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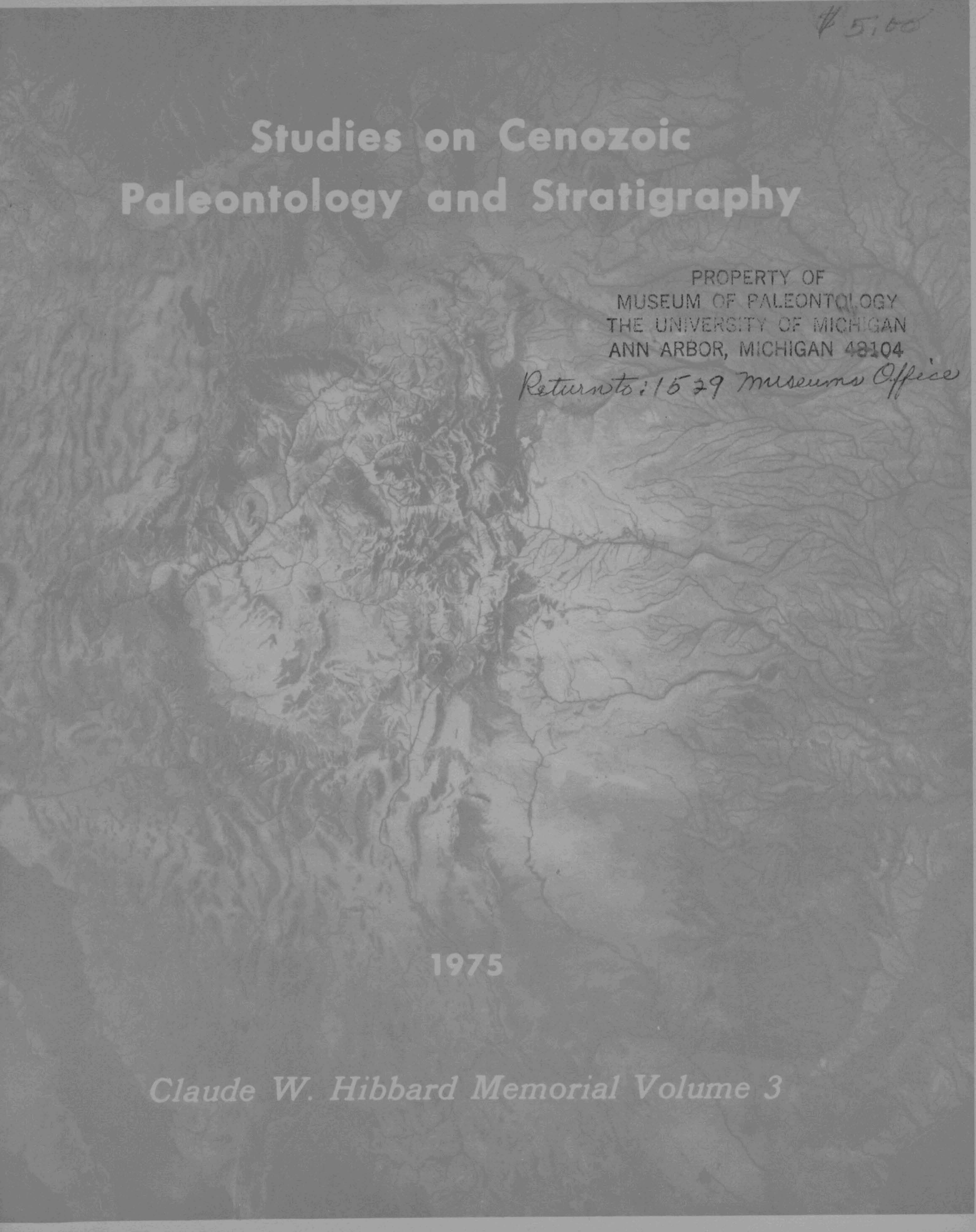

1975

Claude W. Hibbard Memorial Volume 3

CLAUDE W. HIBBARD MEMORIAL VOLUMES (1-5)

Index and Bibliography of Late Cenozoic Freshwater Mollusca of Western North America
Dwight W. Taylor

The Fossil Catfishes of North America
John G. Lundberg

Studies on Cenozoic Paleontology and Stratigraphy
(Papers Presented at Hibbard Memorial Symposium, May, 1974, in Ann Arbor)

Geology and Paleontology of the Early Pleistocene Belleville Formation of North-Central Kansas
Ralph E. Eshelman

Fishes of the Pliocene Glenns Ferry Formation, Southwest Idaho
Gerald R. Smith
and
Fishes of the Miocene-Pliocene Deer Butte Formation, Southeast Oregon
Peter G. Kimmel

Museum of Paleontology
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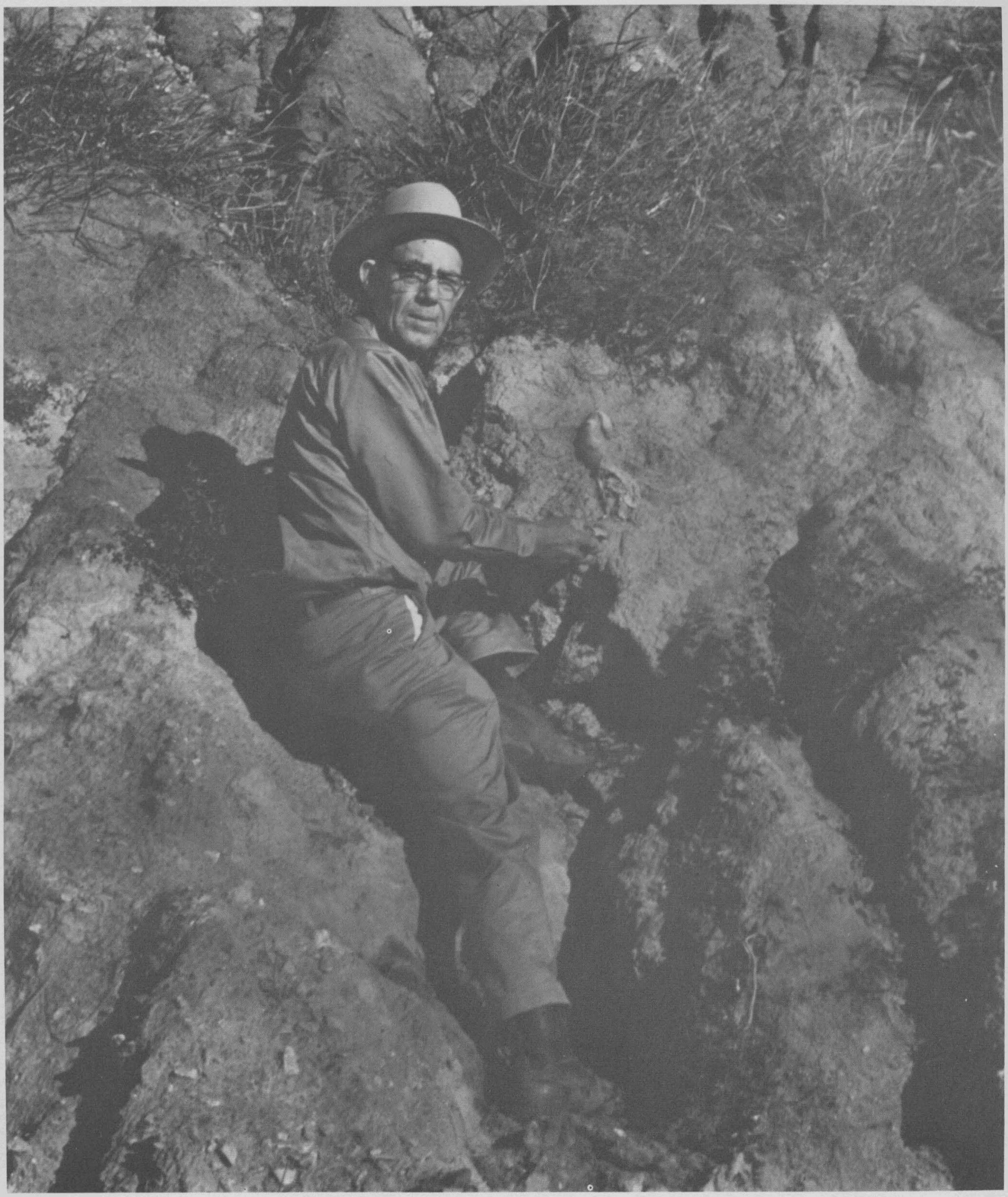
Ann Arbor, Michigan 48104

STUDIES ON CENOZOIC PALEONTOLOGY AND STRATIGRAPHY



Hibbie, 1969

Studies on Cenozoic Paleontology and Stratigraphy

in honor of

Claude W. Hibbard

Curator of Vertebrates, Museum of Paleontology
and
Professor of Geology and Mineralogy
University of Michigan

Edited by
G.R. Smith and N.E. Friedland

1975

Museum of Paleontology
The University of Michigan
Ann Arbor, Michigan 48104

Claude W. Hibbard Memorial Volume 3
Papers on Paleontology No. 12
The Museum of Paleontology
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Gerald R. Smith, Director

APPRECIATION AND ACKNOWLEDGMENT IS EXPRESSED TO THE 1962 CLASS OF THE UNIVERSITY OF MICHIGAN FOR ESTABLISHING AN INSTITUTE OF SCIENCE AND TECHNOLOGY PUBLISHING FUND. THIS FUND AND A CONTRIBUTION BY DWIGHT W. TAYLOR HAVE AIDED IN THE PUBLICATION OF THIS WORK.

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Claude Hibbard appreciated the reasons behind the malapropism, "fest me no more schrifts." But since there are too few other ways to honor the memory of a colleague, we present here a collection of papers that were prepared for the symposium held in his honor May 6 and 7, 1974, at The University of Michigan. The symposium was attended by more than 80 persons; 34 papers were given. The following persons contributed papers to the symposium but are unfortunately not represented in the memorial volumes: Jiri Zidek, Mark Wilson, John W. Cosgriff, Jr., T.N. Todd, Joe A. Tihen, Charles J. Chantell, Robert E. Preston, Charles Meszoely, Ken Campbell, Paul Ramaekers, Russell B. King, C.S. Churcher, John E. Guilday, John A. Howe, William D. Turnbull, John A. Wilson, Margaret S. Stevens, John B. Stevens, John Boellstorff, Michael W. Hager, Gerald E. Schultz, Holmes A. Semken, and Ronald O. Kapp.

Claude W. Hibbard was born in Toronto, Kansas, on March 21, 1905. His early professional training was at the University of Kansas, where he received his Bachelor of Arts degree in 1933 and his Master of Arts degree in 1934. During 1934-35 he was a wildlife biologist with the U.S. National Park Service in Kentucky. He received his Doctor of Philosophy degree in zoology from The University of Michigan in 1941.

During his graduate studies and until 1946 he taught zoology, headed field work, and served as curator of vertebrates at the Museum of Natural History, University of Kansas. He was a member of The University of Michigan faculty from 1946 until his sudden death at the Museum of Paleontology on October 9, 1973.

His broad interests are illustrated by his participation in scientific societies: American Society of Mammologists (Board of Directors), American Ornithological Union, American Society of Ichthyologists and Herpetologists (Board of Governors), the Paleontological Society, Society of Vertebrate Paleontology (Secretary-Treasurer, Vice-President, President), Geological Society of America (Fellow), Kansas Academy of Science (Vice-President, President), Sigma Xi, Phi Sigma, American Geological Institute (Board of Directors), Michigan Geological Society (President), and Michigan Academy of Science, Arts, and Letters (President). He served on the editorial board of "Quaternary Research." In 1967 the University of Kansas honored him with the Erasmus Haworth Distinguished Alumni Honors in Geology. He was the author of about 160 scientific publications and more or less guided through publication more than 50 projects by students in his vertebrate paleontology classes, in addition to supervision of graduate students. He was extraordinarily generous of his materials and time to these student projects, and insisted that the students enjoy sole authorship for their work and ideas. He was an intellectually demanding person, deeply committed to the study of life of the past. His influential philosophy combined the pragmatism of a Kansas farmer with the scholarly curiosity of the great naturalists of the last century. It was a source of great pleasure and satisfaction to him to guide students through their research.

Among his major scientific contributions, three will have the most lasting influence: his development of the faunal sequence for the Plio-Pleistocene rocks in the area of southwest Kansas and northwest Oklahoma, his recognition of evidence for climatic equability in the distributional data for taxa represented in certain Pleistocene faunas, and his development of the large-scale wet-screening technique for fossil concentration.

The painstaking construction of the stratigraphic and faunal framework for the southwestern plains Plio-Pleistocene sequence was the primary object of the nearly 40 field seasons and the incredibly long work-days and work weeks. This monument is still appreciated by too few (a depreciative reference to preoccupation with faunal lists and stratigraphy, written by a leading paleontologist, was one of the most frustrating disappointments in Hibbard's career). At the time of his death it looked as if the major anomalies were being resolved by the chronological information from the ash investigations, and the framework was beginning to resemble the final picture. Many of the papers in this volume contribute to that picture, but without Hibbard the final summary will probably take many more years to develop. The history and current status are reviewed here by Rick Zakrzewski.

In a paper still in preparation, Holmes Semken will discuss the climatic implications of the faunas with discordant zoogeographic elements, a phenomenon first noted in print in 1952 and developed more thoroughly in Hibbard's analysis of the Jinglebob fauna in 1955.

The development of the washing method is presented here in a historical perspective written in a letter to Prof. W.G. Kühne. Naturally, the raconteur touches on a number of other points of special interest to us at this time. With Prof. Kühne's permission, the letter is reproduced here in its entirety (except certain references to eras long-since passed, deleted to preserve the good will of our colleagues in New York).

Excellent biographies of Claude W. Hibbard have been written by Holmes Semken and Rick Zakrzewski (J. Mamm. 56:275-279), Jack Wilson (GSA Memorial, 1974, with bibliography), and Jack Dorr (SVP Bull. 100:59-60), but all of the stories have not been told; perhaps a full history can be assembled while the essential memories are still extant.

A set of volumes like these, but achieving a more definitive summary, was conceived in 1970 by Dwight Taylor. However, the essential source of information and the intended recipient of the honor departed too early. The present volume is therefore just a collection of papers along the way; we hope that they will prove useful in continuing the work.

Many people helped in the preparation of the symposium and this volume: Krystina Butterfield, J.A. Dorr, Jr., James A. Doyle, William R. Farrand, Philip D. Gingerich, Robert Habetler, Ocie M. Hess, Faye Ganfield Hibbard, Robert V. Kesling, Peter G. Kimmel, Russell B. King, Karoly Kutasi, Gerald P. Larson, Gladys Newton, Janet Rudolph, Holmes A. Semken, and Dwight W. Taylor. The frontispiece was provided by Clayton and Caroline Griggs of McPherson, Kansas. The picture was taken during the early summer of 1969 at the White sand and gravel pit, just north of Kanopolis, Kansas.

Finally, I thank all of the participants in the Symposium for their interest and help in honoring Claude W. Hibbard.

GRS

CONTENTS

THE CLASSIFICATION OF OGALLALA SEDIMENTS IN WESTERN NEBRASKA

John Breyer

Abstract.– During the Pliocene, aggrading streams in western Nebraska filled and buried a pre-existing valley system cut deep into Miocene and Oligocene rocks. The alluvial deposits of these streams consist chiefly of sands and silts, but significant amounts of coarser material are present. The gravels are composed largely of granitic debris. Quartz and orthoclase are the most abundant minerals in the sand-size fraction. Shades of pink and red predominate among the sands and silts, but zones with abundant calcium carbonate cement are gray in color. The sediments are characterized by frequent vertical changes in lithology and the limited lateral extent of individual units. The highest remnants of the Ogallala deposits are often capped by a thick caliche deposit. The Ogallala sediments of the study area form a single rock-stratigraphic unit for which the name "Ash Hollow" seems most appropriate.

INTRODUCTION

The Ogallala sediments in western Nebraska occupy and blanket a pre-existing valley system cut deep into Miocene and Oligocene rocks. The topography of the pre-Ogallala surface is dominated by a series of east-west trending valleys and divides (Figure 1). The surface drops to the east at a rate of 23 feet per mile. The sediments consist chiefly of sands and silts but significant amounts of gravel and gravelly sand are present. The sediments are characterized by frequent vertical changes in lithology and the limited lateral extent of individual units (Plate 1).

Lithology

The composition of the Ogallala gravels in this area has been described by Stanley (1971) and Stanley and Wayne (1972). Granitic fragments are the most abundant rock type in the gravels (Table 1). The largest clasts of separate gravel bodies show a marked disparity in size (Table 2).

The sands and silts range in color from shades of pink (5YR 8/3, 8/4, 7/3, 7/4) and red (10YR 6/1, 6/2, 6/3) to brown (5YR 6/3, 6/4). Zones with calcium carbonate cement are more resistant to weathering, forming ledges that are often gray (5YR 8/1, 7/1, 6/1) in color. The sand size fraction of the sediments consists chiefly of quartz and orthoclase. Microcline and plagioclase are present in smaller amounts. Heavy minerals and opaques constitute less than 5% of the 2.0-2.25ϕ size interval. Volcanic shards are the dominant constituent of some sands.

The highest remnants of the Ogallala deposits in this area are often capped by a thick accumulation of calcium carbonate, the Ogallala-climax soil, or High Plains caliche. Cupped pebbles, horizontal laminae, and signs of brecciation and recementation are abundant at this horizon. The calcium carbonate content decreases gradually downward. Coarse sand and gravel may be present even at the highest horizons. The structures and textures of the carbonate layer resemble those described by Aristarain (1970) and Reeves (1970) in the Ogallala caliche deposits of the southern High Plains.

DISTRIBUTION OF SEDIMENT TYPES

A section normal to paleoslope reveals frequent vertical and horizontal changes in lithology (Plate 1). The vertical changes were examined using a statistical tech-

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Texas Christian University, Department of Geology, Fort Worth, Texas, 76129.

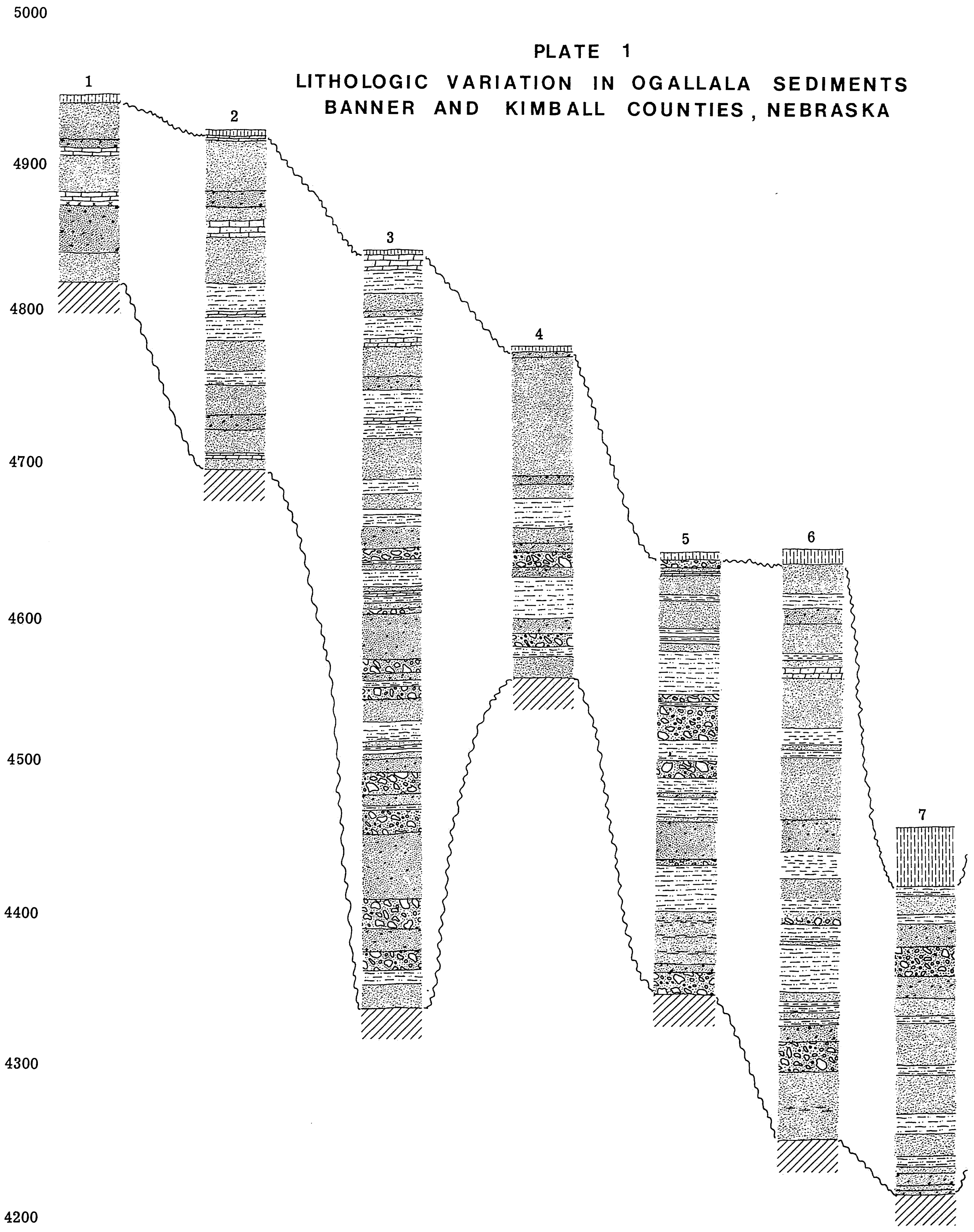
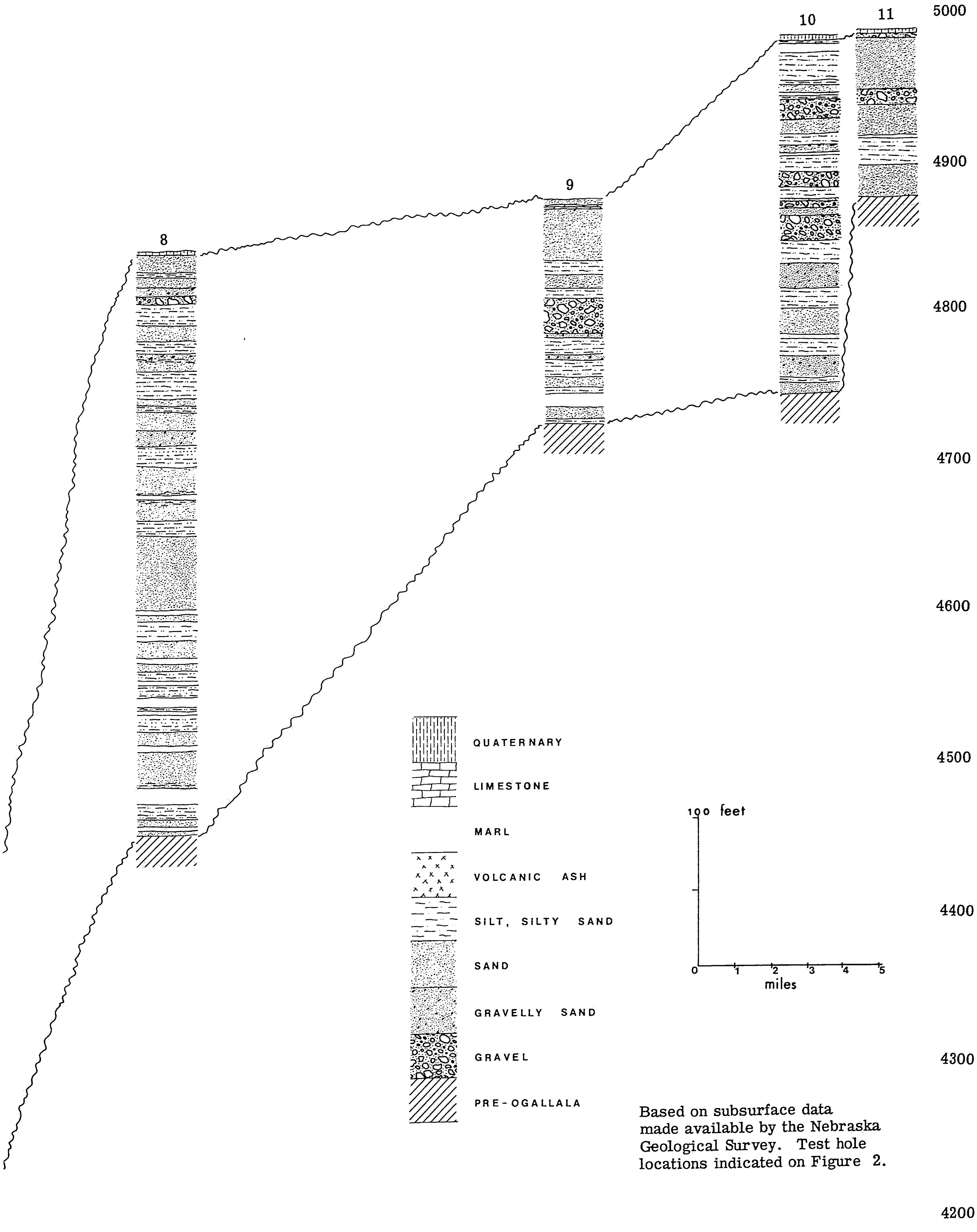


PLATE 1
LITHOLOGIC VARIATION IN OGALLALA SEDIMENTS BANNER AND KIMBALL COUNTIES, NEBRASKA



Based on subsurface data made available by the Nebraska Geological Survey. Test hole locations indicated on Figure 2.

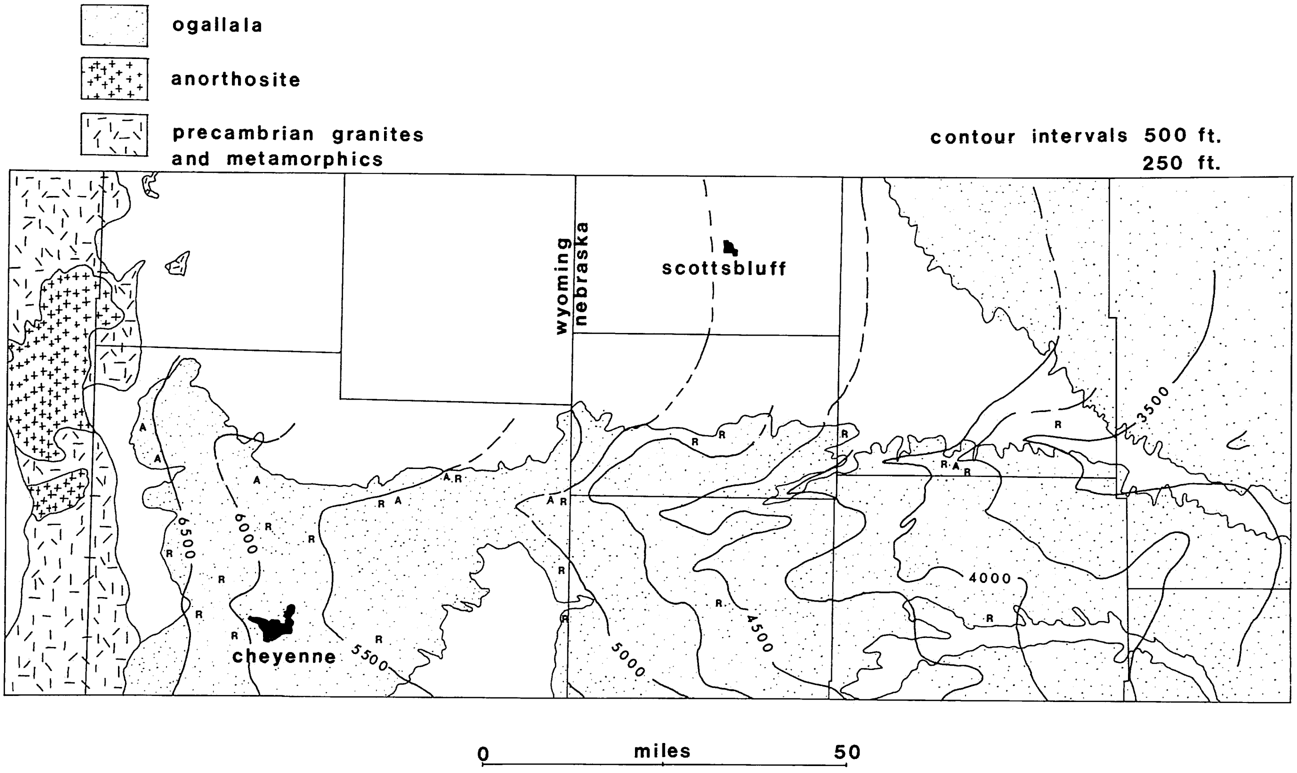


Fig. 1. Topography of the pre-Ogallala surface, eastern Wyoming and western Nebraska. Nebraska contours based on field mapping by the author and more than 200 well logs made available by F.A. Smith of the Nebraska Geological Survey. A=anorthosite bearing gravel. R=rhyolite bearing gravel. Gravel data and Wyoming contours through the courtesy of K.O. Stanley.

Table 1. Average composition of Ogallala gravels (-4.0 to -4.5 phi size interval) in western Nebraska. Quartz and orthoclase pebbles tabulated as granitic clasts. After Stanley (1971).

	Sidney	Bridgeport	Kimball	Greenwood Canyon	Oshkosh
Clast					
Granitic	73	75	90	84	89
Anorthosite	0	trace	2	0	0
Metamorphic	15	15	5	7	4
Sedimentary	5	0	1	0	4
Volcanic	7	10	2	4	1
	100%	100%	100%	95%	98%

nique known as Markov chain analysis in an attempt to detect repetitive lithologic sequences. A transition count matrix for the test holes used to construct Plate 1 is given in Table 3. The matrix records the number of times that all possible vertical lithologic transitions occur. A chi-square test was used to determine which transitions occur at greater than random frequencies. These transitions are indicated by X's in the table.

Only four of the fifty-six transitions occur at greater than random frequencies. The distribution of sediment types in a vertical section is largely random. Coarsening-upward transitions occur as often as fining-upward transitions. Coarsening-upward alluvial sequences are considered diagnostic of braided streams (Costello and Walker, 1972). Costello and Walker argue that reactivation of abandoned stream channels during flood stage produces coarsening-upward sequences. After periods of maximum flow, the decreasing competency of streams, subject to fluctuations in discharge, produces fining-upward alluvial sequences. The scour-and-fill associated with lateral channel migration truncates initial depositional sequences and produces a random vertical distribution of sediment types in the deposits of braided stream systems.

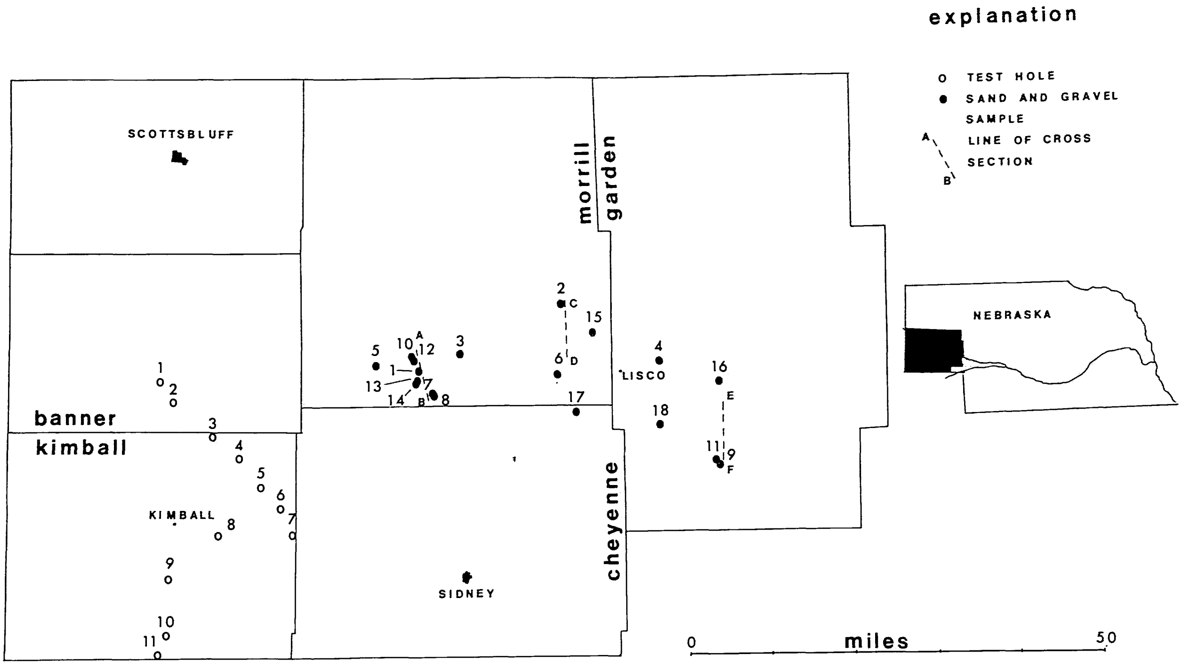


Fig. 2. Index map.

The concentration of gravels and gravelly sands in the lower half of test hole 3 accounts for slightly more than one-third of the gravel-gravelly sand and gravelly sand-gravel transitions in the 11 holes. The preponderance of coarse material at this location (Plate 1) argues for a greater stream competency here than elsewhere at this horizon. The narrow valley in which the stream flowed at this point could have placed restrictions on the width of the channel thereby increasing stream competency.

During the Pliocene, aggrading streams in western Nebraska filled and buried a valley system cut deep into pre-Ogallala rocks (Figure 3). Braided streams flowing eastward from the mountain front deposited a heterogeneous sequence of silts, sands, and gravels. The sediments consist chiefly of granitic debris. The complex nature of the deposit and the random spatial distribution of sediment types are the imprint of the depositional mechanism, i.e., braided streams.

CLASSIFICATION

The Ogallala deposits of the study area form a single rock-stratigraphic unit. No lithologic criteria were observed which would justify the subdivision of these sediments into two or more formations (members). The term, "Ash Hollow", as conceived by Engelmann in 1859 and defined in part by Lugn (1939) seems the most appropriate name for these rocks. The Ash Hollow Formation, as characterized above, extends from the

Table 2. Mean long ($L\bar{x}$) and intermediate ($I\bar{x}$) diameters of the ten largest clasts from sand and gravel sample localities indicated in Fig. 2. Ls, standard deviation of the sample mean, $L\bar{x}$; Is, standard deviation of the sample mean, $I\bar{x}$. Measurements in mm.

Loc.	Stratigraphy	$L\bar{x}$	Ls	$I\bar{x}$	Is
1	Ash Hollow	184	11.76	103	11.14
2	Broadwater	160	19.15	77	13.89
3	Ash Hollow	149	10.04	84	10.91
4	Broadwater	130	11.78	74	5.97
5	Ash Hollow	140	14.63	71	9.80
6	Ash Hollow	117	10.25	51	5.94
7	Ash Hollow	85	9.57	40	4.79
8	Ash Hollow	67	11.00	38	7.42
9	Ash Hollow	77	10.00	41	7.34
10	Ash Hollow	49	5.46	32	3.32
11	Ash Hollow	38	12.43	25	3.82
12	Ash Hollow	56	8.60	39	6.57
13	Ash Hollow	93	15.62	55	6.02
14	Ash Hollow	37	9.67	28	8.50
15	Broadwater	296	20.17	147	10.21
16	Broadwater	146	11.68	75	9.65
17	Ash Hollow	92	17.85	45	6.00
18	Ash Hollow	112	12.65	70	10.07

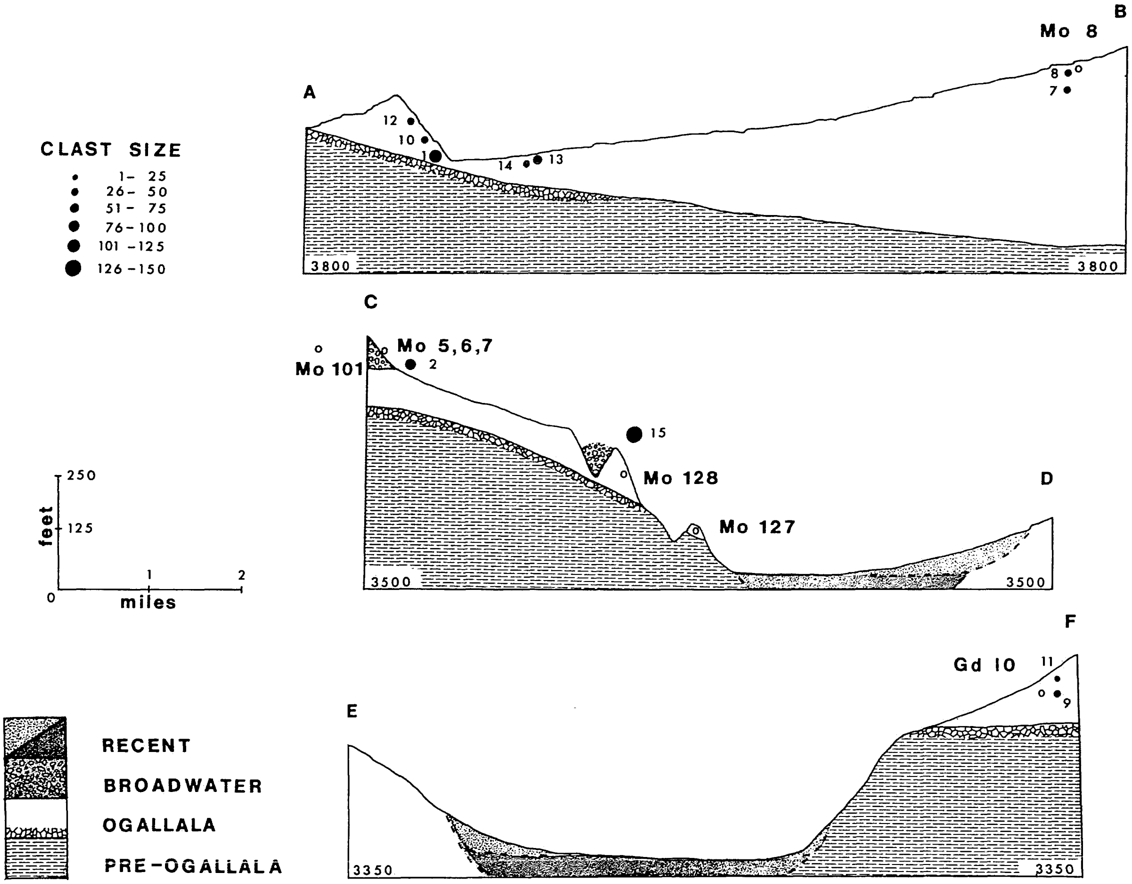


Fig. 3. Clast size measured as the mean intermediate diameter of the ten largest clasts. Measurements in mm. Recent sediments include both eolian and alluvial deposits. Ogallala rocks include a basal pedogenic surface. O=approximate stratigraphic position of University of Nebraska State Museum fossil quarry or locality. Gd-10, Oshkosh Quarry; MO-5, 6, 7, Broadwater Quarries; Mo-8, Dalton Quarry (prospect); Mo-101, Kepler Quarry.

type section on the eastern edge of the study area to embrace all of the Ogallala sediments exposed in western Nebraska and includes the rocks formerly assigned to the Sidney gravel and Kimball formations of Lugn.

Lugn proposed the name "Sidney gravel formation" in 1938. He applied the name to gravel deposits in western and southwestern Nebraska, northeastern Colorado, and northern Kansas. Lugn realized that the Sidney gravel could not be distinguished lithologically from gravels in the Ash Hollow Formation. He used the "importance" of the gravel and its "widespread" occurrence to justify the recognition of a rock-stratigraphic unit. The Code of Stratigraphic Nomenclature (Article 4, Remark c – Independence from inferred geologic history) prohibits this procedure. The widespread occurrence of the gravel has never been demonstrated by tracing the bed from the type section.

The Kimball Formation was named by Lugn in 1938. The formation included the Ogallala sediments above the level of the Sidney gravel and was described as "silt, clay, and fine sand, partly cemented with caliche, with one or two algal limestone beds at the top. It is pinkish to reddish and contains the fossil seeds of the genera *Echinochloa, Panicum,* and *Biorbia.*" Frye et al. (1956) describe the Kimball of northern Kansas: "Except for the basal Sidney gravel lentils, the Kimball member is predominantly fine textured and richly calcareous. . . . In zones where the calcium carbonate content is low, these beds are reddish tan to red brown, but the calcareous material commonly masks the hues of red, giving the entire member an ash-gray color. The calcium carbonate content commonly increases upward, the upper one-half to one-third of the member consisting of impure, relatively soft limestone. . . ."

Thicknesses of silts and fine sands equal to or exceeding the thickness of the Kimball Formation occur at other horizons on the Ogallala deposits of the study area. Accumulations of silts and fine sands are not

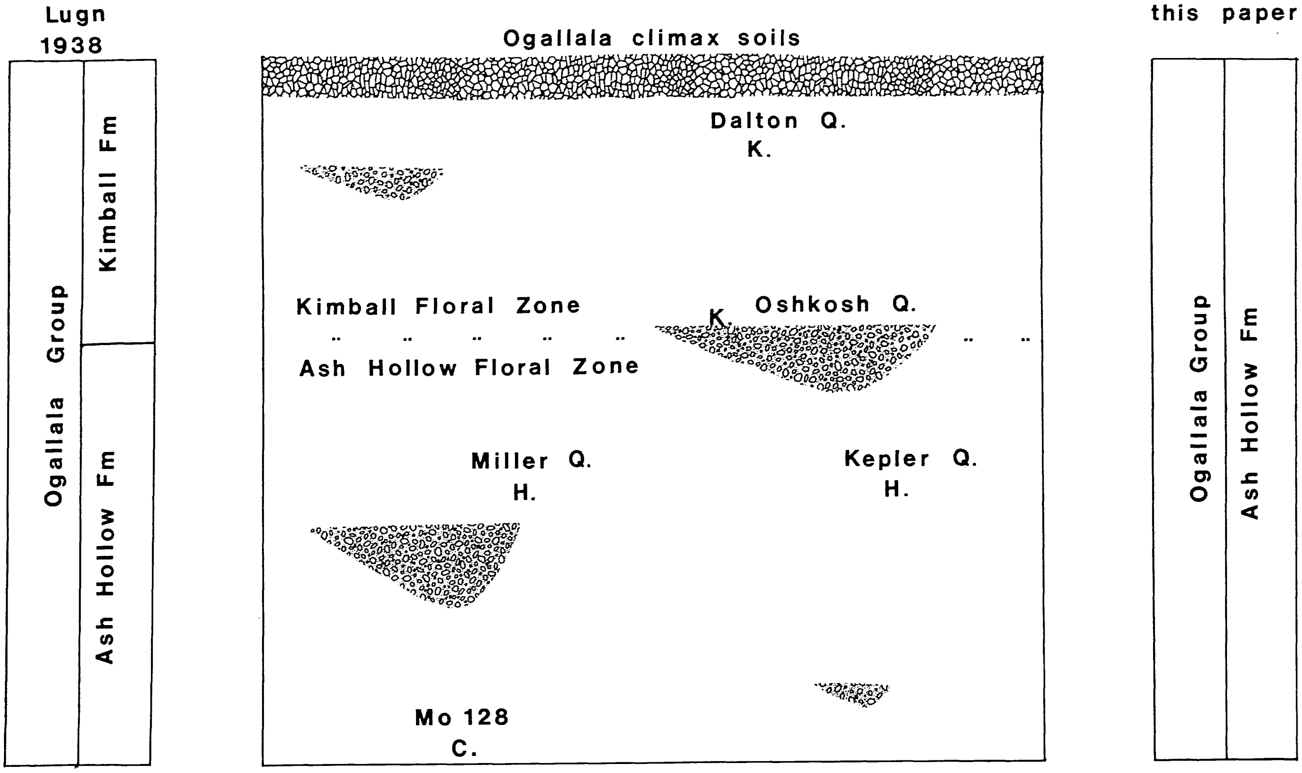


Fig. 4. Nomenclature. Idealized section depicting generally accepted distribution of Ogallala faunas, floras, and gravels in western Nebraska. The Sidney gravel of Lugn (1938) is included as the basal unit of the Kimball Formation. Q, quarry; K, Kimballian fauna (Schultz and Stout, 1948; Schultz, Schultz, and Martin, 1970); H, Hemphillian fauna; C, Clarendonian fauna.

limited to or typical of any particular horizon. The calcium carbonate content and gray color of the Kimball are secondary features associated with a soil-stratigraphic unit, the High Plains caliche, and properly play no part in defining a rock-stratigraphic unit (Code of Stratigraphic Nomenclature, Article 18, Remarks a, b, and c).

Previous researchers have found the upper Ogallala sediments of northern Kansas and western and southwestern Nebraska to contain distinctive vertebrate, invertebrate, and floral assemblages. Frye et al. (1956) discuss the occurrence of these assemblages in the Ogallala deposits of northern Kansas. Schultz and Stout (1948) and Schultz et al. (1970) among others have described the vertebrate faunas found at this horizon in western and southwestern Nebraska. Frye and Leonard (1959, p. 23, Figure 3) depict the floral zones of the Ogallala.

These vertebrate, invertebrate, and floral assemblages have been used as criteria to establish the time equivalence of rocks in widely separated geographic areas. The name "Kimball Formation" has been applied to rocks formed from the sediments deposited during the time interval defined by the presence of these faunas and floras. Frye et al. (1956) state, "The members become

Table 3. Transition count matrix. The matrix records the number of times that all possible lithologic transitions occur. For any transition, the lithology of the lower bed is indicated by the rows of the matrix and the lithology of the upper bed by columns of the matrix. X's indicate transitions which occur at greater than random frequencies (probability of a larger chi-square value = 0.05). The percentage of the total thickness of each lithologic type in the 11 test holes is recorded below the matrix.

Lithology	Code	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Limestone	*1*	-	0	0	1	2	7^{x}	1	0
Marl	*2*	0	-	1	6	3	9	0	0
Clay	*3*	0	0	-	0	0	5^{x}	1	0
Silt	*4*	2	9	2	-	10	31	12	9
Sandy silt	*5*	2	3	0	13	-	10	1	2
Sand	*6*	8	7	3	38	12	-	10	5
Gravelly sand	*7*	1	0	0	12	2	15	-	11^{x}
Gravel	*8*	0	0	0	5	3	3	15^{x}	-
	Code	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
% of total thickness		2	3	1	21	5	42	14	12

meaningful when we consider them to possess approximate age equivalence from place to place. It is in this sense that the members will be used in the following descriptions." This philosophy of nomenclature equates time-stratigraphic units with rock-stratigraphic units. The works of Lugn (1939), Schultz and Stout (1948), and Frye et al. (1956) use biostratigraphic data to define a time-stratigraphic unit to which rock-stratigraphic terms (formation, member) have been applied.

Time concepts, contained fossils, and inferred geologic history are explicit components of both the original definitions and subsequent usages of the terms Sidney gravel and Kimball formation. No lithologic criteria are known which enable these units to be differentiated from the Ash Hollow Formation. This is in clear violation of Article 4, Remarks a, c, and d of the Code of Stratigraphic Nomenclature. Adherence to Article 11 of the code (rule of priority) dictates the use of the name Ash Hollow Formation for all of the Ogallala sediments exposed in western Nebraska.

