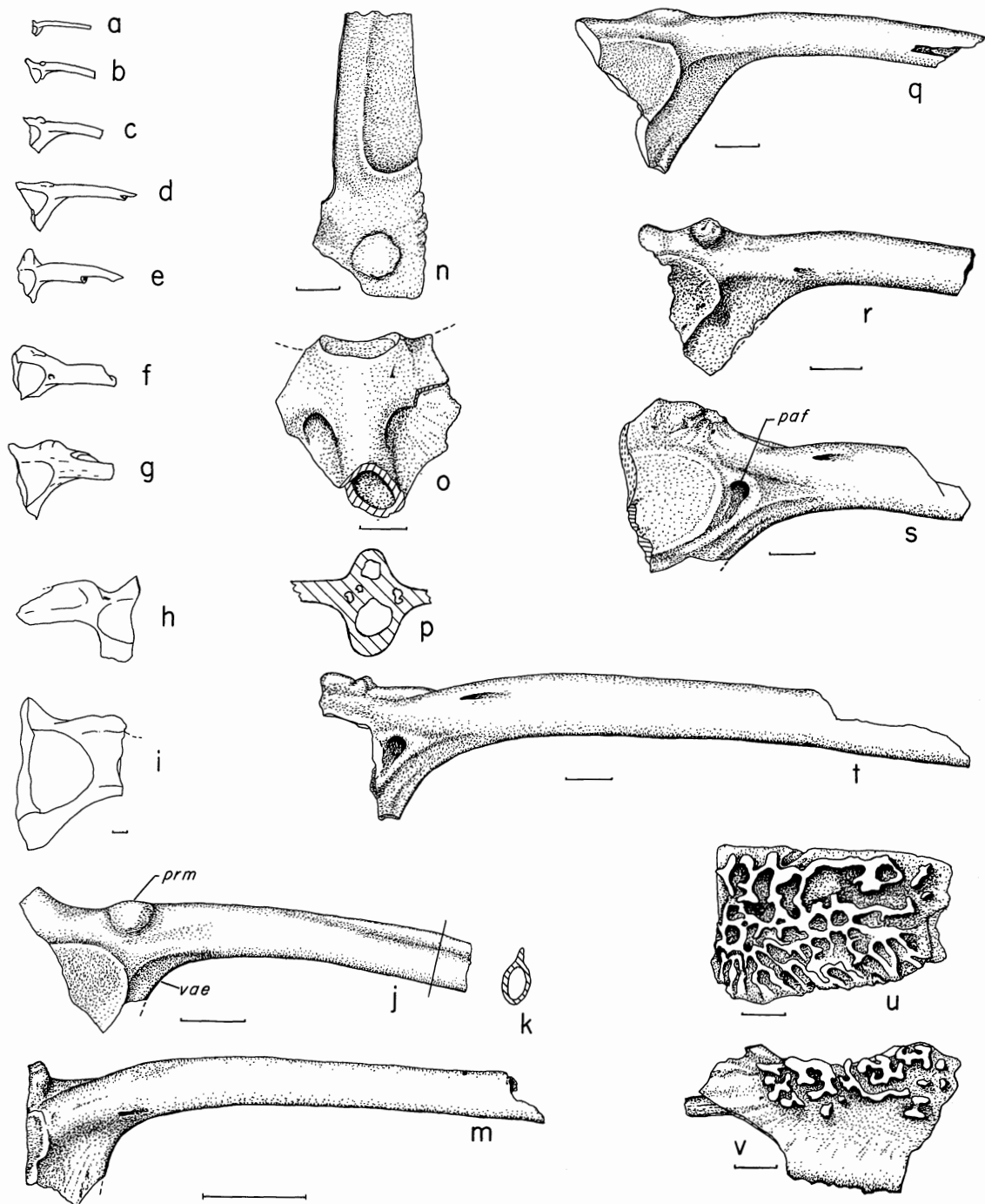
The maxillary fragments are identical to comparable regions in *Scaphiopus couchi*. The larger of these specimens (V55390, text-fig. 7v) is heavily encrusted with dermal ornamentation while the other two maxillae show lesser amounts relative to size.

The otic capsule, while generally indistinguishable from other pelobatids, does show the small (? prootic) foramen characteristic of the subgenus *Scaphiopus* (Kluge, 1966).

The two partial sacrococcyges are similar to those of *S. couchi*, exhibiting complete fusion, dorsal sculpturing, a low dermal keel, and the single lateral nerve opening (text-fig. 70-p).

The referred ilia are identical to *S. couchi* (text-fig. 7s-t). The area of the gluteus muscle attachment is round and distinct rising from the supra-acetabular expansion at a point even with the anterior border of the acetabular fossa. The subacetabular expansion is moderate as in *S. couchi*. All ilia possess a large preacetabular foramen (paf, text-fig. 7s).

Although most of the elements are similar to those found in *S. holbrooki* (Harlan), on



TEXT-FIG. 7.—a-i. Outlines of the various anuran ilia from UM-K6-59 drawn to scale for size comparison. a, *Pseudacris* cf. *P. clarki*, V55414. b, *Acris* sp., V55407. c, *Hyla* cf. *H. gratiosa*, V55410. d, *Hyla* cf. *H. cinerea* or *versicolor*, V55408. e, *Bufo pliocompactilis*, V55433. f, *Scaphiopus couchi*, V55393. g, *Bufo boreas*, V55416. h, *Rana* sp., V55438. i, *Bufo marinus*, V55424. j-k, *Acris* sp., right ilium and cross section of shaft, V55407 (vae = ventral acetabular expansion, prm = prominence.) m, *Pseudacris* cf. *P. clarki*, right ilium V55414, lateral view. n, *Rana* cf. *R. areolata*, right frontoparietal, V55435, ventral view. o-p, *Scaphiopus couchi*, sacrococcyx, V55397, ventral and posterior cross section views. q, *Hyla* cf. *H. cinerea* or *versicolor*, right ilium, V55408, lateral view. r, *Hyla* cf. *H. gratiosa*, right ilium, V55410, lateral view. s-t, *Scaphiopus couchi*, right ilia, V55393 and V55394, lateral views (paf = preacetabular foramen). u, *S. couchi*, right frontoparietal, V55399, dorsal view. v, *S. couchi*, maxilla fragment, V55390, lateral view. All lines represent one millimeter.

the basis of the frontoparietal width and shape (*S. holbrooki* with wider frontoparietal), the specimens are assigned to *S. couchi*. However, the similarity between these two species should not exclude the possibility of the fossil specimens representing an intermediate form or a variation of the species *S. holbrooki*. On the basis of smaller size, greater width of the subacetabular expansion, type of dermal encrustation on the skull bones, and other general characteristics of the ilia (text-fig. 7f), it is most certain that the fossils from this locality are not *Scaphiopus wardorum* Estes & Tihen (1964).

Zweifel (1956) described *S. alexanderi* from the Lower Pliocene Esmeralda Formation in Nevada. Since the anterior portion of the skull of *S. alexanderi* was not recovered, the degree of dermal ornamentation cannot be determined. However, differences in the sacrococcyges and ilia seem sufficient to reject *S. alexanderi* as a taxonomic possibility for the material from the WaKeeney fauna. More precisely, from a ventral aspect the sacrococcyx of *S. alexanderi* exhibits the double sacral expansion with the included nerve foramina being nearly equal. In *S. couchi* the more anterior vertebra is the dominant bridge to the sacral expansion. Tihen (1960) explains this condition on the basis of the first presacral and sacral vertebrae taking part in the formation of the sacrococcyx. The ilium of *S. alexanderi* differs from the ilia of *S. couchi* by the absence of a preacetabular foramen and ridges on the ventral slope of the acetabular fossa. Tihen (1960) places *S. alexanderi* in the *Spea* subgroup (subgenus of authors).

Taylor (1942) described two pelobatid frogs from the Upper Pliocene of Kansas, namely the new genus *Neoscaphiopus* for the species *N. noblei* and *Scaphiopus diversus*. Tihen (1960) considered *Neoscaphiopus* a synonym of *Spea* and *Scaphiopus diversus* a synonym of *Neoscaphiopus noblei*, and both close to *Scaphiopus (Spea) bomifrons*. Tihen considers *S. studei* Taylor (1938) and *S. antiquus* Taylor (1941) (= *S. pliobatrachus*) as belonging to the *Spea* group.

From the osteological differences noted by Zweifel (1956) and Kluge (1966), the *Spea* and *Scaphiopus* subgenera or subgroups are distinct. The specimens from the WaKeeney locality represent a member of the subgenus *Scaphiopus*. Kluge suggests that his Lower Miocene species *Scaphiopus neuter* might represent the point of divergence of the two subgenera from the early pelobatid stock. The fossil occurrence of *S. couchi* referable to the

Scaphiopus subgenus shows that the two lineages were distinct in the Lower Pliocene.

Habit and habitat.—Semi-aquatic, but primarily terrestrial. Fossorial. Fossil characteristics would indicate a near-shore burrowing habitat either within the bordering forest or nearby savanna.

Family HYLIDAE
ACRIS Dumeril & Bibron
Text-fig. 7b, j-k

Holman (1962) and Chantell (1964) have listed several ilial characteristics that allow separation of the genus *Acris* from the various anuran forms in the fauna. On the basis of their criteria, and comparison with extant species, 20 left and 23 right ilia (V55405 through V55407) from locality UM-K6-59 are assigned to *Acris*.

Each ilium possesses a rounded ventral acetabular expansion (vae, text-fig. 7b, j). The dorsal acetabular expansion is convex at the anterior surface and is directed posteriad and dorsad. The prominence (prm, text-fig. 7j) is a rounded knob-like structure anterior to the anterior margin of the acetabular fossa by at least half the length of the base. A low dorsal crest on the ilial shaft is present on unabraded ilia in which the greater portion of the shaft is preserved (text-fig. 7k).

The small size of these ilia make the range of estimated size somewhat unreliable at the minimal limit. The ilia do, however, suggest a maximum size of less than 30 mm.

Skeletal comparisons were made between the two Recent species of *Acris* but separation on the ilial characteristics alone appears hazardous. Holman (1964) noted a tendency for the ventral acetabular expansion to be more pointed in *A. crepitans* Baird than in *A. gryllus* (Le Conte), but this characteristic does not seem to hold for the ontogenetic and geographic series examined. Many hylid fossil remains have been reported from the Great Plains. Chantell (1966, p. 259), summarizing these discoveries, lists additional criteria for separating the two species, but until more complete osteological material is available reference is made only to the genus *Acris*.

Habit and habitat.—Semi-aquatic and near permanent water; in this case a stream. Aquatic and near shore vegetation indicated.

PSEUDACRIS cf. P. CLARKI (Baird)
Text-fig. 7a, m

A single right ilium (V55414, text-fig. 7a, m) missing the anterior portion of the shaft is assigned to *Pseudacris*. The broken free edge appears straight and the anterior margin of

the prominence is nearly even with the anterior margin of the acetabular fossa. The prominence is high and straight, rising from a slight keel. From Chantell's (1966) report, and examination of Recent skeletons, this single ilium falls within criteria listed for *Pseudacris*. The relatively wide ventral acetabular expansion and small size seem to place it near *P. clarki*.

Habit and habitat.—Semi-aquatic but with greater portion of life terrestrial. Abundance and specimen characteristics indicate a form which inhabited the savanna or grassland.

Hyla cf. *H. gratiosa* Le Conte
Text-fig. 7c, r

The more abundant of two large hylids in the fauna is compared with *H. gratiosa* from 15 right and seven left ilia (V55410, V55412 and V55413) and a nearly complete femur (V55411). The ilia are distinguished from those of the other hylid in the fauna by a stout shaft of subrectangular cross section and a foramen on the lateral side of the shaft directly above the connection of the ventral acetabular expansion (text-fig. 7c, r). In addition, the ventral acetabular expansion is very wide anterior to the acetabular fossa and the round knob-like ilial prominence is directed dorsad and laterad. The ilia represent individual body sizes between 35 and 50 mm.

Among the Recent *Hyla* compared, the morphology of *H. gratiosa* as reflected through the ilia compare closely with the fossil ones referred to this species. In general *H. gratiosa* approaches the osteological configuration of certain bufonids.

If correctly associated the femur is morphologically identical to that of *H. gratiosa*. It is only slightly curved and more massive than in the other species of *Hyla* examined.

Habit and habitat.—Semi-aquatic, near shore, fossorial and arboreal. Indicates trees and suitable substrate for burrowing.

Hyla cf. *H. cinerea* (Schneider)
or *H. versicolor* Le Conte
Text-fig. 7d, q

Two ilia, a right (V55408) and a left (V55409), are tentatively assigned to *H. cinerea* or *H. versicolor*. The right ilium is estimated to have come from an individual approximately 48 mm in body length (text-fig. 7d, q).

This form is delineated from the other hylid in the fauna by a more slender rounded shaft, a low smooth ilial protuberance, and the absence of a lateral foramen on the ilial shaft. The ilia are much more delicate than

those referred to *H. gratiosa* from locality UM-K6-59.

The ventral acetabular expansion is wide, a characteristic of *Hyla*. The concave anterior margin of the ventral acetabular expansion has a nearly straight border.

Habit and habitat.—Semi-aquatic, near shore, arboreal. By morphology and abundance a more arboreal hylid is represented along with *H. cf. gratiosa*.

Family BUFONIDAE

In the bufonids the taxonomic assignment of species is based on the frontoparietal. It is within the bufonids that this skull element is morphologically distinct and provides characters necessary for specific placement. Skull and ilial terminology as given by Sanders (1953) and Tihen (1962B).

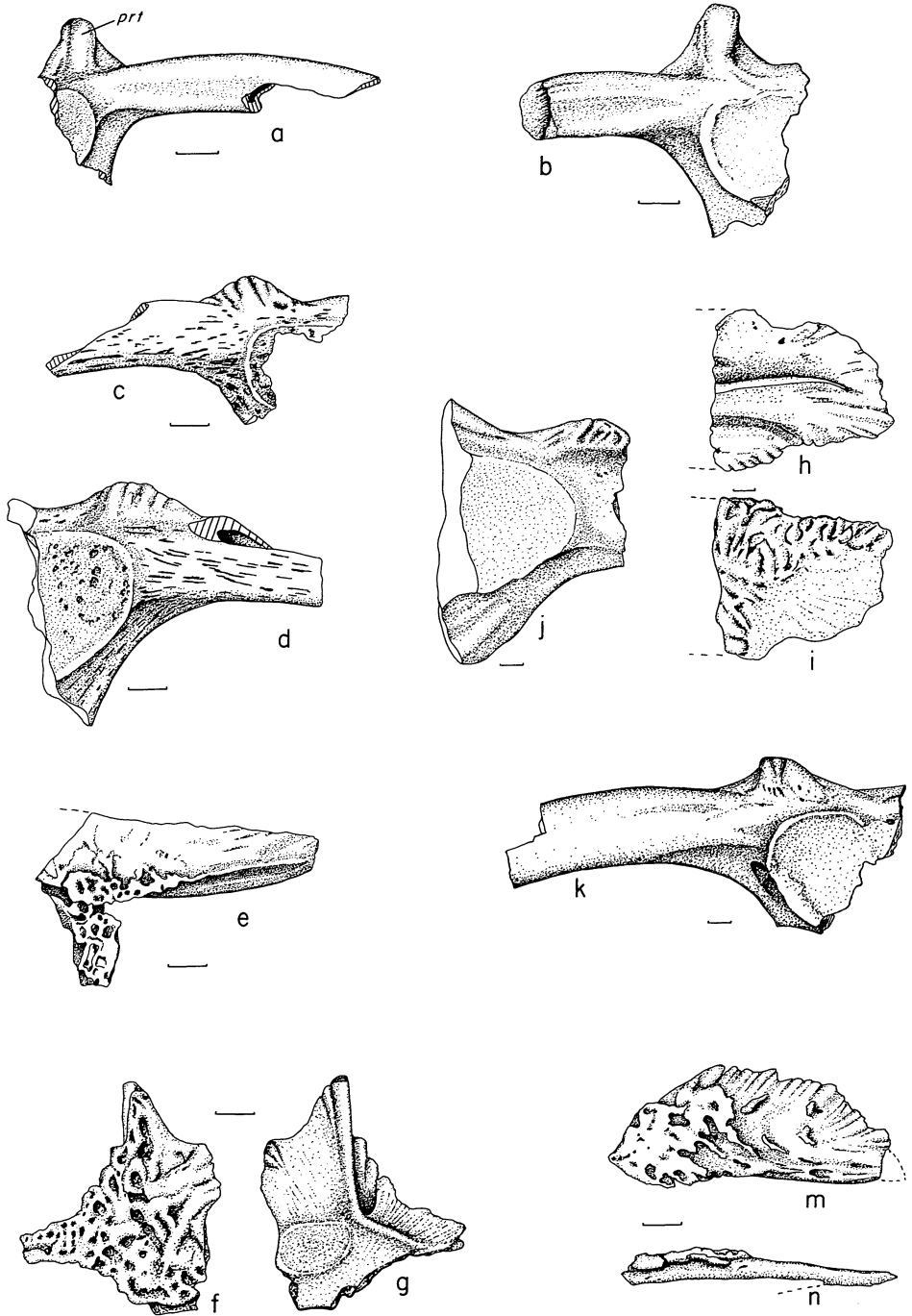
BUFO BOREAS Baird & Girard
Text-figs. 7g, 8c-d, m-n

A single right frontoparietal (V55415), 7.02 mm long and 3.05 mm wide, and six left and three right ilia (V55416 through V55420) are assigned to the extant form *Bufo boreas*.

The frontoparietal thins towards the medial edge and, if it was fused with the opposite frontoparietal, only in the posterior region. The low dermal encrustation (text-fig. 8m-n) is most pronounced posteriad but decreases and terminates toward the anterior half of this element. The dermal deposits form a partial shelf over the canal for the occipital artery. No shelf is developed over the orbital region although the thickest portion of the frontoparietal is directly above the perpendicular laminae.

The ilia (text-fig. 7g, 8c-d) are characterized by a low but variable prominence ranging from 12% to 20% of the base width; a highly curved shaft; a dermally striated appearance to the bone, and a smooth high region on the dorsal portion of the shaft anterior to the acetabular fossa. The ventral expansion is approximately perpendicular to the shaft. The anterior angle ranges from 16° to 28° and the posterior one from 15° to 22°. In four of these specimens the anterior angle is greatest. Variation in seven Recent skeletons of *B. boreas* of variable sizes shows the height of prominence ranging between 12% of the base for the smallest and 19% in the larger forms.