SUMMARY AND RECOMMENDATIONS

The extension of rock-stratigraphic units over wide geographic areas on the basis of nonlithologic criteria is common practice in Ogallala stratigraphy. Faunal and floral assemblages are the criteria most often used to extend rock-stratigraphic names from the type sections in Nebraska southward throughout the High Plains. The term "Ogallala" is best accorded group rank in Nebraska. The Ogallala Group includes the Ash Hollow and Valentine Formations.

The Valentine Formation is a rock-stratigraphic unit characterized by fine-grained, unconsolidated, gray and greenish-gray sands. Johnson (1936) provides an excellent discussion of the use of the terms "Valentine beds" and "Valentine fauna" in the literature. The name "Valentine Formation" should be limited to the areal extent of the characteristic lithology. The formation is well exposed in north-central Nebraska but does not extend southward into western and southwestern Nebraska. The Ash Hollow Formation includes all of the Ogallala rocks exposed in western Nebraska. The Sidney gravel and Kimball formations are not valid rock-stratigraphic units.

The reduction in rank of the Ogallala Group to the Ogallala Formation in Kansas and the southern High Plains seems appropriate and is in accordance with the provisions of the stratigraphic code.

ACKNOWLEDGMENTS

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A SEQUENCE OF RADIOCARBON-DATED WISCONSINAN NONMARINE MOLLUSCAN FAUNAS FROM SOUTHWESTERN KANSAS-NORTHWESTERN OKLAHOMA

Barry B. Miller

Abstract.— This paper summarizes the results of analysis of seven radiocarbon-dated Wisconsinan nonmarine molluscan assemblages from southwestern Kansas and northwestern Oklahoma. Molluscs from three of these faunas, the Classen local fauna, Robert local fauna, and Boyd local fauna, are recorded here for the first time. Sixty-one species were identified from the seven faunas which range in age from about 30,000 to 10,500 years B.P. All of the species found in the Wisconsinan faunas are still extant somewhere in the contiguous 48 states.

The sequence of progressively younger faunas shows decreases in abundance of aquatic species, and of northern species that now reach the southern limit of their range in the Great Plains well to the north of the study area. The reduction of both northern species and aquatic species appears to be related to a climatic trend which brought increasingly warmer and drier summers to this part of the Great Plains. The final depauperization of the fauna occurred within the last 10,500 years and was the apparent culmination of this trend.

The present fauna of the study area is essentially the same as the Wisconsinan assemblages minus most of the northern species. The reduction in northern species has increased the relative abundance of species that are more tolerant of high temperatures and drought. The fauna is now dominated by these climatically catholic species.

INTRODUCTION

The late Cenozoic sediments of southwestern Kansas and northwestern Oklahoma contain one of the most nearly complete nonmarine molluscan faunal sequences that is known for a small area anywhere in the world. Twelve assemblages assigned to the Pleistocene, the Spring Creek local fauna and Sanders local fauna (pre-Nebraskan warm interval; Skinner et al., 1972); the Cudahy fauna (Kansan; Miller, 1968; Couri, 1973); the Berends local fauna, Doby Springs local fauna, Adams local fauna, Butler Spring local fauna, and Mt. Scott local fauna (Illinoian; Miller, 1966); the Cragin Quarry local fauna and Jinglebob local fauna (Sangamonian; Hibbard and Taylor, 1960); and the Bar M local fauna and Jones local fauna (Wisconsinan; Hibbard and Taylor, 1960); have been reported from this area.

The glacial and interglacial faunas frequently contain sympatric occurrences of extant species which now have geographic ranges that are allopatric and that may be separated by hundreds of miles (e.g. *Pupoides inornatus* and *Gastrocopta pellucida hordeacella*). Temperature extremes and available moisture have been suggested as the primary factors controlling the modern distribution of both terrestrial and aquatic molluscs (Hibbard and Taylor, 1960; Taylor, 1960; Clarke, 1973).

The great taxonomic diversity that characterizes the Kansan, Illinoian, Sangamonian, and Wisconsinan assemblages was achieved by the range expansions of many northern, western and eastern species into southwestern Kansas and northwestern Oklahoma. Many of these species are now excluded from this region because of the high summer temperatures and general inadequacy of available moisture. In general, both the glacial and interglacial faunas show a greater diversity than now occurs in the molluscan fauna of this area, and imply a more equable climate at the time these assemblages lived. The equable climate apparently continued in the area until sometime after the Jones and Bar M local faunas lived since both of these assemblages show a greater

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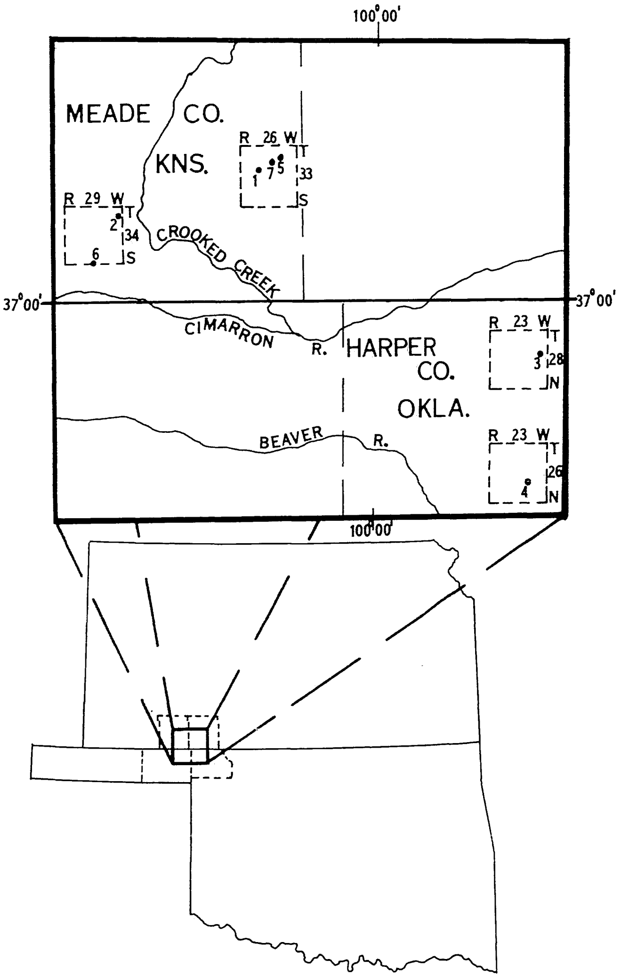

Fig. 1. Wisconsinan faunal localities in study area. 1. Jones local fauna. 2. Bird locality local fauna. 3. Bar M I local fauna. 4. Bar M II local fauna. 5. Boyd local fauna. 6. Robert local fauna. 7. Classen local fauna.

species diversity than the extant fauna of the area. The present study of seven radiocarbon dated molluscan faunas from Meade Co., Kansas and Harper County, Oklahoma (Figure 1) was undertaken in the hope that it would help establish the timing and the nature of the climatic changes that resulted in the present depauperized molluscan fauna. The faunas contain 61 identifiable molluscan species(Table 1), all of which are extant somewhere in the contiguous 48 states, although many have become extirpated from the study area. The faunas span the time interval (Table 2) from about 30,000 years B.P. (Bird locality) to 10,500 years B.P. (Boyd local fauna).

Materials

Some of the Bird locality local fauna, most of the

Table 1. Species List for Seven Wisconsinan Molluscan Faunas

	Bird locality	Jones local fauna*	Bar M locality I*	Bar M locality II*	Classen local fauna	Robert local fauna	Boyd local fauna
AQUATIC SPECIES							
Aplexa hypnorum	–	+	+	+	–	–	–
Armiger crista	–	+	+	+	+	–	–
Ferrissia fragilis	–	–	–	+	–	+	+
Ferrissia parallela	+	–	–	+	–	–	–
Fossaria dalli	–	+	+	+	+	+	+
Fossaria obrussa	–	+	–	+	–	+	–
Gyraulus circumstriatus	+	+	+	+	+	+	+
Gyraulus parvus	+	+	+	+	+	–	+
Helisoma trivolvis	+	+	+	+	–	+	+
Laevapex fuscus	–	+	–	–	–	–	+
Lymnaea stagnalis jugularis	–	+	+	+	–	–	+
Physa anatina	+	+	–	+	+	+	+
Physa gyrina	+	+	+	+	–	+	–
Physa skinneri	–	–	+	+	–	–	–
Pisidium casertanum	+	–	+	+	+	+	–
Pisidium compressum	+	+	+	–	+	+	–
Pisidium ferrugineum	–	+	–	–	–	–	–
Pisidium lilljeborgi	–	+	–	–	–	–	–
Pisidium nitidium	+	+	–	+	–	–	–
Pisidium variabile	–	–	–	?	?	–	–
Pisidium walkeri	–	+	–	–	–	–	–
Promenetus exacuous	+	+	–	–	–	–	+
Promenetus umbilicatellus	+	+	+	–	+	–	+
Sphaerium securis	–	–	–	–	+	–	–
Sphaerium striatinum	–	–	–	+	+	+	+
Stagnicola caperata	+	+	+	+	–	+	+
Stagnicola cockerelli	–	+	+	+	+	–	+
Stagnicola palustris	+	+	+	+	+	–	+
Valvata tricarinata	–	+	+	–	+	+	+
TERRESTRIAL SPECIES							
Carychium exiguum	–	–	+	–	+	+	+
Cionella lubrica	–	–	–	+	+	+	–
Deroceras laeve	–	–	+	–	+	+	+
Discus cronkhitei	–	–	+	+	+	+	+
Euconulus fulvus	–	–	+	+	+	+	–
Gastrocopta armifera	–	+	+	+	+	+	+
Gastrocopta contracta	–	–	+	+	+	–	–
Gastrocopta cristata	±	+	+	–	+	+	+
Gastrocopta holzingeri	–	–	–	–	+	+	–
Gastrocopta procera	–	+	+	–	–	+	+
Gastrocopta tappaniana	–	–	+	+	+	+	+
Hawaiia minuscula	–	+	+	+	+	+	+
Helicodiscus parallelus	–	–	+	+	+	+	+
Helicodiscus singleyanus	–	+	+	+	–	+	+
Nesovitrea electrina	–	–	+	+	+	+	–
Oxyloma sp.	+	–	+	+	–	+	–
Punctum minutissimum	–	–	–	–	+	+	–
Pupilla blandi	+	+	–	+	+	+	+
Pupilla muscorum	–	–	+	+	+	–	+
Pupilla sinistra	–	–	+	–	–	–	–

Pupoides albilabris	+	+	+	+	+	+	+
Pupoides inornatus	–	+	–	–	–	+	–
Stenotrema leai	+	–	+	–	–	+	–
Strobilops labyrinthica	–	–	+	+	+	+	+
Succinea ovalis	–	–	–	–	–	+	–
cf. *Succinea*	+	+	+	+	+	+	+
Vallonia gracilicosta	+	+	+	+	+	+	+
Vallonia parvula	–	–	–	–	+	–	+
Vallonia perspectiva	–	–	–	–	–	+	–
Vertigo elatior	–	–	+	–	+	+	–
Vertigo gouldi paradoxa	–	–	–	–	–	–	+
Vertigo milium	+	+	+	–	+	+	+
Vertigo ovata	+	+	+	+	+	+	+
Zonitoides arboreus	–	–	–	+	+	+	–

*Faunal lists modified from Hibbard and Taylor (1960).

Jones local fauna, and all of the Robert local fauna and Bar M I and II local fauna materials were collected by C.W. Hibbard and field parties from the University of Michigan Museum of Paleontology. All of the Boyd local fauna and Classen local fauna, and some of the Jones local fauna and Bird locality local fauna materials referred to in this report were collected by B.B. Miller and field parties from the Department of Geology, Kent State University.

Table 2. Molluscan Faunas From Southwestern Kansas–Northwestern Oklahoma

Number of Species	Fauna	Age
29	Meade County	Recent, SW Kansas***
36	Boyd	10,790±280 (I-5541)**
38	Robert	11,110±350 (SM-762)*
38	Classen	16,100±250 (I-4930)*
37	Bar M II	17,750±360 (I-3460)*
38	Bar M I	21,360±1250 (SM-763)*
33	Jones	26,700±1500 (I-3461)* 29,000±1300 (I-3462)*
20	Bird locality	29,300±1250 (I-5136)*

* Date from Shell
** Date from carbon layer in silt
*** Data from Hibbard and Taylor, 1960

Collection Localities and Faunal Names

The Bird locality is a name that has been informally used by Hibbard and his associates for materials collected from sediments exposed in a bluff along the south bank of Shorts Creek in the NW¼ SW¼ Sec. 36, T. 33 S, R. 29 W, Meade County, Kansas. Vertebrate fossils from this locality have been reported by Stettenheim (1957). The molluscan fauna, here referred to as the Bird locality local fauna, was collected at the same locality as Stettenheim's material and comes from a one-foot thick zone of light-brown sand, mottled with silt and clay stringers, exposed about 31 ft above the base of the bluff.

The Boyd local fauna is a new name applied to fossils collected from units 19, 21, and 26 (Measured Section 1) of a stratigraphic section measured along the east side of Sand Creek, in the NW¼ NW¼ SE¼ Sec. 3, T. 33 S, R. 27 W, Meade County, Kansas. The Classen local fauna is a new name applied to fossils collected from unit 6 (Measured Section 2) of a section measured along the northeast bank of Sand Creek, in the NW¼ NE¼ SW¼ Sec. 3, T. 33 S, R. 27 W, Meade County, Kansas.

The two localities of the Bar M local fauna originally reported by Taylor and Hibbard (1955) are treated as separate faunas in this study. Differences in their species composition and radiocarbon ages seem to justify the separation. Materials referred to the Bar M I local fauna and Bar M II local fauna are from Localities 1 and 2, respectively, of the Bar M local fauna as described in Taylor and Hibbard (1955) and Hibbard and Taylor (1960).

The location and stratigraphic occurrence of the Jones local fauna, Bar M I local fauna, Bar M II local fauna, and Robert local fauna have been adequately treated in Hibbard and Taylor (1960) and Schultz (1969).

Measured Section I

The section was measured in NW¼ NW¼ SE¼, Sec. 3, T. 33 S, R. 27 W, Meade County, Kansas, at the Boyd locality. It started at the base of the channel of Sand Creek and proceeded eastward toward a gas well on the eastern bank (measured by Stanley Spicer).

Thickness of unit (inches)

28. Top soil; "A" horizon to a depth of 5"; blocky columnar prisms in "B" horizon; gradational contact below. 11.5

27. Silt, fine, tan-brown; caliche particles (to ¼"); some clay; unit 27: mollusks, sharp contact below 11.0

26. Clay, dark brown, some carbon particles; many caliche particles (to 1/8"); essentially no silt; 16 degrees NE dip, N 26 degrees W strike; unit 26: charaphytes, mollusks, and ostracodes, sharp contact below 28.5

25. Sand, medium, tan, cross-bedded, a few caliche particles (to 1/8"); 0.1% gravel, 90% sand, 9% silt, 0.5% clay; slightly gradational contact below 5.25

24. Clay, very dark brown, much carbon, some sand, medium, light tan; sharp contact below 1.75

23. Sand, medium, brown-tan, with some clay; cross-bedded, sharp contact below 6.0

22. Clay, dark brown, with much carbon; same fine sand; gradational contact below 5.0

21. Silt, fine, brown, some limonite stains; one carbon rich layer very near top, another towards base; carbon specks often intermingled throughout; 13 degrees NE dip, N 25 degrees W strike; radiocarbon date of 10, 790±280 years B.P. (I-5541); units 21b and 21a: mollusks, sharp contact below 25.0

20. Silt, fine, yellow, uniform, limonite stained; sharp contact below 3.0

19. Sand, fine-medium, brown-tan, with some caliche particles (to 1/8"); unit 19c: mollusks, ostracodes, and 0.1% gravel, 87% sand, 12% silt, 0.6% clay; unit 19b: grass seeds, ostracodes, mollusks, and 53.4% sand, 46% silt; unit 19a: mollusks, and 0.4% gravel, 58% sand, 41% silt, 0.4% clay; gradational contact below 32.5

18. Silt, brown; laminated with tan medium sand, some limonite stains; unit 18: grass seeds, charaphytes, ostracodes, and 48% sand, 51% silt, 0.8% clay; sharp contact below 6.5

17. Gravel, coarse, brown, with many caliche nodules (to 1½"); sharp contact below 7.5

16. Silt, brown, with intermixed sand and silt; occasional medium grained sand lenses; few caliche nodules (to 1/8"); unit 16b: mollusks, and 38% sand, 57% silt, 4.3% clay; unit 16a: ostracodes, charaphytes, and 0.1% gravel, 71% silt; gradational contact below 18.0

15. Sand, fine to medium, tan, cross-bedded; some limonite stains; more caliche particles near top; slightly gradational contact with slight concentration of caliche 4.25

14. Clay, brown, silty, occasional limonite stains; few caliche nodules (1/8" – ¼"); occasional small lense of brown clay with slightly more silt near base; unit 14b: grass seeds, charaphytes, and ostracodes; unit 14a: mollusks; sharp contact below 10.0

13. Sand, medium, tan, cross-bedded; some chert and caliche nodules (to ¼"); 81% sand, 18% silt, 0.8% clay; sharp contace below 4.75

12. Clay, brown-tan, with very fine grained silt; sharp contact below 10.25

11. Sand, medium-coarse, cross-bedded, limonite stains along bedding plains (¼" thick stain at top); many caliche nodules (to ½"); unit 11: mollusks, sharp contact below 15.0

10. Sand, medium, brown; approximately equal percentage of sand and silt near base with increase of sand upward; unit 10: ostracodes, mollusks, and 0.2% gravel, 56% sand, 43% silt; slightly gradational contact below 6.5

9. Clay, gray-green, uniform, no silt; sharp contact below 9.5

8. Clay, brown (faintly green), very silty; mostly clay, some limonite stains; sharp contact below 2.5

7. Clay and medium sand, yellow brown; approximately equal percentage of each; limonite stained throughout; sharp contact below 1.5

6. Sand, medium, light tan; sharp contact below 1.0

5. Silt, very fine, brown; few caliche nodules (to 1"); gradational contact below 4.0

4. Clay, gray-green, silty; few horizontal limonite stains along bedding; sharp contact below 3.0

Pliocene Series

Ogallala Formation

3. Limestone "caliche", white, massive; slightly gradational contact below................ 22.0

2. Limestone "caliche", white; composed largely of vertical caliche stringers with some red clay intermingled; very slightly gradational contact 10.0

1. Clay, red; very silty; horizontal caliche stringers increase in size (to 3/8") and number upward; base of section covered by stream bed 24.0

Total thickness 23 feet 1.75 inches

Measured Section II

Measured at the Classen locality, the section started on the floor of Sand Creek and was measured along the north bank in NW¼ NE¼ SW¼, Sec. 3, T. 33 S, R. 27 W, Meade County, Kansas (measured by Stanley Spicer).

Thickness of unit (inches)

12. Top soil; "A" horizon to a depth of 5"; blocky columnar prisms in "B" horizon; gradational contact below 11.0

11. Silt, uniform, fine, light tan; very little caliche present; gradational contact below 28.0

10. Silt and clay; fine silt, lighter brown than that below; less clay than that below, not as blocky when dry; very small vertical stringers of caliche; gradational contact below 23.0

9. Silt with much clay; very fine, brown, uniform; clay blocky when dry; very small vertical stringers of caliche; gradational contact below 28.0

8. Clay, uniform, dark brown-black (carbon); not as blocky as one below when dry; no sand; unit 8: mollusks, gradational contact below 24.0

7. Clay, uniform, green-brown, silty to sandy; no iron stains; blocky when dry; sharp contact below 30.0

6. Sand, fine brown; fairly uniform; many vertical limonite stains along old root tubes; unit 6: charaphytes, ostracodes, mollusks, and 0.05% gravel, 77% sand, 22% silt, radiocarbon date of 16,100±250 B.P. yrs.; sharp contact below 16.0

5. Gravel, coarse (to 3/8"), brown; interbedded with medium sand (with clay); some limonite along bedding planes; sharp contact below 10.0

4. Gravel, coarse (to ½"), white (chert and caliche nodules); sharp contact below 4.0

3. Gravel, very coarse (to 3"), yellow-orange-cross-bedded strongly with very coarse sand; 14 degrees SW dip, N 23 degrees W strike; sharp contact below 41.0

2. Sand, medium, pink, some pebbles (to 1"); fairly uniform; a few caliche nodules; sharp contact below 56.5

Ballard Formation

Angell Member

1. Gravel, cemented; covered from stream bed to top of unit but crops out 40 yards to the east 205.5

Total thickness 38 feet 10 inches

METHODS OF FAUNAL ANALYSES

Standard methods utilized in analyzing late Cenozoic nonmarine molluscan assemblages involve comparison with the modern living fauna occurring in the same region as the fossils; comparison with an extant fauna from some other region which contains faunal elements that are similar to those found in the fossil assemblage; or by establishing an area of sympatry for the extant faunal elements (Taylor, 1960, 1965; Miller, 1966). Some analysts have grouped molluscs on the basis of their distribution pattern and plotted changes in the abundance of these climatically significant species groups to interpret climatic changes (Sparks, 1957). Implied in these methods of analysis is the assumption that some aspects of climate have been responsible for the frequently observed differences between the modern fauna and late Cenozoic fossil assemblages found within the same region. The problem has always been one of recognizing which climatic factors limit distribution. In the last several years there have been a number of studies involving both field observation and laboratory controlled experiments which appear to implicate temperature extremes and available moisture as two of the major factors.

Van der Schalie and Berry (1973) have shown that certain aquatic pulmonate and operculate snails are remarkably sensitive to temperature. The species used in their study, *Lymnaea stagnalis, L. emarginata, Helisoma anceps, H. trivolvis, H. campanulatum, Physa gyrina* and *Amnicola limosa* had a normal functional range of between 20C and 30C. Extended exposures to water temperatures below or above this range resulted in reduction in the rate of shell growth and failure of the gonadal tissue to develop. None of the species could be cultured at temperatures much below 12C and none would reproduce if the temperature exceeded 30C. The studies of Randolph (1973) and Elwell and Ulmer (1971) demonstrated the importance of temperature extremes in the functional biology of several species of terrestrial pulmonate snails.

The distributional patterns of nonmarine molluscs also seem to implicate temperature extremes as a primary controlling factor. Taylor (1960), Hibbard and Taylor, (1960), and Clarke (1973) have presented distributional data which suggest a relationship between the north-south limits of range for nonmarine molluscs and temperature extremes.

The importance of available moisture in controlling the distribution of both terrestrial and aquatic gastropods is suggested by the present gastropod fauna of Kansas. The distribution data published in Leonard (1959) was plotted on a map of Kansas that divided the state into 50-mile wide north-south columns. The number of aquatic and terrestrial species within each column were re-

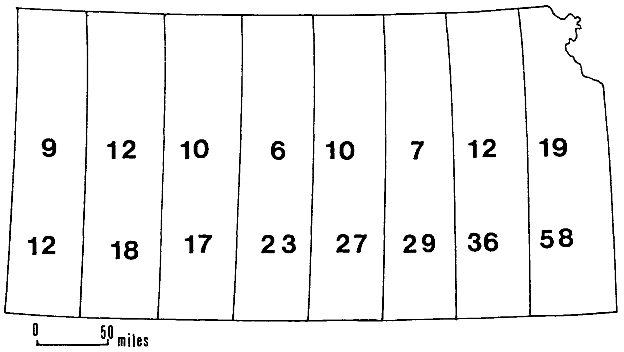

Fig. 2. Map showing gastropod species diversity in Kansas. The upper and lower figures within each 50-mile wide north-south column refer respectively to the number of aquatic and terrestrial species within that column. The data are from Leonard (1959).

corded, with the results presented in Figure 2. Both the terrestrial and aquatic gastropods show decreases in species diversity from east to west. Similar reductions in species diversity occur in the fish of Kansas (Cross, 1967). The reductions in taxonomic diversity from east to west appear to be related to the diminution in the type and number of natural aquatic habitats and to changes in the soil and vegetation, which follow a precipitation gradient that decreases from east to west (Robb, 1941).

In summary, the present state of knowledge concerning the effects of temperature and available water on nonmarine molluscs appears to justify continued use of hypotheses invoking these climatic factors in accounting for the varied species associations found in Pleistocene nonmarine molluscan assemblages.

For purposes of analysis and interpretation, the Wisconsinan and Recent molluscan faunas of the study area have been divided into four general climatic groups. Although these groupings are admittedly somewhat arbitrary since some species are not clearly assignable to one group (e.g. *Succinea ovalis* could with equal justification be considered a northern or an eastern species), they do reflect distribution patterns that are climatically controlled. Changes in the species diversity within these climatic groupings between faunas are primarily responses to climatic change.

Group I includes northern species that are generally distributed in an east-west direction and that have their southern limits in the Great Plains controlled by high summer temperatures. Evidence suggesting this consists of the ability of many species in this group (e.g., *Cionella lubrica, Vertigo elatior* and *Armiger crista*) to extend their range further south at higher elevations in the Appalachian and Rocky Mountains, where the average summer temperatures are generally lower than at the same latitude in the Great Plains.

Group II consists of southerly distributed species whose northward range in the Great Plains appears to be controlled by the length and severity of the winters. This inference is based on the observation that some members of this group (e.g., *Gastrocopta pellucida hordeacella*) are able to extend their range further north along the Atlantic coast where the "oceanic effect" ameliorates the winters.

Group III contains species with north-south distributions that generally occur in the eastern United States, but which range varying distances westward into the Great Plains. The westward range of these species appears broadly to agree with the isohyet pattern in the Great Plains and suggests that the westward distribution of species in this group may be controlled by available moisture.

Group IV includes those species for which there is inadequate range data (e.g., *Vertigo gouldi paradoxa*), whose distribution patterns cannot be obviously related to climatic factors (e.g., *Vallonia parvula*), or that are so widespread that they appear to be rather catholic in their climatic tolerances (e.g., *Pupoides albilabris*).

ANALYSIS OF THE FAUNA

Two striking differences are revealed in a comparison of the modern and Wisconsinan molluscan assemblages from the Meade County area. The modern fauna is dominated by Group IV (48%) species, and is followed in order of diminishing abundance by Group II (28%), Group III (17%) and Group I (6%). In contrast the Wisconsinan faunas are dominated by Group I and IV species. A second obvious contrast between these assemblages occurs in their species diversity. With the possible exception of the Bird locality local fauna, which was obtained from a relatively small sample, the Wisconsinan assemblages contain a greater diversity of species than the modern fauna (Table 2). Both of these differences are in large part due to the reduction in species of Group I (Table 3) that occurred since the Boyd local fauna lived, ca. 10,500 years B.P.

Table 3. Distribution of Group I, II, III, and IV as a Percentage of Total Species in Fauna

	Bird locality	Jones	Bar M I	Bar M II	Classen	Robert	Boyd	Recent Meade County*
Group I	45	48	42	46	42	31	36	7
Group II	10	12	8	5	6	14	11	28
Group III	5	7	16	11	13	16	14	17
Group IV	40	33	34	38	39	39	39	48

*Data from Hibbard and Taylor, 1960

Table 4. Species List for Seven Wisconsinan Molluscan Faunas Arranged by Climatic Group

	Bird locality local fauna	Jones local fauna	Bar M locality I	Bar M locality II	Classen local fauna	Robert local fauna	Boyd local fauna
GROUP 1 (AQUATICS)							
Aplexa hypnorum	–	+	+	+	–	–	–
Armiger crista	–	+	+	+	+	–	–
Ferrissia parallela	+	–	–	+	–	–	–
Gyraulus circumstriatus	+	+	+	+	+	+	+
Lymnaea stagnalis jugularis	–	+	+	+	–	–	+
Physa skinneri	–	–	+	+	–	–	–
Pisidium ferrugineum	–	+	–	–	–	–	–
Pisidium lilljeborgi	–	+	–	–	–	–	–
Pisidium nitidum	+	+	–	+	–	–	–
Pisidium variabile	–	–	–	?	?	–	–
Pisidium walkeri	–	+	–	–	–	–	–
Promenetus exacuous	+	+	–	–	–	–	+
Promenetus umbilicatellus	+	+	+	–	+	–	+
Stagnicola caperata	+	+	+	+	–	+	+
Stagnicola palustris	+	+	+	+	+	–	+
Valvata tricarinata	–	+	+	–	+	+	+
	7	13	9	10	6	3	7
GROUP 1 (TERRESTRIALS)							
Cionella lubrica	–	–	–	+	+	+	–
Discus cronkhitei	–	–	+	+	+	+	+
Gastrocopta holzingeri	–	–	–	–	+	+	–
Nesovitrea electrina	–	–	+	+	+	+	–
Punctum minutissimum	–	–	–	–	+	+	–
Pupilla blandi	+	+	–	+	+	+	+
Pupilla muscorum	–	–	+	+	+	–	+
Pupilla sinistra	–	–	+	–	–	–	–
Pupoides inornatus	–	+	–	–	–	–	+
Strobilops labyrinthica	–	–	+	+	+	+	+
Vallonia gracilicosta	+	+	+	+	+	+	+
Vertigo elatior	–	–	+	–	+	+	–
	2	3	7	7	10	9	6
GROUP 2 (AQUATICS)							
Physa anatina	+	+	–	+	+	+	+
	1	1	0	1	1	1	1
GROUP 2 (TERRESTRIALS)							
Gastrocopta cristata	+	+	+	–	+	+	+
Gastrocopta procera	–	+	+	–	–	+	+
Helicodiscus singleyanus	–	+	+	+	–	+	+
Vallonia perspectiva	–	–	–	–	–	+	–
	1	3	3	1	1	4	3
GROUP 3 (AQUATICS)							
Laevapex fuscus	–	+	–	–	–	–	+
	0	1	0	0	0	0	1
GROUP 3 (TERRESTRIALS)							
Carychium exiguum	–	–	+	–	+	+	+
Gastrocopta armifera	–	+	+	+	+	+	+
Gastrocopta contracta	–	–	+	+	+	–	–
Gastrocopta tappaniana	–	–	+	+	+	+	+
Helicodiscus paralellus	–	–	+	+	+	+	+
Stenotrema leai	+	–	+	–	–	+	–
Succinea ovalis	–	–	–	–	–	+	–
	1	1	6	4	5	6	4
GROUP 4 (AQUATICS)							
Ferrissia fragilis	–	–	–	+	–	+	+
Fossaria dalli	–	+	+	+	+	+	+
Fossaria obrussa	–	+	–	+	–	+	–
Gyraulus parvus	+	+	+	+	+	–	+
Helisoma trivolvis	+	+	+	+	–	+	+
Physa gyrina	+	+	+	+	–	+	–
Pisidium casertanum	+	–	+	+	+	+	–
Pisidium compressum	+	+	+	–	+	+	–
Sphaerium securis	–	–	–	–	+	–	–
Sphaerium striatinum	–	–	–	+	+	+	+
Stagnicola cockerelli	–	+	+	+	+	–	+
	5	7	7	9	7	8	6
GROUP 4 (TERRESTRIALS)							
Deroceras laeve	–	–	+	–	+	+	+
Euconulus fulvus	–	–	+	+	+	+	–
Hawaiia minuscula	–	+	+	+	+	+	+
Pupoides albilabris	+	+	+	+	+	+	+
Vallonia parvula	–	–	–	–	+	–	+
Vertigo gouldi paradoxa	–	–	–	–	–	–	+
Vertigo milium	+	+	+	–	+	+	+
Vertigo ovata	+	+	+	+	+	+	+
Zonitoides arboreus	–	–	–	+	+	+	+
	3	4	6	5	8	7	8
Total Species	20	33	38	37	38	38	36

A number of more subtle faunal changes occurred during the Wisconsinan Stage that were characterized by the following:

1) The number of terrestrial species in Group III increased between about 30,000 years and 20,360 years B.P. The number of terrestrial and aquatic species has remained essentially stable since that time (Tables 4, 5).

2) There has been a gradual increase in the number of species belonging to Group II, with the greatest increase occurring within the last 10,500 years (Table 5).

3) There has been a general decline in Group I species, that started about 18,000 years B.P. and has continued. up to the present. Most of this reduction has been due to a diminution of aquatic species. The greatest depauper-

Table 5. Number of species in Wisconsinan and Recent faunas of study area distributed by species group. A=aquatic species; T= terrestrial species; A&T=aquatic and terrestrial species. Data summarized from Table 4 and Hibbard and Taylor, 1960.

		29,300±1250 Bird locality	29,700±1000 Jones 29,000±1300	21,360±1250 Bar M I	17,700±360 Bar M II	16,100±250 Classen	11,100±350 Robert	10,790±280 Boyd	Recent
Group I	A	7	13	9	10	6	3	7	1
	T	2	3	7	7	10	9	6	1
	A&T	9	16	16	17	16	12	13	2
Group II	A	1	1	0	1	1	1	1	2
	T	1	3	3	7	1	4	3	6
	A&T	2	4	3	2	2	5	4	8
Group III	A	0	1	0	0	0	0	1	0
	T	1	1	6	4	5	6	4	5
	A&T	1	2	6	4	5	6	5	5
Group IV	A	5	7	7	9	7	8	6	9
	T	3	4	6	5	8	7	8	5
	A&T	8	11	13	14	15	15	14	14

ization of Group I species has occurred within the last 10,500 years (Tables 5, 6).

4) The total number of Group IV species has remained relatively stable over the last 21,360 years. Within the last 10,500 years, however, there has been a reduction in the number of terrestrial species with a concomitant increase in the number of aquatic species (Table 5).

5) There has been a reversal in the relative abundance of terrestrial and aquatic species. In general, aquatic species dominated the Wisconsinan faunas from about 30,000 years to 18,000 years B.P. From 18,000 years B.P. to the present, the faunas have been dominated by terrestrial species. This change was primarily the result of Group I aquatic species undergoing a significant reduction in number at the same time Group II, III, IV terrestrial species underwent modest increases (Tables 5, 6, 7).

6) Faunal similarity indices show that the older Wisconsinan faunas, (the Bird locality, Jones, Bar M I and Bar M II), share the most species in common. In contrast, the younger faunas, the Boyd, Robert and Classen show fewer faunal similarities with each other than might be expected when their close proximity of ages is considered (Table 8).

7) Four species, *Gyraulus circumstriatus, Vallonia gracilicosta, Pupoides albilabris* and *Vertigo ovata* are ubiquitous in their occurrence in all of the studied Wisconsinan faunas.

Table 6. Group I, II, III, and IV aquatic and terrestrial species as a percentage of the total number of species within a fauna. (A= aquatic species; T=terrestrial species)

		Bird locality	Jones	Bar M I	Bar M II	Classen	Robert	Boyd	Recent
Group I	A	.35	.39	.24	.27	.16	.07	.19	.03
	T	.10	.09	.18	.19	.26	.24	.17	.03
Group II	A	.05	.03	0	.02	.03	.03	.03	.07
	T	.05	.09	.08	.02	.03	.11	.08	.21
Group III	A	0	.03	0	0	0	0	.03	0
	T	.05	.03	.16	.11	.13	.16	.11	.17
Group IV	A	.25	.21	.18	.24	.18	.21	.17	.31
	T	.15	.12	.16	.14	.21	.18	.22	.17

VARIATIONS IN CLIMATE INDICATED BY THE MOLLUSCS

It is evident from Tables 4-7 that the composition of the molluscan faunas in the study area has undergone numerous oscillations within the past 30,000 years. If we concede that the previously enumerated species groupings are in a general way a reflection of climatic factors controlling the distribution of molluscs, it is reasonable to infer climatic changes from variations in the abundance of these species groups. In the study area northern (Group I) species will increase in diversity in response to cooler summers; eastern (Group III) species should increase in response to more effective moisture; and southern (Group II) species will respond to a decrease in the severity and length of the winters by increasing in diversity.

Diversity changes amongst species groups within the faunas that lived in the study area between about 27,000 years B.P. (Jones local fauna) and 10,800 years B.P. (Boyd local fauna) record a climatic trend in which the summers became increasingly warmer and drier. This increase in the severity of the summers is suggested by the reduction in both the total number of Group I species (Table 5) and in the decrease of Group I species as a percentage of the total number of species in a fauna (Table 3). Increasingly drier summers, which gradually led to the destruction of many of the aquatic habitats, are implied by the general decrease in aquatic species in Groups I, II, and III, and is probably related to increased evaporation rates associated with the warmer summers.

The climate at the time the Jones local fauna lived included cooler, more moist summers than are indicated

Table 7. Distribution of Terrestrial and Aquatic Species in Wisconsinan and Recent Faunas of Study Area

	Bird locality	Jones	Bar M I	Bar M II	Classen	Robert	Boyd	Recent
Total Number Aquatic Species	13	22	16	20	14	12	15	12
% Aquatic Species of Total	65	67	42	54	37	32	42	41
Total Number Terrestrial Species	7	11	22	17	24	26	21	17
% Terrestrial Species of Total	35	33	58	46	63	68	58	59

Table 8. Faunal Similarity Index for Seven Wisconsinan Molluscan Assemblages from Southwestern Kansas–Northwestern Oklahoma.

	Bird locality	Jones	Bar M I	Bar M II	Classen	Robert	Boyd
Bird locality	—	85	75	70	65	75	70
Jones	85	—	70	64	55	61	73
Bar M I	75	70	—	73	74	71	72
Bar M II	70	64	73	—	68	68	64
Classen	65	55	74	68	—	74	69
Robert	75	61	71	68	74	—	67
Boyd	70	73	72	64	69	67	—

by any of the other Wisconsinan assemblages studied. This interpretation is based on the diversity maximum for Group I species and the high percentage of aquatic species. The 26,700±1500 years B.P. date and inferred stadial climate suggests correlation of the Jones local fauna with the bottom of Gruger's (1973) Muscotah core from northeastern Kansas. The pollen profile from this core shows *Betula, Salix,* and *Alnus* increasing with depth below the horizon dated at 23,040±600 years B.P.

The general rate of change toward warmer, drier summers was accelerated between the time the Classen and Robert local faunas lived (Tables 3, 5, 6). It was marked by Group I species declining sharply, especially Group I aquatics, which reached their Wisconsinan diversity low; and by a marked increase in the abundance of southern terrestrial species (Group II). The magnitude of the faunal changes is probably a reflection of the combined effects of the Erie and Two Creek interstadials which occurred between 16,500 to 15,500 years B.P. (Morner and Dreimanis, 1973) and from about 12,500 to about 11,000 years B.P. (Frye et al., 1968).

A return to slightly cooler summers and to less moderate winters than occurred at the time the Robert local fauna lived is implied by the Boyd local fauna molluscs. This return to stadial climatic conditions is indicated by the increase in Group I aquatic species coupled with decreases in Group II and III species. This climatic event appears to correlate with the advance of Valders ice into the Lake Michigan Basin (Frye et al., 1968).

The climatic deterioration which reduced the molluscan fauna in the study area to its present depauperate condition occurred since the time the Boyd local fauna lived, that is within the last 10,500 years. The modern fauna in the study area is dominated by Group IV species, most of which have broad temperature and moisture tolerances. It is interesting to note that although Group IV species now form a greater percentage of the total fauna than at anytime during the Wisconsinan Stage (Table 6), there has been almost no actual increase in the number of species belonging to Group IV since the time the Bar M II local fauna lived (Table 5).

The increasing severity and magnitude of the hot, dry summers within the last 10,500 years have filtered out the Group I species while leaving behind the more tolerant Group IV species.

The increases in southern (Group II) and eastern (Group III) species within the last 11,100 years (Table 3) probably have no climatic significance but are related to the identification of *Quickella vagans* (Group III) and *Succinea concordialis* and *S. vaginacontorta* (Group II) in the Recent fauna of the Meade County area (Hibbard and Taylor, 1960). Specific identification of most succineid taxa including these requires examination of the soft anatomy (Miles, 1958). All of the fossil succineids, therefore, but *S. ovalis* (which can be identified from shell material) were omitted from the analysis of the Wisconsinan assemblages. If these species are omitted from the Recent fauna, the changes in Group II and III species within the last 11,100 years become minimal.

CONCLUSIONS

1) The Wisconsinan molluscan assemblages in general have species diversities that are intermediate between the Illinoian, Sangamonian and Recent faunas of the study area and imply a gradual deviation from the pattern of climatic equability that characterized the Illinoian and Sangamonian Stages.

2) The greatest reduction in species diversity occurred amongst species that are now distributed to the north of the study area within the Great Plains.

3) There was a general reduction in the abundance of aquatic species, with northern aquatic species undergoing the greatest diminution.

4) The reduction of northern species and of aquatic species both appear to be related to a climatic trend

which brought increasingly warmer, drier summers to this part of the Plains.

5) The final depauperization of the molluscan fauna occurred within the last 10,500 years and was the apparent culmination of this trend toward warmer, drier summers.

6) The present molluscan fauna of the Meade County area is essentially the same as the Wisconsinan faunas minus most of the northern species. The reduction in northern species has increased the relative abundance of the more climatically tolerant species which now dominate the modern fauna.

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THE MOLLUSCAN FAUNA OF THE ILLINOIAN BUTLER SPRING SLOTH LOCALITY FROM MEADE COUNTY, KANSAS

Cynthia H. Devore

Abstract.— The previously undescribed fossil mollusks from the Butler Spring sloth locality are described and counted and the geologic range, distribution, and habitat are given for each species.

The fauna was recovered from a marl formed in an alkaline lake during Illinoian times. Comparison with other Illinoian faunas from the High Plains indicates that the assemblage at the sloth locality lived under warmer temperatures than the Butler Spring fauna, but was a cooler assemblage than the Mount Scott fauna. The age of the sloth locality fauna is placed between the Butler Spring and the Mount Scott.

The geologic range of *Gastrocopta cristata* is extended into the late Illinoian, and an alkaline marsh habitat is suggested for *Anisus pattersoni.*

INTRODUCTION

The fauna of the Butler Spring sloth locality is one of six Illinoian fossil faunas studied by the late C. W. Hibbard and field parties between 1936 and 1973. All six localities are located in southwestern Kansas and northwestern Oklahoma, and have yielded both vertebrate and invertebrate fossils.

Since the 1940's, the Illinoian Butler Spring localities have been carefully studied. In 1953 and 1957 over 3 tons of matrix were recovered from five different outcrops. This was washed to yield an extensive vertebrate and molluscan fauna. The fauna from these localities is discussed in Hibbard and Taylor (1960). In 1965, on the basis of pollen analyses, Kapp divided the five Butler Spring localities into two age groups. Localities 2, 3, 4, and 5 of Hibbard and Taylor (1960) contained abundant pollen of pine, composites, grasses, wormwood, and spruce, whereas locality 1 was characterized by pollen of a high percentage of juniper, grasses, and deciduous trees, with very little pine and no spruce. On the basis of the inferred differences in climatic and ecologic conditions, Kapp concluded that the faunas from localities 2, 3, 4, and 5, which were from basal beds, were from the Illinoian glacial maximum. These he renamed the Adams local fauna. The Butler Spring locality 1 was determined to be late Illinoian, representing a transition from glacial to interglacial conditions. For this locality Kapp retained the name Butler Spring.

In 1961 an additional locality was discovered about ½ mile west of the original Butler Spring locality. A ground sloth, *Paramylodon harlani* (Owen), was recovered, as well as a rich fauna of other vertebrates. About 100 yards to the north, another sloth was found in the same bed, associated with a freshwater marl containing abundant mollusks. The vertebrates from this locality were treated in Schultz (1965). The mollusks will be described in this paper. Hopefully the discussion of these mollusks will aid others in the further study of the Illinoian interval in the High Plains region.

AGE AND FAUNAL CORRELATION

In his paper on the Illinoian molluscan faunas of southwestern Kansas and northwestern Oklahoma, Miller (1966) proposed the following chronology for the five Illinoian faunas. They are, from oldest to youngest:

Berends local fauna (B)
Doby Springs local fauna (DS)
Adams local fauna (A)
Butler Spring local fauna (BS)
Mount Scott local fauna (MS)

The evidence of stratigraphy and vertebrate paleontolo-

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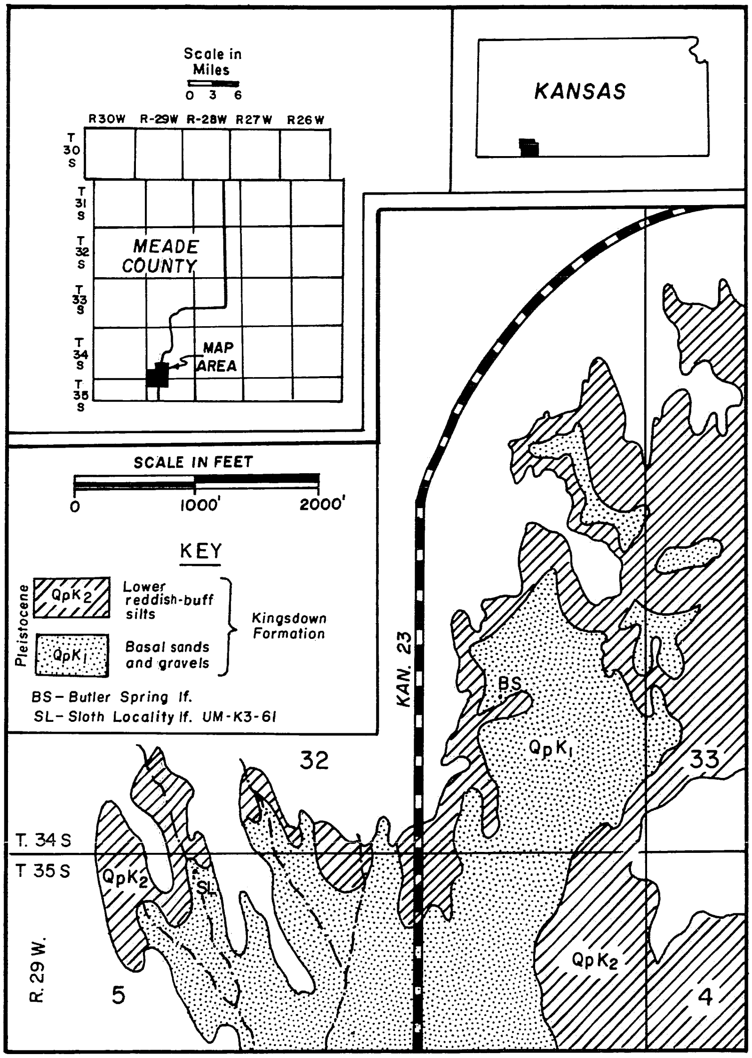

Fig. 1. Geologic map of Butler Spring sloth locality, after Schultz, 1969.

gy indicates that the Berends fauna is early Illinoian (Hibbard and Taylor, 1960). Miller based the relative ages of the four younger faunas on the first and last Illinoian appearances of five molluscan species.

The first Illinoian appearance of the northern species *Probythinella lacustris, Lymnaea stagnalis jugularis, Vertigo elatior,* and *Pupilla muscorum* in the southern High Plains region occurs in the Doby Springs local fauna. These species persist, though diminished in number, through Butler Spring time. (Miller attributes the absence of *P. lacustris, L. stagnalis jugularis,* and *V. elatior* from the Adams fauna to the paucity of material available.) All four species are absent from the Mount Scott local fauna.

The earliest Illinoian appearance of the southern species, *Helicodiscus singleyanus,* is in the Adams local fauna. The species persists through Mount Scott time. This is interpreted by Miller to indicate a warming trend, which allowed the southern form to enter the area.

The molluscan fauna of the sloth locality is very similar to that of Butler Spring. However, the absence of *Probythinella lacustris* and *Lymnaea stagnalis jugularis* from the sloth locality is significant. Ecological evidence indicates that the habitats at the sloth locality would have been ideal for both species. Their absence seems to indicate that at the time the sloth locality fauna lived, the climate was warmer. Therefore it seems that the sloth locality fauna is younger than the Butler Spring. This is not unlikely in spite of the similarity of sediments in which the faunas occur. Since deposition of the cross-bedded riverine sands and gravels would have occurred at different times in different areas, the time lag may have been sufficient to witness a warming of the climate between Butler Spring and sloth locality times.

MOLLUSKS FROM THE ILLINOIAN FAUNAS OF THE HIGH PLAINS REGION

	B	DS	A	BS	SL	MS
CLASS BIVALVIA						
ORDER PRIONODESMACEA						
Uniomerus tetralasmus (Say)	+	–	–	–	–	+
Anodonta grandis Say	–	–	–	+	–	–
Lasmigona complanta (Barnes)	–	–	+	–	–	–
Liguma cf. *L. recta* (Lamarck)	–	–	–	+	–	–
Quadrula quadrula (Rafinesque)	–	–	+	–	–	–
ORDER TELODESMACEA						
Sphaerium lacustre (Muller)	+	–	–	–	–	+
S. occidentale Prime	–	+	–	–	–	+
S. partumecium (Say)	–	–	–	–	–	+
S. rhomboideum (Say)	–	+	–	–	–	+
S. securis Prime	+	–	–	–	–	–
S. striatinum (Lamarck)	–	+	–	+	–	+
S. sulcatum (Lamarck)	–	+	–	–	–	+
S. transversum (Say)	–	–	–	+	–	+
Pisidium casertanum (Poli)	+	+	–	+	+	+
P. compressum Prime	+	+	–	+	–	+
P. nitidum Jenyns	+	+	–	+	+	+
P. obtusale (Lamarck)	+	+	–	–	–	+
P. subtruncatum Malm	–	–	–	–	–	+
P. variabile Prime	+	+	–	–	–	+
P. walkeri Sterki	–	–	–	+	–	+
CLASS GASTROPODA						
ORDER MESOGASTROPODA						
Valvata tricarinata (Say)	+	+	+	+	+	+
Probythinella lacustris (Baker)	–	+	–	+	–	–
ORDER BASOMMATOPHORA						
Carychium exiguum (Say)	+	+	+	+	+	+
Lymnaea stagnalis jugularis Say	–	+	–	+	–	–
L. (Fossaria) dalli (Baker)	+	+	+	+	+	+
L. (Fossaria) obrussa (Say)	+	+	–	+	+	+
Stagnicola caperata (Say)	+	+	+	+	+	+
S. exilis (Lea)	+	–	–	–	–	–
S. reflexa (Say)	+	+	–	+	+	+
Armiger crista (Linnaeus)	+	+	–	–	–	+
Anisus pattersoni (Baker)	–	–	–	+	+	–
Gyraulus circumstriatus (Tryon)	+	+	–	+	+	+
G. deflectus (Say)	–	+	–	–	–	–
G. parvus (Say)	+	+	+	+	+	+
Helisoma anceps (Menke)	+	+	–	+	–	+
H. trivolvis (Say)	+	+	–	+	+	+
Planorbula armigera (Say)	+	–	–	–	–	–
Menetus (Promenetus) exacuous form *kansasensis* (Baker)	+	+	+	+	+	+
M. umbilicatellus (Cockerell)	+	+	+	+	–	+
Ferrissia fragilis (Tryon)	–	+	–	+	–	+
Laevapex fuscus (Adams)	–	+	–	+	–	+
Physa anatina Lea	+	+	+	+	+	+
P. gyrina Say	+	+	–	+	+	+
P. skinneri Taylor	+	+	–	+	+	+
Aplexa hypnorum (Linnaeus)	+	+	–	+	+	+
ORDER STYLOMMATOPHORA						
Cionella lubrica (Muller)	–	+	–	–	–	+
Strobilops labrynthica (Say)	+	+	–	–	–	+
Gastrocopta armifera (Say)	+	+	+	+	+	+
G. contracta (Say)	–	+	–	+	+	+
G. cristata (Pilsbry and Vanatta)	+	+	+	+	+	+
G. holzingeri (Sterki)	+	+	–	+	–	+
G. paracristata	–	–	–	–	+	–
G. pellucida hordeacella (Pilsbry)	–	–	–	–	–	+
G. procera (Gould)	+	+	+	+	+	+
G. tappaniana (Adams)	+	+	+	+	+	+
Pupoides albilabris (Adams)	+	+	–	+	+	+
P. inornatus Vanatta	–	–	–	+	–	–
Pupilla blandi Morse	–	+	+	+	–	+
P. muscorum (Linnaeus)	–	+	+	+	+	–
P. sinistra Franzen	–	–	+	+	–	–
Vertigo elatior (Sterki)	–	+	–	+	+	–
V. milium (Gould)	+	+	+	+	+	+
V. ovata (Say)	+	+	+	+	+	+
Vallonia cyclophorella Sterki	–	–	+	+	–	–
V. gracilicosta Reinhardt	+	+	+	+	+	+
V. parvula Sterki	+	+	–	+	+	+
cf. *Succinea*	+	+	+	+	+	+
Oxyloma sp.	+	+	–	+	+	+
Discus cronkhitei (Newcomb)	–	+	+	+	–	+
Helicodiscus parallelus (Say)	+	+	–	–	–	+
H. singleyanus (Pilsbry)	–	–	+	+	+	+
Punctum minutissimum Lea	–	–	–	–	–	+
Deroceras aenigma Leonard	+	+	–	–	–	+
Euconulus fulvus (Muller)	–	+	–	–	–	+
Nesovitrea electrina (Gould)	–	+	–	–	–	+
Hawaiia miniscula (Binney)	+	+	+	+	+	+
Zonitoides arboreus (Say)	–	+	–	+	+	+
Z. nitidus (Muller)	–	–	–	–	–	+
Stenotrema leai (Binney)	+	+	–	+	+	+

STRATIGRAPHY

The sloth locality is located in the NW¼, NE¼, NW¼, Sec. 5, T. 35 S, R. 29 W, Meade County, Kansas (Fig. 1).

The fossil mollusks occur in a marl bed within the lower member of the Kingsdown Formation of Illinoian and Sangamon age (Qpk 1, of Schultz, 1969). The oldest beds of this unit exposed at the sloth locality are 35 ft of tan to yellow, limonite stained, cross-bedded sands and gravels. Hibbard and Taylor (1960) consider these sands and gravels to have been deposited by the ancestral Cimarron River. Conformably overlying the cross-bedded sands is a 2-foot unit composed of 1- to 2-inch beds of red and gray silts and clays. The marl bed containing the sloth locality local fauna is from this unit.

A measured section from the SE¼, SE¼, Sec. 32, T. 34 S, R. 29 W, Meade County, Kansas, is given below. This section, from Schultz (1969) is from the Butler Spring locality. It is very similar to the stratigraphy at the sloth locality.

Sanborn Group

Kingsdown Formation (*Qs1u* unit of Taylor)

Top eroded away

	Thickness in feet
6. Silty sand, buff to reddish-brown, moderately well-indurated, medium-bedded. Contains nodules and stringers of caliche, most present as rubble on erosional surface	4
5. Clay or mudstone, loosely consolidated, massive, light reddish-brown above lower contact gradational	4
4. Sand, pink to buff to reddish-brown, subangular to subrounded, loosely consolidated with local well indurated lenses; fine grained and well sorted to coarse grained, limonitic and moderately well sorted, with subrounded to rounded pebbles up to 3 in diameter and occasional cobbles of basalt over 6 in diameter. Lower contact irregular	5
3. Silt and clay, reddish-brown, loosely consolidated, massive. Lower contact gradational to irregular	5
2. Sand, clayey, poorly sorted. Generally coarser near the bottom with limonitic streaks and some grit and gravel grading upward into a finer greenish-gray clayey sand and silt at the top. Contains abundant mollusks and small bone fragments (Butler Spring local fauna). (At the sloth locality a 3-5 in marl in this unit). Lower contact irregular	2
1. Sand, medium to coarse, limonitic, with lenses of silt, grit, and indurated sandstone, and occasional large bone fragments (Adams local fauna). Specific lithologies: sand, fine to medium, cross-bedded, white to light pink, well sorted, subrounded, commonly forms an indurated bed at the top of the unit, coarse sand and grit, cross-bedded, black-stained, moderately well sorted, subangular to subrounded; sand, medium, yellow to brown, limonitic, cross-bedded, moderately well sorted, subrounded to subangular with scattered small, rounded pebbles. Base not exposed	15
Total thickness	35

SYSTEMATIC LIST

CLASS BIVALVIA

ORDER TELEODESMACEA

Pisidium casertanum (Poli)	*3/2
P. nitidum Jenyns	4/2
P. sp.	1/2

CLASS GASTROPODA

ORDER MESOGASTROPODA

Valvata tricarinata (Say)	215

ORDER BASSOMATOPHORA

Carychium exiguum (Say)	53
Lymnaea (Fossaria) dalli (Baker)	222
L. (Fossaria) obrussa (Say)	57
Stagnicola caperata (Say)	1697
S. reflexa (Say)	5776
Anisus pattersoni (Baker)	2552
Gyraulus circumstriatus (Tryon)	6643
G. parvus (Say)	20,113
Helisoma trivolvis (Say)	10
Menetus exacuous form *kansasensis* (Baker)	4572
Physa anatina Lea	3236
P. gyrina Say	89
P. skinneri Taylor	871
Aplexa hypnorum (Linnaeus)	2

ORDER STYLOMMATOPHORA

Gastrocopta armifera (Say)	6
G. contracta (Say)	1
G. cristata (Pilsbry and Vanatta)	50
G. holzingeri (Sterki)	3
G. paracristata (Franzen and Leonard)	6
G. procera (Gould)	4
G. tappaniana (Adams)	185
Pupoides albilabris (Adams)	6
Vertigo elatior (Sterki)	3
V. milium (Gould)	20
V. ovata (Say)	481
Vallonia gracilicosta Reinhardt	1
V. parvula Sterki	3
cf *Succinea*	45
Oxyloma sp.	2
Helicodiscus singleyanus (Pilsbry)	20
Hawaiia miniscula (Binney)	3
Stenotrema leai (Binney)	10
Zonitoides arboreus (Say)	1

* /2 indicates the number of single valves recovered.

DISTRIBUTION AND HABITAT

This discussion deals only with the species of mollusks reported from the sloth locality. The species from the Butler Spring locality are thoroughly treated in Hibbard and Taylor (1960) and in Miller (1966). Systematic remarks are included where appropriate.

Family **Sphaeriidae**

Pisidium casertanum (Poli)

Geologic Range.– Early Pliocene (Laverne local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– "Almost cosmopolitan; in the Western Hemisphere from Patagonia to Alaska." (Hibbard and Taylor, 1960, p. 77).

Habitat.– P. casertanum lives in all types of shallow water. It is one of the few sphaeriids which can tolerate desiccation (Herrington, 1962).

Pisidium nitidum Jenyns

Geologic Range.– Early Pliocene (Laverne local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– Holarctic. In North America, *P. nitidum* is to be found from northern Canada to Mexico. It is absent from the southeastern United States (Hibbard and Taylor, 1960).

Habitat.– "Requires cold water, hence found only in deep water, at considerable altitudes, or quite far north." (Herrington, 1962, p. 21).

Superfamily **Valvatoidae**

Valvata tricarinata (Say)

Geologic Range.– Early Pliocene (Laverne Formation, Laverne local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– East Coast, south to Virginia, and the Ohio River, west to central Nebraska and Great Slave Lake (Miller, 1966).

Habitat.– Valvata tricarinata inhabits areas of abundant vegetation in lakes, permanent ponds, and rivers. It is usually associated with the filamentous algae *Oedogonium* and *Cladophora*, and has been observed by Reynolds (1959) feeding on *Vaucheria.* Taylor (1960) reports the snail from a spring-fed pond with water temperature at 15C where it was associated with algae, *Ceratiphyllum,* and *Elodea.* Although *V. tricarinata* has been found on all types of substrate, it seems to prefer firm sediments (Miller, 1966).

Family **Ellobioidae**

Carychium exiguum Say

Geologic Range.– Late Pliocene (Rexroad Formation, Rexroad local fauna) to Recent (Taylor, 1960).

Distribution.– Newfoundland south to Alabama, west to Colorado and New Mexico (Pilsbry, 1948).

Habitat.– Carychium exiguum lives in crevices of fallen logs or among leaf litter in moist areas. Taylor (1960) reports it living among wet leaves along seeps and spring-fed brooks. It ranges from the wet areas immediately adjacent to streams and springs to constantly moist areas on the banks (Hibbard and Taylor, 1960).

Family **Lymnaeidae**

Lymnaea (Fossaria) dalli (Baker)

Geologic Range.– Early Pliocene (Laverne Formation) to Recent (Hibbard and Taylor, 1960).

Distribution.– Northern Michigan west to Montana, south to Arizona and Kansas, east to Ohio (Miller, 1966).

Habitat.– L. dalli prefers areas marginal to bodies of water, and is only rarely found submerged. Leonard (1943) reports it from litter and sedge near pasture ponds. It is common in marshes and around the edges of ponds. Miller (1966) collected it from a seep in Oklahoma where it was associated with *Succinea, Vertigo millium, Gastrocopta tappaniana,* and *Lymnaea obrussa* (Miller, 1966).

Lymnaea (Fossaria) obrussa (Say)

Geologic Range.– Late Pliocene (Rexroad Formation) to Recent (Hibbard and Taylor, 1960).

Distribution.– "From the Atlantic to the Pacific Oceans, and from the Mackenzie Territory, Canada, south to Arizona and northern Mexico" (Baker, 1928).

Habitat.– This species is found on floating vegetation at or near the water's edge. It is common in small water bodies such as creeks and ponds as well as in marsh areas along river banks (Miller, 1966).

Stagnicola caperata (Say)

Geologic Range.– Middle Pliocene (Ogallala Formation, Buis Ranch local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– Quebec and New England, south to Maryland and the Ohio River, west to California, north to the Yukon Territory (Baker, 1928).

Habitat.– S. caperata invariably inhabits temporary ponds, intermittent streams and ditches which become dry for part of the year. It may also inhabit woods pools which dry out from early summer to fall. The species is able to aestivate in the damp mud at the bottom of pools (Hibbard and Taylor, 1960).

Remarks.– S. caperata may be distinguished from other lymnaeids by its small size and very inflated body whorl. Small specimens may be distinguished from *Amnicola crybetes* by *S. caperata*'s more elongate aperture.

Stagnicola reflexa (Say)

Geologic Range.– Late Pliocene (Rexroad Formation, Bender local fauna) to Recent (Miller, 1966).

Distribution.– "Eastern Quebec from approximately 65 longitude, west to Nebraska to about 100° longitude, north to Manitoba to near 50° latitude, south to southern Illinois and southern Kansas, 37° latitude" (Miller, 1966, p. 227).

Habitat.– *S. reflexa* attaches to stones, submerged vegetation, and debris in creeks, ponds, lakes, and sheltered portions of rivers. Some of these habitats dry out in the summer months. Baker (1911) reports this species from woods pools and from ponds in open fields. Apparently it does not require a forest cover. The species has never been reported from large lakes or streams (Baker, 1928).

Remarks.– Immature specimens of *S. reflexa* may be distinguished from *S. caperata* by their more slender appearance and, more reliably, by the sharp angle of the parietal portion of the apperture, which points inward toward the body whorl.

Family **Planorbidae**

Anisus pattersoni (Baker)

Geologic Range.– Middle Pliocene (Rexroad Formation) to late Pleistocene; early Wisconsinan. The last known occurrence in the High Plains is Illinoian (Hibbard and Taylor, 1960).

Distribution.– "Pliocene in southern Idaho, northern Utah, western Wyoming; early Pleistocene in southwestern Idaho, Nebraska, and Kansas; middle Pleistocene in the central Great Plains; late Pleistocene, Ohio" (Hibbard and Taylor, 1960).

Habitat.– Although the habitat of this fossil mollusk can only be inferred from indirect evidence, its abundance at this locality indicates that *A. pattersoni* inhabited moist, swampy areas, marginal to lakes or ponds. It is a prevalent form at this locality, indicating that it may have preferred regions where calcium carbonate was readily available.

Gyraulus circumstriatus (Tryon)

Geologic Range.– Middle Pliocene (Kansan, Cudahy fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– Southern Canada and northern United States, from Labrador west to southern British Columbia, south to the Ohio River and northern Nevada, south in the Rocky Mountains to Arizona (Hibbard and Taylor, 1960).

Habitat.– This species inhabits small temporary bodies of water such as woods pools, flood plain ponds, and marshes (Taylor, 1960).

Remarks.– *G. circumstriatus* can be distinguished from all other *Gyraulus* by the presence of an appertural callus. It is the only North American species to form one. In some specimens, this callus may be lacking, in which case the species may be identified by the slowly expanding whorls, nearly circular in cross-section, which coil almost planospirally. Shells of three coils or less are nearly plane on both sides. Those of *G. parvus* are plane on the right and concave on the left (Hibbard and Taylor, 1960).

Gyraulus parvus (Baker)

Geologic Range.– Middle Pliocene (Rexroad Formation) to Recent (Hibbard and Taylor, 1960).

Distribution.– Eastern North America from Labrador to Florida, west to the Rocky Mountains, and into Alaska (Baker, 1928).

Habitat.– The presence of *G. parvus* in quiet bodies of permanent water depends upon the presence of thick aquatic vegetation (Baker, 1928).

Remarks.– Since this species required perennial water bodies, it is important that it be distinguished from *G. circumstriatus*, which may inhabit temporary waters. This makes distinction of the two species imperative in interpretive work.

Helisoma trivolvis (Say)

Geologic Range.– Early Pleistocene (Nebraskan-Aftonian, Dixon local fauna) to Recent (Taylor, 1960).

Distribution.– "Atlantic Coast and Mississippi River drainages, northward to Arctic British America and Alaska, and southward to Tennessee and Missouri" and Kansas (Baker, 1928, p. 332).

Habitat.– This species is one of stagnant pools and quiet standing water. I have collected it from temporary woods pools in Washtenaw County, Michigan.

Menetus exacuous form *kansasensis* (Baker)

Geologic Range.– Late Pliocene (Rexroad Formation) to late Pleistocene (Kingsdown Formation) (Miller, 1966).

Distribution.– "Pliocene in southern Idaho, northern Texas, and southwestern Kansas; early Pleistocene in Nebraska and Kansas; middle Pleistocene in the Great Plains, from Iowa to Texas; late Pleistocene in southwestern Kansas" (Hibbard and Taylor, 1960, p. 105).

Habitat.– Presumably *Menetus exacuous* form *kansasensis* lives in situations similar to those in which its close relative, *M. exacuous* form *exacuous* lives today. *M. exacuous* form *exacuous* is found associated with submerged vegetation in shallow, quiet, permanent bodies of water, such as ponds, marshes, and backwaters of streams (Hibbard and Taylor, 1960). Three scalariform specimens of *M. exacuous* were recovered.

Family **Physidae**

Physa anatina Lea

Geologic Range.– Late Pliocene (Rexroad Formation, Saw Rock Canyon local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– Detailed studies of this genus have not been completed, "until such time as the entire family is revised, the geographic distribution, ecology, life history and fossil record of members of this group remain unclear" (Miller, 1966, p. 237).

Habitat.– *P. anatina* has been found in all types of permanent shallow water. Taylor (1960) reports it from spring-fed streams and stock tanks. It is able to withstand stagnant conditions.

Physa gyrina form *hildrethiana* Lea

Geologic Range.– Middle Pleistocene; (Kansan, Cudahy fauna) to Recent (Miller, 1966).

Distribution.– Found throughout North America north to Mexico (Miller, 1966).

Habitat.– *P. Gyrina* is an inhabitant of temporary ponds. Most of the specimens recovered from these ponds are immature, but mature individuals may be found burrowed in the wet mud at the bottom of the ponds (Baker, 1928). They have also been reported from stock tanks (Miller, 1966) so are able to withstand stagnant conditions. Baker (1928) reports that in sloughs where the water never completely disappears, large specimens are common. Rest marks on the shells indicate the individuals are from permanent water. Those shells from temporary water do not show these marks (Baker, 1928).

Physa skinneri Taylor

Geologic Range.– Lower Pleistocene (Nebraskan, Dixon local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– North America in a band from about 50 degrees N, to about 44 degrees N, south in the Rocky Mountains to Utah. It has also been reported from Alaska (Miller, 1966).

Habitat.– This species lives in shallow, quiet bodies of water. These may be either temporary or permanent ponds or back waters along streams (Miller, 1966).

Aplexa hypnorum (Linnaeus)

Geologic Range.– Early Pleistocene (Ballard Formation) to Recent (Hibbard and Taylor, 1960).

Distribution.– Circumpolar; in North America it occurs from the Cascade Mountains east to the Atlantic, and from Alaska and Hudson Bay south to Nevada, Colorado, and the Platte River; east to the Ohio River and the District of Columbia (Miller, 1966).

Habitat.– This species is particularly abundant in woods pools. It has also been collected from intermittent streams and stagnant pools (Miller, 1966).

Family **Pupillidae**

Gastrocopta armifera (Say)

Geologic Range.– Early Pliocene (Laverne Formation, Laverne local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– All of eastern North America from Labrador to northern Florida, west to the Rocky Mountains (Miller, 1966).

Habitat.– *G. armifera* is a common species on wooded slopes near streams. It occurs under sticks and leaf litter where there is constant residual moisture (Franzen and Leonard, 1947).

Gastrocopta contracta Say

Geologic Range.– Early Pliocene (Laverne local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– "Maine to Florida; west to Manitoba, South Dakota, central Kansas, west Texas, and Sonora; south in Mexico to the states of Morelos and Vera Cruz. In the Gulf Coastal Plain from Alabama to Texas, and northward in the Mississippi lowlands to Arkansas, the typical form is replaced by another subspecies" (Hibbard and Taylor, 1960, p. 126).

Habitat.– *G. contracta* lives on wooded slopes near rivers and streams. It is found under fallen logs and among leaf litter (Franzen and Leonard, 1947).

Gastrocopta cristata (Pilsbry and Vanatta)

Geologic Range.– Late Pliocene (Bender local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– Indiana, Arkansas, and Louisiana west to Arizona and New Mexico (Miller, 1966).

Habitat.– This species may be found on timbered slopes near streams and also among the roots of dry upland grasses. It is often associated with *Pupoides albilabris*. Both are able to withstand drought (Franzen and Leonard, 1947).

Gastrocopta holzingeri (Sterki)

Geologic Range.– Late Pliocene (Saw Rock Canyon local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– "Ontario and western New York to Helena, Montana, south to Illinois and Albuquerque and Mesilla, New Mexico" (Pilsbry, 1948, p. 883).

Habitat.– *G. holzingeri* occurs on timbered slopes where it lives under sticks and leaf mold.

Gastrocopta paracristata Franzen and Leonard

Geologic Range.– Blancan (Fox Canyon local fauna) to Illinoian (Butler Spring sloth locality). This is an extension of the pre-existing range.

Diagnosis.– This species closely resembles *G. cristata* but differs in that it lacks the subcolumnellar lamella of *G. cristata*. The anterior portions of the lower palatal folds are in contact with the palatal callus; those of *G. cristata* are more deeply immersed. Finally, the peristome of *G. paracristata* is heavier than that of *G. cristata.*

Habitat.– Unknown, but probably similar to that of its close relative, *G. cristata.*

Gastrocopta procera (Gould)

Geologic Range.– Early Pleistocene (Nebraskan or Aftonian, Dixon local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– Mid-Atlantic states west to Arizona and the Black Hills.

Habitat.– *G. procera* inhabits wooded stream slopes, where it lives under stones and fallen logs and among leaf litter (Franzen and Leonard, 1947).

Gastrocopta tappaniana (Adams)

Geologic Range.– Late Pliocene (Rexroad Formation, Saw Rock Canyon local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– New England, south to Virginia and Alabama, west to the Rocky Mountains. In the Atlantic states, it does not extend south of Virginia (Miller, 1966).

Habitat.– This species lives on moist slopes near water, most commonly on wooded slopes near streams. It has, however, been collected from among the roots of grasses on the slopes of an unshaded pasture pond in Kansas (Franzen and Leonard, 1947).

Pupoides albilabris (Adams)

Geologic Range.– Early Pliocene (Laverne local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– This species occurs over eastern North America, west to the Rocky Mountains and across Mexico. It occurs as far north as Maine and south into Bermuda and the West Indies (Hibbard and Taylor, 1960).

Habitat.– *P. albilabris* is able to withstand high summer temperatures and dry conditions. It is common in woods and has been reported from among the roots of grasses far from water (Franzen and Leonard, 1947).

Vertigo elatior (Sterki)

Geologic Range.– Middle Pleistocene (Kansan, Cudahy fauna) to Recent (Miller, 1966).

Distribution.– Newfoundland west to British Columbia, south through the Rocky Mountains to Arizona. Does not extend south of 38 degrees except in the mountains (Miller, 1966).

Habitat.– *V. elatior* requires a cool humid climate. It cannot tolerate hot, dry summers (Franzen and Leonard, 1947).

Vertigo milium (Gould)

Geologic Range.– Late Pliocene (Rexroad Formation, Saw Rock Canyon local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– Maine and Quebec south to the Florida Keys, and into Jamaica and Santo Domingo, west to southeastern Arizona, Mexico and north into Colorado and South Dakota (Pilsbry, 1948).

Habitat.– *V. milium* occurs on moist, timbered stream banks and in marshes. Its absence from southwestern Kansas suggests that it cannot tolerate xeric conditions (Franzen and Leonard, 1947).

Vertigo ovata Say

Geologic Range.– Early Pliocene (Laverne Formation, Laverne local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– Cosmopolitan: Labrador south to the West Indies, west to Mexico and Arizona, north to Oregon and Alaska (Miller, 1966).

Habitat.– *V. ovata* is a species of moist areas immediately adjacent to streams and marshes. In these areas it is often found associated with *Carychium, Fossaria,* and *Pisidium* (Taylor, 1960).

Family **Valloniidae**

Vallonia gracilicosta Reinhardt

Geologic Range.– Late Pliocene (Rexroad Formation, Rexroad local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– The western Great Plains from Minnesota to Manitoba, south to Iowa and Nebraska. It also occurs at high elevations in the Rockies from southern Arizona and New Mexico, north through Alberta to the Northwest Territories (Hibbard and Taylor, 1960).

Habitat.– *V. gracilicosta* inhabits wooded areas under logs and stones and among leaf litter (Taylor, 1960).

Vallonia parvula Sterki

Geologic Range.– Late Pliocene (Bender local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– Western New York west to the Rocky Mountains, south in the Rockies into Arizona and New Mexico, east through Oklahoma into Ohio and southern Ontario.

Habitat.– This species prefers wooded areas where it lives under fallen wood and among leaf litter (Leonard, 1959).

Family **Succinidae**

Succinea

Species of *Succinea* may be distinguished only by examination of the soft parts. They cannot be discerned by shell characteristics alone.

Oxyloma

Species of *Oxyloma* may be distinguished only by examination of the soft parts. They cannot be determined by shell characteristics alone.

Family **Endodontidae**

Helicodiscus singleyanus (Pilsbry)

Geologic Range.– Late Pliocene (Saw Rock Canyon local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– "New Jersey to Florida, west to South Dakota, Colorado, and Arizona (Hibbard and Taylor, 1960, p. 145).

Habitat.– *H. singleyanus* is apparently able to withstand xeric conditions as it is believed to live among the roots of grasses in southwest Kansas (Hibbard and Taylor, 1960).

Family **Zonitoidae**

Hawaiia miniscula (Binney)

Geologic Range.– Late Miocene (Barstow Formation) to Recent (Miller, 1966).

Distribution.– "North America from Alaska and Maine to Costa Rica" (Taylor, 1960, p. 81).

Habitat.– This species is common among grass roots, under logs, and on rocky ledges in moist areas such as flood plains, and wooded slopes. It also occurs in grassy upland situations, but is not abundant there (Leonard, 1943).

Zonitoides arboreus (Say)

Geologic Range.– Early Pliocene (Laverne Formation, Laverne local fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– North America from Costa Rica to northern Canada (Pilsbry, 1946).

Habitat.– This species is common wherever a situation provides local moisture and protection from the sun. It is found in wooded and treeless areas under sticks, stones, and in the roots of grasses (Pilsbry, 1948). In the xeric conditions of southwestern Kansas it is confined to woodlands (Leonard, 1943).

Family **Polygyridae**

Stenotrema leai (Binney)

Geologic Range.– Middle Pleistocene (Kansan, Cudahy fauna) to Recent (Hibbard and Taylor, 1960).

Distribution.– New York state, south to Maryland, west to Kansas and South Dakota (Pilsbry, 1948).

Habitat.– *S. leai* is a species of moist wooded areas, often on the flood plains of rivers, where it lives under sticks, logs, stones, and debris (Miller, 1966).

PALEOECOLOGY

Stratigraphic evidence from Butler Spring and the sloth locality indicates that during mid to late Illinoian times a river larger than the present-day Cimarron deposited cross-bedded sands and gravels as it meandered across its flood plain. At the sloth locality a lake was situated on the flood plain near the river. E.D. Gutentag, who studied the ostracode faunule from the sloth locality, indicated (letter, September 28, 1973) that the lake was stream-fed and at least 10 feet deep. *Chara* grew in shallow portions of the lake. According to Prescott (1970, p. 26) *Chara* "are to be found usually in hard-water or alkaline lakes and slow flowing streams in which calcium is abundant in the form of carbonates or bicarbonates. . . ." Welch (1952, p. 194) states that "*Chara* . . . lives in shallow water and is rooted to the bottom. . . . So abundantly may it grow and so high is the calcareous content that in certain lakes it is said to form the chief, or even the sole, source of marl, and that large marl deposits have resulted from *Chara* alone." The recovery of an oogonium of *Chara* from the sloth locality deposits suggests that this plant may have been a determining factor in the formation of the marl.

In addition to the *Chara* the shallows of the lake probably supported thick growths of plants such as *Oedogonium, Rhizoclonium,* and *Vaucheria,* common pond algae on which *Valvata tricarinata* is known to feed. *Oedogonium* is able to grow in standing water which dries up in the summer. The algae *Rhizoclonium* and *Vaucheria,* like *Oedogonium*, grow attached to the bottom in shallow water and form floating mats which provide food for mollusks over water deeper than the mollusks would normally occupy. The submerged vegetation around the perimeter of the lake afforded food for the large concentrations of *Menetus exacuous kansasensis* and *Gyraulus parvus.* The sticks and debris trapped among the plants would have supported growths of microorganisms and small algae. *Helisoma trivolvis, Physa anatina, P. skinneri, Lymnaea obrussa,* and *Stagnicola reflexa* lived attached to the sticks and debris where they grazed on the algae and microorganisms.

Marginal to the lake was a marsh. The high alkalinity of the water may have permitted precipitation of calcium carbonate in the marsh as well as in the lake. This would explain the occurrence of large pieces of bird egg shell in some of the marl. The marsh itself served as a habitat for *Lymnaea dalli, Pisidium nitidum, Vertigo milium,* and *V. ovata*. The abundance of *Stagnicola caperata* suggests that there were pools in the marsh which were subject to periodic desiccation. This inference is further supported by the prominent rest marks visible on the shells of *Pisidium casertanum*. These rest marks are considered by Miller (1966) to be evidence of desiccation and forced aestivation. *Gyraulus circumstriatus, Physa gyrina,* and *Aplexa hypnorum* also dwelt in these temporary pools. The fact that the five species characteristic of temporary pools comprise almost 33% of the total number of individuals counted (exclusive of *G. parvus*) suggests that this type of habitat was quite prevalent in the area of the lake.

There were numerous deciduous trees near the lake and on the banks of the feeder stream. *Gastrocopta armifera, G. tappaniana, G. cristata, G. contracta, G. procera, Vallonia gracilicosta, Hawaiia miniscula, Pupoides albilabris, Stenotrema leaii,* and *Zonitoides arboreus* lived among the leaf litter and fallen wood of this moist woodland. The ranges of *P. albrilabris, G. cristata,* and *Z. arboreus* probably extended into the grassy uplands above the flood plain.

This ecological reconstruction agrees well with the evidence of vertebrate fossils described in Schultz (1965). The vertebrates recovered were marshy low meadow forms, forms which lived on valley slopes, and those which preferred dry upland prairies.

Climate.– Two far northern forms, *Valvata tricarinata* and *Physa skinneri*, which today do not range farther south than the northernmost states of the Great Plains, existed in the lake at the sloth locality. *Pupilla muscorum,* a land snail with a similar northern distribution, was also present. This suggests that the climate was fairly cool, rather than that the water was cool due merely to the presence of cool springs.

The most overwhelmingly abundant forms at the sloth locality represent species which now range only as far south as northern Nebraska. These are *Stagnicola caperata* and *Gyraulus circumstriatus. Vallonia gracilicosta, Stenotrema leai*, and the mouse *Microtus pennsylvanicus*, which have a similar distribution, are also present.

A few southern forms which range as far north as South Dakota but which are more common farther to the south are present: *Physa anatina, Gastrocopta cristata,* and *Vallonia parvula*. Of these only *P. anatina* is common.

The presence of both northern and southern elements in the fauna implies that the temperatures were more moderate than they are today. The summers were cooler, allowing the northern forms to exist, but the winters were warmer, permitting the southern forms to penetrate the area. Two species which were present in the Butler Spring fauna are absent from the sloth locality. These are *Probythinella lacustris* and *Lymnaea stagnalis jugularis*. Both species prefer the marshy, shallow water environs available at the sloth locality, but both have a relatively northern distribution. Their absence would seem to indicate a warmer climate than that of Butler Spring times.

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CLIMATIC AND BIOGEOGRAPHIC SIGNIFICANCE OF A FISH FAUNA FROM THE LATE PLIOCENE-EARLY PLEISTOCENE OF THE LAKE CHAPALA BASIN (JALISCO, MEXICO)

Michael L. Smith[1], Ted M. Cavender[2], and Robert Rush Miller[3]

Abstract.— Seven species of fishes in six families are described from late Pliocene-early Pleistocene deposits of the Lake Chapala Basin. Six of the species live in the basin today; the other, *Micropterus relictus*, is extinct. The habitat of the fauna was the shallow water of a lake margin or a flowing stream, according to geological and ecological inferences. The climate of the Mesa Central during and since the early Pleistocene was probably not much unlike that of today.

INTRODUCTION

The coastal lowlands of Mexico have served as migration routes for fishes from major faunas located to the north and south, but the uplifted Mexican Plateau has been typified by a high degree of endemism (Barbour, 1973a; Miller, 1976). To some extent, the fish fauna of the Plateau grades into that of the Rio Grande, but the Plateau's southern portion, the Mesa Central (West, 1964, fig. 3), is the probable center of origin of several distinctive groups of fishes.

The fauna of Lake Chapala today is closely tied in with the geological history of the region. Some new aspects of that history are here inferred from a fossil fauna recovered from the Jocotepec Quarry, a gravel pit about 5 km west of the town of Jocotepec, Jalisco, on Hwy. 15. The fossils were collected in June, 1969, by C.D. Barbour and R.J. Douglass; in February, 1971, by Ted Cavender and R.R. Miller; and in November and December, 1972, by R.R. Miller, F.H. Miller, and N.A. Neff.

THE GEOLOGY OF THE LAKE CHAPALA BASIN

Lake Chapala is located in the state of Jalisco except for the southeastern portion which extends into Michoacán. It is the largest lake in Mexico (80 km long and 20 km wide). The Pleistocene history of the lake has been described by Palmer (1926), Downs (1958), Clements (1963), and Barbour (1973b).

The Mesa Central includes the basins of several lakes in addition to that of Lake Chapala. These were formed when the region was uplifted during the mid-Pleistocene. Geological evidence cited by Clements (1963) suggests that the lake was much larger during the Pleistocene than it is today and that drastic post-uplift fluctuations in lake level have occurred. Clements believed that wave action at several levels had formed terraces north of the town of Chapala. Boulders on the terraces are rounded and bear a coating of lime similar to that on boulders of the present shoreline. Clements correlated the terraces with pluvial periods of the late Pleistocene. The terrace deposits bear no fossils, but in Clements' opinion may be comparable in age to fossiliferous deposits of the lake floor. This assemblage is late Pleistocene according to vertebrate fossils (Downs, 1958).

The correlation of the Chapala terraces with Pleistocene pluvial periods is disputed by an interpretation of the diatom stratigraphy of Lake Texcoco, which lies at a latitude about 100 km south of that of Lake Chapala (Bradbury, 1971). Many diatom species are remarkably persistent throughout the stratigraphy of Lake Texcoco, suggesting that climatic changes known to have occurred at more northerly latitudes were not reflected in central Mexico. Interpretation of the geological record is therefore difficult. Barbour (1973b) has suggested that changes in the drainage of Lake Chapala, rather than pluvial episodes, may account for the terraces.

The post-uplift lake lies in a graben formed when blocks north and south of the central block (the present

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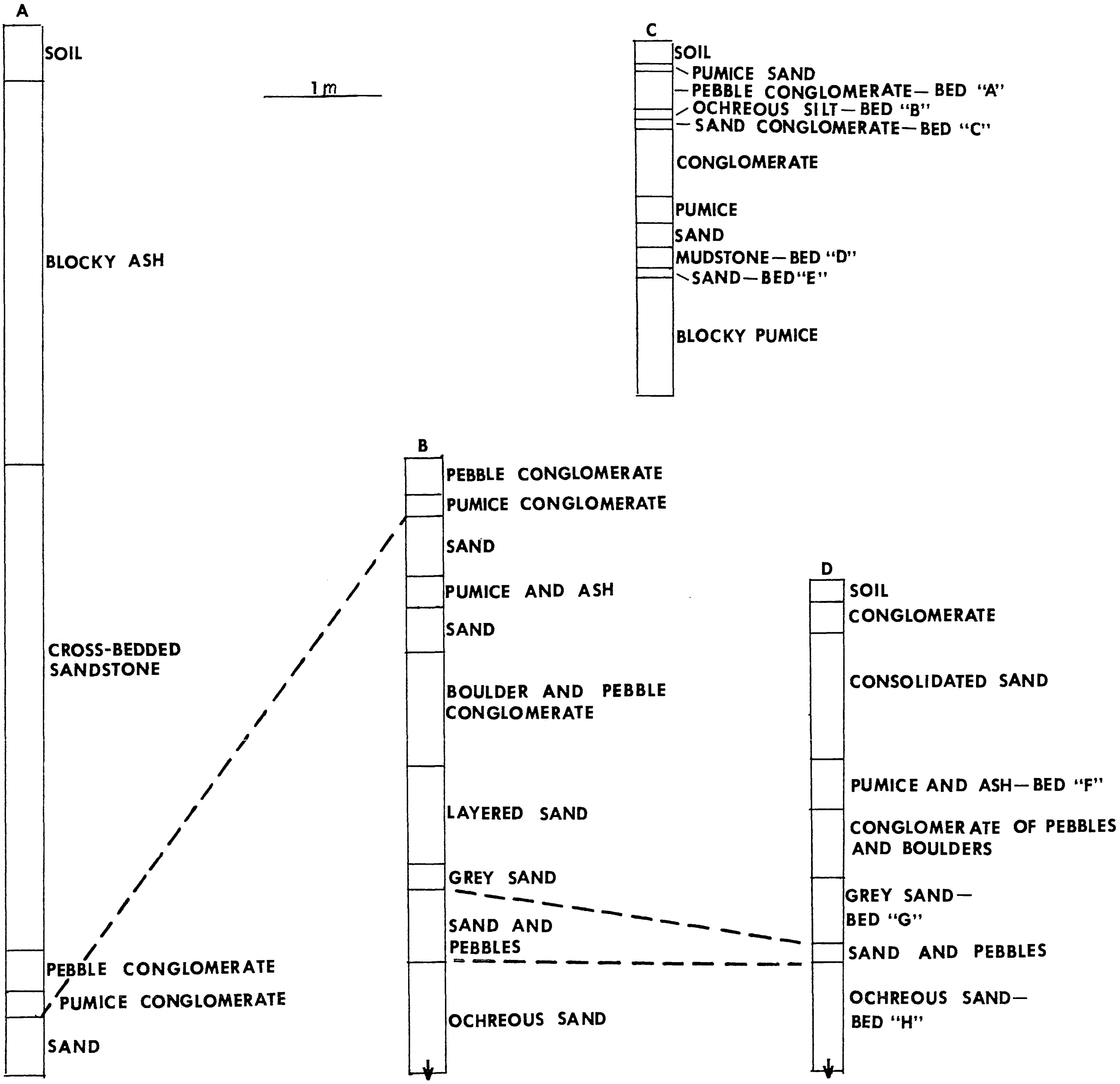

Fig. 1. Geologic section at the Jocotepec Quarry. (A) top vertical section in the west (upper) quarry pit taken 61.0 m north of the highest elevation of the beds. (B) vertical section in the west quarry pit taken 16.2 m north of the highest elevation of the beds. (C) vertical section in the highest west wall of the east (lowest) quarry pit. (D) vertical section in the center of the east wall, east quarry pit. Fossil-bearing strata are indicated as labelled beds.

basin) were further uplifted during the mid-Pleistocene orogeny. Sedimentary deposits of a pre-uplift lake (ancestral Lake Chapala) were tilted and broken at this time. These deposits, called "Chapala Beds" by Palmer (1926) and "Chapala Formation" by Downs (1958), bear remains of diatoms, gastropods, fishes, turtles, a crocodile, water birds, and mammals. The presence of the horse genus *Nannippus* is suggestive of the Pliocene, but the remainder of the fauna seems to be correlated with the lake floor fauna which is late Pleistocene.

Palmer (1926) was first to report the occurrence of apparent stream deposits north of Lake Chapala. The beds consist of cobbles, boulders, and fragments of pumice, all of which are well rounded and suggestive of strong current action. The deposits suggest a wave-worked lake margin or possibly a flowing stream. The fossils of this locality include the six families of fishes discussed in this paper, a frog or toad, a turtle, a bird, *Mammuthus, Neotoma,* and *Sigmodon.* These specimens have been deposited in the Museum of Paleontology, University of Michigan, Ann Arbor (UMMP).

In 1971 a 15 m section of sediment was exposed in an active quarry 5 km west of Jocotepec, a town near the western end of Lake Chapala. Barbour (1973b) obtained fossil vertebrates from this locality and was the first to publish a brief account of the remains. Apparently, local workers had many times come upon fossils in obtaining land fill from the quarry for construction purposes. Some of the fossil material was taken to Dr. Federico Solorzano of Guadalajara.

In general, the Jocotepec Quarry section can be characterized by its abundance of coarse water-rounded volcanic material which is angularly bedded (Fig. 1). The sediments are largely unconsolidated. There are at least two well-marked erosional surfaces. The upper one is cut into a 3 m bed of laminated shale of lacustrine origin. This erosional surface is buried under more than 6 m of cross-bedded pumice conglomerate which forms one of the most striking sedimentary exposures in the entire Chapala basin. The lower erosional surface is also overlain by a 4.5 m thick conglomerate, but this consists of well-rounded cobbles interbedded with layers of cross-bedded sand and gravel and also layers of tuffaceous material. A fossil-bearing zone rich in mammalian fossils was found in contact with the lower erosional surface. Below the contact lies 4 m or more of another conglomerate. The lowermost 2.5 m is an ochreous sand holding rounded black, volcanic (basalt) boulders up to 1 m in diameter. The upper 1 to 2 m is a tuffaceous sand lighter in color with much fewer and smaller boulders. In the 4 m of this sedimentary layer a trend was observed toward diminishing size of the boulders from bottom to top. This stratum shows some bedding structure in the form of small lenses of gravel or siltstone of limited lateral extent. Fish and turtle fragments were found in the sand.

Clements (1963) noted "a rather thick conglomerate overlain by ash and a bed of pumice conglomerate at the west end of the present lake basin. The beds are somewhat north of the lake on the east side of the pass followed by Highway 15." His description closely matches the upper quarry exposures near Jocotepec. Elsewhere in his paper in describing sediments of the Chapala Formation he included "at least one rather thick bed of cross-bedded pumice conglomerate. . ." slightly more than 6 m thick. No such exposure was found along the highway north of Chapala, thus leaving little doubt that Clements was including sediments at the west end of the lake in his definition of the Chapala Formation. Palmer (1926) also mentioned that "extensive tuff and pumice beds occurred in the upper part of the Chapala formation" although he did not give the locality. In the vicinity of Chapala, Palmer only noted "many thin beds of pumice."

The sedimentary section at the Jocotepec Quarry is of considerable interest since it represents a period of uplift, erosion, and deposition in the Chapala basin when there was much moving water, high relief, and a great deal of volcanic activity. This is in decided contrast to the period represented by sediments in the section north of Chapala which show mostly fine, well-sorted sediment deposited in quiet or slow-moving water with occasional moderate volcanic activity and repeatedly uniform conditions.

Lenses in the pumice conglomerate are broken by a number of fracture lines. These fractures are well marked because the displaced alternating lenses are composed of light gray and dark gray pumice particles. The fractures indicate uplift and slumping after deposition of the sediments near Jocotepec. However, one exposure showed cross-bedded pumice channeled into pumice sediment that was already fractured. This indicates uplift may have been taking place at or near the time of deposition. The pumice particles are well rounded and range in size from large gravel to sand. Many of the bands of pumice pinch out in a westerly direction at this exposure. The dip of the foreset beds is in most cases toward the west. Some of the lenses of basalt pebbles and cobbles inter-bedded with the pumice appear to thin out toward the west. No fossils were found in the pumice conglomerate.

Fish fossils were abundant at many different horizons in the middle and lower parts of the quarry section. The middle part in one place contained a small channel of tuffaceous sand which was ochreous in color and resembled the ochreous sand at the lowest level. This channel yielded abundant catfish remains.

The ochreous colored material is reminiscent of scoria and may have been derived from lake beds altered by the overriding basalt. Palmer noted at the south side of the lake near Los Caleras a contact between basalt and diatomitic lake beds. He stated that "for about one meter the liquid lava melted the sediments and converted them into a sort of red hornstone." In another place Palmer observed beds of red scoriaceous material associated with basalt.

It is now possible to integrate what is already known about the geology of the Chapala basin with new information from the sedimentary section of Jocotepec. The following statements summarize this knowledge:

1) The abundance of coarse water-rounded material and buried channels indicate stream deposition with water moving toward the west. Some of the fine deposits are

lacustrine; others may be littoral.

2) Water-rounded basalt particles range in size from gravel to boulders throughout the section and indicate a nearby source of basalt, probably the Estancia basalt of Palmer (1926). This marker formation overlying the type Chapala Formation is actually positioned stratigraphically below the Jocotepec deposits.

3) The coarse material, large boulders, and steeply dipping foreset beds in the water-laid sediment indicate nearby high relief and rapidly moving water.

4) The presence of water-deposited scoriaceous material at the base of the section may represent erosion of lake beds altered by basalt flows. This material is associated with the largest of the basaltic boulders found at the exposure.

5) Fractured sediments indicate uplift took place after deposition; channels cut in fractured sediments at the top of the section indicate uplift was also occurring at the time of deposition of the uppermost beds.

6) Waterlaid ash and finely laminated shales indicate intermittent periods of impoundment or extension of a lake over the area.