The frontoparietal also appears to vary in the Recent forms of *B. boreas* examined. Dermal encrustation is present on some of the mature adults but absent in others. Although the frontoparietals are independent in *B. boreas* the degree of separation is variable. Further-



TEXT-FIG. 8—a-b, *Bufo pliocompactilis*, right and left ilia, V55433 and V55432, lateral views (prt = protuberance). c-d, *B. boreas*, ilia from young and adult, V55420 and V55416, lateral views. e, *B. cognatus*, right frontoparietal, V55441. f-g, *B. pliocompactilis*, holotype, frontoparietal. V55430, dorsal and ventral views. h-i, *B. marinus*, frontoparietal, V55423, ventral and dorsal views. j-k, *B. marinus*, right and left ilia, V55424 and V55425, lateral views. m-n, *B. boreas*, right frontoparietal, V55415, dorsal and lateral views. All lines represent one millimeter.

more, the skull of *B. boreas* and the fossil frontoparietal are similar in having an open canal for the dorsal occipital artery, a frontoparietal with no supraoccipital crest or shelf, and a relatively narrow interorbital region with the width remaining nearly constant from anterior to posterior.

Only *B. boreas* of the Recent New World bufonids examined has a frontoparietal similar to the fossil one assigned to this species. However, the Old World species *B. viridis* and *B. calamita* have many similarities and in fact are nearly indistinguishable osteologically from *B. boreas*. The following similarities in dorsal skull characteristics were noted in comparison of *B. viridis* with *B. boreas*: occipital canal open, frontoparietals relatively smooth and not projecting over the orbit, and other similarities listed by Tihen (1962A) as characteristic of the New World and Old World groups. Furthermore, the skull and body proportions; positions and shape of the skull elements; and the striated appearance of the bone surface, especially in the younger individuals, are similar in the two species. The ilia of *B. boreas* and *B. viridis* have low dorsal crests on the shaft, the prominence is low but variable, the shaft is curved, the ventral acetabular expansion is nearly perpendicular to the shaft, and the acetabular fossa is relatively deep. Characteristics of the other skeletal elements appear to overlap in the two groups. For example, the range of measurements taken on the ilia of *B. boreas* are within the range Tihen (1962A & B) gives for the Old World group, and which were determined from three Recent specimens at the University of Michigan.

One difference between the Old World and New World forms appears to be the fusion of the prootic with the frontoparietal in the latter group (Tihen, 1962B). In *B. calamita* a definite fusion is noted while in adults of *B. viridis* an incomplete fusion is evidenced by the strong suture line and slight separation of the two elements. Fusion seems to be present in some adult *B. boreas* but appears variable between individuals.

Other elements assigned to *B. boreas* include an ilial shaft with a slight ridge developed along the dorsomedial margin, two coccyges (under V55419) showing the characteristic striations, and perhaps the double dorsal keel characteristic of the *calamita* and *boreas* groups. A striking characteristic of all specimens assigned to *B. boreas* from the WaKeeney locality is their deeply striated surface.

It is possible that Tihen's *B. alienus* and *B. suspectus* (the former not examined) were members of the group which is today represented by

B. boreas. From the fossil frontoparietal characterized by a moderate amount of dermal encrustation, the assignment of this element to *B. boreas* seems to be more logical at present. With the variation noted in ilia of Recent *B. boreas* definite placement of *B. alienus* and *B. suspectus* on these elements into a *boreas* stock is not warranted.

Blair (1964) in a series of crosses between the living *B. boreas* group and members of various Old and New World bufonids attempted to clarify the phylogenetic relationships of the former group. Although the relative value of such an experiment remains doubtful, the fossil evidence does support the distinctness of the groups by indicating a long separation between the Old and New World forms.

Habit and habitat.—Semi-aquatic, primarily terrestrial. The extant species occupies many different vegetational zones ranging from grassland to forests. Within the fauna a marginal ecological position is indicated, perhaps bordering the savanna or forest.

BUFO COGNATUS Say
Text-fig. 8e)

A nearly complete right frontoparietal (V55441, text-fig. 8e) is assigned to *B. cognatus*. This distinctive element has the supraorbital crest converging obliquely toward the anteromedial area of the frontoparietal. The groove for the occipital artery is only partially covered by the dermal encrustation.

The relatively small size of the frontoparietal and partially open groove suggest a young individual. The width, including the temporal plate, is 4.33 mm, length, 6.93 mm, indicating a body size of approximately 50 mm.

A left ilium (V55421) conforms to measurements given by Tihen (1962B, p. 28) for those of *B. cognatus*. The height of the ilial prominence of the fossil ilium is 40% of the basal length. The anterior angle at 45° is greater than the posterior one at 40°.

Habit and habitat.—Semi-aquatic, primarily terrestrial, fossorial. Distal to the deposition site. Indicates grassland.

BUFO MARINUS (Linnaeus)
Text-figs. 7i, 8h-k

A right frontoparietal (V55423), a temporal plate (V55426), the distal portion of a right ilium (V55424, text-figs. 7i, 8j), a left ilium (V55425, text-fig. 8k), and two nasal fragments (V55427 and V55428) are referred to the extant species *B. marinus*.

The partial frontoparietal (text-fig. 8h-i) consists of the anterior half that forms the supraorbital shelf. It is broken approximately at

the supra- and postorbital junction. This element has a linear rugose dermal ornamentation which decreases medially from the lateral margins. The lateral crest rises at about a 20° angle from the lower material frontoparietal area. The frontoparietal is broad as in *B. marinus*.

Ventral aspects of the frontoparietal are morphologically identical to the Recent specimens of *B. marinus* that were examined. The slope of the ventral supraorbital shelf, the presence of a groove for the occipital artery at the margin of the inward sloping frontoparietal laminae, terminating at the lateral margin of the occipital crest, and the extreme width of the orbital shelf are characteristic of the fossil element and of *B. marinus*. The fossil frontoparietal and those in *B. marinus* appear identical in size and shape.

Separation of *B. marinus* and *B. valliceps* Wiegmann is based on the frontoparietal, particularly by the absence of a definite supraorbital crest and instead a dorsal outward slope in this region in the former. In *B. valliceps* the ventral surface of the supraorbital area has no pronounced occipital groove as noted in *B. marinus*. The fossil frontoparietal has a greater width than comparable-sized individuals of *B. alvarius* Girard, and is more massive and with less slope to the supraoccipital crest. Dermal encrustation is only slightly developed in the medial region of the fossil element whereas in specimens of *B. alvarius* the ornamentation is well developed toward the center of the skull. However, ventrally the fossil specimen and the frontoparietal of *B. alvarius* are similar except the occipital groove in *B. marinus* trends more dorsad and laterad from the laminae than in *B. alvarius*.

Although the number of specimens do not permit determination of a size range they do indicate a body length of approximately 110 mm.

Tihen (1962B) suggests that *B. marinus horribilis* is a relatively late arrival in North America from an origin in South America. The presence of *B. marinus* in the Lower Pliocene of Kansas indicates an earlier distribution from South America with subsequent range change, or possible origin of this form in North or Central America with dispersal into South America before or after the Lower Pliocene.

Habit and habitat.—Semi-aquatic, primarily terrestrial. Specimens indicate a form living some distance from the deposition site. This form might have traversed several of the different terrestrial habitats.

BUFO PLIOCOMPACTILIS n. sp.

Text figs. 7e, 8a-b, f-g

Holotype.—V55430, a nearly complete left frontoparietal.

Paratype.—A nearly complete left frontoparietal (V55431).

Referred material.—Fifteen left and nine right ilia (under V55432, V55433 and V55434).

Type locality and age.—UM-K6-59. Ogallala Formation, Lower Pliocene.

Diagnosis.—The frontoparietal of the holotype is 4.72 mm long and 3.71 mm in greatest width (text-fig. 8f-g). The holotype and referred specimens represent a small bufonid with a body length ranging from approximately 25 to 40 mm, about half the size of the extant species *Bufo compactilis* Wiegmann. The two frontoparietals show the supra- and postorbital ridges to be absent, with the dermal encrustation greatest toward the lateral border. The orbital shelf has its greatest overlap at the posterior corner of the orbit and in this area covers the anterior opening to the occipital canal. The frontoparietals are incomplete medially and anteriorly, thus apparently joined only in the posterior half of the cranium. Ventrally the frontoparietal includes an oval depression surrounded by a low ridge where a portion of the prootic attached to these roofing bones. The perpendicular laminae of both frontoparietals define the shape of the supra- and postoccipital area and form an angle of about 120°.

Description.—The ilia (text-figs. 7e, 8a-b) referred to *Bufo pliocompactilis* are characterized by an anterior angle of from 35 to 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 percent with some of this variation probably a result of stream abrasion.

Discussion.—The specimens assigned to *Bufo pliocompactilis* show many similarities to those of *B. compactilis* but can be distinguished by the smaller but more massive frontoparietal and the greater amount of dermal encrustation. The shape of the frontoparietal is generally similar in *B. pliocompactilis* and *B. compactilis*. Position of the occipital foramen, width of the occipital shelf, and position of prootic laminae indicate affinities to *B. compactilis*.

Except for size and height of prominence the ilia are nearly identical to those of the larger extant species *Bufo compactilis*. The presence of a small preacetabular foramen, depth of acetabular fossa, the ventral acetabular expansion, and the curvature and shape of the ilia remain similar in the two groups.

Comparison of the fossil specimens of *Bufo pliocompactilis* with other extant bufonid and

pelobatid species suggest no positive affinities to these groups, but two fossil forms do warrant some discussion. Tihen (1962B), in describing *B. spongifrons* from the Middle Pliocene Long Island locality in Kansas, refers three ilia (USNM 22236) to this form, based on a frontoparietal holotype. The frontoparietal of *B. spongifrons* differs from the holotype of *B. pliocompactilis* by the kind of dermal encrustation and relative massiveness. However, Tihen (*op. cit.*) noted the similarity of ilia referred to *B. spongifrons* to those of *B. compactilis*. It is possible that *B. compactilis* or *B. pliocompactilis* was present in the fauna he described. A second form, *B. valentinensis* (Estes & Tihen, 1964) was examined and the difference in dermal encrustation and size serve to distinguish it from *B. pliocompactilis*.

Judging from the geographic area and osteological similarities, *Bufo pliocompactilis* could represent an intermediate species between *B. spongifrons*, *B. valentinensis*, and the living species *B. compactilis*.

Habit and habitat.—Semi-aquatic, near shore, fossorial toad. The specimens would indicate that this vertebrate was a small, fossorial, woodland or forest toad.

Family RANIDAE

RANA cf. *R. AREOLATA* Baird & Girard
Text-fig. 7n

Two nearly complete frontoparietals, a right (V55435, text-fig. 7n) and a left (V55436), compare favorably with those of *Rana areolata*. On the ventral side of these elements a sculptured out area occupied by the forebrain is similar to that of *R. areolata*. The distance from the forebrain to the otic capsule connection which forms a low oval projection, is approximately a third the distance to the anterior edge of the frontoparietal. In those species examined with a noticeable indentation for the forebrain only *R. areolata* appears to have the extreme anterior placement. *R. pipiens* Schreber and *R. clamitans* Latreille have the indentation but it remains more posterior and near the margin of the supraorbital and postorbital junction.

Habit and habitat.—Semi-aquatic, fossorial. Close to the moist river margin or upland.

RANA sp.
Text-fig. 7h

Forty-three left and 38 right ilia (under V55437 and V55438) provide an estimate of abundance of the ranids in the fauna. On the basis of these ilia the body length of individuals would range from approximately 30 to 80 mm. The ilia appear to differ sufficiently in certain characteristics, thus suggesting at least the presence of a second ranid (text-fig. 7h).

Class REPTILIA Order CHELONIA

Within this group the assignment of each form is based on the fragmental material from the main screening site (UM-K6-59) and the floodplain deposits directly above and below it. Because of the isolated and incomplete remains a specific level of identification is not warranted or possible. Carapace terminology is from Lovridge & Williams (1957).

Family KINOSTERNIDAE KINOSTERNON Spix

Two peripherals (V55668) compare favorably with the genus *Kinosternon*. The thick strongly curved margin, the presence of a ridge on the dorsal surface, and size seem to restrict these fragments to this group.

Habit and habitat.—Semi-aquatic, probably often near depositional site.

Family TESTUDINIDAE PSEUDEMYS Gray

Several large shell fragments (V55669 and V56159) from the floodplain deposits above and below the main site, UM-K6-59, compare most closely with the large members of this genus. In nearly every case the bony elements are stream abraded indicating considerable transportation. This form seems to be distinct from the *Chrysemys* in the fauna by the much larger size.

Habit and habitat.—Semi-aquatic, near site but probably transgressed many habitats.

cf. CHRYSSEMYS Gray

Chrysemys is assigned on the basis of a nuchal bone (V55670) and two fragmentary peripherals (V55671). The nuchal is not readily comparable with the extant species *C. picta* (Schneider), but does match this genus most closely.

Habit and habitat.—Semi-aquatic. Primarily aquatic, near bank in shallow water. Indicates existence of profuse aquatic vegetation, little current and muddy bottom.

Family TRIONYCHIDAE TRIONYX Geoffrey St. Hilaire

A single medial pleural bone (V55672) was recovered and assigned to this group. It shows the dermal ornamentation and wide rib extension typical of the softshell turtle.

Habit and habitat.—Semi-aquatic, primarily aquatic. Distal to site but probably moved from deeper water to near shore on occasion.

Order SQUAMATA
 Suborder LACERTILIA
 Family ANGUINIDAE
*GERRHONOTUS MUNGERORUM*¹ n. sp.
 Text-fig. 9e

Holotype.—A frontal (V55674) complete except for small fragments missing from the postero-lateral extremities.

Type locality and age.—UM-K6-59. Ogallala Formation. Lower Pliocene.

Diagnosis.—A large gerrhonotine lizard with massive elongated frontal exhibiting four or possibly six scute areas which are divided generally as in other members of this group; interparietal scute area elevated above adjacent ones; scutellation areas deeply ornamented; frontoparietal scute areas not reaching midline and nearly divided laterally into two separate areas by a ridge or ornamentation; frontal septa separating nasals broad with very little anterior taper; olfactory canal embedded into the antero-ventral portion of frontal; crista cranii massive at base and rounded to surround the olfactory canal.

Description.—The holotype frontal (text-fig. 9e) is 11.25 mm in total length, 3.04 mm across the narrowest supraorbital area, and approximately 6.28 mm wide at the frontal-parietal suture. Estimated snout-vent length of individual is 125 mm. The osteoscuta pattern of the frontal with division of the frontoparietal areas into what appears to be two separate scutes distinguishes this form from other extant species of the genus *Gerrhonotus*.

The wide nearly rectangular frontal septa (0.88 mm at posterior part and 0.5 mm at the anterior, fs of text-fig. 9e) separating the nasals was not observed in any extant species. Although the frontal is much more elongate than in members of *Abronia* it has not reached the slender proportions of the larger species of *Gerrhonotus* such as *G. liocephalus* Weigmann, *G. kingi* (Gray), and *G. multicaudatus* (Blainville). The deep rugose ornamentation appears similar to forms of *Abronia* and certain of the gerrhonotines such as *G. imbricatus* but differs markedly from other members of the group such as *G. kingi*, *G. liocephalus*, and *G. multicaudatus*.

Discussion.—The generic divisions of the gerrhonotine lizards have been modified and rearranged many times (Tihen, 1949; Stebbins, 1958) and at present it is doubtful whether a successful grouping is obtained in the possible

genera *Barisia*, *Gerrhonotus*, *Elgaria*, and *Colytychon*. For the purpose of this report, however, the frontal is assigned to *Gerrhonotus* as used, in a broad sense, to include all members of this general morphological group. The elongated frontal and scute area arrangement should be reason enough to eliminate the possibility of *Abronia*, but certain of the other characters, such as ornamentation, seem more typical of this group. Judging from the diversity of this entire family and especially the genus *Gerrhonotus* (*sensu lato*) a new genus does not seem warranted.

The scutellation pattern would appear criterion enough to separate the WaKeeney species from the extinct California genus *Paragerrhonotus* Estes (1963).

Peltosaurus and *Melanosaurus* from the Lower Tertiary, mid-continental deposits are similar to the modern gerrhonotines (Gilmore, 1928; Tihen, 1949) but apparently differ from them and *Gerrhonotus mungerorum* by the extension of the nasals to the midline of the skull, scute area arrangement and shape of frontals. The heavy sculpture pattern of *G. mungerorum* appears similar to that described for the two older genera and *Paragerrhonotus* (Estes, 1963).

Habit and habitat.—Terrestrial, some distance from depositional site. Probably occupied a variety of habitats from the savanna to grassland.

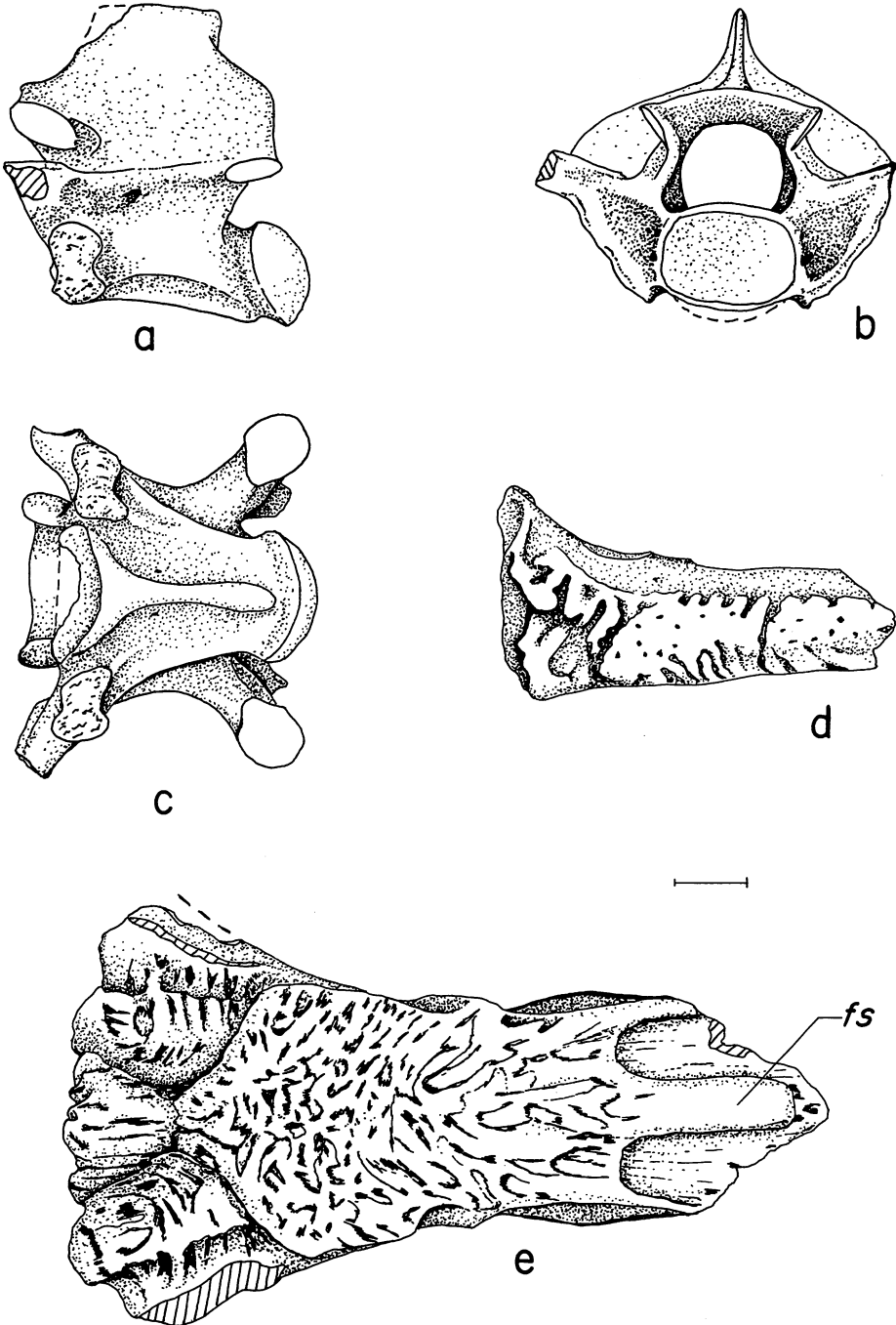
OPHISAURUS VENTRALIS (Linnaeus)
 Text-fig. 9d)

A left frontal (V55675), four nearly complete precaudal and caudal vertebrae (V55676 and V55677), a partial right dentary (V55678) and maxillary fragment (V55679) are assigned to this species.