7) Erosional surfaces followed by periods of deposition may indicate different stages of uplift and landform development. Land mammalian fossils found in contact with one erosional surface indicate buried remains of animals living on, or transported to, that surface; perhaps the fossils were eroded from some earlier deposit.

8) Some of the fossil mammals and fishes are in agreement with those found scattered on the lake bottom and suggest that the source of the lake bottom material is the fossil-bearing zone in the conglomerate represented at Jocotepec. This zone may extend below the present water level or to other parts of the basin.

9) Layers of basalt cobbles found below the thick pumice layer indicate that extrusion of basalt preceded ejection of large amounts of pumice.

10) The cross-bedded pumice conglomerate is so thick and striking in appearance that it may possibly be utilized as a marker bed between adjacent basins. Thick cross-bedded pumice conglomerates were noted in the basin to the northeast along Highway 15 to Guadalajara.

The total section of sediments is distinguished from the "type Chapala section" north of Chapala by the characters enumerated above. Some of the finer material closely resembles deposits in the type section and is strictly lacustrine in origin. The majority of Jocotepec sediments were deposited at the periphery of the old Chapala basin marginal to the ancient lake that occupied that basin. The sedimentary section exposed north of Chapala is probably separated stratigraphically from that at Jocotepec Quarry by a basalt (Estancia basalt).

DESCRIPTION AND DISSCUSSION OF THE FOSSILS

Family **Catostomidae**

Moxostoma Rafinesque

Material.– UMMP 62543-62546.

Discussion.– Specific identification was not possible with the material available. However, the bones examined appear to represent one species of sucker which reached a large size, close to 500 mm in standard length. Assignment to *Moxostoma* is based on gill-cover type as discussed by Nelson (1949) and the following characters: (1) the short opercular arm expanded distally, (2) the extreme narrowness of the opercle at its upper end relative to the lower body of the bone, and (3) a convexity in the lower posterior margin of the cleithrum which is characteristic of most *Moxostoma*. Further agreement of the fossil elements is found with the subgenus *Scartomyzon*. Members of this group exhibit a slight concavity to the anterior margin of the gill cover with a notch for the interopercle located in the lowest part of this margin. The fossil opercle shows an unusual pattern of perforations at the base of the opercular facet on the inner surface. *Moxostoma poecilurum* (Jordan) comes closest to duplicating this characteristic of the osteological material available for comparison.

Family **Cyprinidae**

Algansea tincella (Valenciennes)

Material.– UMMP 62532-62533.

Discussion.– The determination is based on: (1) the evenly tapered posterior limb of the pharyngeal arch, (2) the high walls around the sockets of the teeth, (3) the single-rowed teeth, (4) the presence of an articulating facet for the first branchiostegal ray at the midpoint of the ceratohyal, and (5) the shape of the ceratohyal. The fossils differ from Recent material of this species in the greater robustness of the two anterior teeth.

The genus *Algansea* is restricted to the Rio Lerma basin and adjacent regions of the Mesa Central. It is very closely related to and probably derived from *Gila*, a genus with numerous species that live primarily in western United States (Barbour and Miller, MS). *A. tincella* is a moderate-sized minnow, reaching 15 cm. It is primarily an inhabitant of lakes, although the genus includes stream forms.

Yuriria alta (Jordan)

Material.– UMMP 62538-62542.

Discussion.– Yuriria, proposed as a subgenus of *Hybopsis*, has had a complicated nomenclatural history which is being treated by Miller (1976). Its type species is *Hudsonius altus* Jordan, described from a lake in Guanajuato, Mexico. The osteological evidence indicates that this species is related to cyprinids from western rather than eastern United States, and we follow Alvarez (1970) in retaining it in a monotypic genus. *Yuriria* has the following distinctive osteological traits: (1) preopercle with vertical and horizontal limbs of equal length (the vertical limb apparently reduced in length relative to other western Cyprinidae), the limbs forming an angle of 95 to 100 degrees, the laminar part of the bone between the limbs broadly expanded, (2) supraorbital canal typically extending into the parietal and terminating there in a pore, with this portion of the canal often turning laterad toward the pterotic as in a number of other western Cyprinidae, (3) large numbers of pores in the cephalic sensory canals, about 4 to 5 opening on the pterotic, 7 to 9 (rarely 6) on the dentary, 8 to 12 on the frontal, and 9 to 11 on the preopercle, (4) much enlarged and closely spaced cephalic sensory canal pores, (5) pharyngeal arch with one row of robust teeth resembling those of *Nocomis*, (6) mandible long, nearly straight, with well-developed ramus posterior to the coronoid process, anterior ramus (dentary) slender, tapering anteriorly with a distinctive dorsoventral expansion at the symphysial end, (7) supraethmoid broader than long with front margin deeply notched and with anterolateral corners flared outward over the nasal capsules, (8) vertebrae 40 to 41 with 19 or 20 in caudal series, and (9) pelvic fins with 9 or 10 rays. *Yuriria* resembles *Gila* (type species, *G. robusta*) in items (2) and (3).

The fossils, though unique in some respects, are referred to this species on the basis of: (1) the absence of the minor row of teeth, (2) the anterior position of the teeth relative to the expanded posterior margin of the pharyngeal arch, (3) the short, thick teeth with broad grinding surfaces and slight hooks, (4) the posterior pharyngeal process which is laterally compressed and expanded dorsoventrally, and (5) the horizontal margins of the pharyngeal plate curving ventrolaterally to form points. The following characteristics of the fossils differ somewhat from Recent material: (1) an adductor ridge passing immediately in front of the sensory pores of the preopercle with the laminar part of the bone recessed anterior to the ridge, (2) the basioccipital with low lateral walls only partly enclosing the sagittal recess, and (3) the heavier construction of the dentary, posterior process of the pterotic, and the anterior and dorsal limbs of the pharyngeal arch.

Yuriria alta is widely distributed in lakes and streams throughout the Mesa Central. It is large for a minnow, attaining a length of 35 cm.

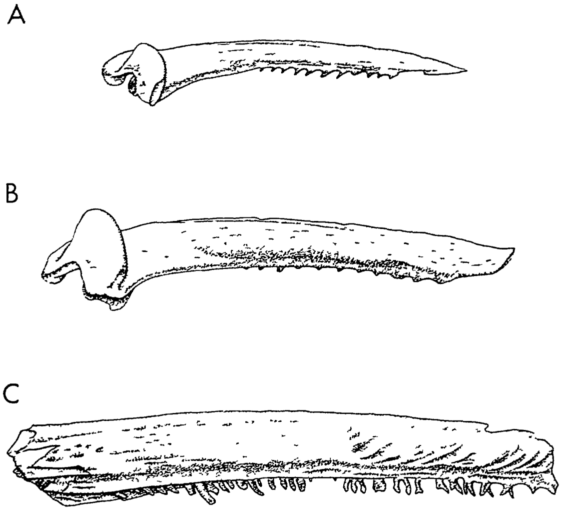

Fig. 2. Lateral views of pectoral spines of *Ictalurus dugesi*. (A) UMMP 62502. (B) UMMP 62512. (C) UMMP 62522. All x 2.

Family **Ictaluridae**

Ictalurus dugesi (Bean)

Material.– UMMP 62501-62531.

Discussion.– Two species of catfishes have been described from Lake Chapala, *Ictalurus dugesi* (Bean) and *I. ochoterenai* (De Buen). Alvarez (1966), however, synonymized these after comparing fossil remains from the Chapala basin. Unless careful comparison of complete neurocrania (not available to us) substantiates two taxa we are inclined to agree with Alvarez. Pectoral spines are usually diagnostic for ictalurids (especially subgenus *Amiurus*) but the fossil spines available to us (Fig. 2) show great variation and do not support the view that more than one taxon is present. Alvarez also concluded that late Pleistocene fossils of *Ictalurus* taken from the beach of Lake Zacoalco (about 15 airline km due west of Lake Chapala – see Fig. 1 in Howard, 1969) and from the floor of Lake Chapala represent *I. dugesi*, a species now extinct in Zacoalco but abundant in Chapala and in the Rio Lerma basin. Although it is possible that more than one catfish may occur in the Jocotepec Quarry beds, we hesitate to assign the fossils to more than one species. We illustrate a normal mandible (Fig. 3) and the one variant mandible (Fig. 4) that may be aberrant or may represent a different taxon.

The fossil material is distinguished from the bullhead catfishes (subgenus *Amiurus*) by: (1) the absence of an anteroventral ridge on the dentary, (2) an elevation at the suture of the dentary and articular which is very high relative to the least depth of the dentary, and (3) tooth rows extending onto the lateral surface of the dentary (Fig. 3). *Ictalurus dugesi* is distinguished osteologically from other members of the subgenus *Ictalurus* by the following combination of characters: (1) usually fewer than three moderately strong and sharp anterior distal serrae on the pectoral spine, (2) anterior ridge and dentations of the pectoral spine few, irregularly spaced and weak to moderate in strength, (3) posterior dentation halves

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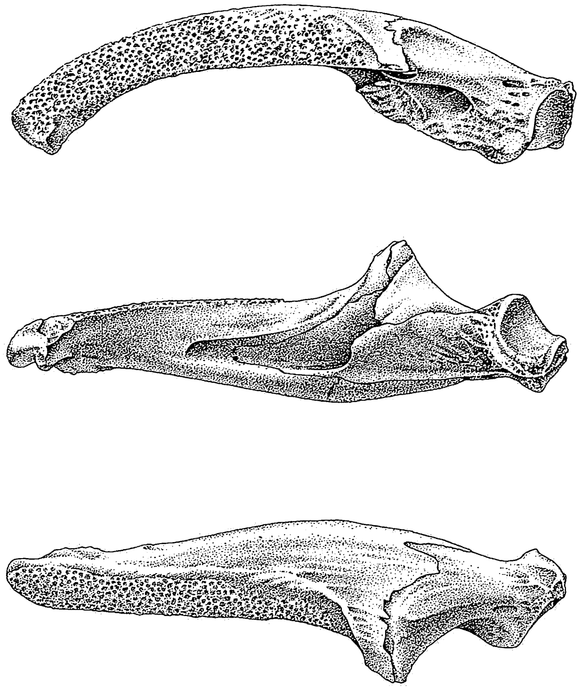

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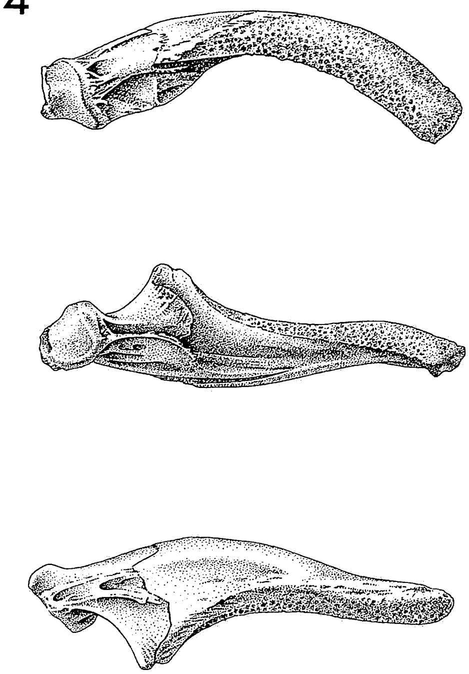

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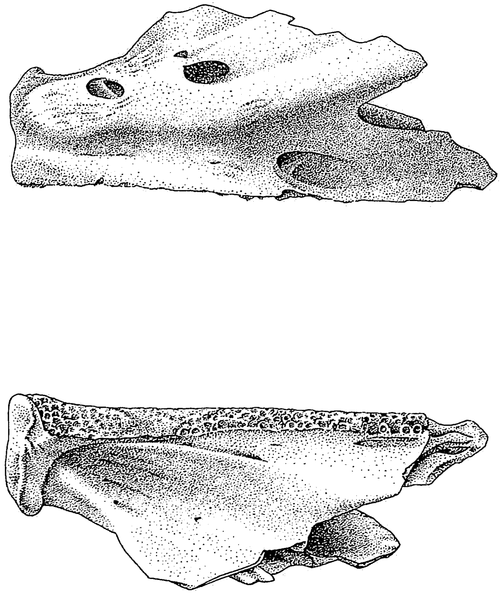

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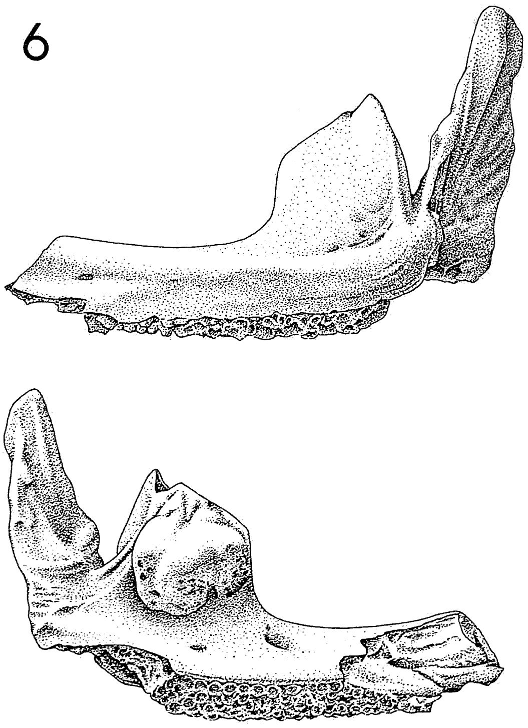

usually aligned, dentations regularly spaced, and unicuspid (sometimes multifid), (4) posterior groove present, dorsal and ventral dentation halves arising from dorsal and ventral spine halves, (5) posterior dentations moderate in size, (6) the short articular bearing a deep pit in its dorsal surface, and (7) the dentary curving evenly over its full length. Pectoral spine character states are based on Lundberg (1970). The material described here differs from Lundberg's description of *I. dugesi* in having moderate-sized rather than weak posterior dentations.

Ictalurus dugesi is found today in the central Mexican states of Nayarit, Jalisco, Zacatecas, Michoacán, and Guanajuato. It occurs in most aquatic habitats within its range, but is not typical of swift water.

Family **Goodeidae**

Chapalichthys encaustus (Jordan and Snyder)

Material.– UMMP 62536-62537.

Discussion.– Although the material is limited, it is referred to this species on the basis of: (1) the pattern of struts around the articulating surface of the opercle, (2) the square-shaped dorsal process of the opercle, and (3) the pattern of furrows on the dorsal surface of the frontal.

The family Goodeidae has its center of abundance in the Rio Lerma basin, from whence the oldest fossil (Pliocene, possibly Miocene) is known (Alvarez and Arreola, 1972). *Chapalichthys encaustus* is restricted to Lake Chapala, the lower Rio Lerma, and the outlet of the lake (Rio Grande de Santiago) above the falls at Juanacatlán. It is found in quiet water. This is one of the most abundant goodeids living in Lake Chapala today.

Family **Atherinidae**

Chirostoma lucius Boulenger

Material.– UMMP 62534-62535.

Discussion.– The determination is based on: (1) the small size of the teeth, in bands in both jaws, (2) tooth bands of dentary wider than in other species of *Chirostoma* and extending laterally to form a dentigerous shelf, (3) lower lateral edge of the dentary slightly concave near the symphysis, and (4) the articular bearing a distinct knob at the anterodorsal limit of the articular-quadrate facet.

Chirostoma comprises 18 species that are primarily restricted to the Mesa Central (Barbour, 1973a, 1974). Ten species occur in Lake Chapala today. *Chirostoma lucius* is known from Lake Chapala and the sluggish part of its outlet, Rio Grande de Santiago, downstream to Poncitlán.

Family **Centrarchidae**

Micropterus relictus Cavender and Smith, new species

Micropterus n. sp. (Miller, 1974)

Material.– UMMP 62462-62500.

Holotype.– UMMP 62499: an incomplete right dentary 33 mm long (Fig. 5) collected by R.R. Miller and party, November 29, 1972. University of Michigan locality UM Mex 1-72: quarry 5 km west of Jocotepec near the west end of Lake Chapala, Jalisco, Mexico. Stratigraphic horizon is Bed A in the highest west wall of the east (lowest) quarry pit, Chapala Formation: late Pliocene-early Pleistocene.

The specimen is from a large individual about 450 mm in standard length. It lacks the articular ramus, but most of the oral margin and coronoid ramus with its toothed surface is preserved, as well as the main body of the bone with three of the anteriormost sensory pores.

Paratype.– UMMP 62500: an incomplete right premaxilla 21 mm long (Fig. 6) from the same locality and horizon as the holotype.

The specimen lacks the posterior ramus. The main body of the bone is intact, as well as the anterior ascending processes and the anterior toothed surface.

Diagnosis.– A large species of *Micropterus* reaching a maximum size close to 600 mm in standard length and a probable weight of over 5.5 kg. *Micropterus relictus* is distinguished from living members of the genus by the following combination of characters: (1) dentary relatively short and deep for a *Micropterus*, its proportions similar to that of the smallmouth bass, *M. dolomieui*, (2) pores of the mandibular sensory canal larger than in *M. salmoides*, corresponding in size to those of *M. punctulatus* and *M. dolomieui*, but not as large as in *M. notius* or *M. coosae*, (3) toothed platform of dentary expanded laterally to form a narrow shelf as in *M. dolomieui*, (4) a deep, well-defined oval pit for the maxillary ligament positioned at the anterior end of the coronoid ramus, (5) the ascending process of the premaxilla meeting the alveolar process at right angles and not obliquely as in Recent species, (6) a dorsal pore located on the commissural branch of the supraorbital canal near its junction with the main canal, (7) vomerine tooth patch with straight posterior border, (8) shaft of vomer convex, (9) preopercle with sensory

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Fig. 3. Right lower jaw of *Ictalurus dugesi*, UMMP 62501; x 1. Top, dorsal view; middle, mesial view; bottom, inverted lateral view.

Fig. 4. Variant left lower jaw of *Ictalurus dugesi*, UMMP 62501; x 1. Top, dorsal view; middle, mesial view; bottom, inverted lateral view.

Fig. 5. Right dentary of *Micropterus relictus*, n. sp., UMMP 62499, holotype; x 2. Above, inverted lateral view; below, mesial view.

Fig. 6. Right premaxilla of *Micropterus relictus*, n. sp., UMMP 62500, paratype; x 3. Above, lateral view; below, mesial view.

canal visibly developed in its vertical limb, (10) ectopterygoid with horizontal and vertical limbs enclosing an angle of 132 degrees, (11) hyomandibular with the vertically oriented adductor ridge extending perpendicularly from its lateral surface, (12) parasphenoid possessing a slight flexure so that the anterior extension of the bone forms a 167 degree angle with a line drawn flush with the ventral margin of the basicranium, (13) ceratohyal relatively deep in relation to its length, perforated by a longitudinal slit near its broken dorsal margin, and (14) supracleithrum with a slender, tapered dorsal end for articulation with the posttemporal.

Discussion.– A readily apparent distinction of *Micropterus relictus* is its unusually large size. This condition in fishes is usually regarded as a specialization. However, *M. relictus* shows primitive structure in the known parts of its anatomy. The primitive characters are related to a somewhat smaller gape and head size than occurs in any living *Micropterus*, although the jaw proportions are not very much less than those of *M. dolomieui*. Although the character of body size is shared with *M. salmoides, M. relictus* possesses none of the extreme jaw specializations of that species.

Several distinctions of *M. relictus*, such as the orientation of the ascending premaxillary process, the parasphenoid flexure, and the dentary pit, can be interpreted as primitive characters since they appear commonly in other centrarchid genera. The extra frontal sensory pore located in the commissural branch close to its junction with the main supraorbital canal is found occasionally in all species of *Micropterus* (Branson and Moore, 1962, but our skeletal material shows it only in *M. dolomieui*) and consistently in seven species of *Lepomis* (*L. auritus, L. marginatus, L. megalotis, L. gibbosus, L. humilis, L. punctatus, L. microlophus*). Elsewhere in the family, this pore occurs only in *Ambloplites* (according to our observations and the above citation). Its apparent stable occurrence in *M. relictus* (in four known frontal bones) and sporadic showing among Recent species of *Micropterus* indicates that it may be a primitive character for the genus that is becoming lost in living forms. Possession of this pore in both *Lepomis* and *Micropterus* is consistent with Branson and Moore's (1962) derivation of these genera from a common ancestor.

Two subgenera of *Micropterus* are currently recognized (Bailey and Hubbs, 1949). *Huro* is monotypic, represented by *M. salmoides*. Three specialized characters distinguish this subgenus: (1) bifid pyloric caeca, (2) loss of scales on the interradial membranes of the dorsal and anal fins, (3) the deeply notched dorsal fin. The five other species are placed in the subgenus *Micropterus* with *M. dolomieui* as the type species. Distinguishing characteristics of this group are (1) simple pyloric caeca and (2) scaled interradial membranes of the dorsal and anal fins. Both of these features are primitive, based on their occurrence among the subfamily Lepominae. Osteological characters supporting two phyletic lines in *Micropterus* are unreported. Bailey and Hubbs (1949) noted parallelism in the trends found in both groups toward the loss of tongue teeth, reduction in scale size (seen in *M. salmoides floridanus*), and change in vertebral count from 14+18=32 to 15+17=32. In general, a more complete dentition is found in members of the subgenus *Micropterus* and they appear to represent the plesiomorphic group. *Micropterus dolomieui* has increased numbers of soft dorsal rays, abdominal vertebrae, and scales, but seems to be related to *M. punctulatus* through the intermediate *M. coosae* (see discussion by Branson and Moore, 1962).

Of the osteological characters used in the diagnosis of *Micropterus relictus*, several indicate a possible tie with *M. dolomieui*. These are the expanded toothed platform of the dentary, the straight posterior border on the toothed platform of the vomer with the shaft convex, and the angle of the ectopterygoid. In addition, the flexure of the parasphenoid and the proportions of the jaws and hyoid bar are most closely approached by *M. dolomieui*, but these are probably primitive as discussed. The quadrate and number of tooth rows on the dentary in *M. relictus* are closer to those of *M. punctulatus*, while the size of the mandibular pores appears to be most like *M. coosae*. In the characteristics of the premaxilla, hyomandibular, preopercle, supracleithrum, and consistent fifth sensory pore on the frontal, *M. relictus* is well differentiated from any Recent *Micropterus*. None of the known characters of *M. relictus* except large body size are shared with the subgenus *Huro*.

The name *relictus* is given as a masculine adjective in the nominative singular and refers to the geographical isolation of the species.

Fossil records of *Micropterus* known to us are the following: *M. salmoides* (Lacépède) from the Pleistocene (late Illinoian) of Kansas (G.R. Smith, 1963); *Micropterus* sp. cf. *M. punctulatus* (Rafinesque) from the lower Pliocene of Kansas (Wilson, 1968); and *Micropterus* sp. from the Pleistocene (late Illinoian) of Kansas (Schultz, 1965) and the lower Pliocene of Kansas and Oklahoma (C.L. Smith, 1962).

DISCUSSION

Hibbard (1955) stressed the importance of correlating evidence from many fields of science in inferring paleoclimates. Geological evidence may suggest general climatic conditions, but biological systems, being sensitive to subtle environmental factors, are probably the best indicators of climatic details. The morphology of an organism may suggest some features of its environment, but morphology alone is not useful in inferring climatic conditions, particularly when morphological information is based on fragmentary remains. However, the ecology of fossil communities can be inferred by applying the principle of uniformitarianism to comparisons of fossil and living species. Close morphological similarity between fossil and Recent populations is considered evidence of ecological similarity. Application of this approach assumes that morphological divergence occurs at the same rate as divergence in ecological tolerances, so that the former can be used as an estimate of the latter. Only slight morphological change (see discussions of *Algansea tincella, Yuriria alta,* and *Ictalurus dugesi*) has occurred between the extant members of the Jocotepec fauna and their Recent counterparts. It is therefore assumed that the ecology of the fossil fishes was similar to that of the same species today.

It seems probable that the climate of the Mesa Central since the early Pleistocene has not been drastically unlike that of today. All but one of the fossil species presently occur in the Lake Chapala Basin. Marked fluctuations seem unlikely since there are no refuges from which the highly endemic fauna could reinvade the area. Any climatic changes must have been within the ecological tolerances of the fishes present since, except for the bass, they were able to survive in place. This view of climatic stability correlates with the diatom stratigraphy of Lake Texcoco. The extinction of *Micropterus* on the Mesa Central is not interpreted as an indication of climatic change. This record represents the extreme southern limit of a principally northern family. Such a peripheral population may have been at the limit of its ecological tolerance, so that even minor climatic changes might have posed significant stress to the population.

The deposits of the Jocotepec Quarry indicate moderate current action at the site, but the fauna includes forms suggestive of a lacustrine habitat. The presence of *Algansea tincella, Chapalichthys encaustus,* or *Chirostoma lucius* in a strong current is unlikely. More than one community seems to be represented at the site, and the faunal list of any one community is probably incomplete. It seems likely that the site was associated with an adjacent body of still water.

The living fauna of Lake Chapala is relatively depauperate for such a large "subtropical" lake (Barbour and Brown, 1974). This fact, coupled with the high degree of endemism in the area, suggests that limits to dispersal have been important in the history of the fauna. Geographical factors influencing fish biogeography in the Mesa Central have been described by Barbour (1973a). The effects of geographical barriers to migration may have been reinforced by the distance of the Mesa Central from its source of immigrants. Fishes from the coastal lowlands have been excluded from the area by both geographical and ecological factors. The representation of Rio Grande faunal elements on the Mexican Plateau shows a marked decline toward the Mesa Central (Miller, 1976), which marks the southern extreme of the Plateau.

The discovery of a centrarchid on the Mesa Central, far south of the known Recent or fossil range of the family, is the most important zoogeographical aspect of this fauna. Centrarchids occur across most of North America between 20 and 50 degrees N latitude, but were thought to have barely extended into northern Mexico (southern coastal limit, Rio Soto la Marina, Tamaulipas; southern Plateau limit, Rio Conchos basin, Chihuahua). *Micropterus relictus* is the only fossil centrarchid yet known from outside the present natural range of the family (cf. Miller, 1959, Fig. 9; see Uyeno and Miller, 1963, regarding the Alaskan record). The occurrence of a centrarchid in southern Mexico suggests a stronger affinity between the fish fauna of the Mesa Central and the North American fauna (Miller, 1976) than previously suspected.

ACKNOWLEDGMENTS

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FISHES OF THE KANOPOLIS LOCAL FAUNA (PLEISTOCENE) OF ELLSWORTH COUNTY, KANSAS

Nancy A. Neff

Abstract.– The Kanopolis local fauna (Pleistocene: Yarmouthian interglacial) contains at least 11 genera and 15 species, comprising the largest fish fauna yet reported from the Pleistocene of the Great Plains. This is the first fossil record reported of *Notropis rubellus, Nocomis biguttata, Ictiobus niger, Lepomis megalotis*, and a *Noturus* in the *furiosus* species group. The representatives of the *furiosus* species group represent a sister group of the ancestor of *Noturus placidus* in the Cottonwood-Neosho system, or a more widespread ancestral form.

Based on the present habitats of the species, this fauna probably represents a permanent, low-gradient, large-stream community. A minor part of the fossil assemblage probably resulted from transport of small stream fish by tributaries into the main channel. Moister climatic conditions can be inferred from the presence of a large stream, permanent-water community, and from the present area of sympatry of that community at lower elevations to the east.

Fish remains from the Kanopolis local fauna of the Pleistocene of central Kansas represent at least 15 species in five families. The fossils were collected from a sand and gravel pit on the property of the White Construction Company of Kanopolis, Ellsworth County, Kansas. The pit lies in the SW¼, NE¼, Sec. 25, T. 15 S, R. 8 W, Ellsworth County, Kansas, at an elevation of 1570 feet. Collections were made in 1969, 1970, 1971, and 1972 by Dr. Claude W. Hibbard of the Museum of Paleontology of the University of Michigan and his field parties. Mr. and Mrs. Clayton Griggs of McPherson, Kansas, located the site and helped in the initial collection of material. The fossils were obtained from the sediments by washing in screen boxes according to the microvertebrate collecting technique described by Hibbard (1949).

The fauna is referred to the Yarmouthian interglacial age on the basis of ecologically inferred warm climatic conditions and stratigraphic evidence (Hibbard, pers. comm.). Holman (1972) has described the herpetofauna from Kanopolis, reporting 20 genera and 21 species.

The fish material consists of more than 1500 individual bones, of which 80% are too fragmentary to be identified. Fragments with diagnostic characters formed the basis for the identifications. Specimens were identified by comparison with recent and fossil comparative material from the Museum of Zoology and the Museum of Paleontology of the University of Michigan.

Permission to study the fossil material was given by Dr. Claude W. Hibbard of the University of Michigan Museum of Paleontology; much of the material was collected under the National Science Foundation grant GB-20249 to Dr. Hibbard. I wish to acknowledge the help and encouragement of Dr. Gerald R. Smith of the University of Michigan Museum of Paleontology.

DESCRIPTION OF THE FAUNA

Family **Lepisosteidae**

Lepisosteus osseus (Linnaeus)

(Fig. 1, A)

Material.– UMMP V59504, 1 right entopterygoid. UMMP V59503, 350 complete or nearly complete scales, 1 entopterygoid, 5 partial dentaries, 1 parasphenoid, 2 preopercles, 4 parietals, 1 posterior part of a vomer, 6 maxillary segments, 1 circumorbital, 1 palatine, 11 dermal skull fragments, 4 vertebrae.

American Museum of Natural History, Department of Ichthyology, New York, New York, 10024.

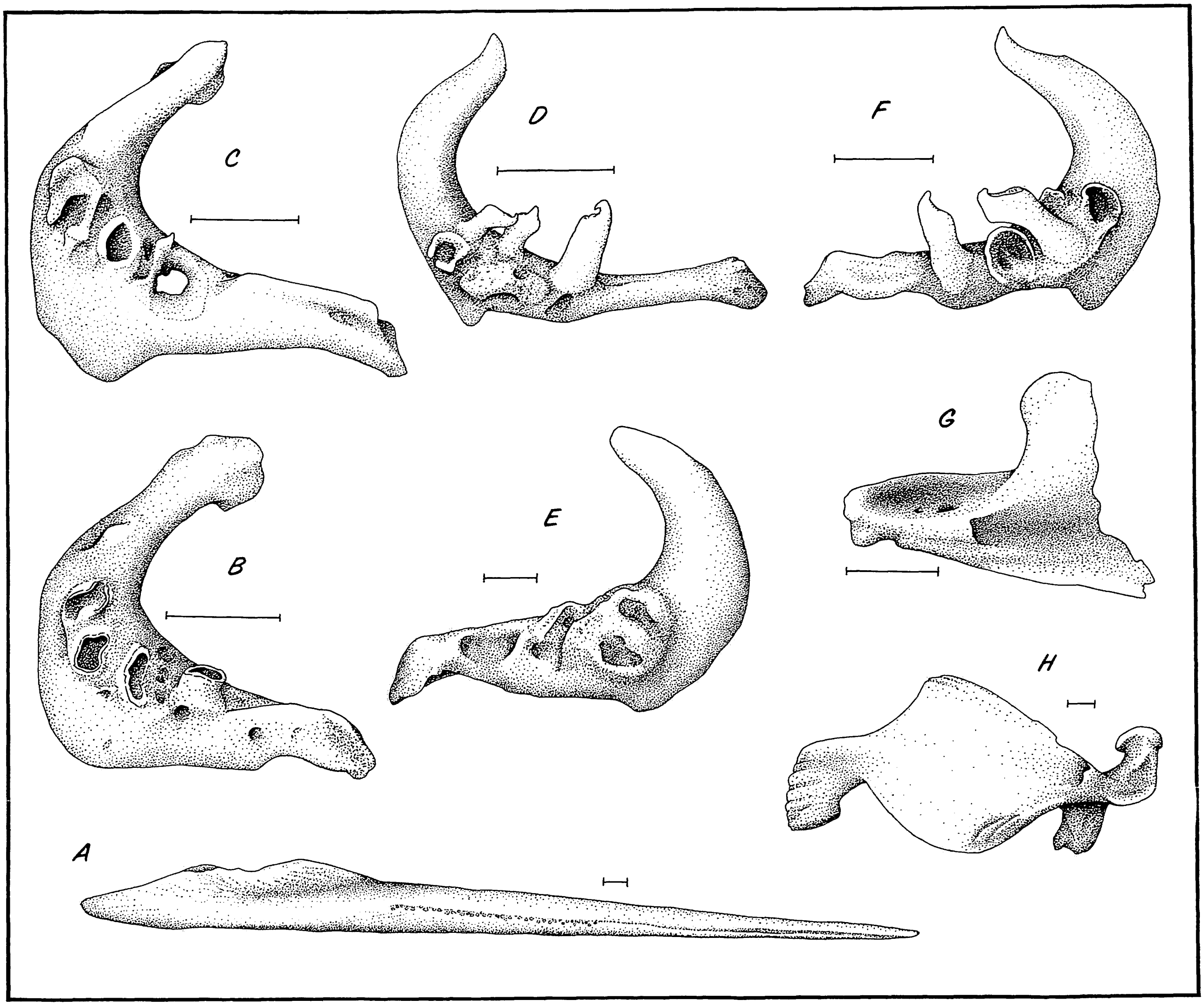

Fig. 1. (A) Right entopterygoid of *Lepisosteus osseus*, ventral view, UMMP V59504. (B) Left pharyngeal arch of unidentified cyprinid, mesial view, UMMP V59523. (C) Left pharyngeal arch of *Campostoma* sp., UMMP V59521. (D) Left pharyngeal arch of *Notropis* cf. *rubellus*, UMMP V59517. (E) Right pharyngeal arch of *Nocomis* cf. *biguttata*, UMMP V59516. (F) Right pharyngeal arch of *Notropis* sp., UMMP V59519. (G) Right dentary of *Pimephales promelas*, mesial view, UMMP V59515. (H) Right maxilla of *Ictiobus niger*, lateral view, UMMP V59505.

Remarks.— The preopercle of *Lepisosteus osseus* can be distinguished from *L. platostomus, L. occulatus* and *L. spatula* by the shape of the posterior half of the exposed dermal surface. In the latter three species, the exposed dermal surface extends some distance dorsally between the subopercle and postorbital bones, while in *L. osseus* and the fossil form there is no extension dorsally. *L. osseus* can also be distinguished by the proportions of the entopterygoid (Gregory, 1933, p. 129) — long and narrow in *L. osseus*, with the posterolateral edge turned sharply ventrally, while in the other three species the bone is wider and has a more obtuse bend in it.

There are slight differences between the parasphenoids of *L. osseus* and *L. platostomus* — the latter is broader posteriorly, with two diagonal ridges on the ventral surface running anteriorly and converging at the level of the basipterygoid facet. The dentary of *L. osseus* is elongated with the symphyseal surface extending posteriorly approximately one-third the length of the dentary. *L. platostomus* and *L. spatula* both have shorter, thicker dentaries with a short symphysis on the mesial side of the anterior end.

Habitat and Distribution.— The long-nosed gar commonly lives in large, open rivers, most often in less turbulent parts – bases of riffles, margins of eddies or in quiet pools and backwaters. The young are often found in shallow backwaters in thick beds of aquatic vegetation.

The long-nosed gar is found throughout eastern North America, from the Mississippi affluents in Montana through the Great Lakes basins (except Lake Superior) to the St. Lawrence-Champlain watershed of Quebec and Vermont, and south throughout southeastern United States to the highlands of northern Mexico.

Fossil Occurrence.– There are numerous records for both the genus and species.

Family **Cyprinidae**

Pimephales promelas Rafinesque

(Fig. 1, G)

Material.– UMMP V59515, 1 right dentary.

Remarks.– The dentaries of *Pimephales promelas* and the fossil differ from *P. notatus, P. vigilax* and *P. tenellus* in being shorter with a deeper cup-like dorsomesial surface of the dentary. The fossil dentary is even slightly more extreme than *P. promelas* but still referable to this species.

Habitat and Distribution.– *Pimephales promelas* is found in streams of all sizes, but is most abundant in pools of small, intermittent headwater creeks or in small streams that are reduced to stagnant pools during dry seasons.

The distribution of the fathead minnow is presently throughout southern Canada (from the Prairie Provinces through to the St. Lawrence drainage of Quebec), extending south, west of the Appalachians, to Tennessee, and further west, south through Montana to New Mexico and into northern Mexico.

Fossil Occurrence.– Pleistocene (Illinoian) of Oklahoma (C.L. Smith, 1958); early Pleistocene of Nebraska (G.R. Smith and Lundberg, 1972).

Notropis cf. *rubellus* (Agassiz)

(Fig. 1, D)

Material.– UMMP V59517, 1 complete left pharyngeal arch. UMMP V59518, 1 partial right pharyngeal arch.

Remarks.– The teeth are small and slightly hooked, almost conical in shape. There are four in the major row and two in the minor. The arch, particularly the anterior limb, is long and slender. The dorsal limb is sigmoid, oval in cross-section, and sharply pointed.

The fossil material is most like the rosy-faced shiner, *N. rubellus*, in these characters, although also resembling *N. atherinoides*. The arch is very much unlike the *N. atherinoides* from Kansas, which Cross (1967) suggests might be a different species.

Habitat and Distribution.– *Notropis rubellus* inhabits small, high gradient streams, only in the eastern portion of Kansas today. The distribution elsewhere is from southern Manitoba, North Dakota and Minnesota eastward throughout Wisconsin and Michigan to the St. Lawrence system. This shiner extends south on both slopes of the Appalachians, in the west to Tennessee and throughout Missouri.

Notropis sp.

(Fig. 1, F)

Material.– UMMP V59519, 1 right pharyngeal arch. UMMP V59520, 3 right pharyngeal arches, 2 left pharyngeal arches.

Remarks.– All of these arches have four teeth in the major row and one in the minor row. The ala is of moderate width with the alar angle opposite the third tooth. The anterior limb is moderately long and slender, with an expansion at the base of the anterior-most tooth. The tooth row extends along approximately two-thirds of the anterior limb. The teeth are strongly hooked, usually with a grinding surface beneath the hook. The dorsal limb is short and strongly curved anteriorly and medially.

Notropis stramineus normally lacks teeth in the minor row. However, the other characteristics of the arch and teeth resemble *N. stramineus* and, to a lesser extent, *N. heterodon*, but are unlike *N. dorsalis, lutrensis, camurus, spilopterus, volucellus* or *cornutus.*

Habitat and Distribution.– Species of the genus *Notropis* are ubiquitous in streams and lakes of eastern North America. *N. stramineus* is very common in shallow, sandy rivers with permanent flow. Its range is from southeastern Canada through the Great Lakes region and south to Tennessee and through the central Great Plains south to the northeastern-most portion of Mexico.

Nocomis cf. *biguttata* (Kirtland)

(Fig. 1, E)

Material.– UMMP V59516, 1 complete right pharyngeal arch without teeth.

Remarks.– The major tooth row extends the entire length of the anterior limb to the broad symphyseal surface. There are four teeth in the major row and one in the minor. The alar angle is not sharp; the dorsal limb is low, broad and slightly rounded. The alveoli are large. The arch has only a moderate platform for the posterior teeth.

Habitat and Distribution.– The hornyhead chub is found in clear, permanent creeks. In Kansas it is found today only in the eastern portion of the state, although there are records from before 1915 in the western portions of the Kansas River drainage.

The distribution is from Colorado and Wyoming, and eastern North Dakota to the western half of the Lake Ontario basin and the Hudson River drainage in New York, and southward into northern Arkansas and Oklahoma, and Tennessee.

Campostoma sp. (Rafinesque)

(Fig. 1,C)

Material.– UMMP V59521, 1 left pharyngeal arch. UMMP V59522, 1 left pharyngeal arch, 1 fragment of arch with teeth.

Remarks.– There are four teeth in the major row and none in the minor row. The teeth are very thin and long with grinding surfaces, and with the ends closer to each other than the bases. The alar angle is not as extreme as in *Hybognathus*. The tooth platform is moderately elevated.

The arch is shaped like *Campostoma* arches in the following characteristics: (1) a fairly broad ala, (2) expansion of the end of the dorsal limb, (3) well-developed muscle origin on the dorsal limb near the tooth row, and (4) an extremely recurved dorsal limb.

The fossil material differs from both *Campostoma oligolepis* and *anomalum* in several aspects. The anterior and dorsal limbs are shorter and the crest on the anterior limb is higher than is found in either *C. oligolepis* or *anomalum*. The arch is also not as slender as *C. anomalum*.

Habitat and Distribution.– *Campostoma anomalum* prefers rocky pools and riffles of clear, permanent streams with moderate to high gradient. *C. oligolepis* inhabits a similar habitat except for preferring larger streams.

The stoneroller occurs in the Lake Michigan and Mississippi River watersheds of Wisconsin, and south through the Mississippi and Arkansas River tributary systems of the Ozark uplands to northeastern Mexico and parts of New Mexico. In the east *C. anomalum* extends from New York southward on either side of the Allegheny Mountains and finally into Gulf tributaries of Alabama and Georgia.

Fossil Occurrence.– Pleistocene (Illinoian) of Kansas, (G.R. Smith, 1963); Pleistocene (Sangamon) of Texas, (Lundberg, 1967).

Genus and species unidentified

(Fig. 1, B)

Material.– UMMP V59523, 1 left arch. UMMP V59524, 1 right arch.

Remarks.– These two arches resemble *Campostoma* in the extremely recurved dorsal limb, the shortness of the limbs, the muscle attachment site on the dorsal limb and the crest on the anterior limb. They differ in having a low, broad ala with no alar margin and a very short anterior limb. The muscle attachment site on the dorsal limb is very strong. There are probably four teeth in the major row and none in the minor.

The presence of the muscle attachment site on the dorsal limb in addition to the usual ones is probably an adaptation for increasing the grinding strength as in *Campostoma*. The recurved dorsal limb, producing a U-shaped arch, is also often found in fish with a grinding feeding habit, perhaps because of dorsal-ventral compression of the arch resulting from dorsal-ventral compression of the head in bottom-dwelling fish (Smith, pers. comm.).

Cyprinidae, indeterminate

Material.– UMMP V59525, 3 frontals, 1 joined pair of frontals, 6 basioccipitals, 3 hyomandibulars, 4 fragments of pharyngeal arches.

Family **Catostomidae**

Ictiobus niger (Rafinesque)

(Fig. 1, H)

Material.– UMMP V59505, 1 complete right maxilla. UMMP V59506, 5 dentaries, 1 premaxilla, 3 incomplete hyomandibulars, 1 subopercle, 2 incomplete pharyngeal arches, 1 pelvic element, 3 maxillae.

Remarks.– The fossil dentaries are referable to *Ictiobus niger* on the basis of the following characters: (1) the length and degree of curvature mediad of the gnathic ramus are intermediate between those of *I. cyprinellus* and *I. bubalus* (the dentary of *I. meridianalis* is like that of *I. bubalus* in these characters), (2) the ridge on the dorsal surface of the gnathic ramus of the dentary is close to center in *I. niger* (and *I. meridionalis*) rather than posterior to center as in *I. bubalus*.

The maxillae in the fossil fauna are referable to *I. niger* on the basis of (1) the greater mesial deflection of the anterodorsal process away from the plane of the body of the bone than in *I. cyprinellus* or *I. bubalus*, and (2) the premaxillary process is directed slightly posterior to the normal to the plane of the body of the bone in *I. niger* rather than more anteriorly as in *I. cyprinellus*. The most complete fossil maxilla is very much like a small specimen of *I. meridionalis*, differing only in the angle of mesial deflection of the anterodorsal process, which is greater in *I. niger* and the fossils. There is some variation in the fossil maxillae in the length of the posterior process, but apparently within the range of variation of recent *I. niger*.

The premaxilla is like *I. niger* or *I. cyprinellus* in having the two limbs of approximately equal length set at about a 120 degree angle to each other, while those of *I. bubalus* and *I. meridionalis* form approximately a 90 degree angle, with a shorter lateral limb in *I. bubalus*.

Habitat and Distribution.– The black buffalo occurs mainly in larger rivers, often in faster currents, preferring

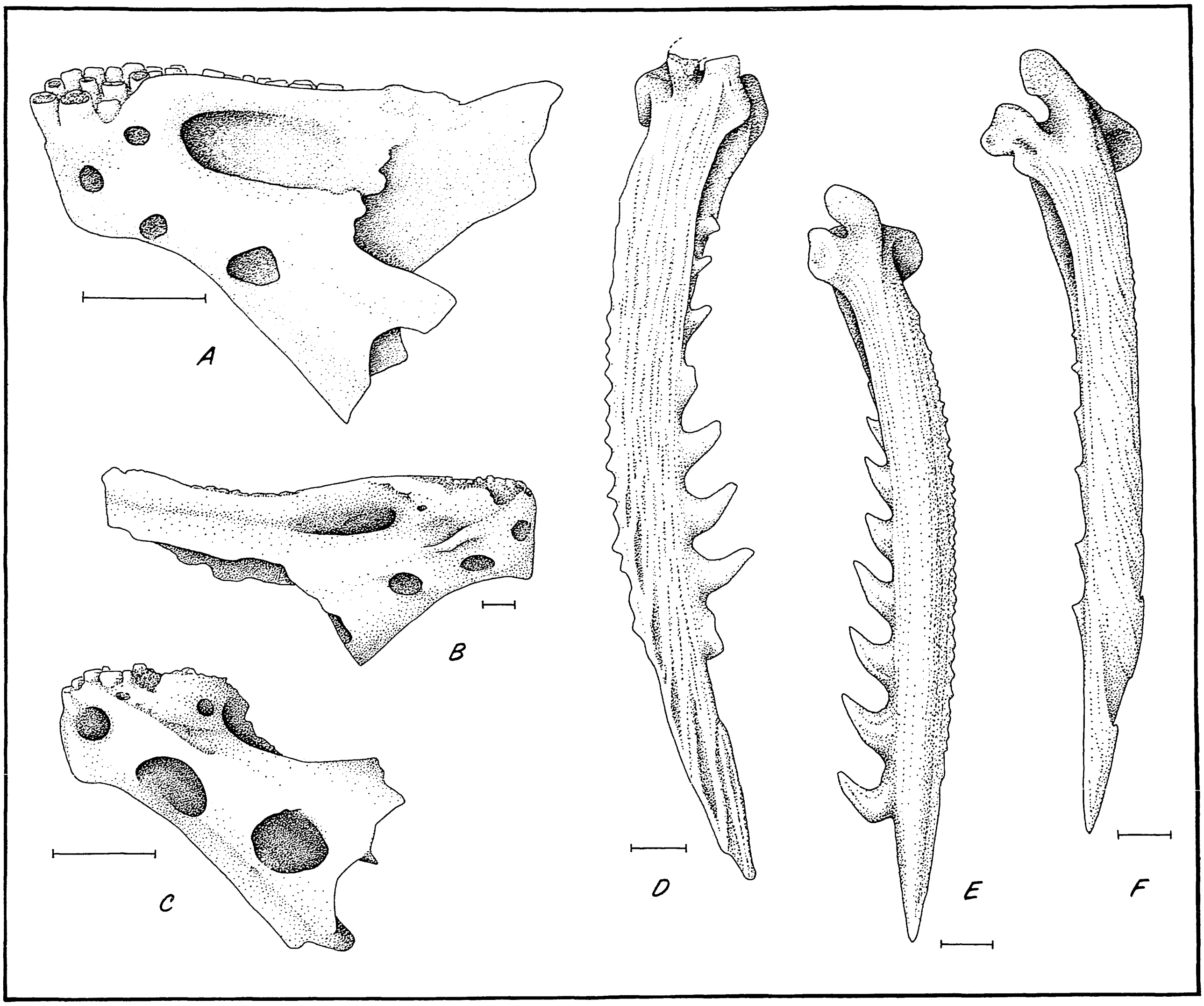

Fig. 2. (A) Left dentary of *Lepomis megalotis*, lateral view, UMMP V59527. (B) Right dentary of *Lepomis cyanellus*, UMMP V59531. (C) Left dentary of *Lepomis* cf. *humilis*, UMMP V59529. (D) Right pectoral spine of *Noturus* cf. *N. furiosus* species group, ventral view, UMMP V59507. (E) Left pectoral spine of *Ictalurus punctatus*, UMMP V59510. (F) Left pectoral spine of *Ictalurus melas*, UMMP V59512.

clear, deep waters.