The complete left frontal is 5.81 mm long, 1.52 mm across narrowest part, and 3.11 mm in width at the frontoparietal suture (text-fig. 9d). The ornamentation is low and restricted to the medial portion. The sutures of the post- and prefrontals nearly meet on the lateral edge of the frontal, being separated by less than 0.5 mm. This condition is identical to *O. ventralis* and *O. compressus* Cope but differs from *O. attenuatus* Baird which has a much wider area of frontal bone forming the supraoccipital region.

The ratio of length of centrum to smallest width of three precaudal vertebrae average 1.35. Using the measurements obtained by Etheridge (1960), the vertebrae would indicate either *O. ventralis* or *O. attenuatus*, the ratios for *O. compressus* being larger than the three taken on the above specimens.

¹ This species is named for Mr. and Mrs. Cecil Munger of Belleville, Kansas, who gave us space to screen and sort the fossiliferous material and allowed us to stay at their ranch.



TEXT-FIG. 9—*a-c*, *Ogmophis kansasensis*, holotype, precaudal vertebra, V55687, lateral, anterior, and ventral views. *d*, *Ophisaurus ventralis*, left frontal, V55675, dorsal view. *e*, *Gerrhonotus mungerorum*, holotype, frontal, V55674, dorsal view. All drawings at same scale. Line represents one millimeter.

The occurrence of *Ophisaurus ventralis* in the Plains fauna during the Lower Pliocene supports Auffenberg's (1955) view that the ancestral form of the North American glass lizards was similar to *O. ventralis*.

Habit and habitat.—Terrestrial, near site of deposition. Fossorial and probably resident of the forest bordering the stream.

Family SCINCIDAE
EUMECES sp.

Elements assigned to this genus include a left and right frontal (V55680 and V55681 respectively), a maxilla (V55682), three dentary fragments (V55683 through V55685), and limb material (V55686).

A specific designation was not attempted because of the osteological similarity between groups examined and being unable to adequately examine a series of each of the 60 or more species under this genus. However, certain inferences can be made concerning this Lower Pliocene form. All elements show little if any transportation, thus suggesting a very close proximity to the site of deposition. All specimens are small, indicating individuals with snout-vent lengths of approximately 90 mm.

Habit and habitat.—Terrestrial, probably arboreal and very near the deposition site.

Suborder SERPENTES

Taxonomic assignment within this group is based on about 100 vertebrae collected from the main quarry, UM-K6-59. The systematic scheme as outlined by Underwood (1967) is used in this section, and osteological terminology will follow Auffenberg (1963).

In each group an attempt is made to define the closest Recent species to the fossil material but a large comparative series was often not available and in some instances not all species of a particular genus were examined. Several vertebrae (under V55720 & V55721) remain unassigned to any of the following categories, and probably represent one or more species aside from the ones identified.

Family BOIDAE

OGMOPHIS KANSASSENSIS n. sp.

Text-fig. 9a-c

Holotype.—V55687. A precaudal vertebra.

Paratypes.—Three precaudal vertebrae, (V55688 through V55690).

Type locality and age.—UM-K6-59. Ogallala Formation, Lower Pliocene.

Diagnosis.—A medium-size boid with a long, thin neural spine extending nearly to edge of zygosphen. Length of centrum slightly greater than horizontal width at the center of vertebra (table 3). Zygosphen slightly arched and wider than cotyle. Cotyle oval and centrum short with hemal keel spatulate. Subcentral ridges distinct.

Description and comparison.—The five vertebrae assigned to this boid each differ to some degree and positive association is not possible. In addition, the type of the genus *Ogmophis oregonensis* Cope is lost (Auffenberg, 1963, and Brattstrom, 1958). Placement is based on Auffenberg's (1963) description of Vanzolini's (1952) assignment of *O. pauperrimas* and 16 vertebrae described from the Lower Miocene of Florida.

The neural spine in *Ogmophis kansasensis* projects far posteriad (text-fig. 9a) distinguishing it from the type of *Ogmophis*. However, the strong interzygapophysial ridges and boid characters such as the oval cotyle, and the short wide vertebrae (text-fig. 9c), conform to the genus *Ogmophis*. Auffenberg (1963) grouped *Boa*, *Constrictor*, *Epicrates*, *Eunectes*, *Sanzinia*, *Boavus*, *Paraepicrates*, and *Pseudoepicrates* into one assemblage, and forms such as *Calamagras*, *Ogmophis*, *Lichanura*, and *Charina* into a second. The boid type from the WaKeeney locality seems to fall into the latter group.

Ogmophis kansasensis is distinct from *Lichanura* and *Charina* by the nearly equal length and minimum width of the centrum. The neural spine of these two living forms is low, short, and nearly oval in cross section while in *O. kansasensis* it is long and thin. *Calamagras* is apparently similar to *Ogmophis* but the thickened neural spine, size and greater elongation of the

TABLE 3—MEASUREMENTS OF PRECAUDAL VERTEBRAE OF TYPE AND PARATYPES OF
OGMOPHIS KANSASSENSIS (in mm)

Measurement	Type V55687	V55688	Paratypes V55689	V55690
Length of centrum	3.85	3.31	4.51	3.55
Width of neural arch	3.02	2.90	3.19	2.80
Width of zygosphen	2.68	—	2.90*	—
Width of postzygapophysial	5.19	4.34	5.10	4.92
Post-presygapophys distance	4.16	3.41	4.37	3.79
Neural arch—height to hemal keel	4.35	2.95	—	—

* Damaged

vertebrae appear to place *O. kansasensis* closer to *Ogmophis*.

Brattstrom (1958), in his discussion of *Charina prebottae*, compared *Charina* with *Ogmophis*. Again, the short, stubby neural spine of *Charina* and *Lichanura* apparently separate these two genera from *O. kansasensis*, *O. oregonensis*, and the other species assigned to *Ogmophis*.

Within the genus *Ogmophis*, four species are recognized by Auffenberg (1963). *O. oregonensis* Cope from the upper Oligocene, *O. compactus* Lambe from the Lower Oligocene, *O. pauperrimus* Vanzolini of the Lower Miocene, and *O. arenarum* Douglas from the Upper Miocene. *O. kansasensis* differs from *O. arenarum* by having two nearly distinct paradiapophysial articular facets and larger size; and from *O. pauperrimus* by the thin neural spine and relatively greater size.

The suggested phylogenies of the North American boids of the genera *Lichanura*, *Ogmophis*, *Charina*, *Aniloides*, and *Calamagras* are given by Auffenberg (1963). Placement of *Ogmophis kansasensis* remains uncertain as the character of the vertebrae suggest a form distinct from *Lichanura* and *Charina*.

Habit and habitat.—Terrestrial, fossorial and near the river margin. Probably from the forest habitat.

Family DIPSADIDAE
HETERODON Latreille

Several precaudal vertebrae (V55691 through V55693) are assigned to the extant genus *Heterodon*. The hemal keel is flat and cunate, extending the length of centrum. Paradiapophyses massive with two well-developed articulation facets. Neural arch low and compressed.

The shape of the hemal keel would best approximate that of *H. nasicus* or *H. simus* of the three extant species. In *H. platyrhinus* the keel is more ridge-shaped (Auffenberg, 1963). Comparison with *H. plionasicus* Peters (1953), on the basis of vertebral characteristics, is difficult as the species is described on cranial elements. Brattstrom (1967) assigned several vertebrae to *H. plionasicus* from Middle and Upper Pliocene localities in Kansas and Oklahoma. The vertebrae assigned here to *Heterodon* are similar to these. However, because of age and hemal keel shape it seems best to leave the species indeterminate for the time being.

Habit and habitat.—Terrestrial, probably a marginal forest-savanna form, but apparently close to depositional site.

cf. PALEOHETERODON Holman

Four precaudal vertebrae (V55694 through V55697) are distinguishable from those assigned to *Heterodon* by their relative height and the more vaulted neural arch. These specimens show the zygosphene to be convex from above and arched from an anterior view as in *Paleoheterodon*. In *Heterodon* from this locality the zygosphene is slightly crenate and nearly horizontal. The accessory process is broken but was apparently short. From Holman's (1964) description the three vertebral elements conform to characteristics listed for *Paleoheterodon* from the Valentine beds of Nebraska.

Habit and habitat.—Terrestrial. Probably distant from the depositional site. The savanna-grassland habitat is indicated by specimens and abundance.

Family NATRICIDAE
NATRIX HILLMANI¹ n. sp.
Text-fig. 10a-e

Holotype.—V55701. A complete precaudal vertebra.

Paratypes.—Precaudal vertebrae (V55702 through V55704).

Referred specimens.—Several vertebrae (V55705) and right maxilla (V55706).

Type locality and age.—UM-K6-59. Ogallala Formation, Lower Pliocene.

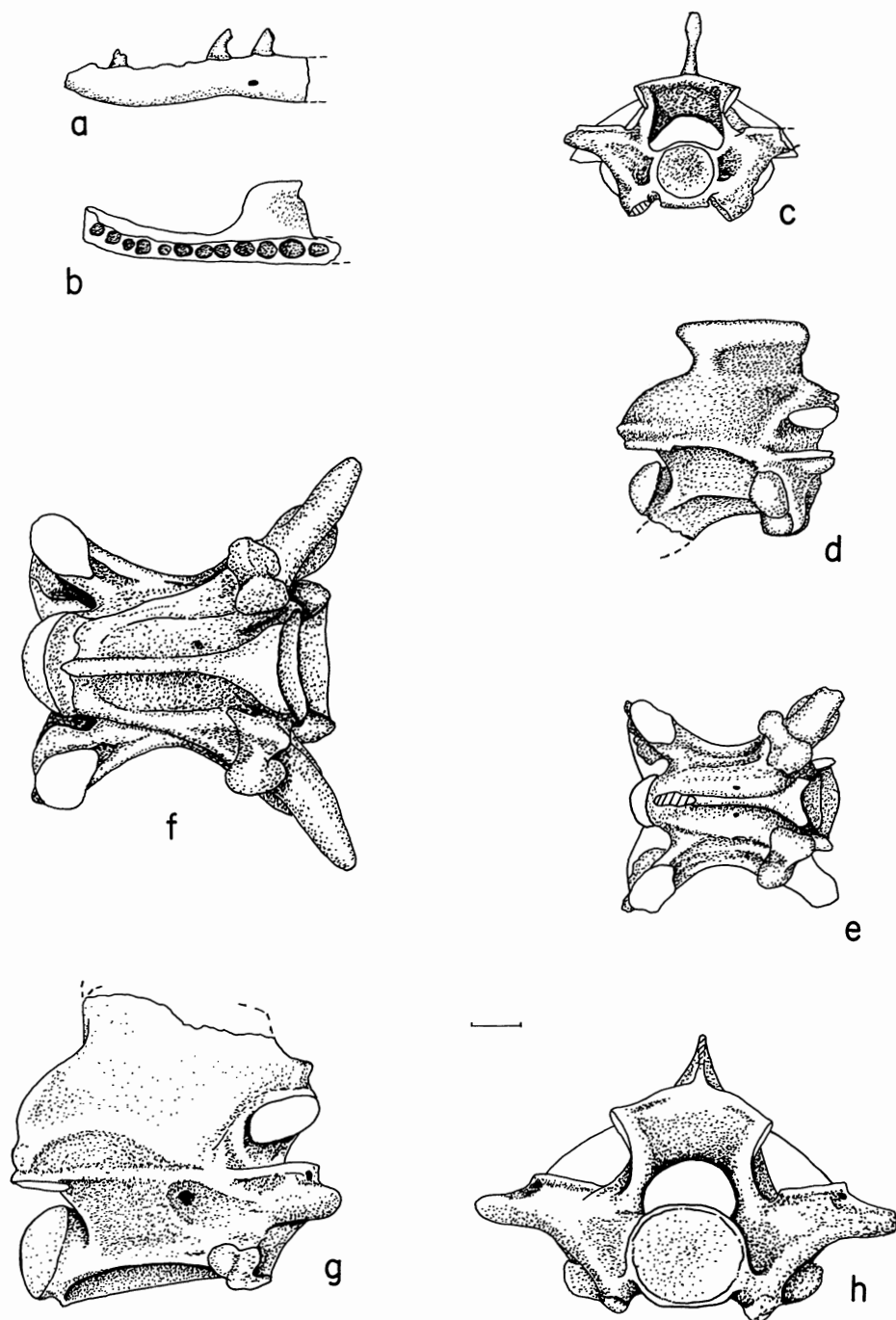
Diagnosis.—A small natricine with a low neural spine thickened at the dorsal and posterior margins; hypapophyses and epizygopophysial spines well developed and zygosphene strongly crenate.

Description.—Rossman (1963) reviewed the taxonomic status of the natricine genera *Liodytes*, *Regina*, and *Clonophis*. *Natrix hillmani* is tentatively placed with the *Natrix* group, but separation from the genus *Regina* seems impossible owing to the uncertainty of the relationship of these two genera. For purposes of this report the genus *Natrix* will be used to include these other genera.

The numerous vertebrae represent a small form (table 4) with body length not exceeding that of the smaller natricine species *grahamii*, *rigidus*, *septemvittata*, and *alleni*.

The grooved dorsal surface of the neural spine (text-fig. 10c-e) appears more developed in the larger specimens. Auffenberg (1963) noted that this character may be sexually dimorphic, ontogenetically variable, and often a pathologic condition. The taxonomic value of the neural spine configuration then must be con-

¹ Named for Mr. Lowell Hillman, owner of the property where the excavation of the WaKeeney local fauna was carried out.



TEXT-FIG. 10—a-b, *Natrix hillmani*, maxilla, V55706, lateral and ventral views. c-e, *Natrix hillmani*, holotype, precaudal vertebra, V55701, anterior, lateral, and ventral views. f-h, *Coluber? plioagellus*, holotype, precaudal vertebra, V55711, ventral, lateral, and anterior views. All drawings to same scale; line represents one millimeter.

TABLE 4—MEASUREMENTS OF PRECAUDAL VERTEBRAE OF THE TYPE AND PARATYPES OF *NATRIX HILLMANI* (in mm)

Measurement	Type	V55702	Paratypes	V55704
	V55701		V55703	
Length of centrum	3.40	3.25	2.25	3.77
Width of neural arch	2.19	2.33	1.56	2.43
Width of zygosphenes	1.96	2.14	1.48	1.95
Postzygapophysial width	3.89	—	—	—
Post-prezygapophysial width	4.78	5.01	2.56	—
Height	3.51	3.84	2.48	3.91

sidered somewhat uncertain until additional evidence is available.

Aside from size and characteristics of the neural spine the vertebrae represent a rather typical natricine snake. The centrum is moderate in length with strong subcentral ridges, well-developed hypapophysial, paradiapophyses projected well below centrum, and an anteroposterior projection of the dorsal suture of the neural spine.

The closest extant species to *N. hillmani* possibly is *Regina alleni* (*R. grahamii* not examined) and differs from this form only by the relatively smaller size and lower neural spine with expanded dorsal and posterior edges.

A maxillary (text-fig. 10a-b) is tentatively assigned to *N. hillmani*. The tooth shape is similar to that described by Rossman (1963) for *R. grahamii*. The maxilla held approximately twelve teeth from the anterior extreme to the posterior margin of the medial process.

Several caudal vertebrae referred to this species, exhibit the wide postero-lateral directed transverse processes as in *R. alleni* and other closely allied species.

Habit and habitat.—Semi-aquatic, near depositional site. Extremely well-preserved vertebral elements indicate a form closely associated with the other shallow-water or river-margin forms.

THAMNOPHIS sp.

A moderate sized snake is referred to the genus *Thamnophis* on the basis of four precaudal vertebrae (V55707 through V55710). The low thin neural spine with overhanging posterior and anterior margins is characteristic of this family. The hypapophysis is directed strongly posteriad. The neural spine which is complete in only one vertebra is thickened medially with a distinctive bulge running from the anterior to posterior edge. The vertebrae assigned to *Thamnophis* seem distinct from *Natrix hillmani* by being more elongate, having a more flattened accessory process, absence of the "ground off" neural spine, and size.

Specific assignment was attempted but the similarity between forms within the genus, and

the lack of a large comparative series for each species, prohibits a suggestion of a species.

Habit and habitat.—Terrestrial and probably distal to site (grassland or savanna).

Family COLUBRIDAE

COLUBER ? *PLIOAGELLUS*¹ n. sp.

Text-fig. 10f-h

Holotype.—V55711, a nearly complete precaudal vertebra missing the dorsal edge of the neural spine.

Referred specimens.—Five precaudal vertebrae (V55712 through V55716).

Type locality and age.—UM-K6-59. Ogallala Formation, Lower Pliocene.

Diagnosis.—A large colubrid (table 5) distinguished from recent forms having similar vertebral elements by extension of the neural spine to the anterior edge of zygosphenes; with high arch to the neural canal and with zygosphenes thickened dorsad and ventrad and projected anterodorsally.