Ictiobus niger is distributed from eastern Nebraska and Minnesota to Lake Michigan and to the Ohio Valley, and southward through the central parts of the Mississippi lowlands to the Gulf Coast and northern Mexico.

Fossil Occurrence.– The genus has been reported from the lower Pliocene of Oklahoma (C.L. Smith, 1962), Pleistocene (Illinoian) of Kansas (G.R. Smith, 1963) and Pleistocene (Sangamon) of Texas (Uyeno and Miller, 1962).

Family **Ictaluridae**

Ictalurus melas (Rafinesque)

(Fig. 2, F)

Material.– UMMP V59512, 1 pectoral spine. UMMP V59513, 15 dentaries, 2 supraethmoids, 16 articular-angulars, 60 pectoral spines.

Remarks.– The supraethmoids are identified as *Ictalurus melas* on the basis of the broad, open anteromedian notch. This character is not as extreme as in *Pylodictis* *olivaris*, nor are the cornua as elongated in *I. melas* as in *Pylodictis.*

The posterior denticulations are weak, and the anterior serrae very weak to absent on the pectoral spines of the fossil form and *I. melas.* The dentaries are probably *I. melas*, since they are heavier and deeper anteriorly, quite distinct from *I. punctatus* or *Noturus.*

Habitat and Distribution.– The black bullhead is found in base- and low-gradient portions of streams, and in backwaters, oxbows, and overflow ponds of larger streams, often in silty water.

The range of *Ictalurus melas* extends from the Hudson Bay watershed of North Dakota through the Great Lakes drainage, including southern Ontario and New York, southward to western Pennsylvania, the Cumberland River system of Tennessee, and through the Gulf states as far west as Texas and northern Mexico.

Fossil Occurrence.– There is an extensive record of *I. melas* throughout the Pleistocene; it is summarized in Lundberg, 1975.

Ictalurus punctatus (Rafinesque)

(Fig. 2, E)

Material.– UMMP V59510, 1 pectoral spine. UMMP V59511, 1 supraethmoid, 2 complete and 4 partial pectoral spines, 1 dentary, 6 articular-angulars, 1 quadrate.

Remarks.– The supraethmoid of the fossil and *I. punctatus* is separable from other species of *Ictalurus* except *I. natalis* and *I. brunneus* by being relatively flat with a closed anteromedian notch. The fossil material is referable to *I. punctatus* rather than either of the others on the basis of the greater length of the lateral cavities posterior to the cornua, and the greater width of the bone behind the cornua. *Ictalurus punctatus* is variable in both the degree of flatness and the width behind the cornua; the fossil material is definitely within this range of variation. From the size of the fossil supraethmoid, the standard length of the original fish is estimated to be at least 300 mm.

The pectoral spines are identified as *I. punctatus* on the basis of the very weak anterior serrae, and the large, strong, simple posterior denticulation. *Ictalurus furcatus* is similar, but can be distinguished by the smaller, more complex (multi-pointed) posterior denticulations.

The dentary of the fossil and recent *I. punctatus* has a long, slender anterior limb, with a shallow anterolateral face, as opposed to the dentaries of the other ictalurid species which are heavier and deeper anteriorly.

Habitat and Distribution.– The channel catfish is found in a variety of habitats but often in large streams of base- or low-gradient, or large deep pools.

Ictalurus punctatus occurs from the Prairie Provinces of Canada and the southern part of the Hudson Bay drainage southward through the Great Lakes-St. Lawrence basin and through most of the Mississippi Valley (as far west as eastern Colorado) as far south as Florida, the Gulf states and northeastern Mexico.

Fossil Occurrence.– The fossil record of *I. punctatus* extends to at least the middle Miocene, with abundant and well-preserved material from the Miocene and Pliocene of Nebraska, and the Pleistocene of the Great Plains (summary in Lundberg, 1975).

Noturus (Rabida) cf. *N. furiosus* species group

(Fig. 2, D)

Material.– UMMP V59507, 1 complete pectoral spine. UMMP V59508, 13 partial pectoral spines.

Remarks.– The pectoral spines are assignable to the *Noturus furiosus* species group as described by Taylor (1969) on the basis of the following characters: (1) the spines of the *furiosus* group are broadly curved, scimitar-like, while those of the *miurus* group are straighter, (2) the presence of very strong, retrorse, posterior denticulations, (3) small, sharp, distinct anterior serrae extend from near the base of the spine to opposite the most distal posterior denticulations and (4) the presence of strong, distal grooves.

Although the fossil material is clearly referable to the *furiosus* species group of the subgenus *Rabida*, it is not strictly referable to any of the four species – *N. furiosus, N. stigmosus, N. munitus,* or *N. placidus* – because of differences in the dentition of the spine. In particular it differs significantly from *N. placidus* in having stronger anterior serrations than that species. The fossil form is not being described as a new species, however, because of the somewhat tentative status of the four existing species. Taylor recognized four species because of consistent morphological differences, but pointed out that the geographic separation of the four species prevents a test of the question of whether they might be subspecies. If it should turn out that the four species are good species, then the fossil material is distinct enough to be recognized as a new species. If, however, they are all part of one species, then the complex encompasses enough variation to include the fossil as part of the same species.

Habitat and Distribution.– *Noturus furiosus* is found only in the Neuse and Tar River systems of North Carolina, in the Atlantic drainage. *Noturus stigmosus* occurs in the Ohio River system, Mississippi River tributaries in western Tennessee, Wabash River in Indiana, Green River in Kentucky, and north to the Detroit, Huron and Maumee Rivers. *Noturus munitus* is restricted to the Pearl River in Louisiana and Mississippi, and tributaries to the Alabama River in Alabama – all Gulf drainages. *Noturus placidus* is found only in the Neosho River drainage in southeast Kansas and Illinois River in Oklahoma – in the

Neosho River, Spring River, and lower course of the Cottonwood River.

Taylor (1969) says that the hiatus in ranges is probably real; the two forms (*N. placidus* and *N. stigmosus*) that occur in the Mississippi drainage are also separated ecologically by a barrier of turbid waters and shifting sand in the lower Arkansas and Mississippi Rivers. Because the species are all characteristic of large lowland streams and rivers, Taylor thinks that simple headwater crossovers between streams probably did not take place. Rather, what remain today are relict populations of a more widely distributed ancestor. Alternatively, there may have been changes in the major streams, but this is unlikely with the populations in the Carolina streams or Gulf coastal rivers, so a more widespread previous distribution is indicated.

The streams in the area of the source of the fossils reported on here, tributaries of the upper Smoky Hill River, are in a separate drainage, the Kansas River drainage, from the Neosho River drainage (part of the Arkansas River system) containing *N. placidus*. Although *N. placidus* is closest geographically, it is less like the fossil than any of the other three. However, the drainage history of the area (Bayne and Fent, 1963) indicates that during Kansan time the upper Smoky Hill River was a tributary to the Arkansas River system, through a valley west of the Neosho (McPherson Valley), and was captured by the lower Smoky Hill River, in the Kansas River system, in early Illinoian, after the date assigned to these fossils. Therefore, this occurrence of a member of the *N. furiosus* species group may represent a sister group of a more widespread ancestor of *N. placidus.*

The habitat preference of all four species is clear water of large streams or rivers, usually moderate to fast current over riffles or rubble (although *N. furiosus* was also reported in abundance in shallow waters with little to no current over coarse sand).

Incertae sedis

Material.— UMMP V59509, 1 dentary.

Ictaluridae, indeterminate

Material.— UMMP V59514, 58 partial pectoral spines, 5 partial opercles, 9 hyomandibulars, 4 partial dentaries, 12 maxillae, 9 quadrates, 10 pterygiophores, 59 cleithra, 45 dorsal spines, 2 urohyals, miscellaneous elements.

Family **Centrarchidae**

Micropterus salmoides (Lacepede)

Material.— UMMP V59526, 12 dentaries, 1 maxilla, 1 vomer, 6 premaxillae, 2 frontals, 3 hyomandibulars, 3 quadrates.

Remarks.— The dentaries are close to *Micropterus salmoides* in the narrowness of the toothed surface and in the shape of the anterior portion of the dentary. There is not a complete enough dentary to distinguish it from *M. punctulatus* conclusively; *M. punctulatus* has a shallower ventromesial flange posteriorly than *M. salmoides* or *M. dolomieui*. A character that did not always separate *M. salmoides* and *M. dolomieui* but was moderately consistent was the presence or absence of a medium-sized pore on the mesial surface of the dentary, halfway from the anterior end and immediately below the toothed surface. In this character the fossils all resembled *M. salmoides* in having the pore present.

The vomer is definitely referable to *M. salmoides*. The toothed surface is elevated above the surface of the bone, extending ventrally and forming a deep recess immediately posterior to it. The shape of the flanges of bone on the dorsal side of the vomer is also distinctively like *M. salmoides.*

The maxilla is distinguishable from *Lepomis* by the absence of the prominence posterolateral to the premaxillary process, by the groove extending dorsally from the premaxillary process and by the deep muscle scar on the mesial surface of the posterior half of the maxilla.

Habitat and Distribution.— The largemouth bass is characteristic of clear, lentic waters, occurring in backwaters and oxbows along major streams and permanent pools of intermittent upland creeks.

The natural distribution of *Micropterus salmoides* is from southern Canada throughout the entire Great Lakes system and Mississippi Valley to northeastern Mexico and in the east from North Carolina down the coastal plain to western Florida.

Fossil Occurrence.— Pleistocene (Illinoian) of Kansas (G.R. Smith, 1963); late Pleistocene of Michigan (Wilson, 1967); Pleistocene (Wisconsinan) of South Dakota (Ossian, 1973).

Lepomis cyanellus Rafinesque

(Fig. 2, B)

Material.— UMMP V59531, 6 complete and 19 partial dentaries, 6 complete and 14 partial maxillae, 2 vomers, 4 frontals, 3 hyomandibulars, 2 premaxillae.

Remarks.— The dentaries in this fossil fauna are clearly separable from all other *Lepomis*, and are referable to *Lepomis cyanellus* rather than *Lepomis gulosus* on the basis of several characters: (1) the acute anterodorsal angle of the dentary is as in *L. cyanellus*, (2) the large muscle scar for the insertion of *m. mandibularis* on the lateral face is further forward than in *L. gulosus*, and (3) the arrangement of the pores of the lateral line canal is as in *L. cyanellus.*

The vomers are referable to *L. cyanellus* on the basis of the shape of the toothed area, the size and number of tooth sockets and the shape of the flanges of bone on the dorsal side of the bone.

Habitat and Distribution.– *Lepomis cyanellus* is found in lakes, ponds and pools of creeks, often in sluggish creeks with intermittent flow, and in fewer numbers in large low- or moderate-gradient streams.

Its range is from Colorado and South Dakota through Minnesota, Wisconsin and the upper peninsula of Michigan to extreme southern Ontario and western New York, southward to Georgia and the Gulf states to northeastern Mexico and eastern New Mexico.

Fossil Occurrence.– Pleistocene (Illinoian) of Oklahoma (C.L. Smith, 1954, 1958); upper Pliocene of Kansas (C.L. Smith, 1962); Pleistocene (Illinoian) of Kansas (G.R. Smith, 1963); Pleistocene (Illinoian) of Kansas (Schultz, 1965); Pleistocene (Kansan) of Texas (Hibbard and Dalquest, 1966); Pleistocene (Sangamon) of Texas (Lundberg, 1967); Pleistocene (Wisconsinan) of Texas (Schultz and Cheatum, 1970); early Pleistocene of Nebraska (G.R. Smith and Lundberg, 1972).

Lepomis cf. *humilis* (Girard)

(Fig. 2, C)

Material.– UMMP V59529, 8 dentaries, 2 maxillae, 4 frontals.

Remarks.– *Lepomis humilis* is recognized by the very large size of the sensory canal pores. There is appreciable variation in the size of the pores in the fossil dentaries, several seeming to have less extreme development of the large pores.

The maxillae are identified as *L. humilis* by the small size of the premaxillary process, the narrowing of the shaft of the maxilla halfway along its length, and the slanted instead of rounded posterior end.

Habitat and Distribution.– The orange-spotted sunfish is tolerant of siltation and high turbidity, and is commonly found in streams with low or intermittent flow, and often in pools of streams.

L. humilis is found as far north as North Dakota in the west, through the Mississippi drainage of southern Minnesota and Wisconsin to extreme southern Michigan and western Ohio. It extends south through the western parts of Kentucky and Tennessee, Alabama and western Mississippi to the Gulf coast, and through the Plains region to Texas and northern Mexico.

Fossil Occurrence.– Pleistocene (Illinoian) of Kansas (G.R. Smith, 1963); early Pleistocene of Nebraska (G.R. Smith and Lundberg, 1972); Pleistocene (Wisconsinan) of South Dakota (Ossian, 1973).

Incertae sedis

Material.– UMMP V59530, 1 vomer.

Remarks.– The specimen is broken, and only tentatively identified as *L. humilis* rather than *L. cyanellus*, on the basis of the shape of the toothed area.

Lepomis megalotis Cope

(Fig. 2, A)

Material.– UMMP V59527, 1 dentary. UMMP V59528, 2 hyomandibulars.

Remarks.– The dentary is identified as *L. megalotis* on the basis of the flatness of the dentary (only weak anteromesial curvature), the smooth curve in the ventromesial margin, unlike the sharper angles in *L. macrochirus* or *L. gibbosus*, and the very large muscle scar for the insertion of *m. mandibularis.*

Habitat and Distribution.– The longear sunfish inhabits still waters of clear lakes, ponds and streams, often associated with considerable aquatic vegetation.

The northern part of the range is through the glacial lake regions from the northern parts of Iowa east throughout the lower peninsula of Michigan and the Lake Erie and Lake Huron drainages of Ontario to the St. Lawrence basin in Quebec and parts of the Allegheny River system in Pennsylvania. The longear is found to the south, through the eastern halves of Kansas and Oklahoma into northern Mexico, and in the east through the Appalachians down to the Gulf states.

Cross (1967) indicates evidence that the longear has become established in the Kansas River basin quite recently through introduction, being previously confined in Kansas to the Arkansas River system. It is known, however, from elsewhere in the Missouri River basin, and may occur in the Kansas River tributary as a relict population.

Centrarchidae, indeterminate

Material.– UMMP V59532, 40 partial dentaries, 2 vomers, 15 maxillae, 50 premaxillae, 48 lower pharyngeal bones with toothed surface, 15 quadrates, 32 articular-angulars, 22 frontals, 7 hyomandibulars, 26 preopercles, 100 spines and pterygiophores.

DISCUSSION

In the Kanopolis local fauna, there are at least 11 genera and 15 species of fishes. It is the largest fish fauna yet reported from the Pleistocene of the Great Plains.

Although most of the forms are not different from the recent populations in the area today, several species do indicate some evolutionary change. The specimens of *Ictiobus niger* are slightly different from recent specimens, *Lepomis humilis* shows considerable variability, and *Noturus* cf. *furiosus* may be a new species altogether, and is certainly different from its nearest living relative.

The Kanopolis fish fauna includes two ecological associations: (1) large-stream and river fishes requiring a base- to low-gradient and (2) species found more often in small streams or semi-permanent waters. The great majority of the species are in the first category; the minnows *Pimephales promelas, Campostoma* sp., *Notropis rubellus*, and *Nocomis biguttata* are in the second category. The fauna is probably from a large stream which, if not low-gradient, must have had permanent still, deep, clear pools and backwaters. The small creek species are sparsely enough represented to be probably fugitive individuals or the result of transport into the larger stream from nearby territories. This is supported by geological evidence that the locality occurs at the confluence of a smaller tributary with the main channel of the river (Hibbard, pers. comm.).

Holman (1972) reported three genera and four species of frogs, six genera and species of turtles, two genera and species of lizards and nine genera and species of snakes from the Kanopolis local fauna. His conclusion was that most of the herpetofauna represented a permanent stream community with relatively deep, slow-moving water.

The only inference that can be drawn about differences in climate from the present is that the area was moister, probably due, at least in part, to a greater annual rainfall than is presently found. This would account for the permanent, large body of water indicated by the herpetofauna and fish fauna. This climatic difference is also indicated by the present geographical location to the east and slightly to the south of the area of sympatry of the fishes in the fauna. The fishes whose ranges do not extend as far west as Ellsworth County today are *Lepisosteus osseus, Nocomis biguttata, Notropis rubellus, Ictiobus niger, Noturus furiosus* species group, and *Lepomis megalotis*. That the area of sympatry is entirely to the east today indicates a moister climate for the Kanopolis area during the time of deposition of the fossils. A similar shift in area of sympatry was noted by Holman (1972) for the herpetofauna of Kanopolis. The fish fauna does not warrant any conclusions about different temperatures or other factors. This agrees well with the placement of the fauna in an interglacial period.

One, possibly two, of the range differences between the fossil fauna and the present fauna are by drainage basins rather than totally climatic correlates. The native occurrence of *Lepomis megalotis* in the Kansas River basin has been questioned (Cross, 1967); its presence in the fossil fauna establishes its Pleistocene range on the high plains. The species of *Noturus* may have been part of a much more widespread population or it may have existed in the upper Smoky Hill River as a continuation of a population ancestral to *Noturus placidus* when the upper Smoky Hill River flowed south through the McPherson Valley into the Arkansas River. After capture by the lower Smoky Hill River into the Kansas River system, extinction of the portions of the *Noturus* population in the Smoky Hill River and throughout the Arkansas River system except for the Neosho and Cottonwood Rivers might have resulted from decreased rainfall and loss of permanent large streams.

Another possibility is that the upper Smoky Hill River during the Yarmouthian interglacial was a tributary of the Cottonwood River, flowing southeast into the Arkansas River system through the Neosho River system. Although the geological evidence as reported by Bayne and Fent (1963) does not indicate this, Miller (1970) has reported both faunal and geological evidence for the drainage of the upper Smoky Hill River through the Cottonwood-Neosho system during Yarmouthian or early Illinoian time. If this drainage pattern existed, then the fossil *Noturus* could represent only a slight extension of the range of the *Noturus furiosus* species group.

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

J. Alan Holman

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

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

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

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

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

INTRODUCTION

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

History of the Site.– The WaKeeney local fauna was discovered by Lester F. Phillis in about 1941. After the discovery, parties from the University of Michigan and from the University of Kansas collected at the site, but these collections were made at the surface and no detailed excavations were attempted. In 1966 Richard L. and Jan

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Michigan State University, Museum, East Lansing, Michigan, 48824.

Wilson removed about 250 "small" sacks of matrix (I interpret this as about two and one-half tons) from the site and wet-screened the material in a nearby spring. The vertebrate fauna from this work was published by Wilson (1968). Shortly after, the Wilsons moved to the west coast, and Claude W. Hibbard of the University of Michigan suggested that I continue excavations at the site in the light of the potentially large and important herpetofauna. Thus, collecting was done in the summers of 1969, 1970, 1972, and 1973. Published references to the site include Hibbard and Phillis (1945), Hubbs and Hibbard (1951), Brodkorb (1962), Feduccia and Wilson (1967), Wilson (1968), Hibbard and Jammot (1971), and Holman (1971).

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

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

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

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

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

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

Class **Amphibia**
  Order **Urodela**
    Family **Ambystomatidae**
      Ambystoma maculatum (Shaw)
      Ambystoma tigrinum (Green)
      Ambystoma sp. indet.

  Order **Anura**
    Family **Pelobatidae**
      Scaphiopus hardeni n. sp.
    Family **Tregobatrachidae** n. fam.
      Tregobatrachus hibbardi n. gen. et sp.
    Family **Bufonidae**
      Bufo cognatus Say
      Bufo marinus (Linnaeus)
      Bufo hibbardi Taylor
      Bufo pliocompactilis Wilson
      Bufo valentinensis Estes and Tihen

- Family **Hylidae**
  - *Acris* sp. indet.
  - *Hyla* cf. *H. cinerea* (Schneider)
  - *Hyla* cf. *H. gratiosa* LeConte
  - *Hyla* cf. *H. squirella* Sonnini and Latreille
  - *Hyla* sp. indet.
  - *Pseudacris* cf. *P. clarki* (Baird)
- Family **Ranidae**
  - *Rana* cf. *R. areolata* Baird and Girard
  - *Rana* cf. *R. pipiens* Schreber
  - *Rana* sp. indet.

Class **Reptilia**
- Order **Chelonia**
  - Family **Kinosternidae**
    - *Sternotherus odoratus* (Latreille)
  - Family **Emydidae**
    - *Terrapene* cf. *T. carolina* (Linnaeus)
  - Family **Testudinidae**
    - *Geochelone orthopygia* (Cope)
    - *Geochelone* sp.
  - Family **Trionychidae**
    - *Trionyx* sp. indet.
- Order **Sauria**
  - Family **Anguidae**
    - *Ophisaurus attenuatus* Baird
    - *Gerrhonotus mungerorum* Wilson
  - Family **Teidae**
    - *Cnemidophorus* cf. *C. sexlineatus* (Linnaeus)
  - Family **Scincidae**
    - *Eumeces hixsonorum* n. sp.
- Order **Serpentes**
  - Family **Boidae**
    - *Tregophis brevirachis* n. gen. et sp.
    - *Ogmophis pliocompactus* n. sp.
  - Family **Colubridae**
    - *Natrix hillmani* Wilson
    - *Thamnophis* sp. indet.
    - *Paleoheterodon* sp. indet.
    - *Coluber* or *Masticophis*
    - *Elaphe* sp. indet.
    - *Lampropeltis similis* Holman

Following is an annotated list of the WaKeeney local fauna herpetofauna. All measurements are in mm. Specimens are either in the Museum, Michigan State University (MSU-VP) or in the Museum of Paleontology at the University of Michigan (UMMP V). In the figures each line equals 2 mm except in *Geochelone* the line equals 40 mm.

ANNOTATED LIST

Class AMPHIBIA

Order URODELA

Family **Ambystomatidae**

Ambystoma maculatum Shaw

Material.— Three trunk vertebrae, MSU-VP 750, Fig. 1 A.

Remarks.— Tihen (1958) divided the genus *Ambystoma* into subgenera and species groups. The 3 vertebrae listed above fit into the *Ambystoma (Ambystoma) maculatum* group, and indeed, on the basis of size and characters are inseparable from the living species *A. maculatum*. The *A. maculatum* group has an interesting present day distribution in that it is divisible into two disjunct areas: (1) along the Pacific Coast from southern Alaska to northern California and east into Montana and (2) south throughout most of the United States east of the Great Plains. Western forms are *A. gracile* and *A. macrodactylum* and eastern forms are *A. jeffersonianum, A. laterale, A. platineum, A. tremblayi,* and *A. maculatum*. Tihen (1958) stated that "the various species groups of *Ambystoma* were established before the Pliocene . . ." and this is borne out by the fossils of *A. maculatum* from the lower Pliocene of Trego County, Kansas. Today, *A. maculatum* occurs in eastern United States and eastern Canada from Ontario, Quebec, and the maritimes south to South Carolina, northern Georgia, coastal Alabama, Mississippi and Louisiana, and eastern Texas.

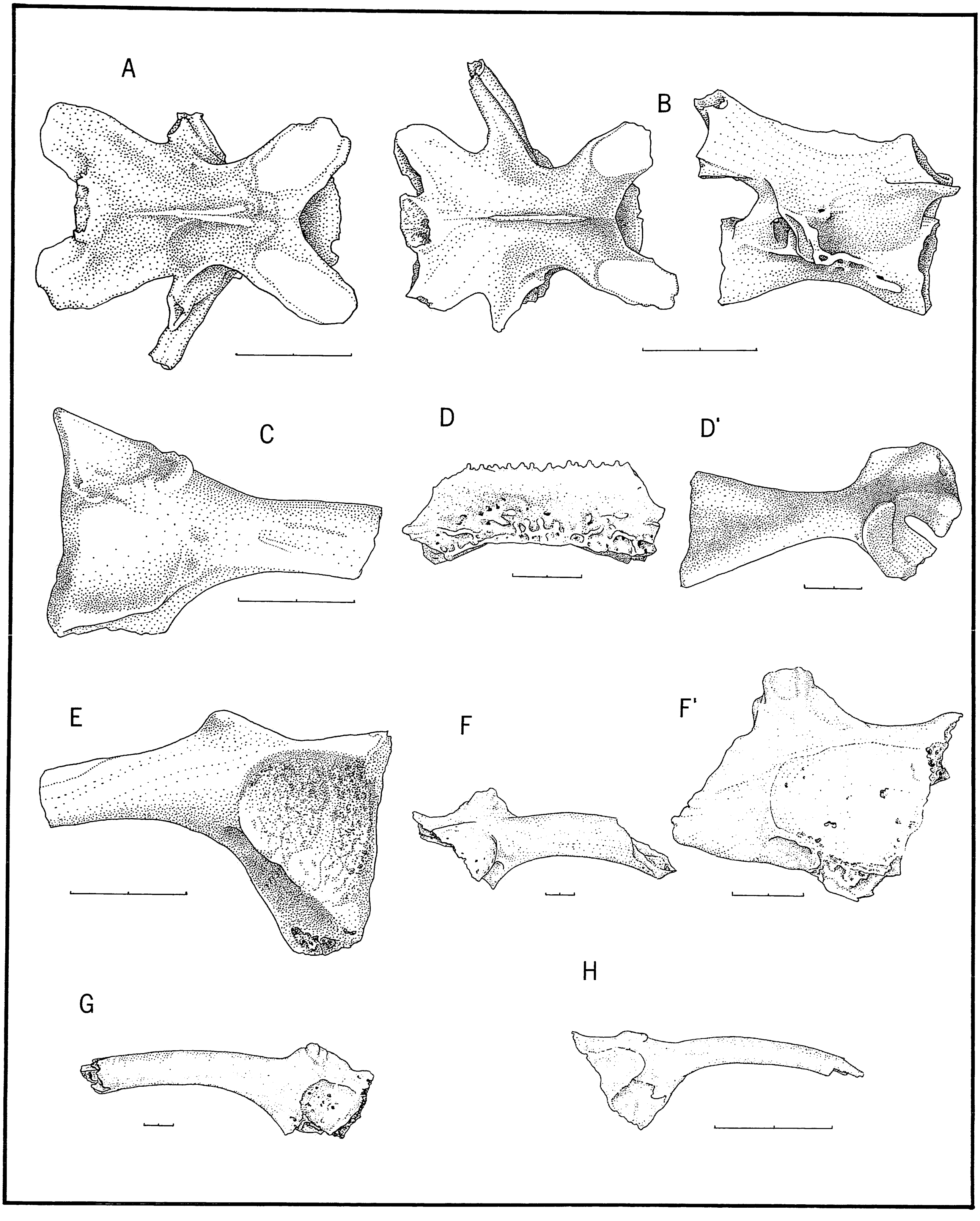
Measurements of the WaKeeney fossils are: width through prezygapophyses 3.2 – 3.7 (3.40) N3; length through zygapophyses 4.8 – 5.7 (5.27) N3.

Ambystoma minshalli Tihen and Chantell of the upper Miocene Norden Bridge fauna of Brown County, Nebraska, is possibly the ancestor to *Ambystoma maculatum* as the Nebraska fossil is characterized as a small *Ambystoma* of the *A. maculatum* group (Tihen and Chantell, 1963). Evidently the evoltuion of *A. maculatum* from *A. minshalli* took place between upper Miocene and lower Pliocene times.

Ambystoma tigrinum (Green)

Material.— Thirteen trunk vertebrae, MSU-VP 751, Fig. 1 B.

Remarks.— These vertebrae seem unquestionably assignable to *A. tigrinum* based on (1) vertebral proportions (Tihen, 1958), (2) the neural arch extending well posterior to the ends of the postzygapophyses, and (3) the upswept neural arch. In size, these fossils are a little smaller than adult *A. tigrinum* of today. This is the earliest record of *A. tigrinum* as a fossil, and we now have two ambystomatid salamanders representing living species by Clarendonian times.


A
B
C
D
D'
E
F
F'
G
H

Measurements of the most complete of the vertebrae are: length through zygapophyses 4.2 – 5.0 (4.70) N4; width through postzygapophyses 2.9 – 3.2 (3.01) N4.

Ambystoma sp. indet.

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

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

Order ANURA

Family **Pelobatidae**

Scaphiopus hardeni n. sp.

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

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

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

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

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

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

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

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

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

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

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

holbrooki and *S. couchi*). The sphenethmoid of *S. wardorum* is unknown.

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

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

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

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

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

Tregobatrachidae n. fam.

Tregobatrachus n. gen., type of the fam.

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

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

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

Tregobatrachus hibbardi n. sp.

Diagnosis.– As for the genus.

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

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

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

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

Family **Bufonidae**

Bufo cognatus Say

Material.– A right partial frontoparietal (UMMP V55441) and a left ilium (V55421) were assigned to this species by Wilson (1968).

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

Bufo marinus (Linnaeus)

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

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

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

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

Bufo hibbardi Taylor

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

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

Bufo pliocompactilis Wilson

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

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

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

Bufo valentinensis Estes and Tihen

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

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

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

Family **Hylidae**

Acris sp. indet.

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

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

Hyla cf. *Hyla cinerea* (Schneider)

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

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

Hyla cf. *Hyla gratiosa* Le Conte

Material.– Four right ilia, MSU-VP 761.

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

Hyla cf. *Hyla squirella* Sonnini and Latreille

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

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

Hyla sp. indet.

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

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

Pseudacris cf. *Pseudacris clarki* (Baird)

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

Remarks.– This form was originally reported by Wilson (1968). The MSU group collected another ilium (MSU-VP 764) that satisfies the criteria of Chantell (1964 and 1966) and Wilson (1968) for the identification of the genus. The MSU ilium is identified as *Pseudacris* sp.

indet. *Pseudacris* cf. *P. clarki* has previously been identified from the upper Miocene of the Norden Bridge local fauna of the Valentine Formation of Brown County, Nebraska (Chantell, 1964).

Family **Ranidae**

Rana cf. *Rana areolata* Baird and Girard

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

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

Rana cf. *Rana pipiens* Schreber

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

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

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

Rana sp.

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

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

Class REPTILIA

Order CHELONIA

Family **Kinosternidae**

Sternotherus odoratus (Latreille)

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

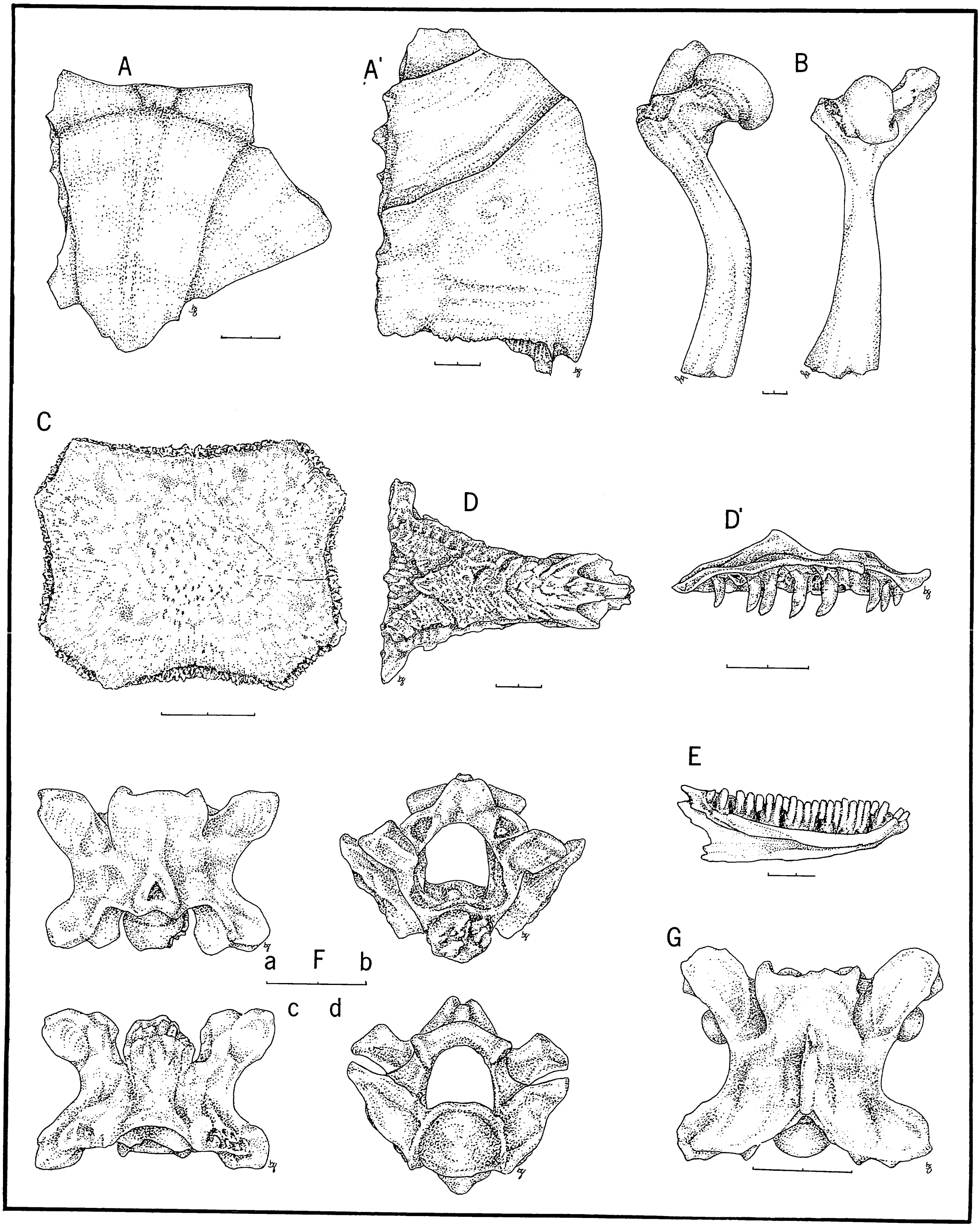
Remarks.– The epiplastral bones of *Sternotherus* (*S. carinatus, S. depressus, S. minor, S. odoratus*) may easily be distinguished from those of *Kinosternon* (*K. acutum, K. bauri, K. cruentatum, K. flavescens, K. hirtepes, K. integrum, K. leucostomum, K. scorpiodes, K. sonoriense* seen only) on the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

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

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

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

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


A
A'
B
C
D
D'
E
a
F
b
c
d
G

Family **Emydidae**

Terrapene cf. *Terrapene carolina* (Linnaeus)

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

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

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

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

Family **Testudinidae**

Geochelone orthopygia (Cope)

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

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

Geochelone sp. indet.

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

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

Family **Trionychidae**

Trionyx sp. indet.

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

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

Other Chelonians

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

Order SAURIA

Family **Anguidae**

Ophisaurus attenuatus Baird

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

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

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

Gerrhonotus mungerorum Wilson

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

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

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

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

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

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

Family **Teidae**

Cnemidophorus cf. *Cnemidophorus sexlineatus* (Linnaeus)

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

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

Family **Scincidae**

Eumeces hixsonorum n. sp.

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

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

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

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

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

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

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

N7; *E. septentrionalis*, 22.

Eumeces hixsonorum differs from the larger skinks of the genus *Eumeces* as follows. It differs from *E. obsoletus* in (1) having less teeth, (2) lower-crowned teeth, (3) more closely spaced teeth, and (4) lacking the swollen crowns of *E. obsoletus*. It differs from *E. laticeps* in (1) having less teeth, (2) lower-crowned teeth, and (3) less closely spaced teeth. It differs from *E. inexpectatus* in (1) being larger and (2) in having lower-crowned teeth.

Order SERPENTES

Family **Boidae**

It was quite surprising to recover, among 1230 vertebrae of snakes, a single vertebra with a structure totally unlike that of any previously reported fossil or recent snake. I am unable to suggest how this unique snake has heretofore eluded being found as a fossil.

Tregophis n. gen.

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

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

Tregophis brevirachis n. sp.

Diagnosis.– As for the genus.

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

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

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

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

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

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

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

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

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

Ogmophis pliocompactus n. sp.

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

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

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

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

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

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

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

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

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

Family **Colubridae**

Natrix hillmani Wilson

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

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

Thamnophis sp.

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

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

Paleoheterodon sp. indet.

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

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

Coluber or *Masticophis*

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

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

Masticophis and may be related to *Coluber constrictor* and/or *Masticophis flagellum.*

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

Elaphe sp. indet.

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

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

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

Lampropeltis similis Holman

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

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

Indeterminate Colubrid Vertebrae

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

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

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

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

DISCUSSION AND SUMMARY

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

Temporal Faunal Elements.— From a temporal standpoint the WaKeeney herpetofauna is divisible into four faunal elements. (I) Elements that are holdovers from earlier Tertiary times. (II) Distinctive forms reported from no other fossil or Recent localities. (III) Extinct Pliocene forms known from other sites. (IV) Species living today.

Group I forms are listed as follows. (1) *Bufo valentinensis* has been reported from upper Miocene localities in Saskatchewan (Holman, 1970) and Nebraska (Estes and Tihen, 1964; Chantell, 1971). (2) *Gerrhonotus mungerorum* has been reported (cf.) from the upper Miocene of Nebraska (Holman, 1973c). (3) *Paleoheterodon* was described from the upper Miocene of Nebraska (Holman, 1964). (4) *Geochelone orthopygia* has been reported from the upper Miocene of Nebraska (Holman, 1973a). (5) *Lampropeltis similis* was described from the upper Miocene of Nebraska (Holman, 1964).

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

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

Group IV forms include: (1) *Ambystoma maculatum*, (2) *A. tigrinum*, (3) *Bufo cognatus*, (4) *B. marinus*, (5) *Hyla* cf. *H. cinerea*, (6) *H.* cf. *gratiosa*, (7) *H.* cf. *squirella*, (8) *Pseudacris* cf. *P. clarki*, (9) *Rana* cf. *R. areolata*, (10) *R.* cf. *pipiens*, (11) *Sternotherus odoratus*, (12) *Terrapene* cf. *T. carolina*, (13) *Ophisaurus attenuatus*, and (14) *Cnemidophorus* cf. *C. sexlineatus*.

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

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

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

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

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

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

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

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

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

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

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

Animals that lived in the stream-basin include *Sternotherus odoratus* and *Trionyx*. Animals that lived in the zone between the edge of the basin and the marshy area include *Bufo pliocompactilis, Acris* sp., *Pseudacris* cf. *P. clarki, Rana* cf. *R. pipiens, Natrix hillmani,* and *Thamnophis* sp.

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

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

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

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

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

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

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

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

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

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

Group I animals are *Ambystoma maculatum, A. tigrinum, Bufo cognatus, Sternotherus odoratus, Terrapene* cf. *T. carolina, Ophisaurus attenuatus,* and *Cnemidophorus* cf. *C. sexlineatus.*

Group II animals are *Scaphiopus hardeni, Tregobatrachus hibbardi, Bufo pliocompactilis, Tregophis brevirachis,* and *Ogmophis pliocompactus.*

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PROFESSOR HIBBARD'S FOSSIL BIRDS

Alan Feduccia

Abstract.– Professor Hibbard's two most important upper Pliocene avifaunas, the Rexroad and Hagerman, are fundamental to our knowledge of Pliocene birds. These avifaunas are compiled here for the first time.

Professor Claude W. Hibbard was a brilliant naturalist; his interests and knowledge spanned all of the vertebrate classes. One of his great joys was to separate avian fossils from his extensive small mammal collections and encourage already established specialists and students to study and report on these interesting finds. The most impressive avian fossil assemblages were those collected from the upper Pliocene of Kansas and Idaho; these have formed the basis of a long series of papers which began in 1944 with a publication by Alexander Wetmore. Wetmore's (1944) paper included descriptions of the first three new extinct species from the Rexroad Formation; at present the fauna contains 17 extinct species, dubious records of three living species, and a number of fragmentary fossils that are identified to the generic level.

Hibbard's other favorite avifauna was from the Hagerman local fauna of Idaho, which now includes a long list of avian species and, along with the Rexroad, forms the fundamental basis of our knowledge of the Pliocene birds of North America. Species continue to be described from both the Rexroad and Hagerman avifaunas, but because no summary of these is current, it is the purpose of this paper to put forth a list of the two with a brief description of their significance.

The birds of the Rexroad Formation come from a number of localities in Meade and Seward counties, Kansas, some of which have been considered to be distinctive local faunas from time to time on the basis of the small mammals. However, there does not appear to be enough of a time interval between the various faunal subdivisions for the birds to be distinctive; therefore, they are treated here as a Rexroad avifauna. The birds are recovered from the various Rexroad localities (Meade and Seward counties) from the upper part of the Rexroad Formation (upper Pliocene). Other important localities are the Fox Canyon locality (UM-K1-47) and the Wendell Fox Pasture locality (UM-K3-53), described by Hibbard (1950) and Woodburne (1961), respectively. Both localities are from Meade County and are assigned to the upper Pliocene, although the Fox Canyon locality is thought to be slightly older than the Rexroad proper. A Saw Rock Canyon locality, from Seward County, Kansas, is located in the lower part (XI Member) of the Rexroad Formation and has been assigned to the early upper Pliocene (Hibbard, 1964).

The Hagerman local fauna is from the Glenns Ferry Formation, Twin Falls, Elmore, and Owyhee counties, Idaho (Malde and Powers, 1962). The fauna is currently considered to be late Pliocene in age (Hibbard et al., 1965; Bjork, 1970), and a potassium-argon date of 3.5 million years B.P. has been obtained (Evernden et al., 1964; Zakrzewski, 1969). Hibbard's view was that the Hagerman represented a slightly younger fauna than the Rexroad.

In Tables 1 and 2 the Rexroad and Hagerman avifaunas are presented completely for the first time. Not only are the specifically identified forms listed, but also those that were only tentatively identified. Many of the Rexroad and Hagerman fossils were fragmentary, and for that reason were not given names, although they are definitely identifiable to the generic level. These are not to be found in catalogues of fossil birds, but do contribute to a better understanding of the avifaunas. It is hoped that this list will provide a comprehensive summary for the non-avian worker who is more interested in the overall avifauna than in the evolutionary affinities of each fossil bird.

To date the preponderance of evidence indicates that

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Table 1. The Rexroad avifauna from Meade and Seward counties, Kansas

Podicipediformes: Podicipedidae (grebes)
Pliolymbus baryosteus, Murray, 1967
Podiceps discors, Murray, 1967
Podilymbus majusculus, Murray, 1967

Ciconiiformes: Ardeidae (herons and bitterns)
Botaurus hibbardi, Moseley and Feduccia, 1975
Egretta sp. (small), Moseley and Feduccia, 1975
Egretta sp. (moderate size), Moseley and Feduccia, 1975

Ciconiiformes: Threskiornithidae (ibises and spoonbills)
Mesembrinibis, gen. & sp.?, Collins, 1964 (listed as *M. cayennensis*)
Phimosus, gen. & sp.?, Collins, 1964 (listed as *P. infuscatus*)
Eudocimus sp., Collins, 1964
Plegadis gracilis, Collins, 1964

Anseriformes: Anatidae (swans, geese and ducks)*
Nettion bunkeri, Wetmore, 1944
Bucephala albeola, sp.?, Wetmore, 1944

Falconiformes: Cathartidae (New World vultures and condors)
Pliogyps fisheri, Tordoff, 1959

Falconiformes: Accipitridae (hawks, Old World vultures, and harriers)
Buteo sp., Wetmore, 1944; Feduccia and Ford, 1970 (close to *B. jamaicensis*)
Accipiter sp., Feduccia and Ford, 1970 (close to *A. cooperi*)

Falconiformes: Falconidae (caracaras and falcons)
Falco sp., Feduccia and Ford, 1970 (close to *F. columbarius*)

Galliformes: Phasianidae (quail, pheasants, and peacocks)
Colinus hibbardi, Wetmore, 1944; Tordoff, 1951

Galliformes: Meleagrididae (turkeys)
Agriocharis progenes, Brodkorb, 1964a

Gruiformes: Rallidae (rails, gallinules, and coots)
Rallus prenticei, Wetmore, 1944
Rallus lacustris, Feduccia, 1968 (originally described as *Porzana lacustris* (Brodkorb, 1958)
Porzana insignis, Feduccia, 1968 (originally *Laterallus*)
Gallinula kansarum, Brodkorb, 1967
Saw Rock Canyon rail indet., Feduccia, 1968
Fox Canyon rail indet., Feduccia, 1968

Charadriiformes: Scolopacidae (woodcock, snipe, and sandpipers)
Sandpiper, gen. & sp. indet., Wetmore, 1944 (size of *Erolia fuscicollis*)
Tringa antiqua, Feduccia, 1970 (Saw Rock Canyon only)

Charadriiformes: Laridae (gulls and terns)
Sterna sp., Wetmore, 1944 (size of *S. forsteri*)

Columbiformes: Columbidae (pigeons and doves)
Zenaidura prior, Brodkorb, 1969

Psittaciformes: Psittacidae (parrots and macaws)
Parrot, gen. & sp. indet., Wetmore, 1944

Strigiformes: Strigidae (typical owls)
Speotyto megalopeza, Ford, 1966
Otus sp., Ford, 1966 (close to *O. asio*)
Asio sp., Ford, 1966
Bubo sp., Feduccia and Ford, 1970 (close to *B. virginianus*)

Piciformes: Picidae (woodpeckers)
Colaptes sp., Feduccia (under study)

Passeriformes: Hirundinidae (swallows)
Hirundo aprica, Feduccia, 1967a

Passeriformes (perching birds)
many diverse species, Feduccia (under study)

* Wetmore (1944) stated that as many as five species of ducks might be represented by the Rexroad anseriform fossils.

all the living species of birds originated during the Pleistocene (Brodkorb; 1966, 1969; Murray, 1967). However, many of the originally reported Rexroad and Hagerman birds were assigned to living species, often on the basis of rather unsatisfactory material. Many of these have now been redescribed, and in all cases have been found to represent extinct species, some ancestral to living counterparts. The last of these was the ancestral Mourning Dove, *Zenaidura prior* (Brodkorb, 1969), which was originally reported by Wetmore (1944) as the living Mourning Dove, *Zenaidura macroura*. Because of the above, in Tables 1 and 2 I have questioned all reports of living species from both the Rexroad and Hagerman avifaunas.

The Hagerman avifauna was primarily an aquatic one, with grebes, a pelican, cormorants, herons, an ibis, a stork, a swan, a goose, a crane, ducks, rails, and a gallinule. In addition, there is an Old World vulture, three owls, and a number of passerines. There is little evidence from the birds to indicate a major difference in climate from the Snake River region of Idaho of today; the avifauna is one of extensive wet areas.

The Rexroad avifauna is somewhat more diverse and contains a relatively smaller percentage of aquatic birds. It contains grebes, herons, ibises, ducks, a condor, hawks, a falcon, a quail, a turkey, rails, a gallinule, two shorebirds, a tern, a dove, a parrot, owls, a woodpecker, and many passerines. The Rexroad fauna tends to indicate that marsh or pond, stream, grassland, and timber communities existed during the period of deposition. Hibbard's (1960) view that during the upper Pliocene, ". . . a subhumid climate with winter temperatures seldom lower than 32F existed as far north as southwestern Kansas and probably into northern Nebraska," is neither confirmed nor denied by the Rexroad avifauna. However, the presence of a turkey (*Agriocharis progenes*) of possible affinity to the tropical turkey, *A. ocellata*, and the presence of an unidentified parrot and four ibises might point to a possibly more moderate climate during the upper Pliocene of Kansas.

Table 2. The Hagerman avifauna from Twin Falls, Elmore, and Owyhee counties, Idaho.

Podicipediformes: Podicipedidae (grebes)
Pliolymbus baryosteus, Murray, 1967
Podiceps discors, Murray, 1967
Aechmophorus elasson, Murray, 1967
Podilymbus majusculus, Murray, 1967

Pelecaniformes: Pelecanidae (pelicans)
Pelecanus halieus, Wetmore, 1933

Pelecaniformes: Phalacrocoracidae (cormorants)
Phalacrocorax idahensis, Wetmore, 1933; Murray, 1970
Phalacrocorax macer, Brodkorb, 1958; Murray, 1970

Ciconiiformes: Ardeidae (herons and bitterns)
Nycticorax sp., Moseley and Feduccia, 1975
Egretta sp., Moseley and Feduccia, 1975

Ciconiiformes: Threskiornithidae (ibises and spoonbills)
Ibis, gen. & sp. indet., Moseley and Feduccia, 1975

Ciconiiformes: Ciconiidae (storks)
Ciconia maltha, Feduccia, 1967b

Anseriformes: Anatidae (swans, geese and ducks; under study by Dr. Glenn Woolfenden)
Olor hibbardi, Brodkorb, 1958, 1964b (originally *Cygnus*)
Anser pressus, Wetmore, 1933; Brodkorb, 1964b (originally *Chen*)
Anas platyrhynchos, sp.?, Brodkorb, 1958
Nettion bunkeri ?, Wetmore, 1933
Querquedula sp., Wetmore, 1933
Bucephala fossilis ?, Brodkorb, 1964b

Falconifromes: Accipitridae (hawks, Old World vultures, and harriers)
Neophrontops slaughteri, Feduccia, 1974

Gruiformes: Gruidae (cranes)
Grus americanus, sp.?, Wetmore, 1933; Feduccia, 1967b

Gruiformes: Rallidae (rails, gallinules, and coots)
Rallus prenticei, Feduccia, 1968
Rallus lacustris, Brodkorb, 1958; Feduccia, 1968 (originally *Porzana*)
Rallus elegans-longirostris group, sp.?, Feduccia, 1968
Coturnicops avita, Feduccia, 1968
Gallinula sp., Wetmore, 1933; Feduccia, 1968

Strigiformes: Strigidae (typical owls)
Speotyto megalopeza, Ford and Murray, 1967
Asio brevipes, Ford and Murray, 1967
Owl, gen. et sp. indet., Ford and Murray, 1967 (close to *Otus asio*)

Passeriformes (perching birds)
many diverse species, Feduccia (under study)

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UPPER PLIOCENE HERONS AND IBISES FROM NORTH AMERICA

Carolyn Moseley and Alan Feduccia

Abstract.– The herons and ibises from the upper Pliocene of North America are discussed along with descriptions of new fossil material from the Rexroad and Hagerman local faunas. A new species of bittern from the upper Pliocene Rexroad Formation is described here as *Botaurus hibbardi* Moseley and Feduccia.

Our present knowledge of the Pliocene avifauna of North America has been gained to a large degree from avian fossils collected by the late Professor Claude W. Hibbard of the University of Michigan Museum of Paleontology. While these fossils come from a variety of localities, the most impressive avifaunas are those of the Rexroad and Hagerman local faunas; these are summarized by Feduccia (in press). In this study the herons and ibises of the Rexroad and Hagerman local faunas are described with a brief summary of the other Pliocene ibises and herons of North America.

During the course of this study skeletons of Recent herons and ibises were examined in the collections of the University of Michigan Museum of Zoology (courtesy of Dr. R.W. Storer), the United States National Museum (courtesy of Dr. R.L. Zusi), the collection of Dr. Pierce Brodkorb (courtesy of Dr. Pierce Brodkorb), and the collection of Alan Feduccia. Pierce Brodkorb kindly permitted the junior author to examine the type of *Nycticorax fidens* Brodkorb. The fossils described herein are in the collections of the University of Michigan Museum of Paleontology (UMMP). The generic classification of ibises and herons follows that of Mayr and Short (1970), and the nomenclature of the bones is primarily that of Howard (1929).

FOSSIL LOCALITIES

The major localities of the Rexroad and Hagerman local faunas are described in detail in a number of publications (Bjork, 1970; Evernden et al., 1964; Feduccia, 1968; Hibbard, 1950, 1959, 1964, 1967; and Woodburne, 1961). The Hagerman local fauna has been taken from the Glenns Ferry Formation (Malde and Powers, 1962) from Twin Falls, Elmore, and Owyhee counties, Idaho. There is a potassium-argon date of approximately 3.5 million years B.P. (Evernden et al., 1964). The Rexroad local fauna is known from the upper part of the Rexroad Formation from Meade County, Kansas. The fauna is generally placed in the upper Pliocene, but Hibbard's view was that the Rexroad represented a slightly older fauna than the Hagerman. Hibbard also recognized several faunas associated with the Rexroad. A Fox Canyon local fauna, older than the Rexroad and from Meade County, Kansas, is distinctive on the basis of the small mammals. A third fauna, the Saw Rock Canyon local fauna from Seward County, Kansas, represents the oldest faunule of the Rexroad Formation. There does not appear to be enough distinction among the birds to subdivide the Rexroad avifauna at this time.

SYSTEMATIC PALEONTOLOGY

Class **Aves**

Order **Ciconiiformes**

Family **Ardeidae**

Genus *Botaurus* Stephens

Botaurus hibbardi, n. sp.

Material.– Distal end (37.3 mm) of left femur, UMMP V41285k, Fig. 1.

Horizon and Locality.– Upper Pliocene, Rexroad Formation. Rexroad local fauna, locality UM-K3-53, Wendell

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Fig. 1. Holotype left femur of *Botaurus hibbardi* (UMMP V41285k), from the Wendell Fox locality of the Rexroad Formation (Rexroad local fauna). From left to right: posterior view of distal femur; anterior view; internal condyle; external condyle. Lower, view of distal end. Actual length, 37.3 mm.

Fox Pasture, S side of Shorts Creek, SW¼, SW¼, Sec. 33, T. 33 S, R. 29 W, Meade County, Kansas. Collected by Dr. Claude W. Hibbard, summer, 1959.

Diagnosis.— Holotype distal end of femur similar to that of Recent *Botaurus lentiginosus* (Rackett), but differing in important characters as follows: anterior ridge of external condyle proximally farther up shaft than anterior ridge of internal condyle; anterior intermuscular line slightly more at middle of shaft; anterior ridge of internal condyle less flaring proximally and running more smoothly into shaft; rotular groove deeper; depression of ligamental attachment more clearly outlined and slightly deeper; attachment of *m. gastrocnemius pars externa* less prominent and less elongate; internal side of internal condyle and external side of external condyle more depressed and more sharply modelled; and internal-external breadth across condyles relatively smaller. Measurements are as follows: width across condyles, 10.6 mm; depth through condyles 9.4 mm; and greatest breadth of shaft, 5.4 mm. Means of equivalent measurements for *Botaurus lentiginosus* (n=7) are 12.3, 10.5, and 6.1 mm.

Discussion.— The distal end of the femur of *Botaurus* is somewhat similar to that of *Nycticorax*, but differs in that: (1) the anterior intermuscular line is considerably more distinct; (2) the shelf above the internal condyle on the posterior side is clearly defined and horizontal; and (3) the attachment of *m. gastrocnemius pars externa* is more prominent. Professor Brodkorb compared the Rexroad fossil with the femur holotype of *Nycticorax fidens* (Brodkorb, 1963b) (lower Pliocene of Florida) and found it to be very distinctive.

Botaurus hibbardi could conceivably be the ancestor of the Recent *B. lentiginosus*; however, the fossil femur is quite distinctive and additional elements will be needed to determine its affinities more precisely. *Botaurus lentiginosus* is known from the Pleistocene of Oregon, California, North Dakota, Iowa, and Florida (Brodkorb, 1963a).

Nycticorax sp.

Proximal and distal ends of left ulnae (UMMP V50232 and V50233, respectively) from the Hagerman local fauna are those of a night heron, and very closely approximate Recent *Nycticorax violacea* in both size and characters. Owing to the fragmentary nature of the material it is impossible at present to determine whether or not these fossils represent a species distinct from *N. violacea*. However, because of the upper Pliocene age of the Hagerman local fauna and the lack of modern species from the fauna (see Brodkorb, 1969), it is probable that these fossils represent a new species, possibly ancestral to *N. violacea*. More material will be needed to answer this question. *Nycticorax violacea* is known from the Pleistocene of Florida, St. Thomas, and Antigua (Brodkorb, 1963a).

Egretta sp. (small to moderate size)

Four upper Pliocene fossils appear to represent an egret very similar to *Egretta caerulea*, but intermediate in size between *E. caerulea* and *E. rufescens.*

The scapular end of a left coracoid (UMMP V53127) from the Hagerman local fauna is an excellent comparison in almost all details with *Egretta caerulea*, differing only in minor details. A nearly complete cervical vertebra (UMMP V52379) from the Hagerman local fauna is extremely close in form to vertebrae of *E. caerulea, E. tricolor,* and *E. rufescens*. It is less stout than that of *E. rufescens.*

The proximal ends of two left tarsometatarsi (UMMP V45422a and an unnumbered specimen), both from the Rexroad local fauna (loc. 3 and the Wendell Fox Pasture locality), are alike and are in perfect agreement with the fossils mentioned above, being close to *Egretta caerulea.*

Again, modern species of other birds are conspicuously absent from the Pliocene, thus making assignment of these fossils to modern species improbable. Additional material will be needed in order to determine the affinities of this form of *Egretta* and the larger one described below.

Egretta sp. (moderate to large size)

The scapular end of a left coracoid (UMMP V47743) from the Rexroad Formation (Bender locality) appears to be of the genus *Egretta*. The closest comparison is with *E. alba*, although the size is close to *E. rufescens*. All the features of the fossil are to be found in some member of the genus *Egretta*. The fossil also bears certain resemblances to *Ardea cinerea.*

Ardeid, gen. and sp. indet.

The distal end of a bill (UMMP V52546) from the Hagerman local fauna is clearly a heron of moderate size, but does not closely resemble any living species. It may be that of one of the above fossil species.

Order **Ciconiiformes**

Family **Threskiornithidae** (Ibises)

Collins (1964) was the first to describe the ibises from the Rexroad local fauna. He identified an ibis, *Plegadis gracilis* Miller and Bowman (1956), which had been originally known from the late Pliocene of Cita Canyon, Texas. In addition, Collins (1964) assigned some fragmentary and unsatisfactory material to two living South American forms, *Mesembrinibis cayennensis* (Gmelin) and *Phimosus infuscatus* (Lichtenstein). These two are probably questionable identifications even at the generic level. Collins (1964) also identified another ibis from the fauna as *Eudocimus* sp., bringing the total number of species to four. Several other fossil ibises have become available in recent years.

Plegadis sp. (gen. tentative)

A proximal end of a right tarsometatarsus missing part of the inner calcaneal ridge (UMMP V29694) represents a small ibis of the Saw Rock Canyon locality of the Rexroad Formation. It is tentatively assigned to *Plegadis gracilis.*

Family Threskiornithidae, gen. and sp. indet.

A proximal end of a left femur (UMMP V49624) from the Hagerman local fauna is that of an ibis, but the bone is too fragmentary to permit a generic identification.

SUMMARY

The Pliocene heron fauna of North America consists of *Ardea polkensis* Brodkorb from the lower Pliocene of Florida, *Nycticorax fidens* Brodkorb from the lower Pliocene of Florida, *Botaurus hibbardi* Moseley and Feduccia from the upper Pliocene (Rexroad Formation) of Kansas, *Nyctiocorax* sp.? from the upper Pliocene Hagerman local faunas, and a moderate to large sized *Egretta* from the Rexroad Formation. The Pliocene ibis fauna is meager, the only highly probable identification being *Plegadis gracilis* Miller and Bowman, which was originally described from the lower Pleistocene of Texas, and later identified in the Rexroad avifauna. However, three other ibises are present in the upper Pliocene of the Rexroad Formation; they are listed here as *Mesembrinibis*, gen. and sp.?, *Phimosus*, gen. and sp.?, and *Eudocimus* sp. In addition there is a single unidentifiable ibis from the Hagerman local fauna.

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THE PROBLEM OF THE HYSTRICOGNATHOUS RODENTS

Albert E. Wood

Abstract.— The use of the masseter muscle-infraorbital foramen complex and the structure of the angular process of the lower jaw have long been used in the classification of rodents. But, since these two features evolved independently, there must have been parallelism in one if not both sets of characters. The Hystricognathi, as revised by Lavocat, include the African Phiomorpha (including the Bathyergidae), the Old World Hystricomorpha (=Hystricidae) and the New World Caviomorpha. The living hystricomorphous Ctenodactylidae, Anomaluridae, and Pedetidae and the Eocene-Oligocene hystricomorphous Theridomorpha have no relationships with the Hystricognathi. The Caviomorpha and Phiomorpha have been thought by many to be directly related because of the extensive identity of structure between members of the two groups. The recent recognition of a subhystricognathous to hystricognathous group of rodents in the Paleocene and Eocene of North and Middle America (a type of rodent that must also have been present at the same time in Asia) supports the idea that the Caviomorpha and the Old World hystricognaths evolved in parallel, developing many identical features independently, an indication that their common ancestors were closely related. An Infraorder Franimorpha is proposed for the Paleocene to Eocene subhystricognathous to hystricognathous ancestral group of the Hystricognathi.

The features of the jaw musculature and of the associated zygomasseteric region of the skull of rodents have been considered of major importance in the classification of the order for over a century and a third (Waterhouse, 1839). The structure of the angle of the lower jaw has been considered of importance for three quarters of a century (Tullberg, 1899). However, when Tullberg combined these two features in the classification of rodents, it greatly complicated matters because the two features were sometimes associated, sometimes not. Therefore, no matter what arrangement of the rodents might be proposed, extensive parallelism must have occurred within the order in at least one of these two features. Because of this, there is still no general agreement as to how to separate parallelism from phyletic relationship in regard to these structures. The rodents about which there has been the most violent disagreement are the hystricomorphous ones, in which the origin of the *masseter medialis* has spread forward from the inner side of the zygomatic arch, through the infraorbital foramen, and out onto the face; and the hystricognathous ones, in which the angle of the lower jaw arises lateral to the plane of the incisive alveolus, instead of in that plane, as in the other rodents, the sciurognaths. Most, but not all, hystricomorphs are hystricognathous; most, but not all, hystricognaths are hystricomorphous (Wood, 1974b). As indicated below, it seems most probable to me that there was parallelism in the evolution of both hystricomorphy and hystricognathy.

The matter is complicated by the zoogeographic problems involved. The hystricognathous, hystricomorphous Caviomorpha were restricted to South America from the early Oligocene to the early Pleistocene, when some of them migrated as far north as North America. The hystricognathous, hystricomorphous Phiomorpha are known from Africa from the early Oligocene to the present; they have been reported elsewhere only from the Miocene of Chios (Tobien, 1968) and the Eocene and Miocene of

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	Hystricognathous	*Hystricomorphous*	*Masseter Lateralis Profundus, Pars Posterior, Deep*	*Fused Malleus and Incus*	*Multiserial Incisor Enamel*	*Sacculus Urethralis*	*Retained* $DP\frac{4}{4}$	*Mesoloph or Mesolophid*
Hystricognathi								
Franimorpha	±	±	±	?	–	?	–	–
Caviomorpha	+	+	+	±[1]	+	±	±[2]	–
Phiomorpha (Excl. Bathyergidae)	+	+	+	+	+	+	+	+
Bathyergidae	+	±	+	+	+	+	?	+
Hystricidae	+	+	+	+	+	+	–	+
Sciurognathi								
Theridomorpha	–	+	–	–	–	?	–	+
Anomaluridae	–	+	–	–	–	–	–	+
Pedetidae	–	+	–	±[3]	+	–	±[4]	–
Ctenodactylidae	–	+	–	+	+	±	–	–
Others	–	5	6	–	–	–	7	8

Fig. 1. Distribution of certain anatomical features among the Hystricognathi, hystricomorphous sciurognaths, and other rodents. + present; – absent; ± present to variable degrees (either sometimes or incipiently present); ? unknown. (1) Not fused in at least some specimens of *Proechimys* sp., *Echimys armatus, Octodon degus, Spalacopus pepigii, Aconaemys* sp. and juvenile *Abrocoma cinereus*. (2) Not in any Deseadan genera, but retention in Colhuéhuapian and later echimyids. (3) Not fused but so closely appressed that motion between them seems impossible. (4) Replacement in *Parapedetes*; dP4 probably retained in *Megapedetes*; no replacement in *Pedetes*. (5) In Dipodoidea. (6) In *Eutypomys*. (7) Sometimes. (8) In many rodents.

Pakistan (Lavocat, 1973, p. 163; Black, 1972, p. 243-246). The hystricognathous, hystricomorphous Hystricidae appear essentially simultaneously in Pakistan, Pikermi and Samos, and Egypt. Lavocat (1973, pp. 167-172) has adopted what is probably the best solution for the classification of these forms, by reintroducing the suborder Hystricognathi, proposed by Tullberg (1899).

Among living rodents, all other groups that have been considered related to the hystricognaths are currently restricted to Africa. These include the hystricognathous but only marginally hystricomorphous Bathyergidae, which Lavocat (1973) has shown were probably derived from the Phiomorpha and therefore belong in the Hystricognathi; and three hystricomorphous but sciurognathous families, the Ctenodactylidae, Pedetidae, and Anomaluridae, that share other features with the hystricognaths besides their hystricognathy (Fig. 1).

The Ctenodactylidae, known from the late Miocene and Pliocene of Africa, India, and Pakistan, are represented by a large number and variety of genera from the Oligocene of central Asia (Bohlin, 1946; Shevyreva, 1971a). They can be followed, in central Asia, as far back as the middle Eocene, where their ancestry merges into a group of rodents that may or may not be ctenodactylids, and that may or may not be sciuravids, but which have some features in common with both (Dawson, 1964; Shevyreva, 1971b, 1972b fig. 1). Shevyreva (1972a) has suggested that these middle Eocene Asiatic genera may have been derived from early Eocene paramyids similar to the European *Pseudoparamys* and *Meldimys*.

The pedetids first appear in the early Miocene of Africa (Stromer, 1926; MacInnes, 1957; Lavocat, 1973), although they are also represented (by one tooth) from the Miocene of Chios (Tobien, 1968). Their ancestry is completely unknown. They show no indications of relationship with either the Phiomorpha or the Ctenodactylidae, although Fischer and Mossman (1969, p. 102) believe the similarity "of the fetal membranes between *Pedetes* and *Ctenodactylus* argues for their close phylogenetic relationship."

Finally, the Anomaluridae are also known from the Miocene of Africa (Lavocat, 1961, 1973), by which time they seem to have fully developed their gliding habits, and Lavocat (1973, p. 196) reports having seen a fragment of the very characteristic olecranon of an anomalurine from the Upper Fayum deposits of Egypt, a specimen that appears subsequently to have been lost. The anomalurids show no clear indications of relationships with any of the other groups discussed here, although Luckett (1971) observed that *Anomalurus* is fundamentally like *Pedetes* and *Ctenodactylus* in the fetal membranes. Lavocat (1973, p. 197) considered the possibility that the anomalurids might have a remote relationship (within or close to the Paramyidae) to the Pedetidae. They cannot have any close relationship to the ctenodactylids.

One last group has often been considered to have some relationship with the hystricognathous groups. These are the sciurognathous but hystricomorphous Theridomorpha of the European Eocene and Oligocene. Schaub (1958) considered that their cheek tooth pattern showed them to have been ancestral to all the hystricognaths. However, so far as I am aware, no one who has studied the material at present considers tham to have anything to do with the ancestry of any of the hystricognath groups.

Relationships between the Hystricidae and the Phiomorpha pose no particular problems, except that the Hystricidae, appearing later than the Phiomorpha, are more primitive than any known phiomorphs in that they retain the normal mammalian replacement of dP^4_4 by P^4_4, a replacement that was already suppressed or greatly delayed in all the early Oligocene phiomorphs (Fig. 1). This, it seems to me, rules out the phiomorphs as possible ancestors to the Hystricidae, although the evolution might have gone in the other direction.

Possible relationships between the Caviomorpha and the Phiomorpha are a more complicated problem. If there is direct relationship between the two groups, there must, apparently, have been a transatlantic migration toward the end of the Eocene, one way or the other. In the days of pontoon land bridges, this was considered no great problem. Then, for many years, it seemed to be an insurmountable one. Recently, the idea of transatlantic crossings has been raised again (Lavocat, 1973) due to the theories of plate tectonics. However, in the late Cretaceous (Cenomanian), the South Atlantic was at least 3000 km wide (Maxwell et al., 1970), which seems to me to indicate that in late Eocene the ocean would have been too wide for crossing by raft. Lavocat disagrees with me on this point and assumes, unjustifiably in my opinion, that in the late Eocene the western tip of Africa and the eastern tip of Brazil were on the same meridian (1973, p. 172). Furthermore, if Bugge (1974, pp. 69-75) is correct that the erethizontids deserve separation from the Caviomorpha as the Erethizontomorpha, this would seem to require two late Eocene rodent invasions of South America.

There are very great similarities between the caviomorphs and the phiomorphs (Fig. 1). If it were not for this, there would be no problem. The similarities are so extensive that Ellerman (1940) placed the two living African genera *Petromus* and *Thryonomys* in the South American subfamilies Octodontinae and Echimyinae, respectively. Landry (1957) pointed out a very large number of features shared by all the hystricognathous rodents and by some of the sciurognathous hystricomorphs. Woods (1972) stated that the myology of *Thryonomys* and *Dasyprocta* are similar to the point of identity. This is especially interesting, as neither would seem to represent the primitive type of rodent for its own continent. Lavocat (1973) emphasized the very close similarities between the ear regions of the Caviomorpha and Phiomorpha and noted that he could find no characters that he could use to separate the two groups. Mossman (1937, pp. 200-203) and Mossman and Luckett (1968) propose the use of the fetal membranes as an independent line of evidence that strongly supports the close relationships of the Caviomorpha and Phiomorpha. However, Luckett (1971) observed that the membranes of *Anomalurus*, *Pedetes*, and *Ctenodactylus* are fundamentally alike so that they must be closely related. As indicated above, the ctenodactylids clearly had an independent ancestry since the early Eocene, so that close similarities in the fetal membranes apparently indicate only rather broad relationships.

Lavocat (1973) considers that the tooth anatomy of the Phiomorpha and Caviomorpha is so close that the former must have been ancestral to the latter; however, he considers that the equal or greater similarity between the phiomorphs and theridomorphs arose by parallelism. He and I differ as to what should be considered the primitive tooth pattern of the caviomorphs. Personally, I believe that the most primitive caviomorphs were those that were brachydont rather than mesodont or hypsodont and that preserve rounded cusps as part of the lophs, rather than merely showing crests where wear results in a slight widening of the dentinal exposure at the locations of the former independent cusps. There are four known Deseadan genera that fit this description —*Platypittamys* (Wood, 1949, fig. 3), *Deseadomys* (Wood and Patterson, 1959, figs. 4-5), *Xylechimys* (Patterson and Pascual, 1968, fig. 2) and *Protosteiromys* (Wood and Patterson, 1959, figs. 30-32). I believe that it is no coincidence that all of these had four-crested lower molars, with no trace of a mesoconid or mesolophid; that the first two (the upper teeth of *Xylechimys* are unknown) had four-crested upper molars; and that the upper molars of *Protosteiromys* show either (depending on the point of view) a very early stage in the development of a fifth crest or a very late stage in the fusion of the fourth and fifth crests. However, in *Proto-*

steiromys (Wood and Patterson, 1959, esp. fig. 30 C), as in the other genera, the third crest from the front ends buccally in an enlargement, apparently the metacone. This would seem to demonstrate that the two posterior crests of *Protosteiromys* (and, presumably, of the high crowned Deseadan genera) are derivatives of the posteroloph. Thus, it seems clear to me, the ancestral caviomorphs had four-crested cheek teeth, with no trace of a mesoloph or mesolophid, whereas the teeth of the ancestral phiomorphs were basically five-crested, with both the mesoloph and mesolophid (Wood, 1968, pp. 38-39, figs. 1-2). Moreover, the Oligocene phiomorphs were clearly in the process of suppressing their permanent premolars, which are rare in the Oligocene fossils and unknown in later ones, whereas there is normal replacement of the premolars in all the known Deseadan caviomorphs from either Patagonia or Bolivia, and it is not until the Colhué-Huapi that the echimyids begin to suppress the eruption of their permanent premolars. This is clearly a case of parallelism between the Caviomorpha (echimyids) and the Phiomorpha.

Until recently there was no fossil evidence that unequivocally countered the morphological similarities between the Caviomorpha and the Phiomorpha. No hystricognathous rodents were known from the Eocene of any part of the world. Lavocat (1973, p. 163) mentions undescribed material from the Eocene of Pakistan. Savage (1971) reported rodents (presumably phiomyids) from the late Eocene or early Oligocene of Libya; he informs me (in lit., 6 Feb. 1973) that these teeth (all isolated incisors) are almost certainly early Oligocene, essentially contemporaneous with those of the lower beds of the Fayum. The nearest approach to Eocene hystricognaths were the Reithroparamyinae, a subfamily of the Paramyidae characterized by incipiently hystricognath angles. The members of this subfamily are known only from North America. The earliest member of the subfamily is the latest Paleocene *Franimys* (Wood, 1962, p. 142; date as corrected by Wood, 1974a, p. 17), where the incipiently hystricognath angle was already present. Wahlert (1972) reported that the late Eocene *Protoptychus* was hystricomorphous and, still more recently, he indicated that it was at least incipiently hystricognathous (1973, p. 14). Wood (1972, 1973) reported and described a lower jaw from the Eocene of the Big Bend area of Texas that was completely hystricognathous, and Black and Stephens (1973) described another hystricognathous rodent from the Eocene of Guadalajara, Mexico. No part of the skull is described for either of these last two animals, so that we do not know whether or not they were hystricomorphous. However, at the present time, the only described possible Eocene ancestry for any of the hystricognaths is from North America. Furthermore, *Protoptychus*, at least, had a cheek tooth pattern (Wilson, 1937, fig. 1) that could easily have given rise to that of the primitive caviomorphs, if I am correct as to what is primitive in that group.

All of this brings me, full circle, back to one of the earlier papers that I wrote (1937), where I said that parallelism, in and of itself, should be treated as evidence of relationship. The similarities between the various living hystricognaths are so great that, it seems to me, they must indicate a special relationship. On the other hand, I still do not believe that rodents crossed the south Atlantic in the late Eocene. The growing number of hystricognathous and subhystricognathous rodents in the Eocene of Middle and North America suggests this area as the source of the caviomorphs. The most reasonable conclusion, it seems to me, is that the New and Old World hystricognaths were independently derived from New and Old World subhystricognathous rodents, presumably all members of the Reithroparamyinae, that had reached both North America and Asia by the early Eocene.

If this view of the evolutionary picture is correct, what should be the classification of the Eocene forms? Should the suborder Hystricognathi be defined as including only those animals that were fully hystricognathous, with the various groups independently derived from members of the reithroparamyine paramyids? Or should the Reithroparamyinae be included in the Hystricognathi by broadening the definition of the latter to include rodents that were only incipiently hystricognathous? The first alternative requires parallelism in the origin of the suborder; under the second, definition of the suborder becomes difficult, as the earliest members were only incipiently hystricognathous, were not hystricomorphous, did not have crested cheek teeth or multiserial incisor enamel, and they had not developed a number of other features of the skull that characterize later hystricognaths (Fig. 1). Furthermore, the Reithroparamyinae are, in all respects except the incipient hystricognathy of the angular process, very difficult to exclude from the Paramyidae. The solution that would most appeal to me would be to leave the Reithroparamyinae in the Paramyidae, but to split that family between the suborders Hystricognathi (subfamily Reithroparamyinae) and Sciurognathi (remainder of the family), a solution that raises problems in formal taxonomy.

Since none of the known North American Eocene hystricognaths seems to fit into the Hystricidae, Phiomorpha, or Caviomorpha (although Wahlert in 1972 tentatively placed the Protoptychidae in the Caviomorpha), a separate ancestral group is needed to receive these forms, for which I propose the term Franimorpha, new infraorder, based on the name of the earliest known included genus. The Hystricognathi may then be divided into four infraorders: the African Phiomorpha, the South American Caviomorpha, the Old World Hystricomorpha (presently restricted to the single family Hystricidae), and the Franimorpha, presently including the Reithroparamyinae, Protoptychidae, *Prolapsus* and *Guanajuatomys*, but which I believe must also have been present in the Eocene of Asia. The presence of subhystricognathous phiomorph ancestors in Asia must be assumed by any explanation for the origin of the Hystricognathi except the derivation of the Old World hystricognaths from the Caviomorpha, a hypothesis currently accepted, so far as I am aware, by no one.

The Franimorpha can be defined as follows: subhystricognathous to hystricognathous; protrogomorphous to incipiently hystricomorphous; with or without a distinct interparietal; alisphenoid does not extend much if any above level of glenoid cavity; at least sometimes a process on the mandible behind the condyle that seems to indicate the differentiation of the *masseter lateralis profundus posterior*, deep portion; molars cuspidate or crested, sometimes with a mesoconid but never with a mesoloph or mesolophid; normal replacement of deciduous premolars; and pauciserial incisor enamel.

According to my interpretation, the split between the sciurognath and hystricognath lines occurred during the Paleocene. From late Paleocene or early Eocene common ancestors similar to *Franimys*, the Franimorpha evolved independently in both North America and Asia, even though none has as yet been recognized from Asia. Probably the caviomorph level of evolution was attained in Middle America in the late Eocene, whence one or more immigrants were able to reach South America; the phiomorph level developed at about the same time in southwestern Asia, some members reaching Africa before the beginning of the Oligocene; and the hystricid level originated at an unknown time in southern or southeastern Asia. All the special similarities shared by the living hystricognaths that were absent in the Franimorpha must have evolved independently, by parallelism.

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OBSERVATIONS ON THE MORPHOLOGY OF THE HEDGEHOG GENUS *PROTERIX* (INSECTIVORA: ERINACEIDAE)

Philip R. Bjork

Abstract.– Additional and more complete skull and skeletal material of the late Oligocene hedgehog genus *Proterix* confirms and refines the description of the genus by Gawne (1968). Two distinct species, *Proterix loomisi* Matthew and *P. bicuspis* (Macdonald) may be justified, yet sexual dimorphism cannot be ruled out. The ear region is typical of modern erinaceids yet the zygomatic and lambdoidal regions are hypertrophied. The thoracic and lumbar vertebrae are hypertrophied as well. A burrowing adaptation is tentatively suggested for *Proterix*.

INTRODUCTION

Among the rare genera of Oligocene mammals from North America, *Proterix* is morphologically most interesting. Matthew (1903) described the genotype, *Proterix loomisi*, on the basis of a fragmentary skull and upper dentition from the upper Oreodon beds of South Dakota. The structure of the skull and vertebral column of this hedgehog was first described by Gawne (1968). She recognized a second species of *Proterix* as well as extending the geographic range of the genus into Nebraska. Gawne recognized the erinaceid affinities of *Apternodus bicuspis* Macdonald (1951) and assigned it to *Proterix*. Macdonald (1961) described the first known lower dentition of *Proterix*. Gawne confirmed Macdonald's assignment of the lower dentition with the description of associated skull and jaws of *Proterix*. Lillegraven (1970) recorded *Proterix* from the upper Oligocene depostis of northwestern South Dakota.

During the summers of 1969, 1971, and 1972, I was fortunate to expand the collection of *Proterix* to include five skulls of varying degrees of completeness (Plate I). In addition many examples of the peculiar ?lumbar vertebrae described by Gawne (1968) and partial atlas, axis and ?thoracic vertebrae were recovered. The new material is significant because it allows confirmation and emendation of conclusions made by Gawne concerning morphology and taxonomy of *Proterix*. Although the additional material is instructive, much skeletal material is lacking which is crucial to an accurate functional interpretation of this peculiar form. All occurrences of *Proterix* known to me are from upper Oligocene deposits of northern Nebraska and western South Dakota.

Materials.– *Proterix loomisi*, SDSM 3215, 7105, 7107, 07256, 07263, 07270, 07274; F:AM 74962. *Proterix bicuspis*, SDSM 7101, 7102, 7103, 7109, 07264, 07266, 07268, 07269, 07272, 07275; F:AM 74961. *Proterix* sp., SDSM 7110, 7114, 7115, 07259.

Abbreviations used in this report include SDSM, South Dakota School of Mines and Technology Museum of Geology, and F:AM, Frick American Museum of Natural History.

THE SPECIES OF *PROTERIX*

Gawne (1968) separated the two species of *Proterix* on the basis of the following characters: presence or absence of I_3, P_2, and protocone on P^3 and the relative depth of the zygomatic arch, posterior extension of palate, height of P^3 compared to P^4, size of hypocone of P^4, length of M^1, shape of M^2, and length of the orbitotemporal region. Based on the new material, most of these characteristics are useful for separation of the two groups. Unfortunately not all specimens are so well preserved as the material Gawne studied, so I have compared the most abundantly preserved elements, P^4 and M^1. P^4 of *Proterix loomisi* is distinguished by the presence of a small hypocone. The hypocone on P^4 is

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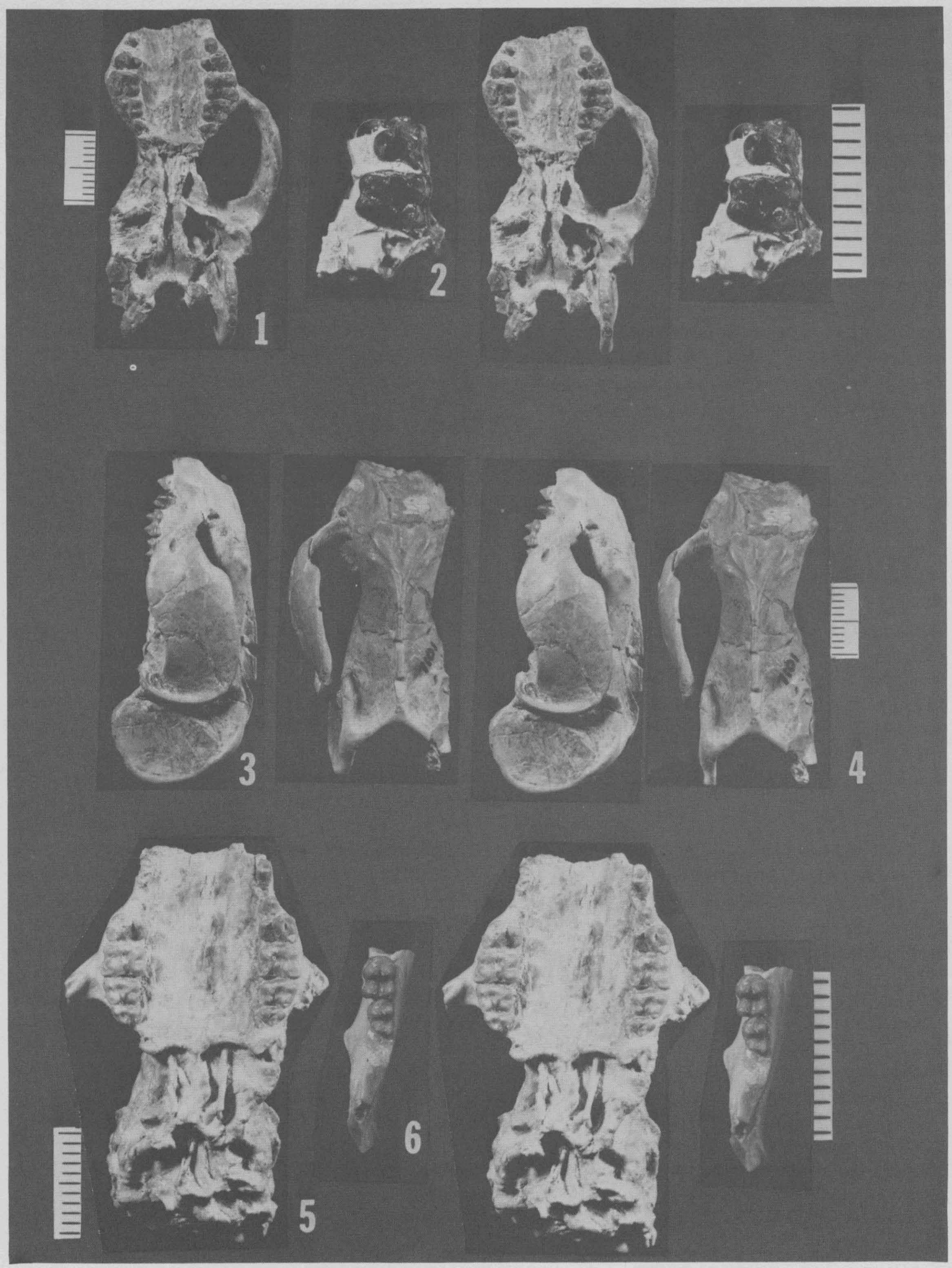

Plate I. Stereograms of the skull and dentition of *Proterix*. All scales are in mm. (1) *P. bicuspis*, ventral view of skull, SDSM 7101. (2) *P. loomisi*, occlusal view of left DP^1 and M^1, SDSM 07274. (3) *P. bicuspis*, left lateral view of skull, SDSM 7101. (4) *P. bicuspis*, dorsal view of skull, SDSM 7101. (5) *P. loomisi*, ventral view of skull, SDSM 07256. (6) *P. loomisi*, occlusal view of left $M_{2\text{-}3}$, SDSM 7117.

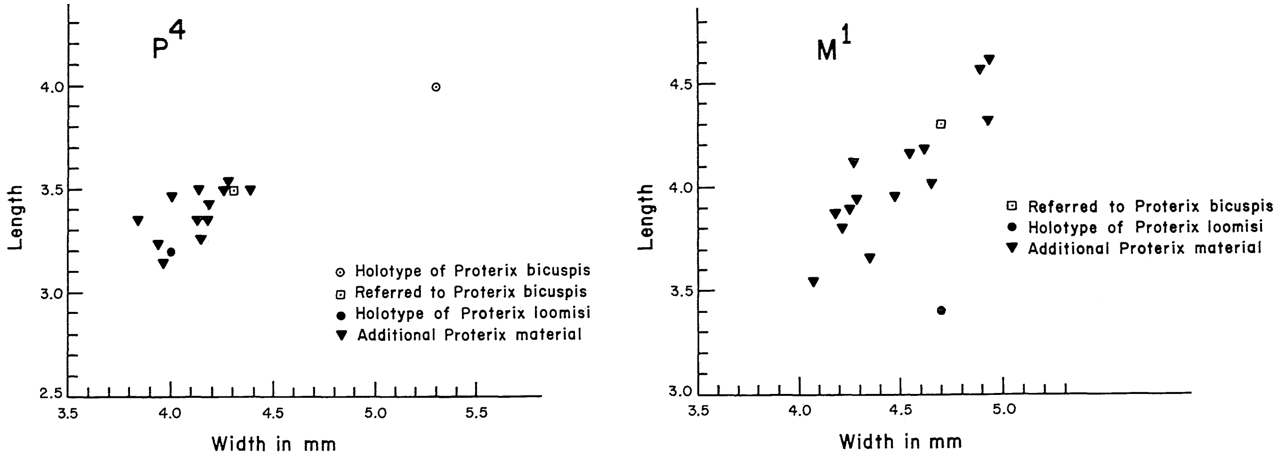

Fig. 1. Scatter diagrams of length and width of P^4 and M^1 of *Proterix* sp.

weakly developed in *P. bicuspis.* A comparison of the measurements of P^4 of known *Proterix* material is given in Text-Fig. 1. The holotype of *P. bicuspis* stands out from all other specimens. Specimens possessing a distinct but small hypocone tend to be slightly smaller than those with a smaller hypocone with considerable overlap. The issue is obscured by a similar consideration of M^1. The holotype of *P. loomisi* stands out as a relatively broad tooth whereas all the others measured are narrower.

Based on association of P^4 and M^1 as well as other cranial characteristics, a variety of interpretations may be offered at this time: two distinct species may be present as recognized by Gawne (1968) but considerable overlap in tooth size is present, an extreme case of sexual dimorphism may be recorded, or more than two species may be present. These interpretations are given in order of personal preference. With the discovery of larger samples these suggestions may be properly tested. Collections made on the Badlands National Monument seem to represent both species and are from a restricted zone 50 to 70 ft below the Rockyford Ash. Those referable to *P. loomisi* are represented by five very incomplete dentitions and no diagnostic skull material. *Proterix bicuspis* is represented by 10 individuals and more complete material including two of the best skulls yet discovered (Plate I, figs. 1, 3, 4 and discussion of skull morphology). A sex ratio of 5:10 (discounting sampling errors of considerable but uncalculable magnitude) might be extreme. On the other hand, both species have a remarkably similar distribution both geographically and stratigraphically. This is the only site from which more than one specimen of *Proterix* has been recovered.

SKULL MORPHOLOGY

The skull of *Proterix* is a remarkable structure. The most striking feature is the development of the back of the skull. On the basis of a fragmentary remains Gawne (1968) correctly noted the existence of a flattened post-zygomatic region which she termed a lambdoidal plate. The lambdoidal plate is made up of the mastoid exposure and the occipital bone. The exact shape of these plates was not known until the discovery of a nearly complete skull (Plate I, fig. 3 and Text-Fig. 2). The expansion of the lambdoidal region appears to be present in both currently recognized species of *Proterix.* The maximum depth of the plate in SDSM 7101 is 20 mm and it extends well below the level of the foramen magnum. The dorsal margin of the plates extends forward well on the skull roof of *P. bicuspis.* This feature is unique among mammals. No trace of an interparietal can be found in the new materials as Gawne had observed but questioned. The lambdoidal plates enclose a pit-like supraoccipital region. Butler (1948) noted that the splenius muscle inserts at the anterior edge of the mastoid exposure of the petrosal bone in modern erinaceids. If the same is true for *Proterix*, a rather massive neck structure and powerful head motion is probable. The deeply excavated supraoccipital region formed an enlarged surface for attachment of the trapezial, transversospinalis, and suboccipital muscle groups.

The zygomatic arch is quite different in the two species. Gawne (1968) described the zygomatic arch of *Proterix loomisi* as heavy for an erinaceid but typical in its general morphology. The lateral face of the maxillary root of the arch has strong dorsal and ventral ridges which mark the origin of the nasal levator muscles. These muscles were probably well developed. This condition is also present in *Proterix bicuspis.* The rest of the arch in *P. bicuspis* is extraordinary (Plate I, fig. 3). On the basis of some fragments of the arch and impressions from enclosing matrix, Gawne (1968) correctly stated that the

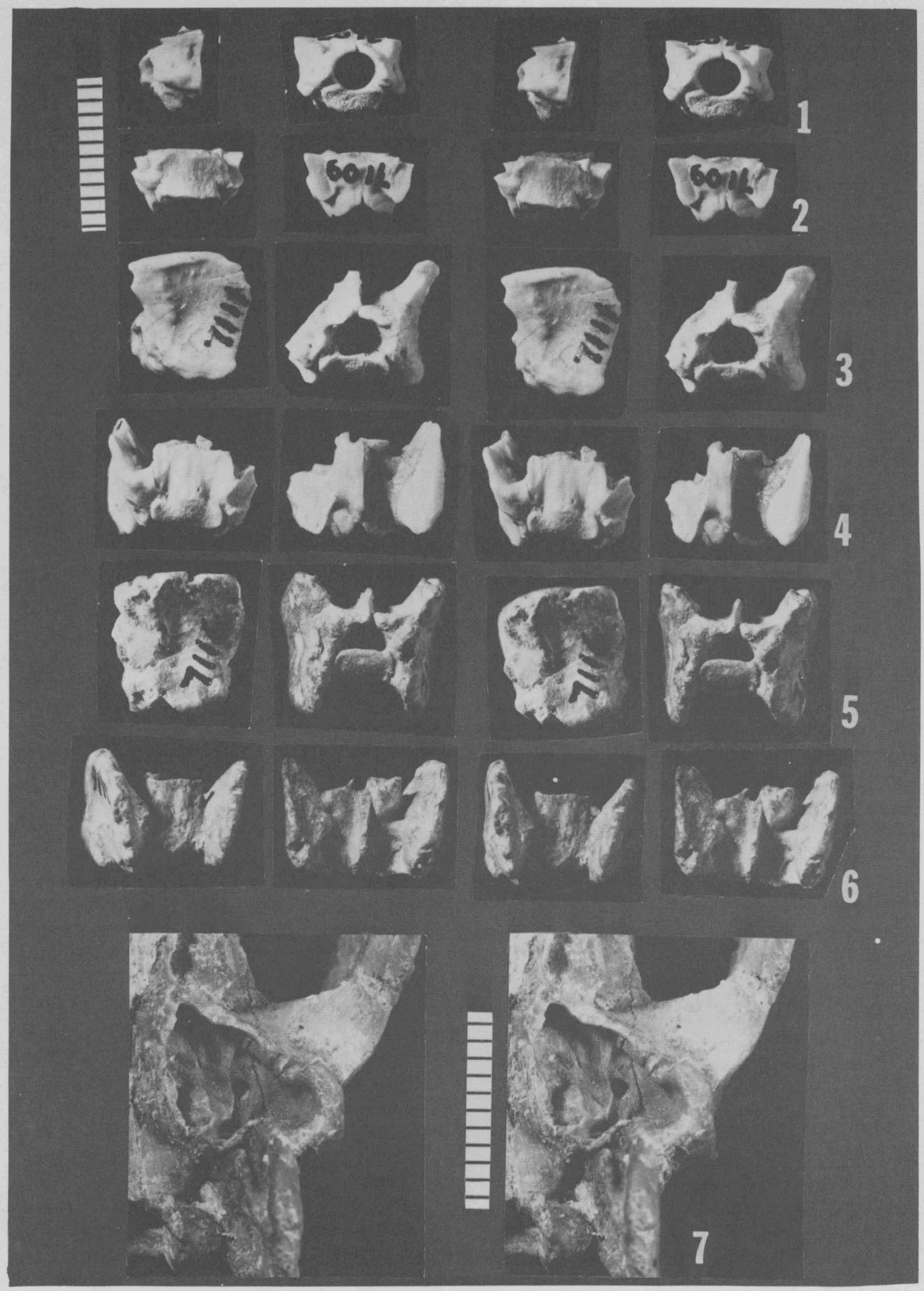

Plate II. Stereograms of vertebrae and otic region of *Proterix*. All scales are in mm. (1) Lateral and anterior views of thoracic vertebra, SDSM 7109. (2) Ventral and dorsal views of thoracic vertebra, SDSM 7109. (3) Lateral and anterior views of anterior lumbar vertebra, SDSM 7111. (4) Ventral and dorsal views of anterior lumbar vertebra. SDSM 7111. (5) Lateral and anterior views of posterior lumbar vertebra, SDSM 7116. (6) Ventral and dorsal views of posterior lumbar vertebra, SDSM 7116. (7) Left otic region of *P. bicuspis*, SDSM 7101.