Description and comparison.—In general, the vertebrae conform to those of *Coluber* and *Masticophis* and in certain characters are similar to *Pituophis*, *Salvadora*, *Drymarchon*, and other attenuate snakes. The type (text-fig. 10f-h) is more massive than either *Masticophis* or *Coluber* with a heavy neural arch as reflected by the thickened posterior edge and zygosphenes. Accessory processes slightly divided posteriorly with the prezygapophysial articular surface strongly obovate. Hemal keel pronounced and slightly spatulate extending posteriorly nearly to the condyles. The paradiapophyses with well-developed articular facets are nearly ventral, projecting below the level of the hypapophysis. The cotyle is oval and epizygapophysial spines moderate.

From Auffenberg's (1963) discussion of *Coluber* the presence of well-developed epizygapophysial spines will separate this genus from other colubrids. The relative size of the cotyle and condyle appear to distinguish *Salvadora* and *Ophedryx* from *Coluber* ? *plioagellus*. The

¹ *agellus*, L. dim. of *ager* meaning "field."

TABLE 5.—MEASUREMENT OF PRECAUDAL VERTEBRAE OF THE TYPE AND REFERRED SPECIMENS OF *COLUBER* ? *PLIOAGELLUS* (in mm)

Measurement	(type)	Paratypes				
	V55711	V55712	V55713	V55714	V55715	V55716
Length of centrum	5.15	4.58	3.45	5.99	5.26	—
Width of neural arch	3.01	2.95	2.09	4.85	3.24	5.07
Width of zygosphene	3.92	—	1.66	—	2.63	4.18*
Postzygapophysial width	5.49	—	3.58	—	—	7.98
Post-prezygapophysial width	5.54	—	4.86	7.25	—	6.94
Height	5.37*	4.32	—	6.5*	5.36	—

* Damaged

overall structure of the type, particularly the massiveness, conforms to the vertebral elements of *Salvadora*.

Habit and habitat.—Terrestrial. Vertebrae transported but because of the large size not destroyed. A grassland or shrub habitat is indicated.

PITUOPHIS Holbrook

Three vertebrae; an anterior precaudal (V55717) and two medial precaudals (V55718 and V55719) are assigned to the extant genus *Pituophis*. The anterior vertebrae is characteristic of the genus with vertebral parapophyses posterior to cotyle, no epizygapophysial spines, prezygapophysial articulation surfaces horizontal, zygosphene wider than cotyle, and accessory process obsolete. The nearly central projecting ventral tip of the spine is identical to vertebrae in the anterior region of *Pituophis*. Confusion over the taxonomic placement of the anterior vertebra is possible with various vipers with similar characteristics observed in the posterior region of *Lachesis* and *Bothrops*.

The medial precaudal vertebra compares favorably with that of *Pituophis* with thin zygosphene and a moderate centrum length. The strong subcentral ridges, concave zygosphene, and size appear to separate it from *Elaphe*, but positive elimination of this genus appears impossible on the basis of vertebral elements.

Habit and habitat.—Terrestrial. Probably from the tree-grass margin (or savanna) habitat(s).

Class AVES

The rare specimens of birds represent three new forms. The first bird (a teal, *Nettion ogalalae*) from the WaKeeney local fauna was described by Brodkorb in 1962. Two new avian forms reported by Feduccia & Wilson (1967) represent two additional families, the Cracidae and Picidae.

Family CRACIDAE

ORTALIS AFFINIS Feduccia & Wilson

This cracid is named on the basis of a right carpometacarpus (V55784) screened from UM-K6-59. *Ortalis affinis* is most similar to the extant species *Ortalis vetula* (Wagler) but differs by having a larger carpal trochlea, shallower distal metacarpal symphysis, more robust process of metacarpal I, and more pronounced external ligamental attachment (Feduccia & Wilson, 1967).

Habit and habitat.—Volant, and arboreal. A subtropical forest bird with related living forms in South and Central America and southern North America.

Family PICIDAE

PLIOPICUS BRODKORBI Feduccia & Wilson

This small woodpecker is described from a tarsometatarsus (V55785) screened from UM-K6-59. Characters of the new genus and species are given by Feduccia & Wilson (1967). The new woodpecker seems to be most closely allied to the extant genus *Melanerpes*.

Habit and habitat.—Volant and arboreal. Indicates wooded areas very close to the river.

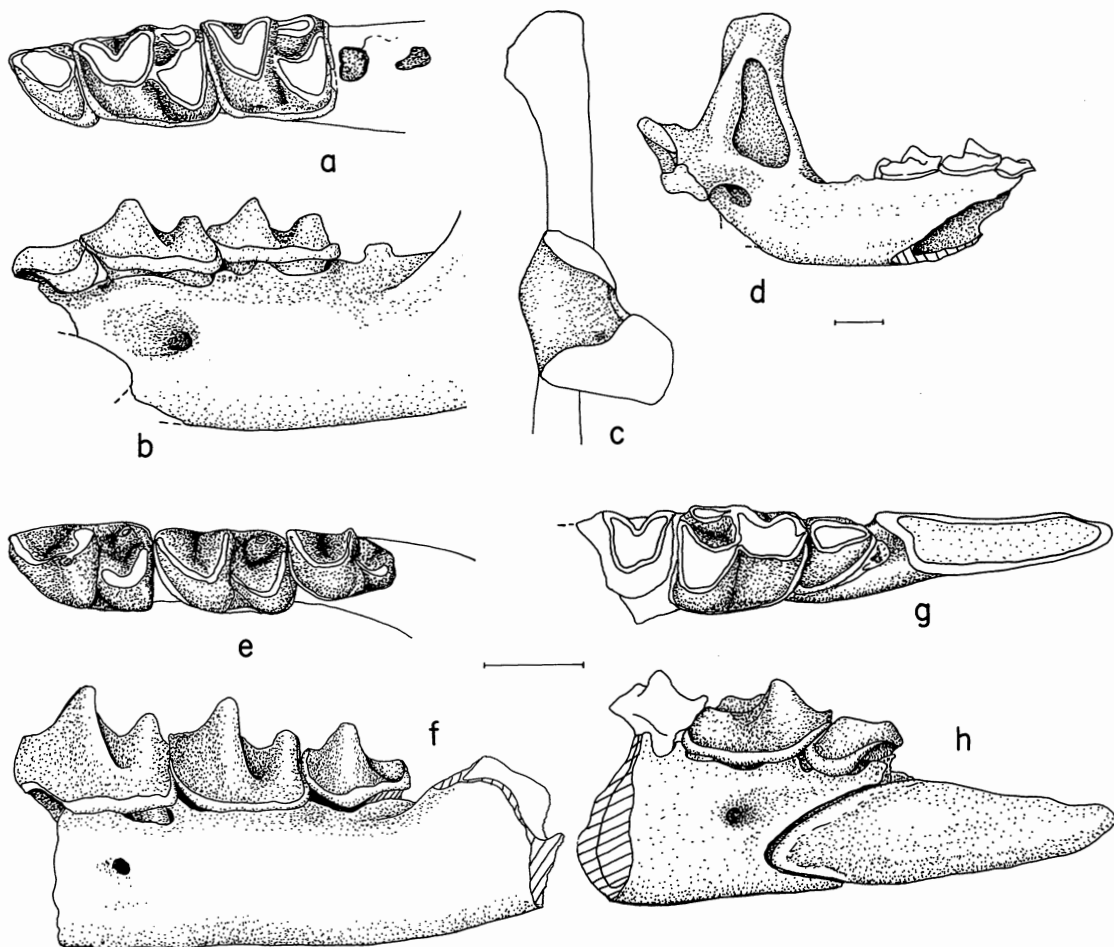
Class MAMMALIA
Order INSECTIVORA
Family ERINACEIDAE
Subfamily ERINACEINAE
Gen. et sp. indet.
Text-fig. 12a-b

A right M₁ (V55722) is that of an erinaceine hedgehog close to the European *Amphecinus*. I am grateful to Malcolm C. McKenna for this identification.

Family SORICIDAE
LIMNOECUS Stirton
Text-fig. 11e-f

A left lower jaw fragment (V55723) bearing M₁-M₃ is referred to the extinct genus *Limnoecus*. The inferior margin of the dentary is nearly horizontal with the small I₃ alveolus below the M₁. The mental foramen is below the middle of M₁.

The metaconid and paraconid of M₃ are



TEXT-FIG. 11—Soricidae. a-d, *Parydrosorex concisus*, holotype, left lower jaw, V55724; a, occlusal view; b, labial view; c, posterior view of condylar process; d, lingual view. e-f, *Limnoecus* sp., left lower jaw, V55723, occlusal and labial views. g-h, *Parydrosorex concisus*, referred specimen, right lower jaw, V55725, occlusal and labial views. All drawings, except d, to the same scale. Lines represent one millimeter.

equivalent in size with both located at the lingual margin of the tooth. The talonid of the M_3 is reduced to a small keel with a single postero-medial cusp. This keel (crista obliqua) runs medially from the cusp to a medial point on the protolophid. The cingulum on M_3 terminates posteriad beneath the base of the cusp. These conditions compare favorably with those given by James (1963, p. 31) in his discussion concerning *L. tricuspis*.

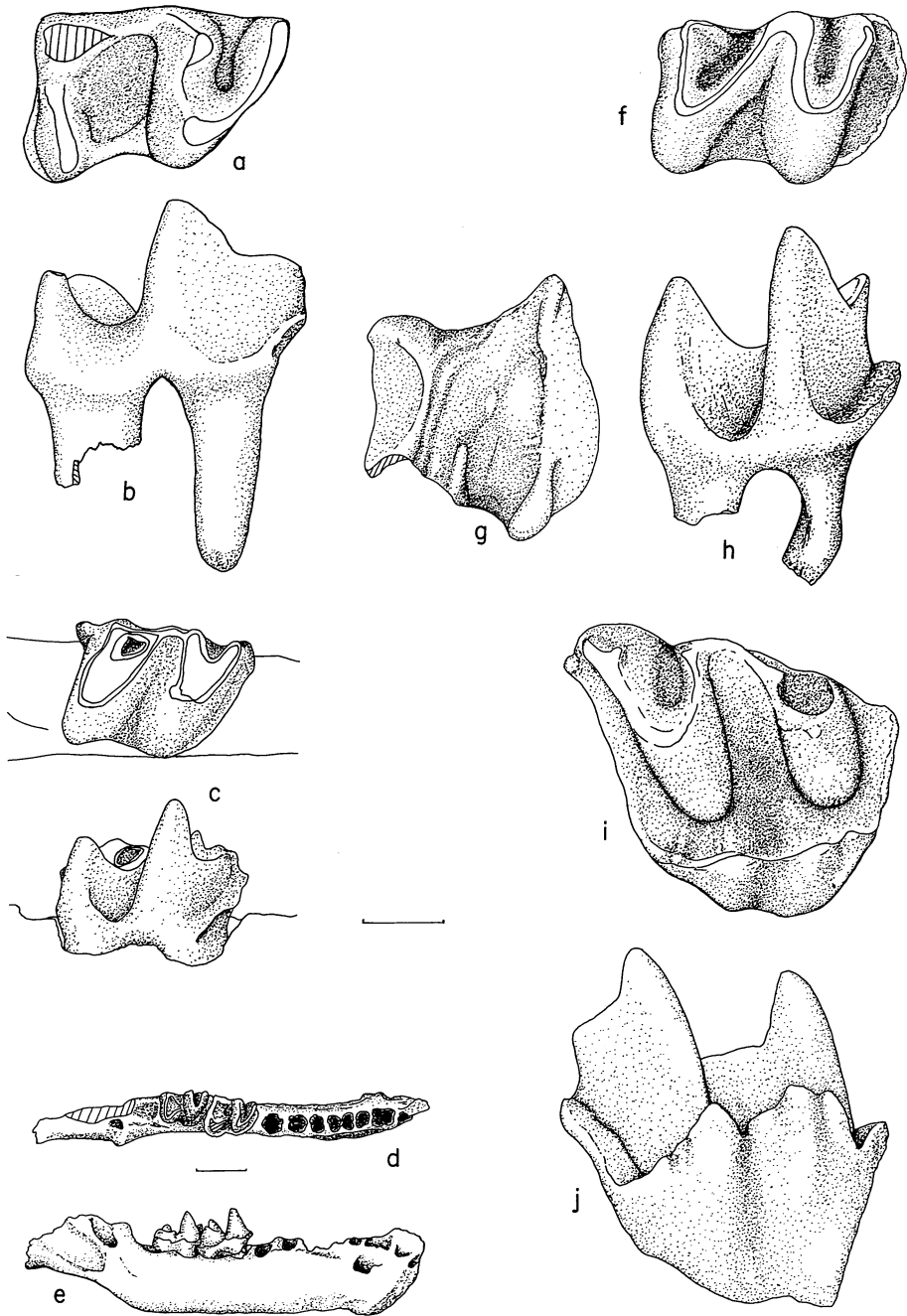
The teeth under normal light appear to be pigmented although this is not certain. James (1963, p. 40) and Repenning (1967, p. 5) discuss the value of pigmentation in shrew taxonomy. In the latter report it was noted that pigmentation was very important and usually

preserved on the fossil teeth. Therefore, if the interpretation of color is correct, the jaw assigned to *Limnoecus* compares favorably with species James (*op. cit.*) regarded as *Limnoecus* (table 6), and is quite distinct from the other soricids in the fauna.

Habit and habitat.—Terrestrial. Near stream margin but possibly a marginal shrub or savanna form.

TABLE 6—MEASUREMENT OF DENTITION IN *LIMNOECUS*, V55723 (in mm)

Measurement	M_1	M_2	M_3
Anteroposterior	1.48	1.39	0.99
Transverse	0.91	0.90	0.69



TEXT-FIG. 12—Insectivora and Chiroptera. a-b, Erinaceine gen. et sp., indet., right M_1 , V55722, occlusal and labial view. c, Talpid gen. et sp., indet., right M_2 , V55750, occlusal and labial views. d-e, *Myotis* sp., right lower jaw, V55752, occlusal and labial views. f-j, *Domininoides mimicus*; f and h, holotype, right M_2 , V55732, occlusal and labial views; g, left clavicle, V55744, posterior view; i-j, right upper molar, 55737, occlusal and lingual views. All drawings same scale. Line represents one millimeter.

PARYDROSOREX CONCUSUS¹ n. gen. et n. sp.

Text-fig. 11a-d, g-h

Holotype.—Left lower jaw (V55724) bearing moderately worn P₄-M₂ and the ascending ramus. Alveolus of I₃ present.

Referred Specimen.—Anterior portion of right lower jaw (V55725) with I₃, P₄, M₁ and broken M₂ (text-fig. 11g-h).

Type locality and age.—UM-K6-59. Ogallala Formation. Lower Pliocene.

Diagnosis.—Generic and specific diagnosis the same. A moderately sized shrew with a compressed lower jaw (table 7); mental foramen small, surrounded by shallow depression and centered on the ramus just anterior to the posterior root of M₁; entoconid on M₁ and M₂ well developed and nearly medial between the posterior margin and the metaconid; molars possess well-developed entolophids; alveolus border of I₃ is located below the middle of M₁; heavy uninterrupted cingulum present on both lower molars and on the posterior, external, and internal sides of the P₄; ventral articular facet (Gaughran, 1954) is subtriangular with the internal area wider; ridge connecting the two lingual articulation areas of the ventral and dorsal articular facets of the condyle forms the internal margin of the condular process; ascending ramus narrow with a deep internal temporal fossa; mandibular foramina confluent and below the neck of the condyle; M₂ nearly rhombic in shape; no pigmentation is present.

Description and comparison.—The holotype is broken below the P₄ with the anterior portion missing (text-fig. 11a-d). The angular process is missing. The coronoid process is oval in cross section and is directed anteriorly at the dorsal extremity. The deep posterointernal ramal fossa (Hibbard, 1953, p. 23) is subtriangular in outline with the ventral margin anteriorly convex. There is no transverse limula. The dorsal and ventral articular facets are separated by a small intermediate fossa or depression. The ventral facet is nearly horizontal and flat with

the internal portion of the facet broader than the external. The dorsal facet is relatively small and round (text-fig. 11c). The positions of the facets and their placement on the ramus are similar to those of *Blarina* and *Cryptotis* but differ from most *Sorex*.

In occlusal outlines the M₁ is trapezoidal and the M₂ is rhombic. The shapes of these molars are emphasized by continuous, heavy cingula on all sides. The entoconid is large but is situated more posterior than in *Hesperosorex* Hibbard (1957).

The unicuspid P₄ has a low rounded crown. This is different from the blade-like P₄ of the *Sorex* (s. l.) group. This tooth is small and compact with cingulum continuous except on the anterior border. On the P₄ the single valley opens lingually.

The small alveolus for the P₁ (or canine of authors) under the anterior end of P₄ is nearly horizontal to the ramal axis. The extremely small diameter of this root indicates that the next tooth is very small. In the referred specimen there is only one alveolus between the incisor and the P₄ (text-fig. 11g-h).

Discussion.—This genus is distinct from all extant shrews by the following combination of characters: the small P₄ with the valley opening to the lingual margin; shape of the condyle; shape of the posterointernal ramal fossa; confluence of the mandibular and postmandibular foramina; posterior position of the dental foramen and I₃; and the shape and crown height of the lower molars.

Among the fossil forms, *Alluvisorex arcadentes* Hutchison (1966) and ? *Hesperosorex chasseeae* Tedford (1961) (now *Alluvisorex chasseeae*, see Repenning, 1967, p. 33) seem to represent forms closest to *Parydrosorex concisus*. They are similar in the general shape of the lower molars, size of P₄, shape of the ascending ramus and condyle facets, and the entoconid placement and size. However, the short jaw with the more posterior position of the incisor, molar compression, confluent mandibular foramen, and position of the P₄ sulcus distinguish the two genera. Trends in this lineage would seem to include characteristics common with a compressed

¹ *parydros*, Gr. meaning "living near water"; *concisus*, L. meaning "brief, short," in reference to the short lower jaw.

TABLE 7—MEASUREMENT OF DENTITION OF THE TYPE AND REFERRED SPECIMEN OF *PARYDROSOREX CONCUSUS* (in mm)

Specimen	I ₃		P ₄		M ₁		M ₂	
	AP*	Tr*	AP	Tr	AP	Tr	AP	Tr
Holotype V55724	—	—	0.68	0.82	1.25	1.00	1.19	1.04
Paratype V55725	2.15	0.54	0.63	0.72	1.23	0.98	—	—

* AP = anteroposterior; tr = transverse.

sion of the lower jaw such as the loss of the P_3 and the dental shortening.

Parydrosorex concisus possibly represents a near terminal member of the *Alluvisorex* lineage in North America which Repenning (1967, p. 61–62) suggests is represented by the later occurrences of *Blarinella* and *Petenya* of Eurasia.

Habit and habitat.—Terrestrial. Probably resident near the stream margin and into the savanna.

Soricids gen. et sp. indet.

Three right maxillary fragments possibly represent three *Sorex*-like shrews in the fauna. At present it appears best to describe these forms on the P^4 and relate to associated features in each maxilla. A lower jaw fragment (V55729) and several isolated teeth (V55730) are probably from this group. The upper dentitions from *Limneocus* are poorly known, thus any of the following specimens might represent a small form of this genus. A second possibility is that each of the three maxillary fragments represent variations of one or two species. All of the specimens are nearly equal in size.

Form A

A maxillary fragment (V55726) with a P^3 , broken P^4 , and alveolae for five teeth anterior to P^3 conforms to the dental formula of a number of soricid genera including *Sorex*. The P^3 is under the anterior border of the P^4 . The P^3 is a minute single cusp with a transverse blade-like crown. The large anterior incisor probably had a double root as evidenced by the alveolus with a medial partition. The remaining portions of the P^4 show the protocone to be present, but no hypocone. A cingulum surrounds the talonid keel and appears to terminate at the protocone.

This maxillary fragment is broken just posterior to the P^4 . No infraorbital foramen is present on the specimen. The entire specimen shows a compression of the unicuspid with the alveolae small and nearly uniform in size. The two small alveolae anterior to the P^3 are oval and compressed anteroposteriorly. The slope of the maxilla along the nasal opening is pronounced, as in species of extant *Cryptotis*. The specimen suggests a soricid like form with short rostral area and crowded unicuspid.

Form B

A maxillary fragment (V55727) with P^4 – M^2 and alveolus of P^3 is similar to Form A by having a small posterior indentation in the talonid area. A heavy cingulum surrounds the talonid keel and continues uninterrupted along the base of the protocone. Judging from the alveolus, the P^3 , although close enough to the P^4 to

cause a notch in the anterior border of the latter, seems to be larger than in Form A. The two molars have massive cingula on the posterior and lingual margins. The talon valley and posteriorly directed keel are weak and progressively decrease from the P^4 to the M^2 . The M^1 and M^2 are much wider than long. The infraorbital foramen is dorsal to the P^4 .

Form C

A maxillary fragment (V55728) differs from Forms A and B in the shape of the P^4 talon keel, and by having no notch for the P^3 in the anterior margin of P^4 . The infraorbital foramen begins at the posterior margin of the P^4 .

Family TALPIDAE

DOMNINOIDES MIMICUS¹ n. sp.

Text-fig. 12f–j

Holotype.—V55732. A right lower second molar.

Paratypes.—Two left M_1 's (V55733 and V55734); two right M_3 's (V55735 and V55736).

Referred specimens.—Upper right molar (V55737); two P^4 's (V55738 and V55739); two left and two right M^3 's (V55740 through V55743); a partial left humerus (V54849); a left clavicle (V55744); two calcanea (V55745 and V55746); two scapulae (V55747 and V55748); and miscellaneous material including radii, phalanges, etc., under V55749.

Type locality and age.—UM-K6-59. Ogallala Formation, Lower Pliocene.

Diagnosis.—A large fossorial mole showing many features parallel to the modern *Scapanus* group; width of the anterior cingulum on M_2 is approximately one fifth of anteroposterior length of the tooth; posterior cingulum absent or nearly so and a deep posterolingual reentrant valley (between entoconid and metaconid) opens at a line drawn from the posterior to the anterior terminations of the cingulum; lingual cusps are low relative to the labial cusps.

Description.—The holotype a right M_2 (V55732) is only slightly worn (text-fig. 12f, h). It is two rooted, the anterior root being smaller and more compressed anteroposteriorly than the posterior root (table 8). The high protoconid and the adjacent lower paraconid and metaconid form the major blade of the tooth and are positioned somewhat medially on the base (text-fig. 12f and h). The hypoconid and entoconid form the posterior loph and the posterior margin of the tooth. A slight bulge at the

¹ *mimicus*, L. meaning "imitative." In reference to the osteological similarity of this large fossorial mole to the western species of *Scapanus*.

TABLE 8—MEASUREMENTS OF TYPE, PARATYPES, AND REFERRED TEETH OF *DOMNINOIDES MIMICUS* (in mm)

Specimen	M ₁		M ₂		M ₃		M ¹ or M ²		M ³	
	AP**	Tr**	AP	Tr	AP	Tr	AP	Tr	AP	Tr
V55733	2.76	2.49								
V55734	2.80	2.24								
V55732 (type)			3.10	2.02						
V55735					2.61*	1.72				
V55736					3.13	1.95				
V55737							4.09	3.01		
V55740									2.13	2.57
V55741									2.44	2.76
V55742									2.20	2.50
V55743									2.05	2.32

* Damaged

** AP = anteroposterior; Tr = transverse.

junction of the ridge from the hypoconid at the metaconid is probably a small reduced metastyloid.

The M₁ is two-rooted with only slight anterior and posterior cingula. The metaconid is the dominant lingual cusp with paraconid and entoconid much lower. The paraconid is nearly obsolete and ridge-like.

The two M₃'s are relatively large with massive anterior cingula. No posterior cingula are present. Width of anterior cingula same as the distance between paraconid and metaconid. The talonid cusps are much smaller than the trigonid cusps.

The large unworn right upper molar (M¹ or M²), assigned to *Domninoides mimicus*, has heavy anterior and posterior cingula which join the protocone and hypocone, respectively (Fig. 12i-j). The protocone is blade-like. The hypocone and protocone are separated by a shallow continuous groove. The metamesoloph has a small cusp at its posterolabial termination. There are no posterior and anterior accessory processes, their function apparently taken over by the massive cingula in these two areas. The two dominant cusps, the paracone and metacone, are similar to those of the large *Scapanus*. There is no labial cingulum.

Two left M³'s and two right M³'s are assigned to *D. mimicus*. Their range of size is quite variable (table 8). In many respects the M³'s differ markedly from all extant genera of large fossorial moles. A pronounced anterior cingulum extends to the protocone and the metacone is reduced and ridge-like. Three of the four roots are large, and the fourth is small and medial to the two labial ones.

A large partial humerus (V54849) is assigned to *D. mimicus*. It is 16.49 mm long and approximately 13 mm wide (brachialis process broken). Comparison with *D. valentinensis* Reed was made with illustrations loaned by Howard Hutchison of the University of Cali-

fornia; and except for the greater size of the WaKeeney specimen, the humeri seem similar.

A nearly complete left clavicle (V55744) is also assigned to *D. mimicus* (text-fig. 12g). The maximum length is 6.01 mm and width of the facet of the internal articulation is 7.78 mm. A portion of the clavicle is broken from the anteroventral corner but does not include the facet of the humeral articulation. The clavicle is generally similar to that of the large *Scapanus* but differs in some respects. The internal (sternal) articular facet is not perpendicular to the anterior surface of the clavicle as in *Scapanus* but is rotated posteriad, thus changing the angle of projection of the element. The humeral facet is rotated counterclockwise (lateral view) with respect to the proximal facet. In *Scapanus* these two facets are nearly parallel.

The large vascular foramina present in *Scapanus*, *Scalopus*, and *Parascalops* is absent on the fossil clavicle. No indentation (for the foramen) is present on the ventral margin near the area of articulation with the small heterotropic bone as in *Scapanus*. In *Scalopus* this foramen is not marginal but pierces the clavicle nearly medially. In general the clavicle is broader and thinner than those of extant fossorial moles.

Other elements assigned to the large mole *Domninoides mimicus* include two partial scapulae (V55747 and V55748). These elements show the nearly continuous tendinal groove as in *Parascalops*. Two calcanea (V55745 and V55746), fragments of radii and miscellaneous material are assigned to the WaKeeney mole.

Discussion.—From the three other described species of *Domninoides*, namely, *D. riparensis* Green (1956), *D. valentinensis* Reed (1962), and *D. evelynae* Macdonald (1963), the larger size, absence of a posterior cingulum on M₂ and M₃, and absence of a mesostyle on the lower molars are distinctive differences.

Habit and habitat.—Terrestrial, fossorial.

Probably burrowed in the moist sandy or silty soil beneath the larger vegetation near the river margin.

Talpid gen. et sp. indet.
Text-fig 12c

A right jaw fragment with M_2 and alveolae for P_4 , M_1 and M_3 (V55750), a left upper molar (V55751, probably an M^2), and the proximal portion of a humerus are unassignable to *Domninoidea mimicus*. The teeth represent a smaller mole about the size of *Parascalops* (table 9).

TABLE 9—MEASUREMENTS OF TOOTH AND JAW FRAGMENT (V55750) LISTED AS TALPID GEN. ET SP. INDET. (in mm)

Measurement	Specimen V55750
M_2 anteroposterior	2.18
M_2 transverse	1.41
M_1 – M_3 alveolae length	5.89
Thickness of jaw below M_2	2.33

The M_2 has a narrow anterior cingulum with no cingulum on the other three sides (text-fig. 12c). The posterior accessory cusp is well developed. This tooth is moderately worn and the mesostyle to mesoconid relationship is not clear. However, examination of similar stages of wear in extant forms show the fossil specimen to be similar to *Parascalops*. Other characteristics of the M_2 such as the posterior accessory cusp, cingulum, general shape and size also approximate *Parascalops*.

The upper molar has a cingulum on each side and the only lingual cusp is the protocone. The anterior accessory cusp is developed. The tooth is compressed and thus unlike forms such as *Scapanus*.

The humeral fragment is similar to that of *Parascalops* among Recent forms examined. It differs from *Domninoidea mimicus* in shape and position of the greater and lesser tuberosities and bicapital groove.

Order CHIROPTERA
Family VESPERTILIONIDAE
MYOTIS Kaup
Text-fig. 12d–e

A small right dentary (V55752) containing M_1 and M_2 compares favorably with several members of the *Myotis* group (text-fig. d–e). However, on the basis of jaw morphology, alveolar placement which shows tooth enlargement and position, and size, this specimen is similar to many species of *Myotis*, namely: *lucifugus* (Le Conte), *sodalis* Miller & Allen, *volans* (Allen), and *yumanensis* (Allen).

Habit and habitat.—Near depositional site. Possibly rested in the larger trees.

Order CARNIVORA
Family MUSTELIDAE
*MARTES STIRTONI*¹ n. sp.
Text-fig. 13a–b

Holotype.—V55754; fragmentary skull. Reconstructed maxillae and premaxillae contain both upper molars, RP^4 , LP^3 , RP^3 , RP^2 , and alveoli for remaining teeth. Fragments of remaining areas on skull under this number are used in the generic and specific assignments.

Referred specimen.—V55755; a right ? P_3 .

Type locality and age.—UM-K6-59. Ogallala Formation. Lower Pliocene.

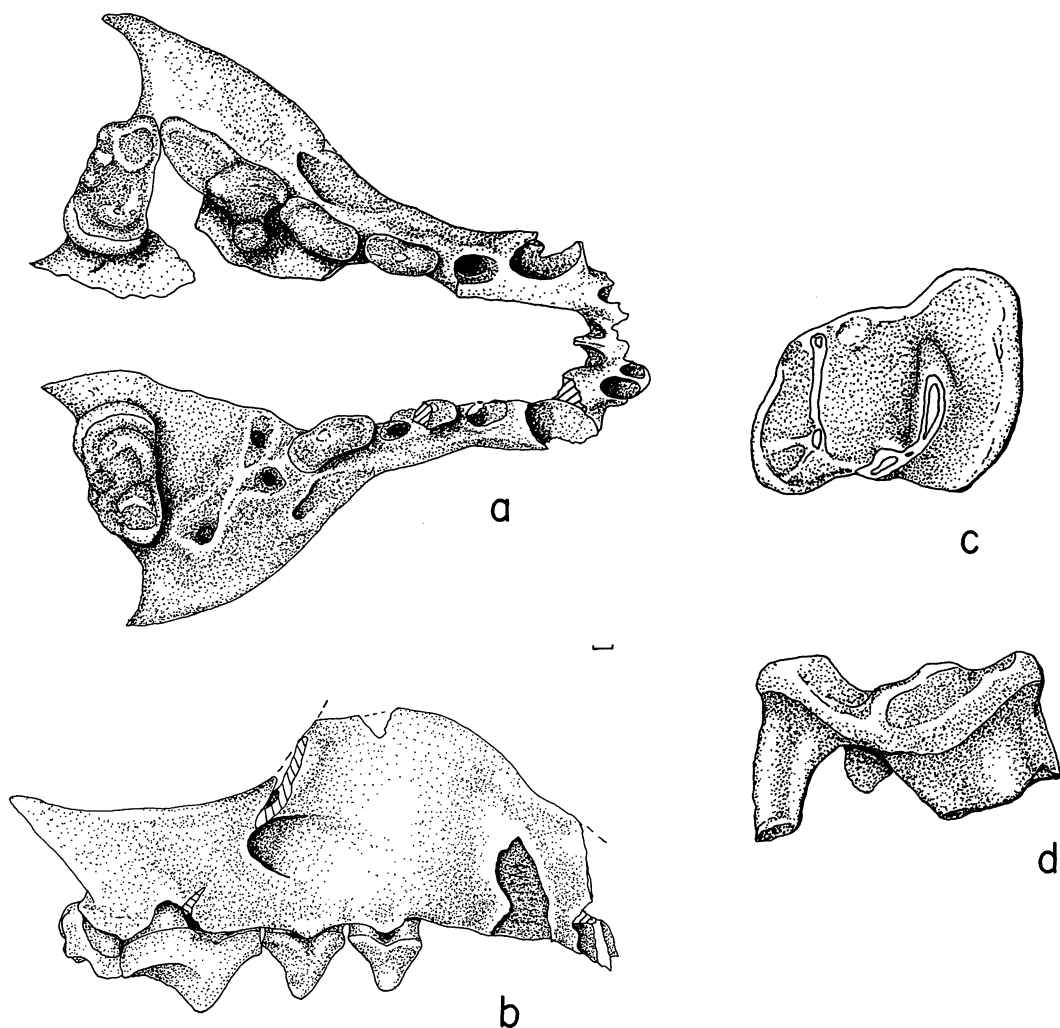
Diagnosis.—A small mustelid with upper dentition I^1 – I^3 , C, P^1 – M^1 , upper premolars not crowded; M^1 with posteromedial cusp (metaconule); upper molars with the lingual anteroposterior width slightly greater than labial, and with the anteroposterior margins nearly straight; P^4 with prominent, sharp protocone on an arm extending slightly anterior of the parastyle, slender main blade and without a shelf on the lingual side of paracone; P^3 oval with a small anterior and posterior shelf; I^3 's much larger than other medial incisors; temporal crests present but weak; occipital condyles relatively large and somewhat more flattened than in extant species of the genus *Martes*.

Description.—Smaller than *Martes americana* (table 10); rostrum elongate with a small diastema between the root of P^1 and the two adjacent roots; infraorbital foramen opens above the anterior root of P^4 ; premolars not crowded with all lateral teeth nearly aligned, but with C and P^1 displaced somewhat laterally leaving the shortest distance across the

TABLE 10—MEASUREMENTS OF TYPE OF *MARTES STIRTONI* (in mm)

Measurements—right side	V55754
P^2 , anteroposterior	3.64
P^2 , transverse	1.59
P^3 , anteroposterior	4.19
P^3 , transverse	1.81
P^4 , anteroposterior	7.09
P^4 , transverse at protocone	4.06
P^4 , transverse across talon	2.37
M^1 , anteroposterior, lingual margin	3.29
M^1 , anteroposterior, labial margin	4.05
M^1 , transverse	7.08
Total: I^3 alveolus to M^1	27.22

¹ Named in honor of the late Dr. Ruben Arthur Stirton, the University of California, for his work on the Late Tertiary mammals of the Plains region.



TEXT-FIG. 13—Carnivora. a-b, *Martes stirtoni*, holotype, fragmentary skull, V55754, occlusal and labial views. c-d, *Plesiogulo* sp., left M¹, V55756, occlusal and anterior views. Drawn to same scale. Line represents one millimeter.

palate between the P²'s; I³ nearly twice the size of I² as evidenced by the alveolae; root of canine oval and slightly curved posteriad; P² and P³ simple, oval in outline, without accessory cusps, and with the major cusp nearly centered; small cingula present on the anterior and posterior margins of this tooth; P⁴ thin with protocone positioned on a narrow neck and projected anteriorly of the parastyle; parastyle minute but obvious; no internal shelf at the base of the paracone but a thin cingulum entirely surrounds the tooth; anterior indentation between paracone and protocone pronounced.

The M¹ has straight and nearly parallel anterior and posterior sides. The paracone and

metacone are separated by a groove with the former cusp larger and centered near the anterior border. Protocone is large with a ridge running antero-externally to meet the cingulum anterior of the paracone. Lingual shelf, of this tooth, has a pronounced cingulum. The M¹ is arched with the lingual and labial margins high as in members of the *Martes* group (text-fig. 13a-b).

Several fragmental regions of the skull compare closely with *Martes*. One area reconstructed includes the right supraoccipital with the occipital condyle. The inflated medial area above the foramen magnum, position of lambdoidal crest to foramen magnum and the relative distance between the condyles is similar to

Martes. However, the relationship of condyle size to rostral and tooth size is greater in *Martes stirtoni* with the condyles somewhat flattened and larger. The left condyle and a portion of the basicranium show that the position of the anterior condyloid foramen is similar to *Martes*.

Another assembled region contains the anterior portion of the left tympanic bulla, the internal portion of the glenoid cavity and part of the bone surrounding the external auditory meatus. These structures compare favorably with *Martes*.

The referred lower premolar (?P₃) is oval in occlusal outline and a lingual cingulum is present. The posterior heel is narrow. The posterior crest, ascending from the heel to the principle cusp, is steplike with a small cuspid developed. The tooth is narrow compared with living *Martes*, particularly in the posterior region. However, the small cusp or step-like posterior ridge is present in the genus *Martes*.

Generic designation.—The genus *Martes* is used here on the basis of several morphological characteristics. Among the major criteria that can be compared with the fossil specimen are: the non-crowded four upper premolars; absence of M²; anteroposterior length of P⁴ and transverse distance of M¹ are equal or nearly so; P⁴ with well-developed sharp protocone projecting anteriorly at about 60° from the anteroposterior tooth axis; and the position and relative size of the infraorbital foramen. Further, the general shapes of the teeth, their relative placement, length and width relationship of rostrum, positions of foramina in *M. stirtoni* are exhibited by members of the genus *Martes*.

Comparison.—Since the holotype represents a morphological form close to the Recent species of *Martes* a general review of the many Upper Tertiary mustelid genera is not attempted.

Martes stirtoni differs from *M. campestris* Gregory (1942) by its smaller size and presence of a metacone on the M¹. On the basis of size and the narrow P⁴, with protocone on narrow neck, *M. stirtoni* may be distinguished from other members of the genus. The geographic position and the subtropical environment further support the difference of this form from other extant North American *Martes*.