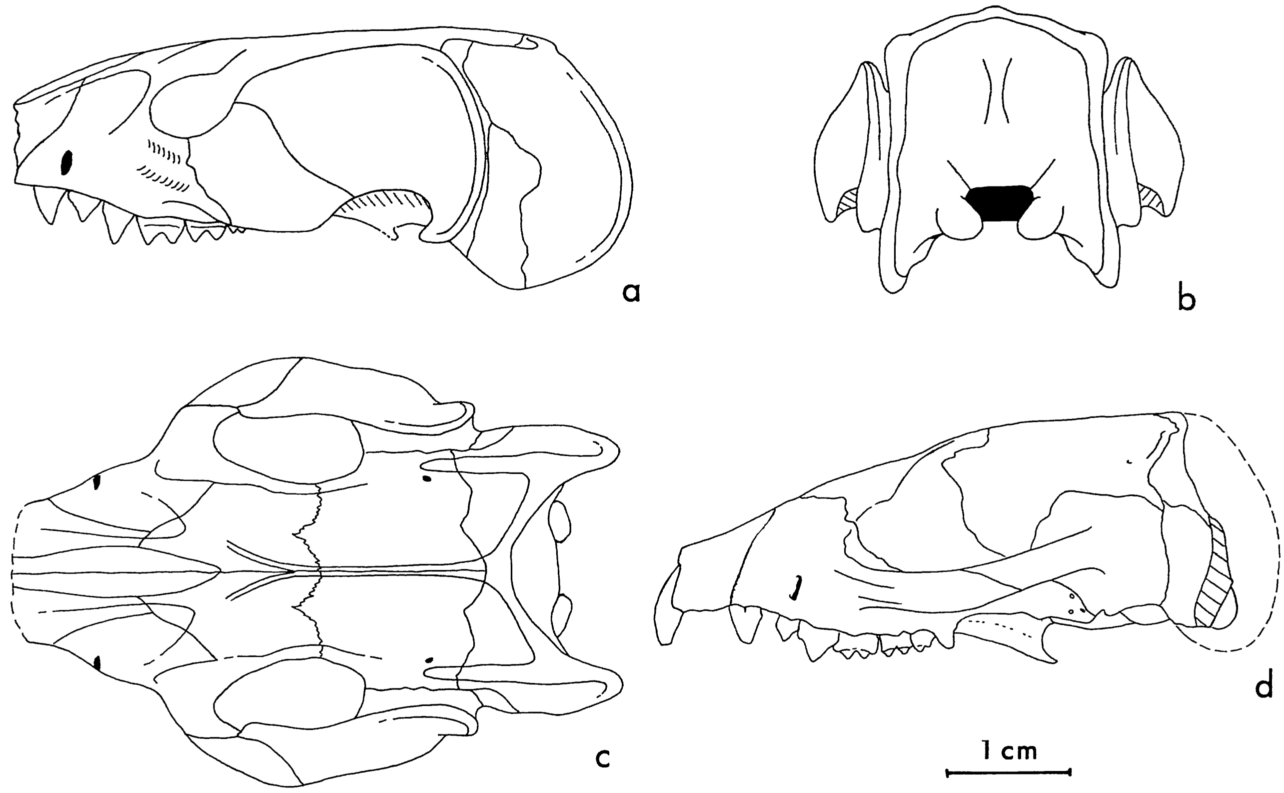

Fig. 2. Reconstructions of the skulls of *Proterix bicuspis* and *Proterix loomisi*. Scale is approximately one cm. (a) Lateral view of the skull of *P. bicuspis*. (b) Posterior view of the skull of *P. bicuspis*. (c) Dorsal view of the skull of *P. bicuspis*. (d) Lateral view of the skull of *P. loomisi*.

arch is deep (11.2 mm in SDSM 7101). The squamosal portion of the arch is unique among mammals. A strong vertical ridge marks the posterior border of the arch. The posteroventral border curves forward and merges with a rim marking the external auditory meatus (Plate II, fig. 7). The glenoid fossa is a broad, flattened, and triangular surface in front of the external auditory meatus.

Three of the partial skulls (SDSM 7101, 7102, 7117) have well-preserved otic regions (Plate II) in addition to the structure which Gawne described as the type of *Proterix bicuspis*. In general her interpretation of the ear structures is accurate except for the location of certain foramina. The foramen for the superior ramus of the stapedial artery cannot exit the otic region in the position (Text-Fig. 3) indicated by Gawne. Preparation of the type of *P. bicuspis* and three additional otic regions (Plate II) indicates a well-developed, anteriorly-directed pit. This observation requires a revision of Gawne's reconstruction of the arteries and nerves passing through the otic region. The interpretation is facilitated by the discovery of another foramen just anterior to the fenestra ovalis. I believe this foramen to be the exit of the facial branch of nerve VII. The superior ramus of the stapedial artery probably exited the skull through the foramen which Gawne indicated for the facial branch of the VII cranial nerve. A comparison of the two interpretations is in Text-Fig. 3. The otic region of *Proterix* is similar to that of modern *Erinaceus* in the location of foramina for nerves and arteries as described by Butler (1948). The external auditory meatus is ventrally deflected, a condition common among burrowing insectivores (Hildebrand, 1974).

DENTITION

Previous workers have adequately described the known dentition of *Proterix*. Only two additions to those descriptions can be made on the basis of the new material. Complete M_{2-3} of *Proterix loomisi* was found associated with cranial fragment and partial atlas (SDSM 7117). These teeth were damaged or lacking in the lower jaw material available to Gawne. The trigonid of M_2 and M_3 is not so compressed anteroposteriorly as in *P. bicuspis*. The anterior and labial cingula are more strongly developed in *P. loomisi*. The entoconid of M_3 projects posteriorly in *P. loomisi*.

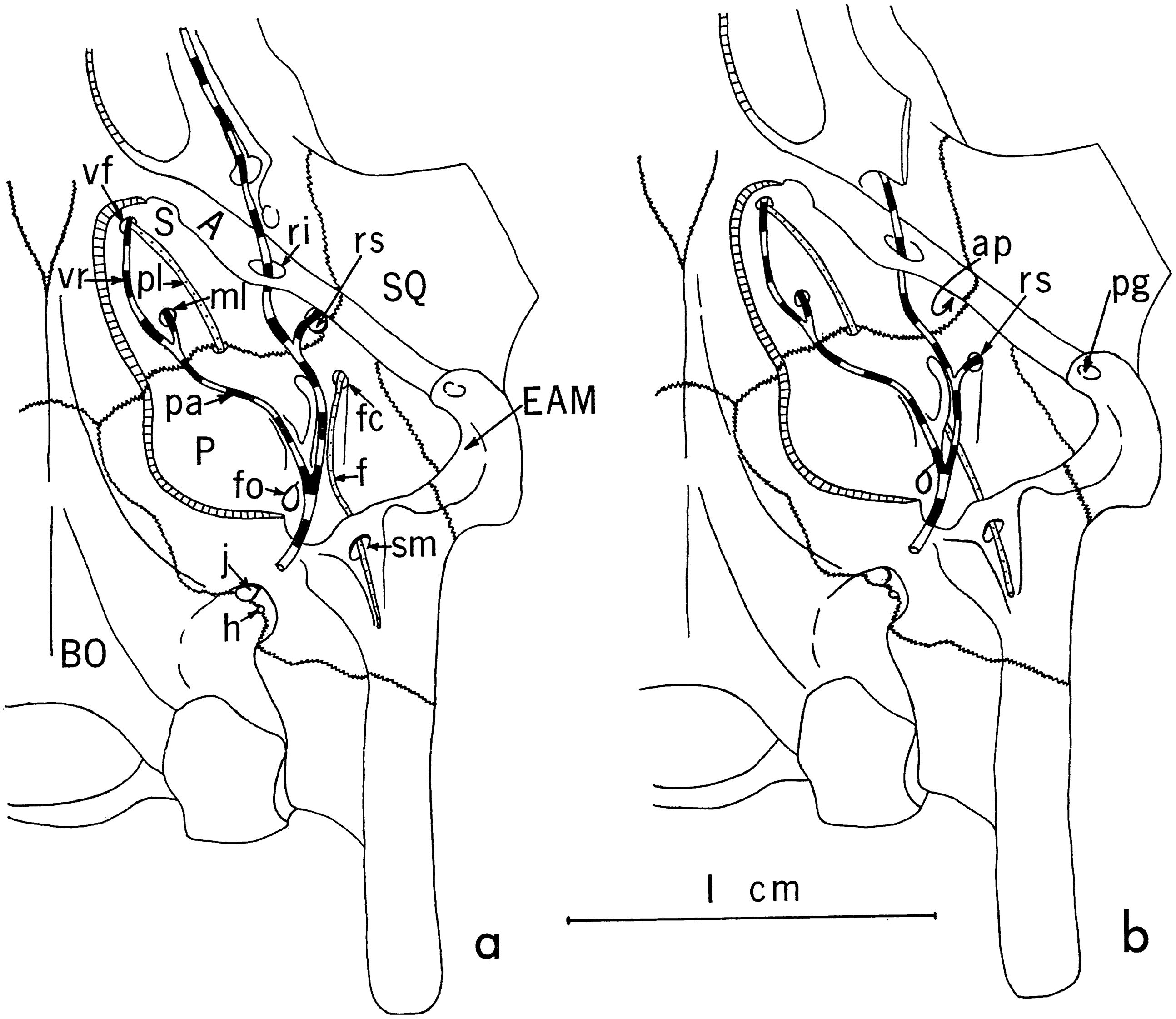

Fig. 3. Comparison of the interpretations of the otic region of *Proterix*. Diagrams are modified versions of Text-fig. 9 in Gawne, 1968. Scale is approximately one cm. (a) Interpretation of Gawne, 1968. (b) Alternative interpretation based on three skulls of *Proterix bicuspis* and one of *P. loomisi*. Abbreviations: A, alisphenoid; BO, basioccipital; EAM, external auditory meatus; P, petrosal; S, sphenoid; SQ, squamosal; ap, anterior pit; f, facial branch of VII nerve; fc, facial canal; fo, fenestra ovalis; h, hypoglossal foramen; j, jugular foramen; ml, middle lacerate foramen; pa, pulmonary artery; pg, postglenoid foramen; pl, palatine branch of VII nerve; ri, foramen for inferior ramus of stapedial artery; rs, foramen for superior ramus of stapedial artery; sm, stylomastoid foramen; vf, vidian foramen; vr, vidian ramus of promontory artery.

The DP^4 (SDSM 07274) is the first record of a deciduous tooth for *Proterix* (Plate I, fig. 2). Compared with the P^4 of *Proterix*, DP^4 is relatively low crowned. A prominent cusp in the position of the paracone forms the anterior portion of a low blade extending back to a small posterior cusp (metacone). The protocone is low and broad with a steep anterior face and a gently sloping posterior face. The hypocone is absent and no cingula are developed. The P^4, with hypocone, is visible just above the DP^4, thus the specimen may be referred to *Proterix loomisi*. The DP^4 is 3.1 mm long and 3.4 mm wide.

VERTEBRAE

The vertebrae of *Proterix* are as peculiar as the back of the skull. Gawne reported on 10 vertebrae, two associated with *P. loomisi* and eight articulated vertebrae associated with *P. bicuspis.* In each case the vertebrae are remarkably uniform. They are massive in appearance with relatively low neural spines and broad lateral plates, which flare out laterally from front to back and dominate the vertebrae when viewed from every aspect. Gawne assigned all these vertebrae tentatively to the lumbar series because of the lack of vertarterial canals and lack of rib articulations. In the sample at hand 34 vertebral fragments have been recovered. Almost all duplicate the morphology described by Gawne. Three of the vertebral fragments are clearly assignable to other regions of the column. A partial atlas was found in association with a skull fragment of *Proterix loomisi.* Even in this fragment the lateral wings turn slightly (upward?) suggesting that lateral plates may be a cervical feature as well. The axis fragment (SDSM 07173) is incomplete especially on the posterior margin, although it is massive in character. A third vertebra (SDSM 7019, Plate II, figs. 1-2) is quite possibly a posterior cervical or anterior-most thoracic, based on the narrow separation and dorsal convexity of the prezygapophyses. The centrum is appreciably shorter than in the other vertebral types. Unfortunately, the lateral plates on this specimen are broken. No trace of any rib articulations is known to me. The remaining 31 partial vertebrae are massive structures as briefly described by Gawne (1968) and above. Certain other features of the lumbar series are noteworthy. Because most of the vertebrae were found isolated, additional morphologic information is available (Plate II, figs. 3-6). Anterior lumbar vertebrae have relatively smaller lateral plates which do not extend below the centrum. In ventral view all lumbar vertebrae possess an emargination at the juncture of the lateral plate and the centrum. The emargination of anterior lumbar vertebrae is rounded, rather than acute as in the posterior lumbar vertebrae. The neural spine does not completely separate the prezygapophyses in the anterior lumbar as in the posterior. The anterior lumbar postzygapophyses are not the robust rod-like structures as in the posterior lumbars. In the entire lumbar series the anterolateral border of the lateral plates is a broad, curved, articular surface which articulates with the internal side of the posterior margin of the lateral plate of the vertebra immediately anterior. As Gawne (1968) pointed out, this severely limits the movement of the lumbar series to the sagittal plane. The anterior face of the centra of the lumbar series slopes posteriorly. The posterior face of the centrum is nearly vertical. The resulting articulation between centra allows for the same vertical motion of the vertebra. The single thoracic vertebra has centra which have vertical faces fore and aft.

The lumbar vertebrae seem to be extremely well developed for very strong vertical movements. If the lateral plates restrict motion and serve as the origin or insertion of the longissimus dorsi and quadratus lumborum muscles, then a peculiar mode of locomotion must have been utilized by *Proterix*.

CONCLUSIONS

Two species of *Proterix* are maintained although the nature of variability in teeth suggests considerable overlap in size and proportions. Until significantly larger samples are available, sexual dimorphism must be kept in mind.

A minimum of eight lumbar vertebrae is suggested for *Proterix*. No ribs or sacral vertebrae have been recognized. A survey of the vertebral counts of modern erinaceids (Flower, 1885) indicates a maximum of seven lumbar vertebrae. In those mammals in which the lumbar series is lengthened, it is at the expense of the thoracic or sacral vertebrae. The direction of expansion of the lumbar series is not known in *Proterix*. Cetaceans emphasize vertical motion of the vertebral columna dn have elongated lumbar series with reduced sacral series. Is a similar mode of locomotion possible in a terrestrial form such as a hedgehog? The lack of rib and limb material is not uncommon in extinct taxa of mammals, but the possibility of reduced appendages in *Proterix* must be kept in mind. Perhaps locomotion in *Proterix* parallels that of amphisbaenid reptiles. A strong nasalmusculature, neck structure, ventrally directed external auditory meatus, and restricted vertebral movements suggest a fossorial way of life. Confirmation of this suggestion depends on the discovery of complete postcranial skeleton.

Butler (1948) placed *Proterix* close to the ancestry of the erinaceid subfamily Erinaceinae but in a monotypic tribe, Protericini. McKenna and Simpson (1959) questioned this assignment on the basis of the lack of primitive erinaceines from Eurasia. Gawne (1968) concluded that *Proterix* stands alone among known erinaceids, a conclusion that is strongly supported by the bizarre character of the head and vertebral column. As the Eocene and Oligocene ancestors of *Proterix* become known, such a taxonomic distinction may be fully justifiable.

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SUR LA FAUNE DE VERTÉBRÉS PLÉISTOCÈNES DE LA ROUMANIE

Nec. Macarovici[1]

Abstract.– The Pleistocene vertebrate fauna of Rumania is rather rich. The author presents this fauna according to the three principal subdivisions of the Pleistocene (lower, middle, and upper). He considers the beginning of the Pleistocene as the time when the genus *Elephas* appears in the fauna of Europe (including Rumania), i.e., the time of the Tulceşti fauna (south Moldavia). Then the author reviews the whole fossil vertebrate fauna, particularly the mammal fauna, known from the three great subdivisions of the Pleistocene of Rumania. The list of fossil mammals reviewed shows that in the Pleistocene more mammals lived in the territory of Rumania than live there today.

Résumé.– La faune des Vertébrés pléistocènes de la Roumanie est assez nombreuse. L'auteur fait une présentation de cette faune d'après les trois subdivisions importantes du Pléistocène (inférieur, moyen, et supérieur). Il considère comme commencement du Pléistocène le moment où apparaît dans la faune de l'Europe (la Roumanie y comprise) le genre *Elephas*, c'est-à-dire le moment lorsque se constitue la faune de Tuluceşti (du S de la Moldavie). Ensuite l'auteur passe en revue toute la faune fossile de Vertébrés, en particulier celle de Mammifères, connue dans les trois grandes subdivisions du Pléistocène de la Roumanie. La liste des Mammifères fossiles passés en revue montre qu'au Pléistocène vivaient sur le territoire de la Roumanie plus de Mammifères qu'aujourd'hui.

La faune des vertébrés pléistocènes connue de la Roumanie est relativement nombreuse. En dehors de la faune d'âge würmien (Pléistocène supérieur), connue en général de la plupart des terrasses inférieures des rivières de la Roumanie, le reste de la faune de vertébrés pléistocènes est connu des points éloignés les uns des autres. Aussi, il est assez difficile de faire la corrélation entre eux. Si l'on considère le Pléistocène de la Roumanie d'après les trois divisions importantes (inférieur, moyen, et supérieur), on trouvera les données suivantes sur la faune pléistocène:

I. *Pléistocène inférieur.*– Nous partons de l'idée – admise aussi par d'autres auteurs – que le Pléistocène commence en Europe au moment où apparaît la plus ancienne espèce de *Elephas*, à côté de laquelle *Mastodon (Anancus) arvernensis* Cr. et Job. (apparu au Pliocène supérieur) persiste encore quelque temps. Ainsi la plus ancienne faune de vertébrés appartenant au Pléistocène inférieur, connue en Roumanie est la faune de Tuluceşti (distr. de Galaţi) du sud de la Moldavie. Cette faune a été décrite par Sabba Athanasiu (1915) et est, du point de vue chronologique, descendente de la faune de Măluşteni-Bereşti du sud de la Moldavie. Cette dernière faune est attribuée au Pliocène supérieur (=Roumanien=Czarnotien=Villafranchien s. str., c'est-à-dire supérieur, Azzaroli).

La faune de Tuluceşti est formée par: *Anancus arvernensis* Cr. et Job., *Archidiskodon meridionalis* Nesti, forme primitive (=*Elephas planifrons* Falc., Sabba Athanasiu, 1926), *Cervus (Elaphus) issidorensis* Cr. et Job., et une molaire de *Mastodon (Zygolophodon) borsoni* Hays, dont

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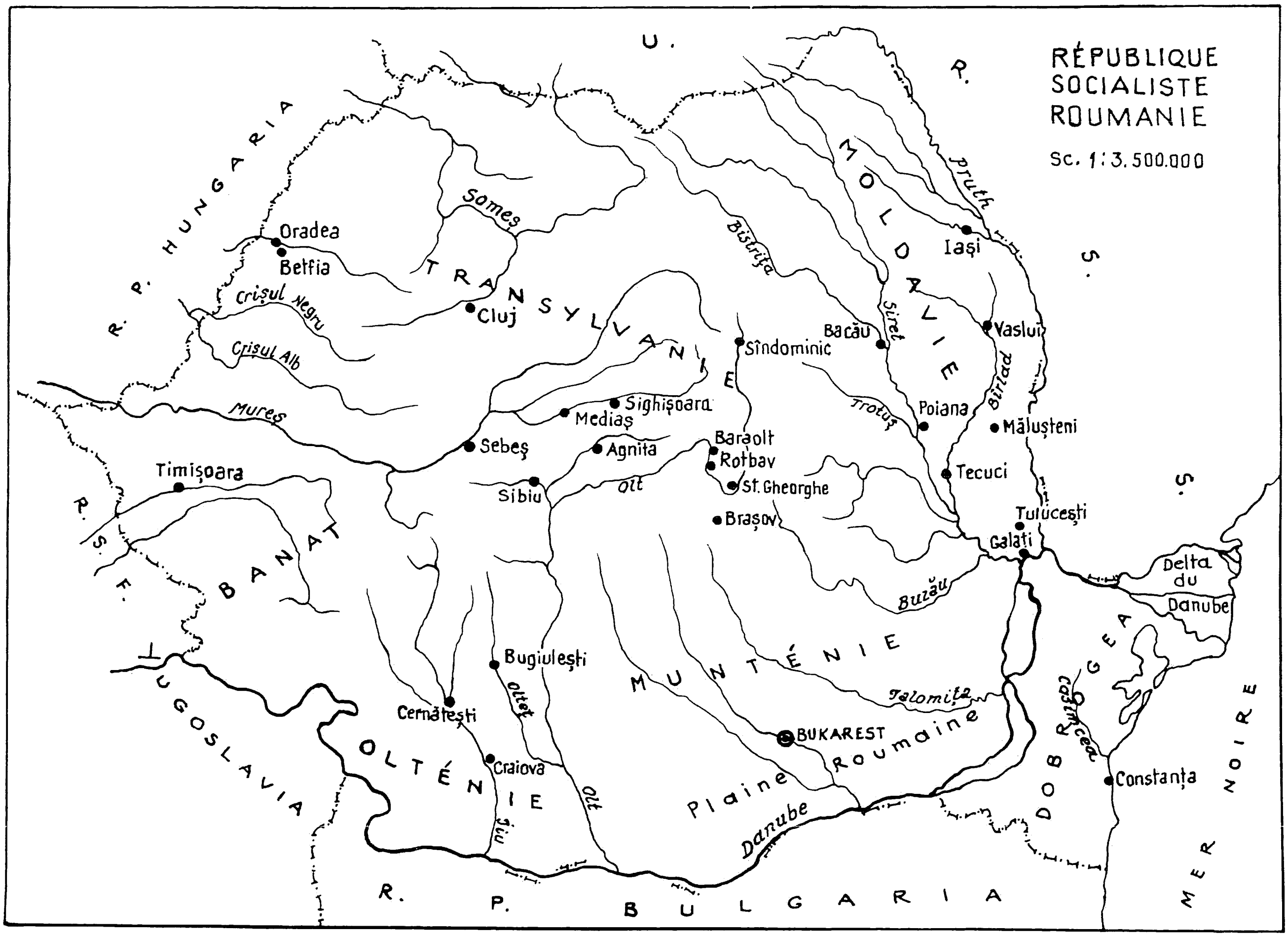

le point de provenance n'est pas bien connu. A cette liste de faune C. Ghenea et C. Rădulescu (1964) ajoutent la description d'une mandibule incomplète (trouvée toujours à Tuluceşti) de *Camelus (Paracamelus) alutinensis* Stef. et d'un métacarpien de *Hippotigris stenonis* Cocchi. Pour compléter cette liste de faune, trouvée à la base du Pléistocène inférieur, il faut ajouter les deux mandibules connues de *Archidiskodon meridionalis* Nesti, provenant du piedmont du côté gauche du Siret, de la localité de Poiana-Nicoreşti. La base de ce piedmont appartient toujours au Pléistocène inférieur. Des molaires de ce proboscidien sont connues également du piedmont situé entre le Siret et le Trotuş, d'où proviennent aussi des molaires de l'*Anancus arvernensis* Cr. et Job. (I. Atanasiu, 1940). Mais, pareilles molaires ont été trouvées également sur la terrasse supérieure (160 m) de la Bistriţa, de la même région subcarpatique (Saraiman et al., 1965).

Une faune très proche en âge de celle de Tuluceşti (Galaţi) a été décrite par Ecat. Schoverth et al. (1963) à Cernăteşti (dans Dealul Calului) (distr. Gorj, Olténie), à la confluence du Jiu avec le Motru et l'Amaradia. Cette faune comprend: *Anancus arvernensis* Cr. et Job., *Archidiskodon meridionalis* Nesti (=? *Elephas planifrons* Falc.), *Rhinoceros* cfr. *etruscus* Falc., *Equus* sp. (=?*E. mosbachensis abeli* Antonius) et une molaire de *Mastodon borsoni* Hays, qui paraît être remaniée de dépôts plus anciens.

De toutes ces formes, *Anancus arvernensis* Cr. et Job. est assez souvent cité dans les dépôts pliocéno-pléistocènes de l'Olténie, tandis que *Archidiskodon meridionalis* Nesti est relativement souvent cité dans les "Graviers de Cîndeşti" (Apostol, 1968) de la Plaine Roumaine. Pourtant on ne peut pas affirmer si *A. meridionalis* est connu seulement dans des dépôts appartenant au Pléistocène inférieur ou bien aussi dans des dépôts plus récents. Dans la Plaine Roumaine sont citées – très rarement – dans les mêmes dépôts, certaines molaires de *Elephas (Palaeoloxodon) antiquus* Falc., de même que des molaires de *Elephas planifrons* Falc. (décrites, par ex. à Orodelu, SW de l'Olténie, par Sabba Athanasiu, 1926).

Au Pléistocène inférieur est attribuée également l'ancienne faune (inférieure) de Bugiulești (C. Rădulescu et P. Samson, 1968), qui comprend: *Archidiskodon meridionalis* Nesti, *Dicerorhinus etruscus* Falc., *Hippotigris stenonis* Cocchi, *Sus strozzi* Maj., *Dama nestii* Maj., *Euctenoceros ctenoides* Maj., *Libralces gallicus* Azz., *Pliotragus ardea* Dep., *Leptobos* sp., *Megalovis latifrons* Schaub, *Canis etruscus* Maj., *Crocuta perrieri* Cr. et Job., *Castor plicidens* Maj., *Trogontherium cuvieri* Fisch., *Dolichopithecus gallicus* Necrasov, etc.

Sont connus des restes de *Archidiskodon meridionalis* Nesti, de *Libralces gallicus* Azz. (Apostol, 1972) et de *Cervus* cfr. *perrieri* Cr. et Job. (Sabba Athanasiu, 1914-15) dans la haute terrasse (73-75 m) du Danube de la Plaine Roumaine, cette terrasse étant attribuée également au Pléistocène inférieur.

Dans le bassin de Brașov, la partie inferieure dé l'horizon III de Baraolt du point de Rotbav-Silvestru est attribuée (par Rădulescu, Samson, et al., 1965, 1969) aussi au Pléistocène inférieur. L'horizon III de Baraolt comprend la faune suivante: *Archidiskodon meridionalis* Nesti, *Dicerorhinus etruscus* Falconer, *Hippotigris* cfr. *stenonis* Cocchi, *Hippotigris süssenbornensis* Wüst, *Equus aluticus* Răd. et Sams., *Cervus* sp. (groupe *Rusa*), *Trogontherium* cfr. *boisvillethi* Langel, *Orthogonoceras verticornis* (Dawk) Kalke 1951 (=*Allocaenolaphus arambourgi* Răd. et Sams., 1967).

Il faut observer que dans cette faune est absent *Anancus arvernensis* Cr. et Job., qui fait défaut aussi dans la faune ancienne (inférieure) de Bugiulești.

Dans la partie NW de la Roumanie, ă Betfia (Dealu Sumlea) près de Băile Episcopiei (au SE de Oradea Mare), est connue une faune de Mammifères nombreuse (plus de 50 espèces), décrite par I. Kormos (1913-1914) et M. Kretzoi (1941, 1960-61). M. Kretzoi (1960-61) attribue cette faune ă la partie finale du Pléistocène inférieur (au Cromerien). Elle est formée d'abord par 20 espèces de carnivores (*Felis silvestris* Schreib., *Leo gombaszögensis* Kretzoi, *Machairodus latidens* Owen, *Epimachairodus hungaricus* Kretzoi, *Crocuta* sp., *Martes* cfr. *intermedia* Heller, *Mustella palerminea* Petényi, *Putorius* cfr. *stromeri* Kormos, *P. praeglacialis* Kor., *Pannonictis pliocaenica* Kormos, *Meles meles praeglacialis* Kormos, *Canis mosbachensis* Soergel, *Canis* sp. (?*gigas* Kretzoi), *Alopes vulpes* L., *Cynalopes praecorsae* Kormos, *Ursus spelaeus* Ros. et Heins., *U. stehlini* Kretzoi, *U. arvernensis* Cr. et Job., *Ursus* sp., *Gulo schlosseri* Kor.).

Suivent ensuite 14 espèces de rongeurs (*Sciurus* sp., *Citellus primigenius* Kormos, *Spalax* sp., *Cricetus* sp., *Cricetus cricetus praeglacialis* Schaub, *Allocricetus bursae* Schaub, *Pitymys hintoni* Kretzoi, *Clethrionomys* sp., *Mimomys* sp., *Microtomys* aff. *catianus* Hinton, *Pliolagus töthi* Kretzoi, *Lagotherium brachygnathum* Kormos, *Castor fiber* L., *Lepus* sp.).

Sont connues également deux espèces d'insectivores (*Erinaceus* sp. et *Sorex margaritodon* Kormos). Viennent ensuite 10 espèces de périssodactyles et artiodactyles (*Opsiceras etruscus* ssp., *Rhinoceros kronstadtensis* Toula, *Equus (Allohippus)* sp., *Capreolus* sp., *Alces* cfr. *latifrons* Johnston, *Megaceros euryceros* Aldrov., *Megaceros* cfr. *depuisi* Stehlin, *Bison priscus* Boj., *Bison schoetensacki* Freudenberg). A ces espèces nous ajoutons *Equus scythicus* Răd. et Sams., connu également ă Galoșpetreu (Bihor).

De la faune de Bretfia sont connues aussi quelques espèces d'oiseaux décrites par Kretzoi, ă savoir: *Pelargosteon töthi* Kretzoi, *Anas platyrhyncha* L., *Falco tinnunculus* L., *Falco* cfr. *subbuteo* L., *Lyrurus partium* Kretzoi, *Perdix jurcsaki* Kretzoi, *Otis lambrechti* Kretzoi, *Turdicus tenuis* Kretzoi, *Corvus betfianus* Kretzoi, etc.

Il y a lieu ă observer que, étant donnée l'absence des espèces de *Elephas*, on peut admettre que cette faune représente plutôt une faune de steppe.

La faune que nous avons citée jusqu'ici comme appartenant au Pléistocène inférieur, peut être attribuée également au Villafranchien supérieur dans le sens d'Azzaroli (1967).

II. *Pléistocène moyen.*— Pour la partie orientale de la Roumanie cette subdivision du Pléistocène ne peut pas être établie d'après la faune fossile de Mammifères; elle a été établie seulement d'après la faune de mollusques (la faune de Barboși-Babele). Mais pour Olténie est connue une faune fossile de Mammifères qui peut être attribuée au Pléistocène moyen. Telle est la faune nouvelle (supérieure) de Bugiulești, formée par les espèces suivantes: *Elephas (Parelephas) trogontherii* Pohlig, *Hippotigris* cfr. *süssenbornensis* Wüst., *Equus aluticus* Răd. et Sams., *Soergelia elisabethae* Schaub., *Bison* cfr. *schoetensacki* Freudenberg, *Trogontherium cuvieri* Fisch., etc. (Samson et Rădulescu, 1968).

Une autre faune de Mammifères fossiles, proche de la précédente en ce qui concerne le contenu, a été décrite par C. Rădulescu, P. Samson, et al. (1965) ă Rotbav – Dealul Tiganului, dans la dépression de Brașov (Transylvanie SE) et qui comprend: *Elephas (Parelephas) trogontherii* Pohlig (forme archaîque), *Dicerorhinus kirschbergensis* Jaeger, *Equus mosbachensis* v. Reichenau, *Praealces latifrons* Johnston, *Dolichodoryceros savini* Dawkins (=*Dol. süssen-*

bornensis Kahlke), *Capreolus capreolus* L., *Cervus* cfr. *elaphus* L., *Bison* cfr. *priscus* Bojanus, *Castor fiber* L., etc.

Nous devons mentionner ici que le *Dicerorhinus kirschbergensis* Jaeger et le *Dolichodoryceros savini* Dawkins sont connus dans le bassin de Braşov, surtout ã Araci-carrière.

Une faune pas trop nombreuse est décrite par Sabba Athanasiu (1912) dans la terrasse moyenne (40-50 m alt. rel.) du versant droit de la vallée Drăghici (au S de Cîmpulung-Muscel). Cette faune, attribuée par l'auteur mentionné au Pléistocène moyen, est formée par: *Machairodus latidens* Owen, *Hyaena crocuta spelaea* Goldf., *Sus scrofa* L., *Cervus* cfr. *elaphus* L., *Bos* cfr. *primigenius* Bojanus.

Avant d'en finir avec la liste de la faune de Mammifères fossiles du Pléistocène moyen, il faut rappeler aussi la faune de même âge, connue dans le bassin intramontan de Ciuc (de la Transylvanie orientale, sur la vallée supérieure de l'Olt), ã la localité de Sîntdominic. Elle est formée (D'aprẽs Samson et Rădulescu, 1968) par: *Rhinoceros (Coelodonta) antiquitatis* Blum, *Equus* cfr. *steinheimensis* v. Reichenau, *Cervus elaphus* L., *Rangifer tarandus* L., *Bison* cfr. *priscus* Boj., *Ursus spelaeus* Ross et Heins., *Sorex* cfr. *minutus* L., *Sorex* cfr. *araneus* L., *Castor fiber* L., *Glis* cfr. *glis* L., *Muscardinus* cfr. *avellanarius* L., *Cricetus* cfr. *cricetus* L., *Pliomys lenki* Heller, *Lagurus* cfr. *lagurus* Pallas, *Microtus oeconomus* Pallas, *Microtus gregalius* Pallas, etc.

Il est très difficile de répartir chronologiquement, dans le cadre du Pléistocène, la faune mentionneé plus haut. En ce qui concerne ce problẽme P. Samson et C. Rădulescu (1968) font la proposition d'attribuer la faune supérieure de Bugiuleşti et celle de Rotbav-Silvestru au *Günz*, et celle de Rotbav-Dealul Tiganilor au *Günz-Mindel*.

Les deux espẽces de cervidés de Araci-Carriẽre marqueraient le *Mindel*; la faune de Drăghici avec celle de Sîndominic marqueraient le *Mindel-Riss*.

Enfin, dans le bassin de Sf. Gheorghe (les points "La Moară" et "La Carrière-Sud") est connue une faune plus récente que celle mentionnée plus haut et formée par *Parelaphus trogontherii* Pohlig (forme évoluée), *Coelodonta antiquitatis* Blumb., *Marmota* sp., et *Equus* sp. Samson et Rădulescu (1968) attribuent cette faune au Rissien. Mais toutes ces attributions d'âge, mentionées plus haut, sont plus ou moins hypothétiques, puisqu'elles ne s'appuient pas sur une stratigraphie d'une vigoureuse succession, établie sur des dépôts se succédant verticalement. Les points fossilifẽres mentionnés sont isolés et éloignés les uns des autres; aussi on peut trouver beaucoup de lacunes dans leur succession.

III. *Pléistocène supérieur.*— La faune de Vertébrés caractéristique au Pléistocène supérieur est connue surtout des terrasses des riviẽres de la Roumanie et parfois du loessoîde couvrant ces terrasses, de même que des cavernes et grottes remplies par des loessoîdes (par ex., dans la vallée de la Casimcea dans la Dobrogea). D'autres fois cette faune est connue dans les dépôts laissés dans les cavernes par l'homme paléolithique ou même dans les abris-sous-la roche utilisés par celui-ci.

Examinons successivement les terrasses inférieures, en commençant par celle du versant droit du Prut ã Stînca Ripiceni (N de la Moldavie). Dans les dépôts de cette terrasse Nec. Moroşan (1938) cite: *Elephas (Mammuthus) primigenius* Blumb., *Rhinoceros tichorhinus* Cuv., *Bos primigenius* Boj., *Equus cabalus fossilis* Cuv. (=?*Equus germanicus* Nehring).

Ces formes correspondent, en général, au Würmien. Des molaires de *Mammuthus primigenius* Blumb. sont citées de la même terrasse inférieure du Prut moyen ã Drănceni. Pareils restes de Mammouth sont connus également dans les terrasses inférieures de certains affluents du Prut. Tel est le cas de la terrasse inférieure de confluent de Miletin et de la Jijia, ou bien le cas de la terrasse inférieure (de 15-20 m) du versant gauche du Bahlui prẽs de Jassy, ã Holboca, d'oũ on a décrit (Macarovici et Zaharia, 1963) un crâne presque entier de *Elephas trogontherium* Pohlig (forme évoluée), ã côté de molaires de *Elephas (Mammuthus) primigenius* Blumb. et d'une mandibule de *Rhinoceros (Coelodonta) antiquitatis* Blumb. (=*R. tichorhinus* Cuv.).

Dans les "sables de Ciric" de la terrasse moyenne du versant gauche du Bahlui ã Jassy sont connues (R. Sevastos, 1903) des molaires et des os de *E. (Mammuthus) primigenius* Blumb., *Rhinoceros tichorhinus* Cuv., *Megaceros euryceros* Aldrov., *Bos primigenius* Boj., *Bison priscus* Boj. Les "sables de Ciric" se trouvent aussi dans la terrasse supérieure du versant gauche du Bahlui (ã 160 m d'altitude) d'oũ est connue une molaire de *Paleoloxodon antiquus* Falc. (Et. Patte, 1936).

A mesure qu'on avance vers le S, on constate que la faune de Vértébres fossiles ne change pas beaucoup dans les dépôts de certaines terrasses inférieures des riviẽres. Anisi, de la terrasse inférieure du Vaslueț (ã Hulubăț — ville de Vaslui) sont connues plusieurs molaires et défences de *E. (Mammuthus) primigenius* Blumb., os et crânes de *Rhinoceros tichorhinus* Cuv. et cornes de *Bison priscus* Boj., *Bos primigenius* Boj., et *Megaceros euryceros* Aldov. (Macarovici, 1959).

De la terrasse inférieure de la riviẽre du Bîrlad sont connus les mêmes Mammifères fossiles, à Negrileşti et à Ungureni. Mais la plus nombreuse faune de Mammifères fossiles würmiens est connue de la terrasse inférieure du Bîrlad à Rateş (près de Tecuci). De cette terrasse sont connus (Macarovici, 1959, 1969; Apostol, 1970): *E. (Archidiskodon) meridionalis* Nesti (très rarement), *E. (Mammuthus) primigenius* Blumb., *R. (Coelodonta) antiquitatis* Blumb., *Bison priscus* Boj. (crânes), *Bos primigenius* Boj. (crânes et os), *Equus germanicus* Nehring, *Equus scythicus* Răd. et Sams., *Sus scrofa ferus* L., *Camelus* sp. (remanié).

En ce qui concerne *E. (Mammuthus) primigenius* Blumb., de cette liste, celui-ci a été rencontré non seulement dans les localités moldaves mentionnées, mais aussi dans les terrasses inférieures de la vallée du Siret entre Poiana et Paşcani, et dans celles du nord de la Moldavie (Apostol, 1968).

Le même proboscidien a été rencontré – assez rarement, c'est vrai – dans la Plaine Roumaine, en particulier dans certains points des environs de Bucarest, dans les graviers qu'y sont à la base des loessoîdes. Puis, sont connus certains points le long du Danube (S du distr. Ilfov) et à l'embouchure de Jiu où des restes de *E. (Mammuthus) primigenius* Blumb. furent trouvés.

En échange, beaucoup de points à faune de Vertébrés fossiles quaternaires sont connus en Transylvanie, entre les rivières Olt et Mureş. Ainsi, un point riche en pareille faune est connu à Guşteriţa (Hammersdorf), au N de Sibiu, dans la terrasse inférieure du Cibin (au confluent de celui-ci avec la vallée Ruscior). La faune de ce point a été décrite par Akner (1850-1852) et se trouve conservée pour la plupart dans la collection du Musée de Sciences Naturelles de Sibiu. Cette faune comprend les espèces suivantes: *Elephas (Mammuthus) primigenius* Blumb., *Cervus (Megaceros) euryceros* Aldrov., *Cervus elaphus* L., *Bison priscus* Boj., *Rhinoceros tichorhinus* Cuv., *Felis spelaea* Goldf., *Hyaena spelaea* Goldf., *Ursus arctoides, Equus germanicus* Nehring (=*E. caballus fossilis* Cuv.).

Une faune semblable (constituée par: *E. primigenius* Blumb., *Bison priscus* Boj., *Bos primigenius* Boj., *Cervus (Megaceros) euryceros* Aldrov., *Cervus elaphus* L., *Alces palmatus* Ham. Smith, *Capra* sp.) est gardée aussi dans le Musée de la ville de Sighişoara. Elle a été collectionnée dans la terrasse inférieure de la rivière de Tîrnava Mare, aux environs de cette ville. Dans le Musée de Sciences Naturelles de Sibiu se trouve, restauré, un squelette de *Bison priscus* Boj. (Otto Phleps, 1906), trouvé dans le Kreuzberg – Dealul Crucei – près de Sighişoara. Toujours dans la même terrasse inférieure de la Tîrnava Mare, à la localité Brăteiu (à l'E de Mediaş), sont connus des os de *Rhinoceros (Coelodonta) antiquitatis* Blumb., *Equus germanicus* Nehring, et *Alces* sp.

Une liste de faune, approximativement identique en âge, est connue aussi de la terrasse inférieure de la Tîrnava Mică, à la confluence de celle-ci avec le ruisseau Bogaciu. Cette faune est constituée par *E. (Mammuthus) primigenius* Blumb., *Alces* cfr. *palmatus* Ham. Smith, *Megaceros euryceros* Aldrov.

Une faune relativement nombreuse de vertébrés est connue également de la terrasse inférieure du ruisseau Hîrtibaciu (affluent gauche du Cibin), semblable à celle de Sighişoara. Telle est la faune connue de cette terrasse à Apoş (au NW de Agnita) et à Hosman, faune formée par: *E. (Mammuthus) primigenius* Blumb., *Rhinoceros (Coelodonta) antiquitatis* Blumb., *Cervus (Megaceros) euryceros* Aldrov., *Cervus alces* (=*Alces palmatus* Ham. Smith), *Cervus (Dama) vulgaris* L., *Cervus elaphus* L., *Bos primigenius* Boj., *Bison priscus* Boj., *Capra* sp., *Equus* sp.

Les trois premiers éléments de cette liste sont connus aussi dans la dépression de Făgăraş, à Bruiu (sur le côté droit de l'Olt).

Dans le bassin de Braşov sont connus certains Mammifères fossiles indicant le Pléistocène supérieur. Tel est *Rhinoceros kronstadtensis* Toula (provenant de la ville même de Braşov), après lequel suivent les restes de *E. primigenius* Blumb. et ceux de *Megaceros giganteus* Blumb. de Rotbav (le point "Cariera de sub brazi") et de Ghidfalău. En même temps, est connue du bassin de Sf. Gheorghe (sur l'Olt supérieur) la faune suivante: *Elephas (Mammuthus) primigenius* Blumb., *Rhinoceros (Coelodonta) antiquitatis* Blumb., *Equus germanicus* Nehring, *Megaceros giganteus* Blumb., *Bison priscus* Boj., *Felis spelaea* Goldf., *Marmota* cfr. *bobac* Müller, etc.

Une faune très proche de celle de Sf. Gheorghe est connue aussi de la terrasse inférieure de la rivière de Sebeş, à la ville homonyme.

Sur la limite occidentale de la Roumanie, entre Oradea et Arad, existent beaucoup de points dans la plaine entre les Crişuri, d'où sont connus de nombreux restes de *Elephas (Mammuthus) primigenius* Blumb., trouvés soit à la base des loessoîdes, soit dans les graviers des terrasses inférieures.

Avant de terminer avec l'énumération de la faune de vertébrés fossiles quaternaires connus en Roumanie, nous nous arrêterons un instant sur la faune de Mammifères fossiles connue du loessoîde sédimenté dans les cavernes des calcaires jurassiques du centre de la Dobrogea. Telle est la caverne dite "La Adam" et d'autres cavernes de la vallée de Casimcea dans lesquelles s'est déposé le soit disant "nouveau loessoïde." Dans la masse de ce loessoïde existe huit niveaux de faune. Quatre de ces niveaux contiennent une faune "froide" (arctique), représentée par *E. (Mammuthus) primigenius* Blumb., *R. tichorhinus* Cuv., *Rangifer tarandus* L., *Megaceros giganteus* Blumb., *Ursus spelaeus* Goldf. Avec ces quatre niveaux à faune "froide" alternent les quatre autres niveaux contenant de la faune "chaude" de steppe, représentée par: *Saiga tatarica, Vulpes corsac, Equus przewalskii, Asinus hydruntinus*. Cette alternance de faune est en liaison directe avec la migration de la faune würmienne, suivant que le climat devanait plus chaud ou plus froid pendant la période würmienne.

Il convient d'y ajouter aussi la faune découverte dans quelques cavernes de Transylvanie (par ex. dans la Peştera Ohaba) et d'Olténie (par ex. la Peştera Muerii).

De ces cavernes est connue, en particulier, une faune de carnivores (*Ursus spelaeus* Ros., *Leo spelaeus* Goldf., *Alopex lagopus* L., *Panthera pardus spelaeus* Koch., *Crocuta spelaea* Goldf., *Gulo gulo* L., *Vulpes vulpes* L., *Canis lupus* L., *Mustela erminea* L.).

De la liste de Mammifères fossiles que nous avons présentée plus haut, il résulte que sur le territoire de la Roumanie, au Pléistocène ont vécu plus de Mammifères que n'y vivent aujourd'hui. C'est grâce à ces migrations et à l'évolution générale que s'est constituée la faune actuelle de Mammifères de l'Europe et, en même temps, celle de la Roumanie.

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ALLOPHAIOMYS KORMOS FROM THE PLEISTOCENE OF NORTH AMERICA

Robert A. Martin

Abstract.– *Allophaiomys* Kormos is reported from the Kentuck local fauna of McPherson County, Kansas and the Java local fauna of Walworth County, South Dakota. These are the first records of this genus in North America. Both faunas are considered to be of latest early Pleistocene age and broadly contemporaneous with European deposits containing *Allophaiomys*. An Asian epicenter of evolution and dispersal is suggested, and descendant taxa are discussed.

INTRODUCTION

Allophaiomys is an extinct genus of vole first recorded from deposits in Hungary by Kormos (1933). This genus represents the earliest evolutionary grade of voles with rootless cheek teeth and cementum in the reentrant angles. Since Kormos' (1933) original description *Allophaiomys* has been recorded from numerous deposits throughout Europe (Chaline, 1970, 1972, 1973; Kowalski, 1960; Malez, 1961; Pasa, 1947; Kretzoi, 1965; Terzea and Jurcsak, 1968, 1969; Fejfar, 1961; Musil, 1966; Van Der Meulen, 1972; Rabeder, 1972, 1973). With the exception of Pidoplicka's (1955) report of *Allophaiomys* from Cortkov in the Ukraine, adequate documentation of Asiatic records is lacking. Kretzoi (1956) postulated its presence at Chou-Kou-Tien in China and Kowalski (1960) mentioned the presence of an undescribed species from the Altai Mountains of the USSR (I. Gromov, oral comm.).

The purpose of this paper is to report the occurrence of *Allophaiomys* from two local faunas in the Great Plains region of North America: the Kentuck local fauna of McPherson County, Kansas (=the Kentuck assemblage of Hibbard, 1952) and the Java local fauna of Walworth County, South Dakota (Martin, 1973a, b). RAM=personal collection of R.A. Martin.