Ecologically the stone martin of Eurasia might best approximate this fossil form. Novikoc (1956, p. 192) in listing habitats for *M. forina* Erxleben says it is found in "floodland forests and established shelter belts," with a range into China, Syria, Iran, and other countries having warmer climates. This Lower Pliocene form, judging from the associated faunal types, is probably ecologically replaced today, in a similar environment, by the weasel, *Mustela frenata*. The genus *Tayra* from South America also probably occupies a comparable ecologic situation today as did *M. stirtoni* in the Lower Pliocene.

Habit and habitat.—Terrestrial. Probably an active predator of the small forest-savanna vertebrates along the river border.

PLESIOGULO Zdansky

Text-fig. 13c-d

One left, upper first molar (V55756, text-fig. 13c-d), is assigned to *Plesiogulo*. Transverse length, 12.94 mm; narrowest anteroposterior width, 8.15 mm; greatest diameter at lingual margin, 10.78 mm.

Martin (1928) described *Brachypsalis marshalli* (= *Plesiogulo marshalli*) from Sherman County, Kansas. Little comparison can be made from his description but certain differences are noted. Martin's specimen was approximately a third larger. The protocone is lower in the M¹ of the Trego County specimen with the metacone and paracone smaller and widely separated. This tooth has well-developed labial roots with the large lingual root formed by a fusion of two of sub-equal size. The protocone is low and crest-like and a ridge runs from this cusp to the anteromedial border where it forms a slight projection. The metacone is situated at the posterolateral corner on the margin of the tooth. Shotwell (1956) described a *Plesiogulo* from McKay reservoir in Oregon. His specimen differs from the one found at Wa-Keeney by its larger size, and position of metacone.

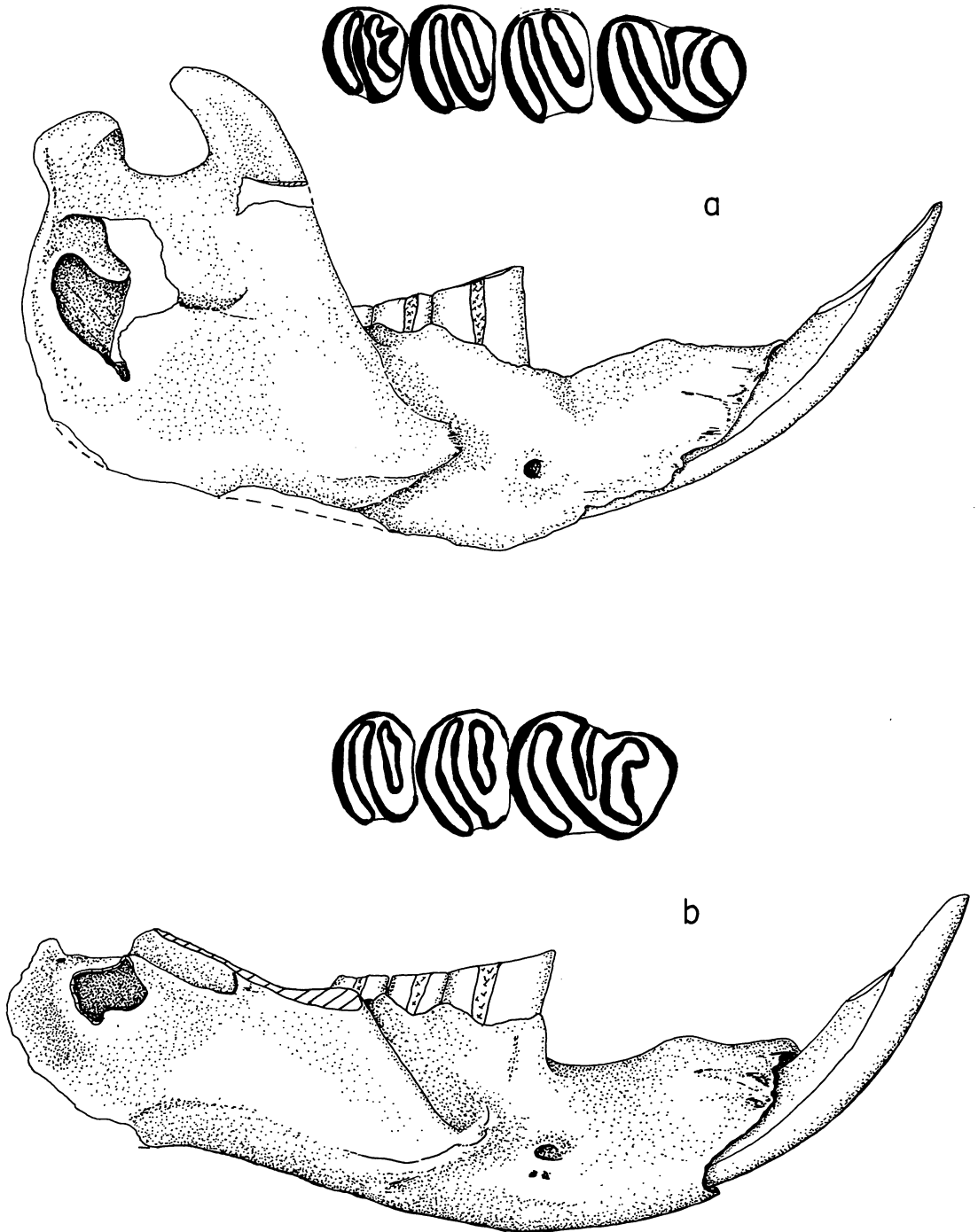
The *Plesiogulo* from this fauna probably represents the earliest record for North America, and thus the size and modifications of M¹ probably reflect evolutionary changes in the later occurrences.

Family CANIDAE

Gen. et sp. indet.

The presence of a foxsize canid in the fauna is based on a right M¹ (V55760) and the distal portion of a humerus (V55758).

The upper molar measures 12.63 mm transversely and 8.98 mm anteroposteriorly across the widest portion. All cusps are low with the paracone and metacone separated by a deep narrow groove. Metacone is positioned near the posterolabial border. The protocone is near the anterior border with a low ridge extending to the posteromedial margin of the tooth. Comparison with various canids proved unsatisfac-



TEXT-FIG. 14—*Eucastor phillisi*. a, Part of skeleton of holotype, right lower jaw, V55764, occlusal and labial views. b, Right lower jaw, KU6885, occlusal and labial views. Same scales for occlusal views with side views reduced. Lines represent one millimeter.

tory. The tooth is more rectangular than in *Vulpes* and *Canis*.

The partial humerus compares favorably with members of the genus *Canis*, except for the greater width of the olecranon fossa (9.8 mm) relative to width of the distal end (22.8 mm from medial epicondyle to capitulum).

? Family CANIDAE

? HADROCYON Stock & Furlong

A fragmentary lower molar (V55759) was collected from the floodplain deposits six feet above the main screening site UM-K6-59 (Unit C of Fig. 2A).

Among the large canids most of the molars appear to have roots of nearly equal diameter; however, in *Hadrocyon* the roots of M_2 are unequal. On the broken tooth the anterior root is wide transversely with the much smaller posterior root directed posteriad. Largest diameter of the anterior root is 11.4 mm while the posterior one measures 5.7 mm. The roots originate close together as in the M_2 of *Hadrocyon*. The anteroposterior length of the tooth is approximately 20 mm. Separation from *Aeluroidon* is not certain but the latter has roots of nearly equal diameter on the M_2 .

An incisor (V54831) belonging to a large canid may belong to the same form as the molar just described. It has three anterior lobes and the occlusal face is parallel to the dorsal surface of the root.

Order RODENTIA

Family MYLAGAULIDAE

EPIGAULUS MINOR Hibbard & Phillis

Text-fig. 15g-i

Only one tooth, a right P_4 , V55763, was collected from the main screening site (text-fig. 15g-i). Three other well-worn premolars (V54835, V55761 and V55762) are assigned to *Epigaulus minor* (table 11). They were surface collected from the UM-K6-59 locality.

The unerupted lower premolar has no os cementum, with the crown unworn and the base open. The base of this tooth is equidimensional to the type of *Epigaulus minor* (from

TABLE 11—MEASUREMENTS AND NUMBER OF LAKES OF PREMOLARS ASSIGNED TO *EPIGAULUS MINOR* (in mm)

Specimen Number	AP*-Base	AP-Sur-face	Tr*	Hgt.	No. of Lakes
V55763	10.40	6.81	4.80	9.26	8
V55761	8.85	9.07	5.54	7.72	7
V54835	6.58	8.71	5.12	7.38	6
V55762	2.23	4.72	3.89	6.50	4

* AP = anteroposterior; Tr = transverse.

KU Loc. 29, Trego County, Hibbard & Phillis, 1945).

Habit and habitat.—Terrestrial. Distant to site. Morphologically one of the grassland forms.

Family CASTORIDAE

EUCASTOR PHILLIS¹ n. sp.

Text-fig. 14a-b, 15a-f

Eucastor cf. *tortus*, 1945, Hibbard & Phillis. (Right lower jaw, University of Kansas No. 6885).

Holotype.—V55764, a partial skeleton including: right lower jaw, femur, astragalus, radius and ulna; left tibia-fibula and humerus; a pelvis in fragmentary condition; and many vertebrae, tarsals, carpals and phalanges.

Type locality and age.—KU Loc. 29, Trego County, Kansas. Lower Pliocene, Ogallala Formation.

Paratypes.—V55765, associated left P_4 - M_3 ; V41452, left lower jaw with M_1 and M_2 ; V54850, left P_4 ; V54832, left jaw fragment with M_2 ; V55766, left M_1 and M_2 ; V55767, an upper molar; V41453, two P_4 's; V55768-V55773, P_4 's; V55774, a DP_4 ; V55775, DP_4 ; V55778-V55781, four calcanea; V55777, two astragali, and V55776, miscellaneous teeth. (All paratypes from Locality UM-K6-59).

Diagnosis.—A moderate-sized *Eucastor* with elongate lower jaw (text-fig. 14a-b). Diastemal distance, as measured from anterior edge of the P_4 at the alveolar margin to lower incisor along a line of the alveolae, equal to or greater than anteroposterior length of P_4 - M_3 (table 12); M_3 nearly as large as M_2 ; P_4 with metafossettid in early wear stage and parastriid much shorter than mesostriid; enamel pattern of the upper premolar in early stage of wear nearly as wide as long with 'S' pattern

TABLE 12—MEASUREMENTS OF TYPE SKELETON OF *EUCASTOR PHILLISI*, V55764 (in mm)

Element and Measurement	Value
Lower jaw, length	54.3
Lower jaw, occlusal length	15.8
Lower jaw, length of diastema	15.9
Depth lower jaw below M_1	13.0*
Height cornoid process above M_2	16.1
Width of ascending ramus at condyle base	16.8
Humerus, length	35.1
Ulna, length	50±*
Radius, length	39.5
Radius, distal width	5.1
Femur, length	50.2
Femur, distal width	13.2
Tibia-fibula, length	65.2
Tibia-fibula, distal width	10.6

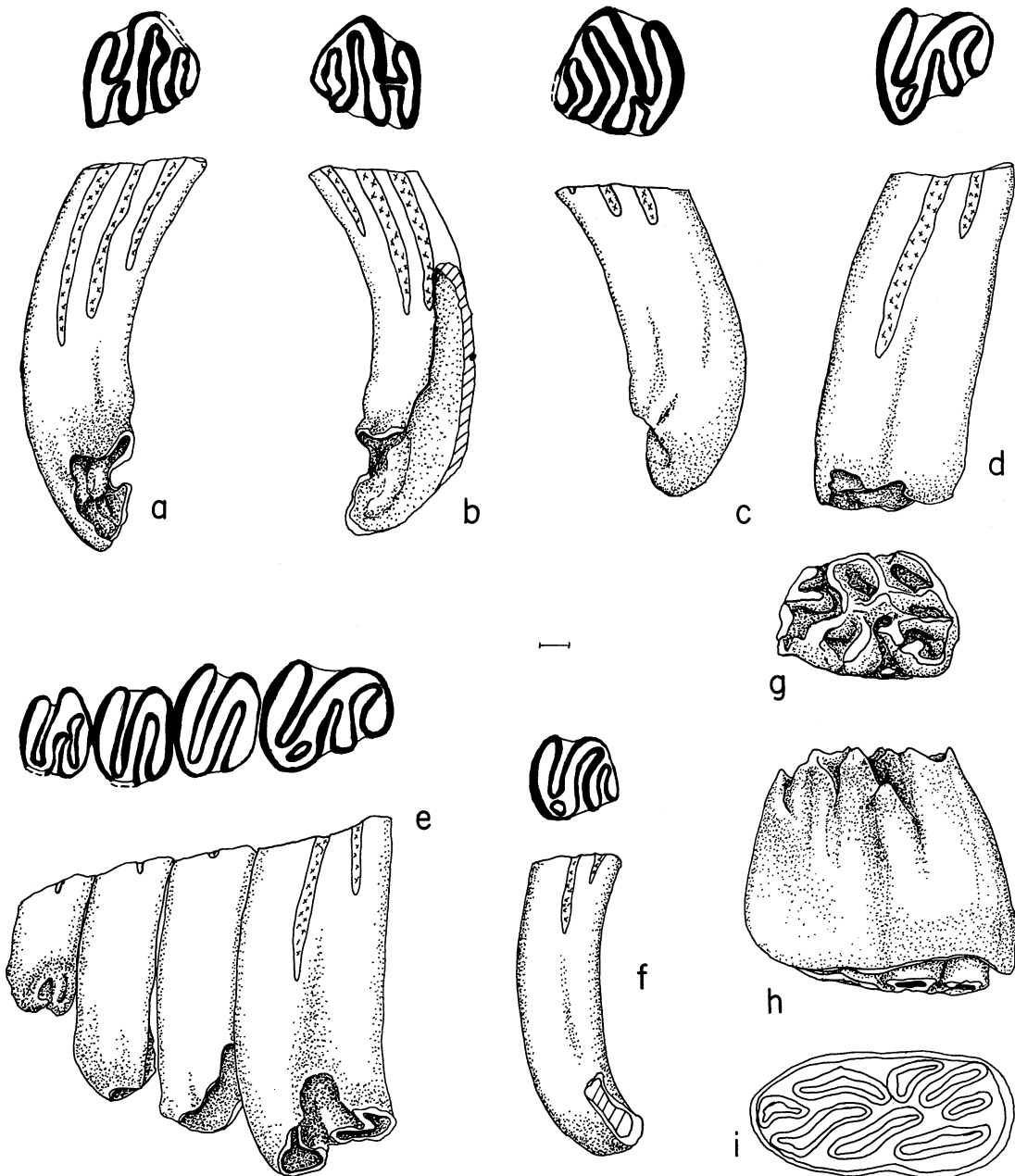
* Damaged

¹ Named for Mr. Lester F. Phillis who discovered and reported this fauna from Ogallah, Kansas.

developing before disappearance of the meta-fossettid (text-fig. 15e, d); roots develop early before wear eliminates parastrid; P⁴'s with unequal lingual striae with the parastrae usually longest, and with hypostrae persistent until roots are well formed and internal striae disappear (text-fig. 15a-c, f); anterior and pos-

terior sides of the P⁴ are parallel; posterior enamel border on the lower molars is much thicker than the anterior.

Description.—The lower dentition appears compressed anteroposteriorly with M₁ and M₂ nearly equal in size (table 13). The P₄ in early stage of wear nearly as wide as long, with



TEXT-FIG. 15—a-f, Cheek teeth of *Eucastor phillisi*, lingual and occlusal views; a, right P⁴, V41453a; b, left P⁴, V41453b; c, left P⁴, V55768; d, left P₄, V54850; e, associated lower dentition, V55765; f, upper molar, V55767. g-i, *Epigaulus minor*, right P₄, V55763, occlusal, side, and ventral views. All drawings same scale; line represents one millimeter.

TABLE 13—MEASUREMENTS OF LOWER TEETH OF *EUCASTOR PHILLISI* (in mm)

Specimen Number	P ₄		H*	M ₁		H	M ₂		H	M ₃		H
	AP*	Tr*		AP	Tr		AP	Tr		AP	Tr	
V55764 (type)	5.46	4.08	—	3.35	4.16	—	3.29	3.80	—	3.01	3.37	4.18
KU 6885	6.08	4.67	—	3.62	4.65	—	3.25	4.11	—	—	—	—
V55765	5.01	4.11	11.91	3.18	4.15	9.95	3.08	3.65	8.33	3.07	3.46	—
V55850	4.50	4.20	12.21	—	—	—	—	—	—	—	—	—
V41452	—	—	—	3.93	4.39	8.41	3.48	4.32	—	—	—	—
V54832	—	—	—	—	—	—	3.59	4.21	—	—	—	—

* AP = anteroposterior; Tr = transverse; H = height of tooth.

nearly parallel sides and the base not expanded as in *E. dividerus*.

The lower jaws are elongate but shaped generally like other *Eucastor* and *Dipoides*. The mental foramen is anterior to the base of P₄ and the dental foramen is positioned as in other *Eucastor*. The ventral projection of the angle, beginning below the posterior margin of the M₃, is more lingual than in *Castor*. The anterodorsal projection of the diastemal region anterior of P₄ is low, the symphysis being more horizontal than in other *Eucastor* and *Dipoides* with the possible exception of *E. tortus*. The posterior portion of the jaw does not have the pronounced inferior notch below the condyle as in *Castor* but instead a strong ridge runs nearly ventrad. The condyle is low and relatively massive and not inflected inward as in *Castor*. The incisor terminates in a distinct capsular process located in the extreme posterolabial border of the jaw at the base of the condyle.

The four P₄'s have three internal striae which vary in relative lengths. The parastriae are longer than or equal to mesostria. The paraflexi and hypoflexi of P₄ are tightly compressed at the inner portion of the reentrant (text-fig. 15a-c). Root closure of the upper teeth occurs during moderate wear while the striae are still quite long (table 14).

Among the postcranial elements the interesting factor is the apparent individual morphological similarities of certain elements to both *Castor* and *Ondatra*. The thoracic and pelvic limb bones show the strongest resemblance to *Ondatra* and *Neofiber*. The relatively

short and stocky humerus has a lateral condyloid crest extending to the medial portion of the shaft. The deltoid tuberosity is narrow and projects from the shaft for a distance nearly equal to shaft width. The inner condyle projection and associated fossa are similar to those of *Ondatra*.

The radius and ulna are relatively massive as in *Castor*. However, the ulna does not have the sharp anteromedial border like *Castor* but is more rounded at the margin similar to *Ondatra* and *Neofiber*.

The femur of *Eucastor phillisi* is like those of *Ondatra* and *Neofiber* in the positions and shapes of the three trochanters, the shaft configuration and the length-width ratios. Only the slight transverse broadening of the shaft in the distal portion shows a dissimilarity to *Ondatra* but is identical to *Neofiber*. The modern beaver has a short, flattened femur with the distal trochanter at and ventrad to the middle of the shaft unlike *E. phillisi*, *Neofiber*, and *Ondatra*.

Unlike *Castor*, the tibia-fibula are completely fused in the lower third of the shaft, and again the similarity of these elements to *Neofiber* and *Ondatra* is nearly perfect including the curvature, rotation of articular facets, proportions of tibia to fibula and flare of the lateral margins. The measured ratios of lengths and widths of femur to tibia in *Ondatra* and *Neofiber* are nearly identical to *E. phillisi*.

The astragalus and calcaneum of *E. phillisi* are more like *Castor* than the microtines, but differ in details from the modern beaver. Similarities of the calcaneum with *Castor* and differences from the *Neofiber-Ondatra* foot include: the rounded massive posterior part of the external surface, the large lesser process, and the absence of an extending peroneal tubercle. The astragalus, while similar to the microtines and *Castor*, has the shortened neck, the continuous internal calcaneal and head facet (scaphoid articulation) and wide external calcaneal articular facet similar to the extant beaver.

Another striking parallel to *Ondatra* and *Neofiber* is seen in the relationship of caudal

TABLE 14—MEASUREMENTS OF UPPER PREMOLARS OF *EUCASTOR PHILLISI* (in mm)

Specimen Number	AP*	Tr*	Total length	Stria length
V55769	3.27	3.05	7.64	7.08
V41453a	4.24	3.87	13.91	5.68
V41453b	4.27	4.24	15.88	7.54
V55768	4.95	4.87	11.91	1.41

* AP = anteroposterior; Tr = transverse.

to precaudal vertebrae. The anterior caudal vertebrae are much longer and more massive than the trunk. They have a thick continuous transverse process and the paired ventral and dorsal processes are nearly symmetrical. The caudal vertebrae of *E. phillisi* although differing from *Ondatra* and *Neofiber* in relative massiveness and continuation of the shelf-like transverse process are in dorsal and ventral aspect quite similar.

From the limb structure and axial skeleton the locomotion and habits of *E. phillisi* would appear to parallel closely those of the large microtines, *Ondatra* and *Neofiber*. Homologies to the Castoridae would include the tooth pattern and the tarsals and phalanges.

Comparison.—The following five species of *Eucastor* are recognized from North America; *tortus* Leidy, *dividerus* Stirton, *planus* Stirton, *lecontei* (Merriam), and *malheurensis* Shotwell. *E. phillisi* is distinguished from *E. tortus* by the larger third molars. The beaver most similar to *E. phillisi* seems to be *E. planus* Stirton (1935) which differs from *phillisi* by the unequal striids on the P_4 and the longer diastema of the lower jaw. *E. phillisi* differs from the other species by the unequal length of the internal striids on P_4 , relatively early root closure, oval to equidimensional lower premolars, relative length of the diastema, tooth pattern, tooth size, and persistence of a metafossettid.

Habit and habitat.—Semi-aquatic, fossorial. Probably wide ranging and often present over the depositional site. Habit judged to be similar to *Ondatra* and *Neofiber*.

Family SCIURIDAE

? *TAMIAS* Illiger

Several lower molars, V55782, and upper molars, V55783, compare favorably with extant *Tamias* and fit characteristics discussed by Black (1963, p. 128).

Upper molars with no or only slightly developed metaconules, proto-loph extended to protocone with small protoconule, and subquadrate in outline.

M_1 or M_2 with angular posterointernal corner and rhombic shape. M_3 outlines and cusp arrangement as in *Tamias*.

Family GEOMYIDAE

Gen. et sp. indet.

A small geomyid is assigned to the fauna on the basis of several isolated teeth (V55881 through V55887). Apparently the teeth began to close off soon after erupting. In the later wear stages (when root length equals crown height) the enamel is interrupted on the lingual and labial sides.

The teeth are isolated from their respective elements and some have been abraded and encrusted.

Habit and habitat.—Terrestrial. Fossorial. Specimens show considerable transportation thus indicating a grassland form.

Family HETEROMYIDAE

PEROGNATHUS Maximilian

The following specimens are assigned to *Perognathus*: one right and three left P^4 's (V55867 through V55870); six molars (V55875 through V55880); two jaw fragments, one with P_4 (V55871 and V55872), and a maxillary fragment with M^1 (V55873).

These teeth and jaw fragments represent a form the size of *Perognathus parvus* (Peale). The P^4 's are in three stages of early wear. The protocone is low and small and nearly isolated from the three posterior cusps. The lower P_4 has four nearly uniform-sized cusps with the mesoconid slightly smaller.

Habit and habitat.—Terrestrial. Abundant unabraded material indicates a form living close to depositional site. Probably occupied the forest or savanna area.

? Family DIPODIDAE

? Subfamily SICISTINAE

MACROGNATHOMYS NANUS Hall

Text-fig. 16c-d

A right jaw fragment bearing M_1 (V55864) compares favorably with the genus *Macrognothomys* (Hall, 1930). The tooth measures 0.96 mm long and 0.77 mm wide across the posterior cusps. The M_1 has a low mesolophid reaching the lingual margin of the tooth. Anteroconid low and rounded, projecting slightly anteriorly and nearer protoconid (text-fig. 16c-d). Klingener (per. comm.) reexamined Hall's type and noted several differences from the original illustration.

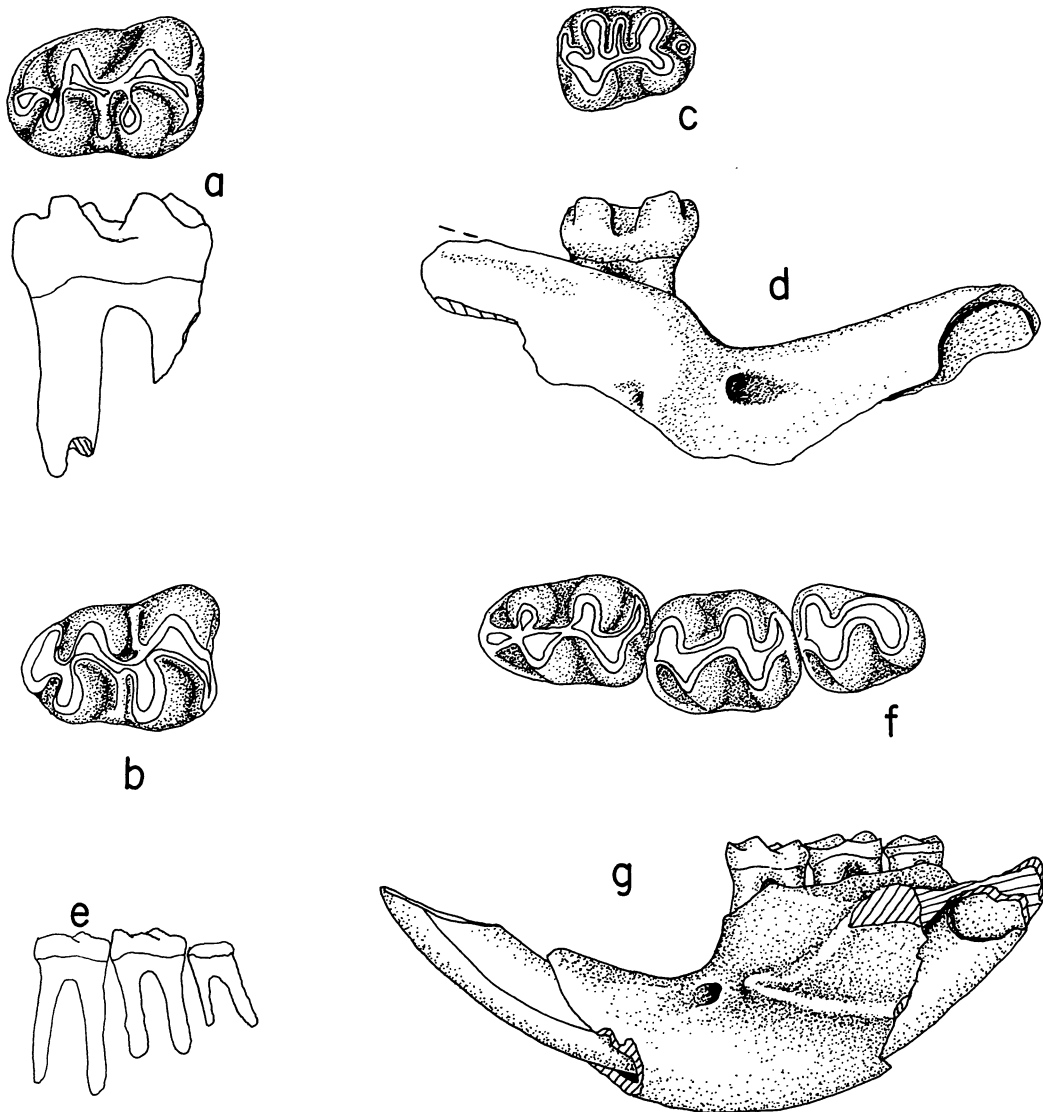
The mental foramen is directly below the lowest portion of the diastema as in *Sicista*. The M^1 is 0.96 mm anteroposteriorly; 0.77 mm transversely across the posterior cusps, and 0.62 mm across the anterior cusps.

Klingener (1966, p. 7) discusses the possible evolutionary and biogeographic positions of North American sicistines. The position of *Macrognothomys* is uncertain and a subfamily rank of either Sicistinae or Zapodinae must be tentative.

Habit and habitat.—Terrestrial, near shore. Probably a woodland sicistine.

? SICISTINAE gen. et sp. indet.

A second possible sicistine form is assigned to the fauna from a RM_1 (V55815), LM^1 and



TEXT-FIG. 16—a-b, *Peromyscus* sp., a, right M_1 , V55800, occlusal and lingual views; b, right M_1 , V55801, occlusal view. c-d, *Macrognothomys nanus*, jaw fragment and M_1 , V55864, occlusal and labial views. e-g, *Tregomys shotwelli*, holotype, left lower jaw, V55787; e, root outline from x-ray; f, occlusal view; g, labial view of jaw. Scale for upper drawings the same, e and g as indicated. Both scales indicated by lines representing one millimeter.

LM_2 (V55960). It is much larger and higher crowned than the lower jaw fragment assigned to *Macrognothomys*.

The M_1 measures 1.4 mm by 1.1 mm. The anteroconid is high and sharp. A mesolophid and small mesoconid are present. The high, pointed cusps are nearly perpendicular to the tooth base.

The M_2 has a small anteroconid with two distinct ridges running to the protoconid and metaconid. A pronounced mesolophid termin-

ates at the lingual margin of the tooth. The posterior lophid from the metaconid joining the medial portion of the tooth at a point of origin of the mesolophid is absent in the Wa-Keeney form.

Habit and habitat.—Terrestrial. Although uncertain of the association and reasons for the apparent rarity of this form, the teeth are unabraded, seem to retain the tartar staining and have very small roots which would allow the tooth to come free of the mandible or

maxilla. This form probably occupied the forest habitat, near the river margin.

? Subfamily ZAPODINAE
Gen. et sp. indet.

A ?RM¹ and ?LM¹ (V55865 and V55866) are similar to those of *Zapus* but are much less complicated and more bulbous. The pattern differs in many respects from *Megasmithus* and in general appears simplified from that illustrated by Klingener (1966, p. 6) for this species. The two teeth are zapid-like but without associated dentitions and skull material a positive taxonomic position is impossible to determine.

Family CRICETIDAE

The number of forms assigned to this family from the WaKeeney local fauna give evidence of several factors unique to the fauna. First, the exact ecological and age situation apparently has never been thoroughly sampled in the Plains before; next, the majority of cricetids were small, and zonation based on habitat types was present. At least five morphological cricetid types are present but the affinities and generic classification must remain in doubt until other samples from this age and similar paleo-habitats are known. The fossil record of Upper Miocene-Lower Pliocene cricetids is very poorly known with less than six genera recognized (Clark *et al.*, 1964, p. 42; Shotwell, 1967). Of these forms it is doubtful whether more than two or three have affinities with those of the WaKeeney local fauna.

Wood (Clark *et al.*, 1964) discusses the possible phylogenetic relationships of Late Tertiary North American cricetids and places the forms which are known from that time into a sequence where *Copemys* (*sensu lato*) would be ancestral to *Peromyscus*. From the WaKeeney local fauna the mouse assigned to *Peromyscus* and those ascribed to *Copemys* appear distinct with both genera being contemporaneous and occupying adjacent habitats. The habitat preference seems to be the forest or savanna areas which were probably quite extensive to support the large number of rodent forms present.

It is impossible to suggest affinities for most of the cricetids without material from ages prior to and following the deposition of this fauna. They are generally quite small and unique as an associated group. They exhibit, in some cases, primitive tooth characteristics quite similar to certain European forms (e.g., *Democricetodon* Fahlbush, 1964), and more advanced characters defining a cricetine which resembles extant species of *Peromyscus*.

An attempt was made to separate the cricetids on a combination of individual characters but many intergrades are noted. The following key to the WaKeeney forms will illustrate the main criteria used. Cusp terminology from Hooper (1957) and Hershkovitz (1962).

- 1a. Metaconid and protoconid of M₁ alternate. Anteroconid lingual with associated labial cingulum well developed relative to the lingual cingulum *Peromyscus* sp.
- 1b. Metaconid and protoconid of M₁ alternate. Protoconid sloping posteriad toward hypoconid forming lingual margin of tooth. Anteroconid medial 2
- 1c. Metaconid and protoconid of M₁ nearly opposite. Size small; M₁ anteroposterior length less than 1.30 mm. Cusps high and tooth bases bulbous. Masseteric ridge pronounced *Gnomomys saltus* gen. et sp. n.
- 2a(1b). M₂ wider than M₁. Size small, M₁ anteroposterior length less than 1.25 mm. Cusps low, anteroconid on M₁ medial with no accessory cusps present. Jaw thin and deep, the distance below M₁ greater than M₁-M₂ length. Posterior root of M₁ at moderate wear stage nearly twice the occlusal length of this tooth *Tregomys shotwelli* gen. et sp. n.
- 2b. Anteroconid blade-like. Metaconid separate from or attached by low thin mure to protoconid. Size moderate, M₁ length greater than 1.30 mm. Accessory cusps present 3
- 3a(2b). Cusps low with round metaconid attaching to medial mure by thin low ridge. M₁ length range between 1.35-1.45 mm. Roots relatively massive *Copemys pisinnus* n. sp.
- 3b. M₁ cusps high and tooth bulbous. Hypoconulid present. Metaconid oval and attached to anteroconid. Roots short and round. ? *Copemys*

PEROMYSCUS Gloger Text-fig. 16a-b

The following specimens are assigned to the genus *Peromyscus*: V55796 through V55801, five right and one left M₁'s; V55802 through V55807, two left and four right M₁'s; V55808, RM₂; V55847 and V55848, LM₂'s; V55809 through V55813, two LM₂'s and three RM₂'s; V55849 and V55850, a right and left M₂; and V55814, a lower jaw without teeth.

These specimens represent a small *Peromyscus*, the greatest anteroposterior length of the M₁'s not exceeding 1.5 mm (table 15). Metaconid and protoconid are alternate and the anteroconid is lingual to the midline of the

TABLE 15—MEASUREMENTS OF THE M₁ AND M¹ OF TEETH ASSIGNED TO *PEROMYSCUS* (in mm)

Specimen No.	M ₁			M ¹		
	AP*	TrA*	TrP*	AP	TrA*	TrP*
V55796	1.40	0.97	0.81			
V55797	1.38	0.95	0.79			
V55798	1.36	0.97	0.80			
V55799	1.35	0.92	0.77			
V55800	1.32	0.90	0.84			
V55801	1.43	0.98	0.83			
V55802				1.62	1.04	1.02
V55803				1.64	1.04	1.03
V55804				1.63	1.03	0.98
V55805				1.59	0.99	0.97
V55806				1.65	1.09	1.02
V55807				1.53	1.02	0.97

* AP = anteroposterior measurement; TrA = transverse measurement across anterior cusps; TrP is across posterior cusp.

tooth (text-fig. 16a-b). The anterolabial cingulum is well developed while the anterolingual cingulum is absent. A mesolophid is present on all six M₁'s with one of the anterior cingula having a low ectolophid and ectostylid.

The upper molar assigned to *Peromyscus* is nearly identical to certain extant species such as *P. polionotus*. It differs only by the absence of a bifurcate anterocone and relatively lower accessory cusps and lophes.

If correctly associated, the lower jaw relative to the teeth is massive. However, the shape of the jaw, the mental foramen, and the masseteric ridges are as in *Peromyscus*.

Habit and habitat.—Terrestrial. Probably occupied the brushy marginal zone between the forest and savanna-grassland.

TREGOMYS SHOTWELLI gen. et sp. n.
Text-fig. 16e-g

Holotype.—V55787, fragmentary left lower jaw with I, M₁-M₃.

Paratype.—V55788, left lower jaw fragment with M₁ and M₂.

Referred specimens.—V55789, RM₁; V55790, LM₂; V55791, right maxilla fragment with M¹-M³; V55793, RM¹; V55794, RM² and V55795, LM².

Type locality and age.—UM-K6-59. Ogalala Formation, Lower Pliocene.

Diagnosis.—Generic and specific diagnoses the same. A small cricetid with low-cusped, simple molars (table 16); M₁'s with medial anteroconids and subequal anterior cingula; metaconid and protoconid nearly opposite with the

posterior side of the latter sloping farther posteriorly; M₂ squarish and relatively large, wider than M₁; second lower molar with heavy cingulum on the anterolabial side; masseteric crests low, terminating anteriorly at the level of the laterally positioned mental foramen; jaw relatively thin, the depth below M₁ greater than the total length of the lower molars; M₁ length less than 1.2 mm in well worn specimens; M₃ relatively large with greatest transverse width nearly equal to other lower molars; roots on lower molars long.

Description.—The lower dentition is relatively short with the second molar the largest tooth in the series. The long rooted M₁-M₃ have no accessory cusps. The M₁ is subtriangular in shape and the M₂ is nearly square (text-fig. 16f-g). The M₃ is simple with only three cusps.

M₁ with anteroconid conical and medial with the anterolabial and lingual cingula subequal in length. Anteroconid attaches to metaconid and protoconid by an anterior mure at the junction of these two major cusps. The protoconid slopes farther posteriorly than the metaconid. A wide valley separates the metaconid and entoconid. The posterior cingulum is wide with no apparent development of a hypoconulid. The anterior root of M₁ is nearly twice the length of occlusal surface.

Cusps of M₂ are alternating low and separated by relatively wide valleys. The anterior cingulum runs dorsad onto the metaconid.

The lower third molar is nearly triangular with an "S" pattern developed after considerable wear. Apparently only one posterior cusp (the entoconid) was present.

The lower jaw is deep and transversely compressed; the molar roots extend deep into the jaw (text-fig. 16e). The masseteric ridge terminates below the anterior part of M₁. The inferior crest is much more pronounced than

TABLE 16—MEASUREMENTS OF *TREGOMYS SHOTWELLI* (in mm)

Measurements	V55787 (Type)	V55788* (Paratype)
I, anteroposterior	1.01	
I, transverse	0.53	
M ₁ , anteroposterior	1.19	1.19
M ₁ , transverse—posterior	0.82	0.82
M ₁ , transverse—anterior	0.72	0.75
M ₂ , anteroposterior	1.05	1.10
M ₂ , transverse	0.86	0.85
M ₃ , anteroposterior	0.93	
M ₃ , transverse	0.79	
M ₁ -M ₃ , anteroposterior	3.16	
Depth Ramus below M ₁	3.31	
Diastema length	2.81	

* Abraded

¹ Generic name for Trego County, Kansas. Specific name for Dr. J. Arnold Shotwell, Museum of Natural History, University of Oregon, who has worked with many Upper Tertiary mammals and in particular the cricetids.

the superior one. The mental foramen is on the labial side of the jaw. The incisor is very flat with the dorsoventral depth nearly twice the transverse width (table 16).

The maxilla (V55791) with M^1 - M^3 referred to *Tregomys shotwelli* is abraded but shows several characters consistent with the type. The low cusps on all molars are nearly adjacent. The M^3 is large and rounded. The M^2 and M^3 both exhibit a concave anterior margin for placement of the adjacent tooth.

Habit and habitat.—Terrestrial. This form probably occupied a savanna or marginal grassland some distance from the depositional site.

GNOMOMYS SALTUS¹ gen. et sp. n.
Text-fig. 17a-c

Holotype.—V55826, partial right lower jaw bearing a nearly unworn M_1 .

Paratypes.—V55827, right lower jaw fragment with M_1 ; V55828, a right jaw fragment with M_1 ; V55828, left M_1 ; V55830, LM_1 ; V55841, RM_1 ; and V55829 a right lower jaw without teeth.

Referred specimens.—V55832, RM_1 ; V55834, LM_1 ; V55835, LM_1 ; V55836, LM_2 ; V55837, RM_1 ; V55838, RM_2 ; V55839, RM_2 ; V55840, LM_2 ; V55843, RM_1 ; V55844, RM_2 ; and V55825, jaw fragment with M_1 .

Type locality and age.—UM-K6-59. Ogallala Formation. Lower Pliocene.

Diagnosis.—A very small cricetid with simple bulbous and moderately high cusped teeth; anterior bases of metaconid and protoconid opposite on M_1 ; anteroconid a simple medial cusp with cingula subequal in length; anteroconid joins protoconid by low narrow mure; lower jaw small with masseteric crests terminating as distinct knob high on jaw below anterior root of M_1 ; mental foramen relatively large and on the labial side of the diastema.

Description.—The lower first molar of *Gnomomys saltus* is bulbous (text-fig. 17a-c) with high pointed cusps. The rounded major cusps on the M_1 's are projected vertically from the tooth base. The M_1 is two-rooted, the posterior

root greatly enlarged and more oval relative to the anterior one. The metaconid is connected to the protoconid by a narrow mure in the early wear stages. All M_1 's are extremely small with the greatest anteroposterior diameter being 1.28 mm (table 17).

The dentaries containing the M_1 's and the edentulous jaw show a characteristic terminal knob and an upper curved portion of the masseteric crest.

Other teeth are referred to *Gnomomys saltus* on the basis of crown height, and cusp arrangement. The five upper first molars are small, the occlusal length ranging between 1.2 and 1.28 mm (table 17). These teeth have heavy cingula originating at or surrounding the anterior margin of the anterocone which runs posteriad to the base of the hypocone and completely surrounds the protocone. The M_1 's present a square outline with corners all approaching or equaling 90°. The roots are long on the M_1 's; the two posterior ones with nearly equal posterior margins.

Discussion.—Klingener (in press) in a description of the Norden Bridge rodent fauna discusses a small unassigned muroid M_1 . From his description it would seem that this tooth matches the type described under the new genus *Gnomomys*.

The dental pattern and size distinguish *Gnomomys saltus* from other previously described Miocene or Pliocene cricetids, and from those in this fauna. The adjacent metaconid and protoconid are different from extant cricetids from North America. The amount of tooth variation appears extreme in this form and strongly suggests more than a single species.

Habit and habitat.—Terrestrial. Near river margin. A woodland form is indicated.

COPEMYS PISINNUS¹ n. sp.
Text-fig. 17d-e

Holotype.—V55819, lower jaw bearing M_1 and M_2 .

Paratypes.—V55820, left lower jaw with M_1 ; V55822, a right M_1 ; V55855, a right M_2 .

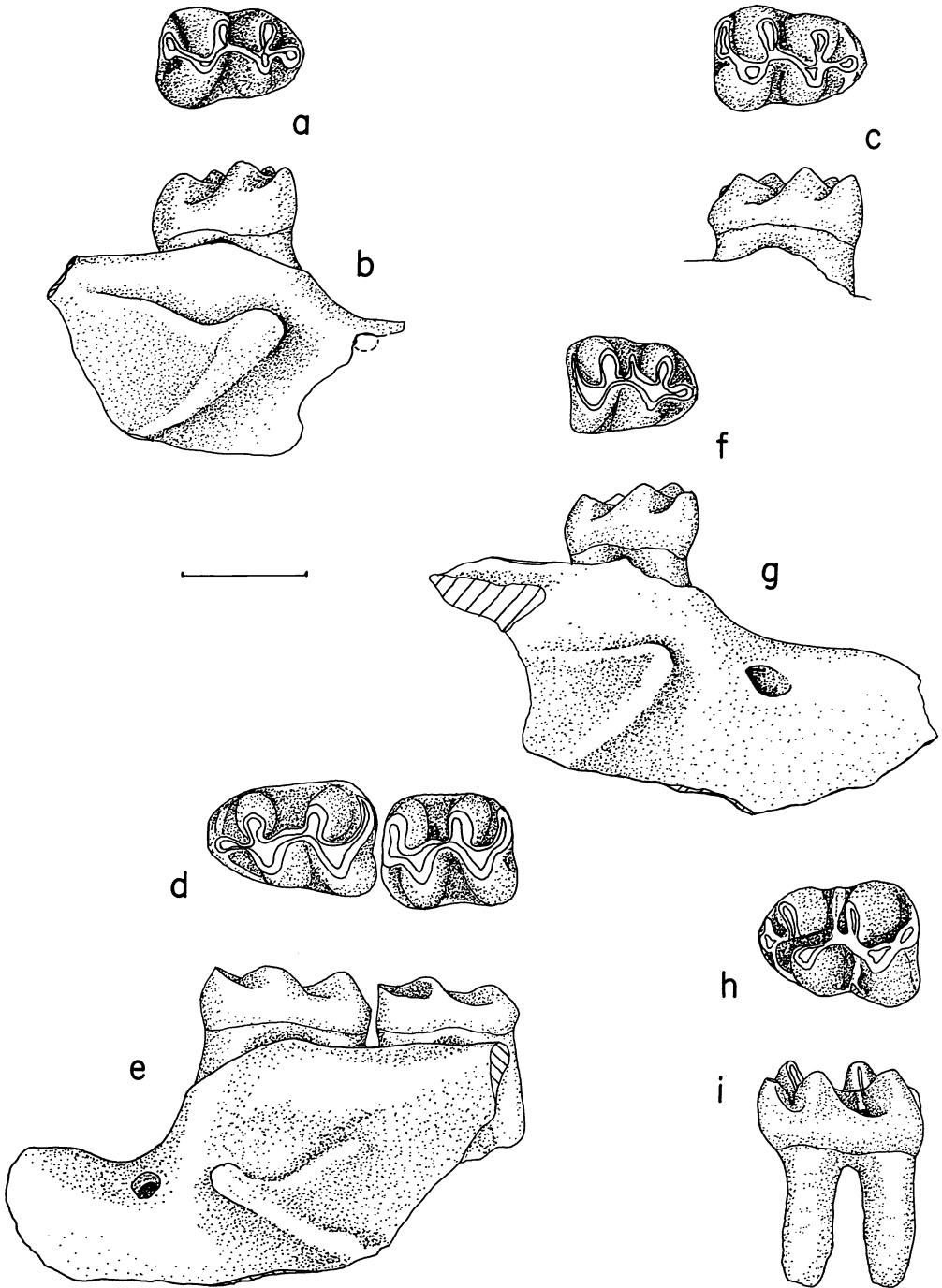
Type locality and age.—UM-K6-59. Ogallala Formation, Lower Pliocene.

¹ *pisinnus*. L. meaning "small or little."

TABLE 17.—MEASUREMENTS OF M_1 'S OF *GNOMOMYS SALTUS* (in mm)

Measurement*	Type	Paratypes					
	V55826	V55825	V55823	V55827	V55828	V55830	V55841
AP	1.20	1.19	1.25	1.28	1.25	1.23	1.20
TrA	0.82	0.81	0.89	0.97	0.91	0.91	0.88
TrP	0.71	0.70	0.70	0.82	0.78	0.82	0.73

* AP = anterior posterior; TrA = transverse measurement across anterior cusps; TrP = transverse measurements across posterior cusps.



TEXT-FIG. 17—Cricetidae, a-b, *Gnomomys saltus*, holotype, right M_1 and dentary fragment, V55826, occlusal and labial views. c, *G. saltus*, right M_1 , occlusal and labial views. d-e, *Copemys pisinnus*, holotype, left lower jaw with M_1 and M_2 , V55819, occlusal and labial views. f-g, cricetid indet., right jaw fragment with M_1 , V55825, occlusal and labial views. h-i, cf. *Copemys*, left M_1 , V55816, occlusal and labial views. Same scale for all drawings, line represents one millimeter.

Diagnosis.—A small cricetid (table 18) with medial anteroconid and moderate alternation of metaconid and protoconid on M_1 ; a relatively small round metaconid attaches low to the medial mure by a thin ridge, being nearly isolated from the protoconid; M_2 with small anteroconid and mesolophid; M_2 as wide as M_1 ; lower molars with long oval roots, the posterior root of M_1 nearly as wide as transverse diameter of the tooth.

Description.—The anteroconid of M_1 is a high sharp cusp with subequal lingual and labial cingula. The protoconid extends far posterior, compromising the labial margin of the M_1 . A mesostylid is present on M_1 and M_2 . There is no hypoconid on either M_1 or M_2 (text-fig. 17d-e).

Copemys pisinnus differs from the *Peromyscus* in the fauna by position of the anteroconid, the shape of the metaconid and protoconid, their degree of alternation, and shapes and lengths of roots. The M_1 of *C. pisinnus* is more pointed anteriorly than those of *Peromyscus*.

Copemys pisinnus differs from the type of *Copemys*, *C. loxodon* (Cope), by its smaller size, and wider area between the anteroconid and metaconid. However, the posterior slope of the protoconid, cusp alternation, and positions of cingula conform closely to those of the genus *Copemys* as described by Wood (1936).

Habit and habitat.—Terrestrial. The specimen condition indicates a forest and near stream margin form.

cf. COPEMYS Wood
Text-fig. 17h-i

One left M_1 (V55816, text-fig. 17h-i) and a right M^1 (V55818) are markedly different from the teeth assigned to *Peromyscus* and *Copemys pisinnus*. They exhibit many characteristics of *Copemys* as originally described (Wood, 1936, p. 5). The M_1 is relatively high crowned with the sharp anteroconid medial and low. Metaconid is separated from protoconid by a deep groove, the anteroconid attaching only to the protoconid. A well-developed mesolophid and

ectolophid are present. The posterior arm of protoconid extends posteriad as a distinct marginal crest to the hypoconid base interrupting the ectolophid. Roots are relatively short and round. The size (table 19), metaconid separation, slight alternation of cusps, and position and shape of anteroconid suggest a form related

TABLE 19—MEASUREMENT OF LM_1 AND RM^1 ASSIGNED TO *CF. COPEMYS* (in mm)

Specimen No.	AP*	TrA*	TrP*
V55816	1.42	0.90	1.07
V55818	1.87	1.14	1.15

* AP = anteroposterior; TrA = transverse measurement across anterior cusps; TrP = transverse measurement across posterior cusps.

to *Copemys*. The upper molar has a bifurcate anterocone and like the M_1 has high cusps.

Habit and habitat.—Terrestrial. Probably a large, rare woodland mouse.

Cricetid gen. et sp. indet.
Text-fig. 17f-g

A lower jaw of an old adult with M_1 - M_3 (V55821), molars completely worn, is unassignable to any of the previously described cricetids.

This cricetid was moderate in size with occlusal length of 3.72 mm (table 20). The upper masseteric crest is traceable only for a short distance posteriad. A large mandibular foramen is located in a shallow fossa between the M_3 and the ascending ramus which is much different from the condition observed in *Tregomys* and *Copemys pisinnus*.

A very small jaw fragment with the M_1 (V55825) is not assignable to the species and genera described. It seems to differ from the M_1 's assigned to *Gnomomys* by the following: a mesolophid is present, the anteroconid is sharp and the metaconid is round and nearly isolated from the protoconid. No posteroconulid is developed (text-fig. 17f-g).

TABLE 20—MEASUREMENT OF CRICETID LOWER JAW (V55821) REFERRED TO AS CRICETID GEN. ET SP. INDET. (in mm)

Measurement	Value*
M_1 , anteroposterior	1.40
M_1 , transverse	0.97
M_2 , anteroposterior	1.28
M_2 , transverse	0.99
M_3 , anteroposterior	1.05
M_3 , transverse	0.82
Total occlusal length	3.72
Depth of ramus below M_1	3.98

* Measurements taken on very worn teeth.

TABLE 18—MEASUREMENTS OF *COPEMYS PISINNUS* (in mm)

Measurement	Type	Paratypes	
	V55819	V55820	V55822 V55855
M_1 , anteroposterior	1.41	1.35	1.44
M_1 , transverse-anterior	0.80	0.77	0.85
M_1 , transverse-posterior	0.98	0.95	1.00
M_2 , anteroposterior	1.19		1.21
M_2 , transverse	0.97		1.01

Order LAGOMORPHA
 Family LEPORIDAE
 ? HYPOLAGUS Dice

About 40 isolated teeth and several postcranial elements (V54840, V56144–V56146) are from a small rabbit the size of *Hypolagus*. No associated dentitions or lower P₃'s were obtained, making a more definite taxonomic assignment impossible.

The rabbit probably occupied a marginal ecological position between the forest and grassland habitats. The individual specimens although not indicating a great amount of transportation are separated and broken, probably by stream transportation. The extreme fragility of rabbit cranial material, distance to the site, and size selection by the stream accounts for the relatively abundant yet disassociated material.

Order ARTIODACTYLA
 Family CAMELIDAE *
 ? PROCAMELUS Leidy

A fragmental dentary with fractured M₁ and M₂ (V56147) was collected from the lower flood plain deposit (Unit A, Fig. 2A) about 100 feet due west of KU Trego County Loc. 29. It was collected by Claude W. Hibbard in 1967.

Although the size is comparable to *P. grandis* Gregory (1942) the condition of the specimen warrants only a tentative generic designation.

A calcaneum (V56154) picked up as surface float at KU Loc. 29 is tentatively assigned to *Procamelus*.

Habit and habitat.—Terrestrial and far from site. Grassland perhaps above the flood plain itself.

Family ANTILOCAPRIDAE
 ? MERYCODUS Leidy

The posterior portion of a skull (V56148), several teeth (V56149), and postcranial elements (V56150) are tentatively assigned to the small antilocaprid *Merycodus*.

No horns were present on the preserved portion of the skull (broken through the anterior portion of orbits).

The distance from the glenoid cavities to the condyles in the fossil skull is relatively greater than in the extant genus. The presphenoid is massive and ventrally rounded into a keel and differs from the sharp linear process in *Antilocapra*.

The six teeth are brachydont, well rooted and most likely represent premolars of the small antilocaprid.

The absence of horns and associated dentition makes the assignment of the small artio-

dactyl nearly impossible. However, the basiocranium corresponds most closely with Antilocapridae and would thus seem to allow the suggestion of this group rather than the Cervidae, or other Upper Tertiary families.

Habit and habitat.—Terrestrial. Material suggests a form living near the depositional site. Probably a woodland-savanna form.

Order PERISSODACTYLA
 Family EQUIDAE

Morris F. Skinner, of the Frick Laboratory The American Museum of Natural History, assigned the following horses from the Trego County deposits.

ASTROHIPPIUS Stirton

Astrohippus is assigned on four upper cheek teeth; V54858, V56151, V56153 and V54843. These teeth were collected from KU Trego County Loc. 29.

NEOHIPPARION cf. *N. AFFINE* (Leidy)
 Two upper molars (V56156) from KU Loc. 29 are placed in *N. cf. affinis*.

NEOHIPPARION cf. *N. OCCIDENTALE* (Leidy)
 Three upper cheek teeth, V54859, V54857 and V54853 are assigned to the *occidentale* group by Morris Skinner. They were obtained from KU Loc. 29.

HIPPARION cf. *H. LENTICULARIS* (Cope)
 Two upper cheek teeth 6889 (Univ. of Kansas) and V54860 were compared with *H. lenticularis*.

cf. PLIOHIPPIUS Marsh

A lower tooth (V56152) compares most closely with that of *Pliohippus*. It was the only horse tooth obtained at UM-K6-59 during the screening process.

cf. GRIPHIPPUS Quinn

V54856, an upper molar, is comparable to *Griphippus* according to Morris Skinner. This tooth was collected from KU Loc. 29.

Order PROBOSCIDEA
 Family INCERTA SEDIS

A single phalange (V56158) from a relatively small proboscidean was found in the main screening site, UM-K6-59. It probably is from a member of either the gomphotheriids or mammutids, comparing closest with these two groups.

Habit and habitat.—Terrestrial. Distant to site but data inconclusive.

Vertebrata indet.

Several coprolites were obtained from the screening site UM-K6-59. To the ecological in-

ferences of the site these would support the idea that a portion of the fauna was deposited under conditions approaching a quiet or standing water situation. These remains, the basal clay and excellent condition of many fossils are taken together to indicate a phase of nearly stable deposition without any great effects from the river current.

CONCLUSIONS

The WaKeeney local fauna is a Lower Pliocene vertebrate assemblage. The earth history of this site can be interpreted from the geological data and the faunal types recovered.

The sedimentary deposit displays geologic characteristics such as crossbedding and well-sorted quartzose sand of a stream or river deposit. The fishes indicate a water habitat that was close to or within a large stream or river. The fish assemblage further indicates that the river had a low gradient, aquatic vegetation was present, and the water was nearly free of suspended clastic material.

The amphibians, reptiles, birds, and mammals indicate that the deposit accumulated at the river margin. They suggest the general areas of adaptation, including an arboreal environment which bordered the river and a savanna and grassland environment some distance from the depositional site.

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