SYSTEMATIC PALEONTOLOGY

Order **Rodentia**

Family **Cricetidae**

Subfamily **Microtinae**

Allophaiomys cf. *A. pliocaenicus* Kormos 1933

=*Microtus (Pedomys) llanensis* of Hibbard, 1952. Univ. Kansas Contr. Paleont., Vertebrata, Art. 2:1-14.

=*Allophaiomys* of Martin, 1973. Bull. New Jersey Acad. Sci., 18(2):48-56.

Referred Specimens.– KU (University of Kansas) 7380, 7381, 7382, 7351, three right mandibles and one left mandible, all with M_1-M_2; and 7384, isolated teeth.

UMMP (University of Michigan) 34710, 24505, two left mandibles with M_1-M_2; 34707, one left mandible with M_1-M_2 and one right mandible with M_1 only; and 50516, isolated teeth.

SDSM (South Dakota School of Mines and Technology) 8031, blanket number covering all *Allophaiomys* material from the Java local fauna, including mandibles, palates, and isolated teeth.

Locality and Age.– Kentuck local fauna, NW¼, Sec. 13, T. 18 S, R. 4 W, McPherson County, Kansas – latest early Pleistocene.

Java local fauna, NW¼, Sec. 26, T. 123 N, R. 75 W, Walworth County, South Dakota – latest early Pleistocene (?early Kansan).

Remarks.– The specimens from the Kentuck local

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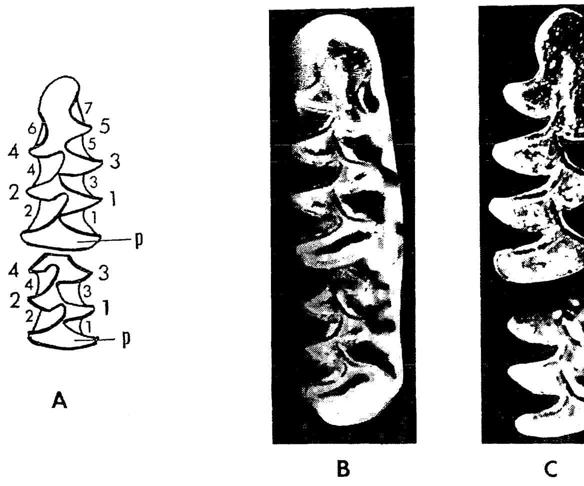

Fig. 1. *Allophaiomys* cf. *A. pliocaenicus* from the Kentuck local fauna of Kansas (A, UMMP 34710, left M_1-M_2) and the Java local fauna of South Dakota (B, SDSM 8031, right M_1-M_2; C, SDSM 8031, right M_1-M_2). Small numbers correspond to reentrant angles. Large numbers are located at the apices of triangles. p= posterior loop. For scale refer to measurement in Table 1.

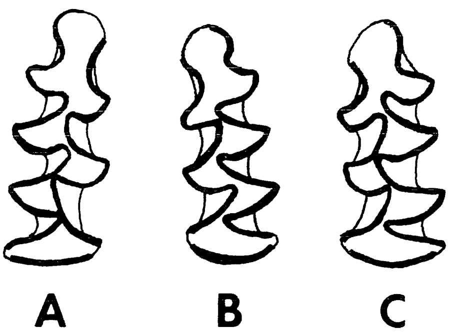

Fig. 2. *Allophaiomys pliocaenicus* from the Kamyk local fauna, Poland. Variation of the first lower molar. (A) RAM-VP 77, right M_1. (B) RAM-VP 77, left M_1. (C) RAM-VP 77, left M_1. x 7.0.

fauna described here as *Allophaiomys* were originally allocated to *Microtus (Pedomys) llanensis* Hibbard 1944, but differ from that species in possessing two fewer triangles on the first lower molar. As described by Hibbard (1944, p. 730), the holotype of *M. llanensis* possesses a first lower molar consisting ". . .of a posterior loop and three tightly closed triangles. The fourth and fifth triangles confluent and open broadly into a small anterior loop." Sixth and seventh incipient triangle buds appear on the anterior loop, and this pattern is also consistent for topotype material of *M. llanensis* described by Paulson (1961).

Diagnosis of Allophaiomys pliocaenicus *Kormos.– Allophaiomys pliocaenicus* is a small microtine rodent with rootless cheek teeth and cementum in the reentrant angles. The first lower molar (M_1) possesses a posterior loop, three closed triangles, and a simple, but somewhat variable anterior loop (Figs. 1, 2). The third lower molar demonstrates a posterior loop, two confluent triangles, and a small anterior loop (or, if one considers the anterior loop of M_2 and M_3 to be composed of triangles, triangles three and four are small and confluent).

Features of the M_1 are sufficient to separate both the genus *Allophaiomys* and the species *A. pliocaenicus* from all microtines except *Arvicola* and *Phaiomys*. Characteristics of the M_3 are included simply to exclude *Arvicola*, in which the well-developed anterior loop (or triangles three and four) on M_3 produces a pattern identical to the M_2 in all known species (Martin, 1974). However, in no way can any aggregation of dental and mandibular characters satisfactorily separate *Allophaiomys* from the extant *Phaiomys* (e.g., *P. leucurus*). For this reason, I (1974) synonomized *Allophaiomys* Kormos 1933 under *Phaiomys* Blyth 1863. Here, I present the more conservative classification held by other researchers and accept the integrity of both taxa. I hasten to add that I do not favor this classification, and I await a definitive diagnosis of *Allophaiomys* which will separate it from *Phaiomys* on some grounds other than chronology.

Measurements of isolated teeth of *Allophaiomys pliocaenicus* from the Kamyk deposit of Poland, as published by Kowalski (1960) are as follows (l=length, w=width, number in parentheses following tooth measured=number of measured specimens. Subsequent numbers represent the observed range and the mean): lM_1(7), 2.7-2.9(2.8), wM_1(9), 1.2-1.3(1.3); lM_2(8), 1.6-1.8(1.7); lM_3(8), 1.4-1.6(1.5); lM^1(9), 2.2-2.7(2.4); lM^2(9), 1.7-1.9(1.8); lM^3 (14), 1.7-2.0(1.8).

Conformity in size between the Kamyk specimens and those from the Java and Kentuck local faunas can be seen by comparing the above data to those in Table 1.

DISCUSSION

Originally described as the Kentuck assemblage by Hibbard (1952), this aggregation of fossils is now regarded by the author and others (H. Semken and R. Zakrzewski, oral comm.) as a local fauna of uncertain stratigraphic relationships. Semken (1966) emphasized the fact that the Kentuck deposit was not lithologically related to the McPherson Formation (as redefined by Semken, 1966), and thus not related to the Illinoian Sandahl local fauna. The Kentuck local fauna includes a number of misidentified taxa (R.A. Martin and C.W. Hibbard, unpublished), and is obviously in need of further study. Based upon the presence of *Allophaiomys* and an extinct *Sigmodon* similar to *S. curtisi* (Hibbard, 1972; Martin, 1974) it appears that

Table 1. Measurements in mm of *Allophaiomys* from the Java local fauna of South Dakota and the Kentuck local fauna of Kansas. N=number of specimens, OR=observed range, $\bar{x}$=mean, s=one standard deviation, C.V.=coefficient of variation.

		N	O.R.	$\bar{x}$	s	C.V.
JAVA						
M_1	Length	20	2.75-3.40	3.01	±0.15	4.98
	Width	20	1.17-1.40	1.27	0.07	5.51
M_2	Length	20	1.54-1.92	1.79	0.09	5.03
	Width	20	1.00-1.23	1.13	0.06	5.31
M_3	Length	20	1.48-1.85	1.63	0.10	6.14
	Width	20	0.84-1.05	0.92	0.06	6.52
M^1	Length	20	2.30-2.67	2.53	0.10	3.95
	Width	20	1.28-1.63	1.45	0.09	6.21
M^2	Length	20	1.79-2.15	1.98	0.09	4.55
	Width	20	1.15-1.37	1.25	0.06	4.80
M^3	Length	20	1.72-2.12	1.89	0.12	6.35
	Width	20	0.96-1.17	1.06	0.06	5.66
KENTUCK						
M_1	Length	11	2.60-3.01	2.84	0.15	5.28
	Width	13	1.10-1.32	1.22	0.07	5.74
M_2	Length	6	1.61-1.85	1.73	0.08	4.62
	Width	6	1.06-1.12	1.08	0.03	2.78
M_3	Length	3	1.40-1.61	1.52	0.11	7.24
	Width	3	0.87-0.95	0.90	0.04	4.44
M^1	Length	4	2.22-2.49	2.34	0.12	5.13
	Width	4	1.35-1.47	1.39	0.05	3.60
M^2	Length	11	1.68-2.01	1.86	0.11	5.91
	Width	11	1.10-1.30	1.21	0.07	5.79
M^3	Length	6	1.71-2.20	1.91	0.18	9.42
	Width	6	0.83-1.23	1.07	0.16	14.95

the Kentuck local fauna is older than the Sandahl local fauna and broadly contemporaneous with the Java local fauna. It may or may not ultimately be shown to be exactly contemporaneous with the latter.

As I have indicated (Martin, 1973a, b), the Java local fauna is post-Borchers (Hibbard, 1941, 1972) and pre-Cudahy (Hibbard, 1944, 1949, 1972; Paulson, 1961) in age. According to Hibbard and Dalquest (1973), this indicates a block of time roughly between 2 million K/Ar years and .6 million K/Ar years B.P. (see Hibbard and Dalquest, 1973, for discussion of dates and stratigraphic interpretation). Since the Cudahy fauna of Kansas is considered to be of latest Kansan age (Paulson, 1961; Hibbard, 1972), and since the Java fauna, although older than Cudahy, contains some extinct species in common with the Cudahy fauna (e.g., *Ondatra annectens, Reithrodontomys moorei*) and is also a "cool" fauna, I (1973a) relegated the Java local fauna to the latest early Pleistocene and, tentatively, to an early phase of the Kansan glaciation at approximately one million years B.P. The earliest European records of *Allophaiomys* are from local faunas in France (Balaruc 1, Chaline, 1970), Holland (Brielle, noted by Chaline, 1973), Poland (Kamyk, Kowalski, 1960), and Yugoslavia (Marjan, Malez, 1961). These faunas are considered by Chaline (1973) to be of a boreal nature and to correspond to an early phase of the Gunz glaciation. Chaline (1972) further indicates that this "fauna" existed in Europe approximately one million years B.P. (K/Ar documentation lacking). Temporarily accepting this date, the above faunas correspond roughly to the North American Kansan glaciation. There is neither any evidence nor any suggestion by recent European research that *Allophaiomys* appeared any earlier in Europe than it did in North America. Since conspecificity of European and American *Allophaiomys* is likely, dispersal routes cannot be determined at the present time, except insofar as the lack of *Allophaiomys* from both continents prior to the (?) Kansan/Gunz glaciation suggests a double corridor from Asia developing during this time.

Extinct and extant microtines from North America have not as yet been studied in detail with regard to derivation from *Allophaiomys*, but convincing evidence is presented by Chaline (1970, 1972, 1973) for the evolution of extant European vole taxa from *Allophaiomys*. In essence, Chaline implies a polyphyletic origin for species of the genera *Microtus* and *Pitymys* from various populations of *Allophaiomys pliocaenicus*. Although I do not agree with his taxonomy in its entirety (e.g., by my definition any vole with at least five well-developed triangles and an anterior loop on M_1 cannot be assigned to *Allophaiomys*) Chaline's model is not inconsistent with biological reality (see Martin, 1970) and, in my opinion, can be expanded to include *Neodon, Alticola, Tyrrhenicola,* and probably *Anteliomys* (=*Eothenomys*) as well. Other extant voles with ever-growing cheek teeth and cementum are apparently not, however, derived from *Allophaiomys*. *Arvicola* appears as early in the fossil record as does *Allophaiomys* and, according to Chaline (1966), it has an independent origin. The North American *Neofiber* traces its ancestry to *Proneofiber* (Hibbard and Dalquest, 1973), a genus with rooted cheek teeth. Kretzoi (1969) emphasizes the distinction of *Lagurus* and its extinct relatives by classifying them as the tribe Lagurini.

SUMMARY

1) *Allophaiomys* cf. *A. pliocaenicus* is recorded from two local faunas in the Great Plains region of North America.

2) The Kentuck assemblage of Kansas (Hibbard, 1952) is considered to be a local fauna and broadly contempora-

neous with the Java local fauna of South Dakota (Martin, 1973a). Both local faunas are tentatively assigned to an early phase of the Kansan glaciation.

3) According to published accounts by European paleontologists (notably Chaline, 1970, 1972, 1973), *Allophaiomys* appears in faunas of Europe and North America approximately at the same time (?Kansan/Günz glaciation). Lack of *Allophaiomys* records prior to this time on both continents suggests an Asian epicenter of evolution and dispersal.

4) *Allophaiomys*, considered as an evolutionary grade, is believed to have been ancestral to *Microtus, Pitymys, Neodon, Alticola, Tyrrhenicola,* and probably *Anteliomys.*

ACKNOWLEDGMENTS

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MICROTINE RODENTS FROM THE OGALLALA PLIOCENE OF NEBRASKA AND THE EARLY EVOLUTION OF THE MICROTINAE IN NORTH AMERICA

Larry D. Martin

Abstract.– Screening operations in the upper portion of the Ogallala Group in Nebraska have resulted in the recovery of numerous microtine rodent jaws and teeth. This new material has significantly increased our knowledge of the early evolution of the microtines. Two new genera and three new species are described. One genus is affiliated with *Microtoscoptes* while the other seems similar to *Pliophenacomys*.

Prior to the development of underwater screening techniques (Hibbard, 1949) very little was known about the fossil history of North American microtines. Extensive screening operations resulted in large collections of these rodents and the number of extinct genera known from North America rose from two to around 14. They are presently the most useful biostratigraphic tool for the correlation of continental sediments Blancan in age or younger and have proved to be useful indicators of local environments.

The usefulness of microtines in sediments older than Blancan has been seriously hampered by inadequate collecting, with most records concentrated around Oregon, Idaho, and Wyoming (Fig. 1). During the summers of 1971 and 1972 I was able to add several new sites from the late Ogallala Pliocene of Nebraska. These new localities add substantially to our knowledge of the early microtine radiation. They double the known diversity of microtines of this age and provide some additional insight on the early evolution of the Microtinae. They are all from sites which are Hemphillian or slightly younger in age.

SYSTEMATICS

Class **Mammalia** Linnaeus, 1758

Order **Rodentia** Bowdich, 1821

Superfamily **Muroidea** Miller and Gidley, 1918

Family **Microtidae** Cope, 1891

Subfamily **Microtinae** Miller, 1896

Tribe **Microtoscoptini** Kretzoi, 1955

Genus *Microtoscoptes* Schaub, 1934

Genotype. – *Microtoscoptes praetermissus* Schaub,1934

Diagnosis.– Small voles with relatively low-crowned molars, having broad, straight reentrant angles lacking cement; molars consisting of pairs of broadly confluent triangles opposite each other and separated from other pairs by a thin central connection of enamel; M^2 with four roots and two lingual reentrant angles; M^3 with two labial and three lingual reentrant angles; M_1 with small anterior loop and no enamel islet.

Microtoscoptes disjunctus (Wilson, 1937)

(Fig. 2)

Goniodontomys disjunctus Wilson, 1937.

Microtoscoptes disjunctus (Wilson), Hibbard, 1959; Repenning, 1968; Hibbard, 1970.

Emended Diagnosis.– Larger than *M. praetermissus*; anterior loop of M^1 without enamel pit even in fairly young stages of wear.

Geological Range and Distribution.– ?Clarendonian; Hemphillian of Oregon, Idaho, and Wyoming.

University of Kansas, Museum of Natural History and Department of Systematics and Ecology, and University of Nebraska State Museum, Research Affiliate.

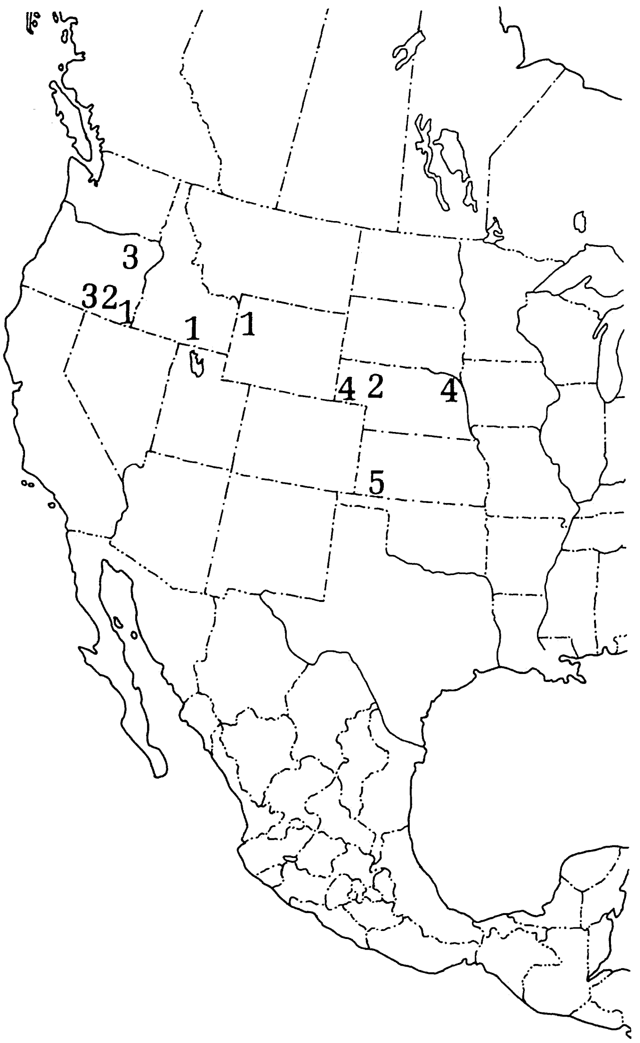

Fig. 1. Distribution of pre-Blancan microtines in North America. (1) *Microtoscoptes.* (2) *Paramicrotoscoptes.* (3) *Promimomys.* (4) *Propliophenacomys.* (5) *Ogmodontomys.*

Discussion.– *Microtoscoptes disjunctus* has been discussed in detail by Hibbard (1959, 1970a) and by Repenning (1968). It appears to be closely similar to the genotypic species, *M. praetermissus.*

Paramicrotoscoptes gen. nov.

Genotype.– *Paramicrotoscoptes hibbardi* sp. nov.

Diagnosis.– A small microtine with rooted molars, no cement or dentine tracts, and triangles on lower molars and M^1 tending to be directly opposite of each other and confluent. *Paramicrotoscoptes* differs from *Microtoscoptes* in having a single large lingual reentrant angle on M^2 and only two on M^3, and at least one posterior enamel pit on M^3.

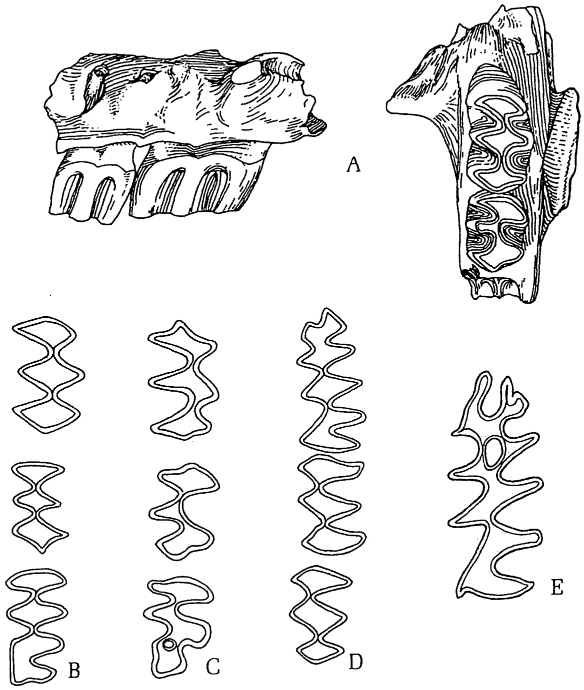

Fig. 2. *Paramicrotoscoptes* and *Microtoscoptes.* (A) *Paramicrotoscoptes hibbardi,* UNSM 47504, holotype, right maxilla with M^1-M^2, labial and occlusal views, x 6. (B-E) occlusal views, not to scale. (B) *Microtoscoptes disjunctus,* right M^1-M^3 (from Repenning, 1968). (C) *Paramicrotoscoptes hibbardi,* right M^1-M^3 (from Shotwell, 1970). (D) *Microtoscoptes disjunctus,* left M$_1$-M$_3$ (from Repenning, 1968). (E) *Paramicrotoscoptes hibbardi,* left M$_1$.

Paramicrotoscoptes hibbardi sp. nov.

(Figs. 2-4)

Microtoscoptes disjunctus Shotwell, 1970

Holotype.– University of Nebraska State Museum (UNSM) 47504, right maxilla with M$^{1\text{-}2}$. Collected in the summer of 1971 by Larry D. Martin and party.

Horizon and Type Locality.– Hemphillian (upper part of Ogallala Pliocene), Ash Hollow Formation, Ogallala Group, UNSM Coll. Loc. Kh-101, SE¼, SE¼, SW¼ Sec. 3, T. 15 N, R. 40 W, 4.5 mi W of Lemoyne, Keith County, Nebraska.

Referred Material.– A partial right maxilla and 59 isolated teeth from the same locality and horizon as the holotype.

Description.– Slightly smaller than *Microtoscoptes disjunctus*; palate with anterior root of zygomatic arch across from anterior loop of M^1; palate fairly deep with vertical margins; maxillary portion terminating posteriorly near anterior loop of M^2; posterior margin of incisive foramen across from anterior edge of M^1; M^1 consisting of an anterior loop and four alternating triangles with first and second, and third and fourth arranged opposite and confluent with each other; anterior face of tooth with

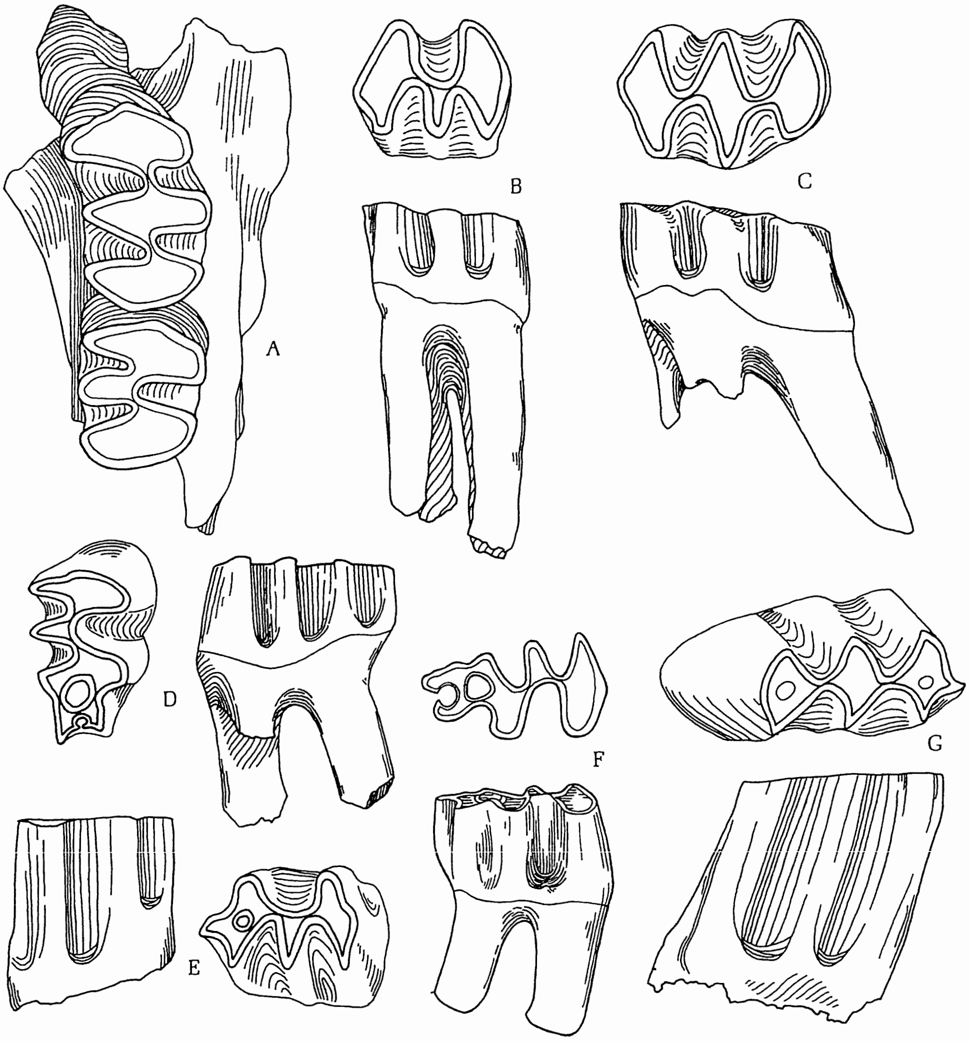

Fig. 3. *Paramicrotoscoptes hibbardi*. (A) KU 28290, right maxilla with M^1-M^2, occlusal view. (B-E) occlusal and labial views. (B) UNSM 47505, left M^2. (C) UNSM 47504, left M^1. (D) UNSM 47502, right M^3. (E) UNSM 47506, left M^2. (F) UNSM 47501, right M^3, occlusal and lingual views. (G) UNSM 47503, right M^1, occlusal and labial views. All x 12.5.

low dorsal-ventral median ridge and posterior face with a distinct posterior ridge, in young teeth reentrant angles touch closing off each dentine rhombohedron from the other but the amount of closure is reduced with wear; young teeth with distinct circular anterior pit and shallow posterior pit (both lost with wear), three roots, anterior root largest, posterior lingual root next in size and slightly farther anterior than posterolabial root; M^2 with large anterior loop and three alternating triangles, one across from single, large lingual reentrant angle and two confluent posterior triangles with enamel pit in early stages of wear (Fig. 3 E), two labial reentrant angles present, low median ridge down posterior face of tooth, and four long roots; M^3 with three roots, anterior roots across from each other and labial one small, anterior loop, two alternating triangles and posterior loop present, first triangle closed and opposite broad lingual reentrant angle, second triangle broadly confluent with posterior loop, posterior loop rectangular in shape with large anterior enamel islet (lost only with extreme wear) and smaller posterior islet, posterior islet open to the rear and lost with wear.

All lower molars with two roots; M_1 with very large anterior loop, anterior loop consisting of two confluent posterior triangles, anterior portion with deep anterior groove creating two anteriorly projecting "horns," large enamel pit present in young specimens, posterior loop confluent (except in early wear, see Fig. 4 C) with first alternating triangle forming "V," second and third alterna-

Table 1. Measurements of cheek teeth in mm, *Paramicrotoscoptes hibbardi*

		N	Range	Mean	S.D.
M^1	Length	14	1.89-2.35	2.09	0.13
	Width	14	.92-1.58	1.24	0.24
M^2	Length	7	1.46-1.72	1.61	0.08
	Width	7	1.00-1.37	1.29	0.13
M^3	Length	6	1.85-2.22	1.94	0.16
	Width	6	1.11-1.44	1.21	0.15
M_1	Length	14	2.15-2.56	2.38	0.14
	Width	14	.98-1.41	1.16	0.14
M_2	Length	11	1.66-1.93	1.82	0.08
	Width	11	1.06-1.40	1.29	0.12
M_3	Length	7	1.48-1.87	1.73	0.23
	Width	7	.83-1.23	1.05	0.14

ting triangles confluent and nearly opposite each other; M_2 consisting of posterior loop and four alternating triangles broadly confluent and opposite each other (the enamel pattern of the tooth forms three diamonds joined near the midline of the tooth); M_3 small and narrowing posteriorly; posterior loop rounded posteriorly, first and second, and third and fourth alternating triangles broadly confluent and nearly opposite each other.

Etymology.– Paramicrotoscoptes for its close similarity to *Microtoscoptes*; *hibbardi* for the late Claude W. Hibbard who was the foremost student of fossil microtines in North America.

Discussion.– In 1963 Shotwell reported an M_2 of *Microtoscoptes disjunctus* from the Bartlett Mountain local fauna in Oregon. He later (Shotwell, 1970) illustrated a number of teeth of this rodent and commented on some differences between the M_1 of it and those from the type area (Rome local fauna). However, he did not think that the differences present warranted separation at the species level. Examination of Shotwell's figures shows that the microtine from the Bartlett Mountain local fauna is essentially identical with that from UNSM Coll. Loc. Kh-101, and that there are considerable differences between M^{2-3} of this rodent and *Microtoscoptes disjunctus*. These teeth are usually conservative in crown pattern in microtines (especially M^2) and the differences noted (one lingual reentrant in M^2 and two in M^3) seem adequate to separate the two forms at the generic level.

Basically, *Paramicrotoscoptes* is less specialized than *Microtoscoptes*. The triangles on the molars are more alternating and less closed. In *Microtoscoptes* the triangles on the molars are arranged in confluent pairs that form "diamonds" connected centrally by very thin enamel. The anterior loop of M_1 is large in *Paramicrotoscoptes* and in young teeth contains an enamel pit. Enamel pits occur on a number of the other teeth, and most appear to have been depressions on the unworn occlusal surface. Enamel pits are unreported for *Microtoscoptes*. *Paramicrotoscoptes* and *Microtoscoptes* are not known to occur together and the exact age relationship of the two forms is presently unknown, although both occur in localities that have been called Hemphillian. They both appear to have been aquatic rodents and the Nebraska population occurs in ponded water sediments in association with *Dipoides* and another small beaver.

Tribe **Microtini** Simpson, 1945

Genus *Promimomys* Kretzoi, 1955

Genotype.– Promimomys cor Kretzoi

Diagnosis.– Small voles with relatively low-crowned molars lacking cement and having broad straight reentrant angles; M_1 with simple anterior loop and cricetine islet; hypoconal complex simple and sometimes separated from anterior part of tooth in M^3; all upper molars with three roots (modified from Repenning, 1968).

Promimomys mimus (Shotwell, 1956)

Prosomys mimus Shotwell, 1956; Kowlaski, 1960; Sulinski, 1964; Fejfar, 1964.

Microtodon mimus (Shotwell), Kowalski, 1960.

Promimomys mimus (Shotwell), Repenning, 1968.

Emended Diagnosis.– Slightly smaller and with less expanded anterior cingulum than *Promimomys cor*; anterior loop less complicated than in other European *Promimomys*.

Geological Range and Distribution.– Hemphillian of eastern Oregon.

Discussion.– I have chosen to follow Repenning (1968) in the synonymy of *Prosomys* with *Promimomys*. *Promimomys mimus* is apparently older and more primitive than any known true microtine from Eurasia.

Ogmodontomys Hibbard, 1941

Genotype.– Ogmodontomys poaphagus Hibbard, 1941

Diagnosis.– Voles with low-crowned rooted teeth, lacking cement; M^1 with a posterior loop, three alternating triangles and an anterior loop complicated by a prism fold and enamel pit in early stages of wear; apices of reentrant angles on lingual side of M^1 not turned anteriorly, and M^3 usually with three roots.

Ogmodontomys sawrockensis Hibbard, 1957

Cosomys primus Wilson. Hibbard, 1949, 1953.

Ogmodontomys sawrockensis Hibbard, 1957; Zakrzewski, 1967.

Diagnosis.– Smaller and lower crowned teeth than in *Ogmodontomys poaphagus*, also differing from that spe-

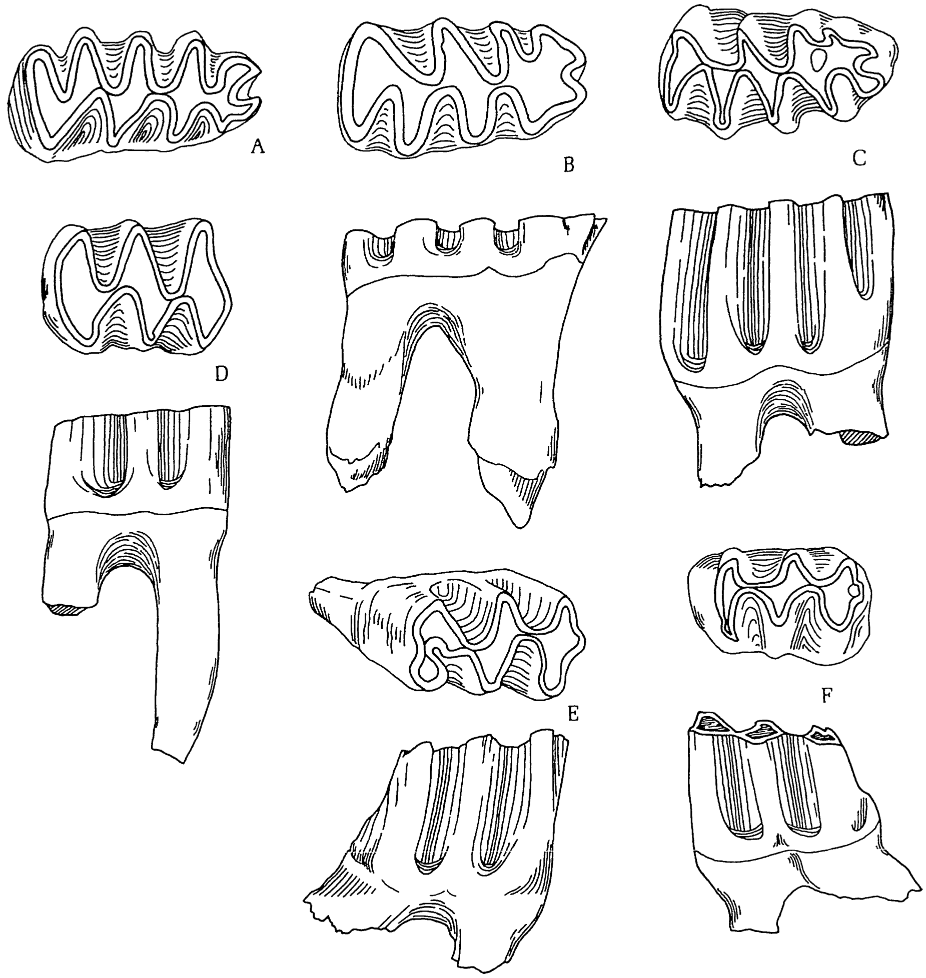

Fig. 4. *Paramicortoscoptes hibbardi.* (A) UNSM 47523, right M$_1$, occlusal view. (B-C) molars, occlusal and lingual views. (B) UNSM 47521, left M$_1$. (C) UNSM 47522, left M$_1$. (D) UNSM 47542, right M$_2$, occlusal and labial views. (E) UNSM 47532, left M$_3$, occlusal and lingual views. (F) UNSM 47533, left M$_3$, occlusal and labial views. All views x 12.5.

cies in having steep vertical walls to the palate, deeper palatal grooves, and lacking development of dentine tracts.

Geological Range and Distribution.— Hemphillian of southwestern Kansas.

Discussion.— *Ogmodontomys* represents a slow evolving lineage of microtines. The Saw Rock Canyon local fauna is Hemphillian on the basis of its beaver and rhinoceros (Schultz, Tanner, and Martin, 1972). It ultimately gives rise to *O. poaphagus*, a species which differs only in increased size, hypsodonty, and minor changes of the palate, although the time span between the known populations of the two species may be several million years. *Ogmodontomys* may be derived from a microtine like *Promimomys.*

Propliophenacomys gen. nov.

Genotype.— *Propliophenacomys uptegrovensis* sp. nov.

Diagnosis.— Medium size microtine with palate and palatal grooves shallow; molars rooted and lacking cement; lingual reentrant angles turned posteriorly and alternating triangles closed.

Propliophenacomys uptegrovensis sp. nov.

(Fig. 5)

Holotype.— UNSM 31391, partial rostrum with palate and M$^{1\text{-}2}$.

Horizon and Type Locality.— Kimball Formation, Ogallala Group, Pliocene, from UNSM Loc. Cn-101, NE¼ Sec. 23, T. 15 N, R. 49 W, Cheyenne Co., Nebraska.

Diagnosis.— Same as genus.

Description.— Snout short, incisors highly curved with broad, slightly rounded, orange enamel surfaces; infraorbital foramina relatively large and dorsal; anterior zygomatic

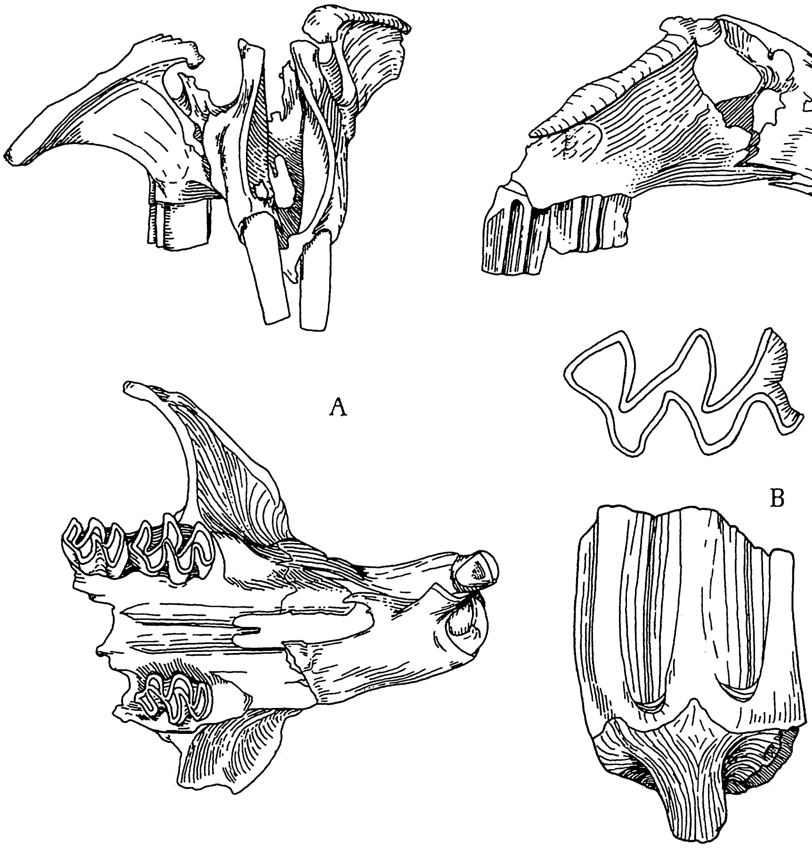

Fig. 5. *Propliophenacomys uptegrovensis.* (A) UNSM 31391, holotype, partial rostrum with M^1-M^2, anterior, lateral and occlusal views, x 5. (B) *Propliophenacomys parkeri*, right M^1, occlusal and labial views, x 15.

plate broad, triangular, and across from anterior portion of M^1; incisive foramina large and elongate with posterior margin anterior to M^1; small palatal spine present; palate shorter between anterior border of palatal foramina and posterior border of incisive foramina than in *Ogmodontomys sawrockensis*; palate and lateral palatal grooves very shallow and palatal foramina small; molars rooted but relatively high crowned, and lacking cement and dentine tracks; M^1 with two well-developed roots and an incipient third root on lingual side, anterior loop and four alternating triangles all more closed than in *Ogmodontomys sawrockensis*; width of M^1 1.52 mm and length 2.23 mm; M^2 with two roots and anterior loop with three slightly open alternating triangles; width of M^2 1.45 mm and length 1.88 mm.

Etymology.– *Propliophenacomys* for its presumed relationship to *Pliophenacomys*; *uptegrovensis* for the Uptegrove local fauna.

Discussion.– This is one of the most advanced microtines known from the Ogallala in terms of its relatively high-crowned teeth and closed triangles. The Uptegrove local fauna includes *Spermophilus kimballensis, Perognathus, Calippus, Neohipparion, Pliohippus, Nanippus, Teleoceras, Aphelops, ?Pliauchenia,* and a giant camelid (Kent, 1967). It represents a more upland fauna than those associated with other Ogallala microtines. The shallow palate and short rostrum of *Propliophenacomys* are suggestive of *Pliophenacomys* and the new genus is probably more closely related to it than to *Ogmodontomys.*

Propliophenacomys parkeri sp. nov.

(Figs. 5-6)

Holotype.– UNSM 47597, partial left ramus with M_1.

Horizon and Type Locality.– From unnamed beds in the upper part of the Ogallala Group, UNSM Coll. Loc. Kx-113, SE¼, Sec. 24, T. 33 N, R. 4 W, Devil's Nest Airport, Knox County, Nebraska.

Referred Material.– Two partial left rami with M_{1-2}, Kansas University (KU) 25302, UNSM 47598; right M_1, KU 25303; partial right M^1, UNSM 47599.

Horizon and Localities.– Same as holotype except KU 25302, which is from KU-Neb 36 on roadcut S of Santee, Knox County, Nebraska.

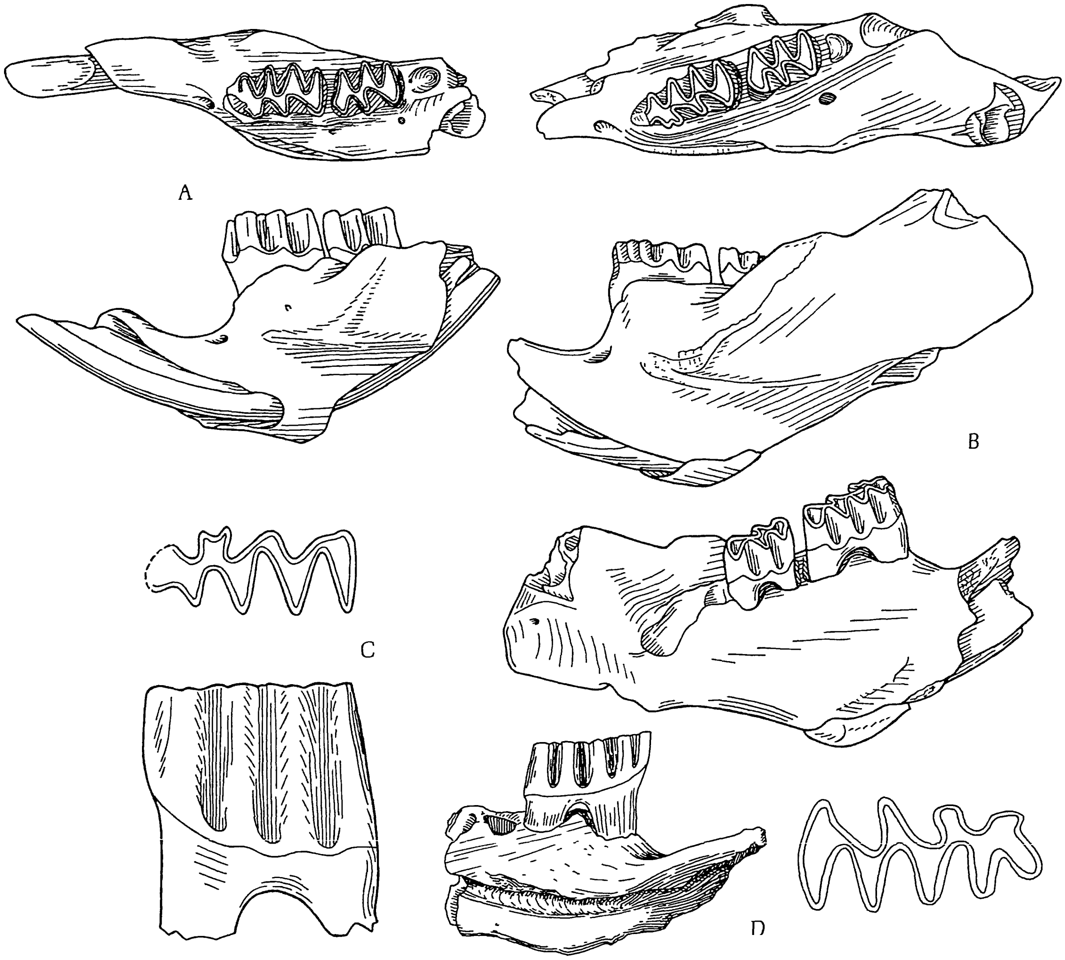

Fig. 6. *Propliophenacomys parkeri.* (A) UNSM 47598, left ramus with M_1-M_2, occlusal and labial views, x 5. (B) KU 25302, left ramus with M_1-M_2, occlusal, labial, and lingual views, x 5. (C) KU 25303, right M_1, occlusal and lingual views, x 11. (D) UNSM 47597, holotype, left ramus with M_1, occlusal view, x 12.5, and lingual view, x 6.

Diagnosis.— A vole, lower-crowned than *Propliophenacomys uptegrovensis*, with rooted molars lacking cement and dentine tracts; anterior loop of M_1 complicated but lacking enamel pit even at early stages of wear.

Description.— A small microtine slightly larger than *Nebraskomys*; lower molars with two roots; molars lacking cement and dentine tracts; M^1 with an anterior loop, three alternating triangles and a posterior loop, apparently 3 roots, reentrant angles broader and straighter and triangles not so closed as in *P. uptegrovensis*, labial triangles small; ramus with masseteric lines meeting below posterior loop of M_1 and continuing forward as shelf below anterior loop of M_1; mental foramen small and dorsal; symphyseal angle prominent; microtine groove (Repenning, 1968) present; broad depression between M_2 and ascending ramus; capsular process indistinct; incisor smooth; M_1 with anterior loop, three to four alternating triangles and posterior loop; anterior loop more complicated than in *Promimomys*, but lacking enamel pit, reentrants broad and straight, alternating triangles open; M_2 with posterior loop and four alternating triangles with the third and fourth broadly confluent. Measurements (in mm): UNSM 47599, right M^1, length, 2.20, width, 1.09; UNSM 47597, holotype, left M_1, length, 2.54, width, 1.16; KU 25303, right M_1, length 2.50, width 1.03; UNSM 47598, left M_2, length 1.72, width 1.11; KU 25302, left M_2, length 1.83, width 1.14.

Etymology.— Named for Gilbert D. Parker in appreciation of his assistance during the field season of 1973.

Discussion.— *Propliophenacomys parkeri* is a small rodent with a more complicated M_1 than in *Promimomys.* Two types of M_1 seem to be represented in the small sample and more than one taxon might prove to be present if additional material is collected. In one type the M_1 has an anterior loop with a prism fold and three alternating triangles, and in the other there is no distinct prism fold and a fourth triangle seems to be separating off the anterior loop. There is no enamel islet on the anterior loop of KU 25303, which is a fairly young tooth. A palate of *P. parkeri* or a lower dentition of *P. uptegrovensis* would greatly clarify the relationships of these two taxa.

CONCLUSIONS

Microtine rodents are probably not uncommon in the upper Ogallala deposits of the central Great Plains and their rarity is the result of collecting bias. A greater diversity of these rodents (five genera) appears to occur in North America than in Europe. They must have undergone a truly "explosive" radiation as they are presently one of the most numerous and widely distributed mammalian groups, although they were one of the last major mammalian groups to appear. The earliest record of microtine rodents is from the Clarendonian of North America and they must have achieved a Holartic distribution soon after their origin, because *Microtoscoptes* and *Promimomys* are known from the Pliocene of both North America and Eurasia. Both the Recent and fossil distributions of the microtines suggest that the subfamily had a northern radiation.

It is not yet clear whether microtines originated in North America or Eurasia, although most of their early record is presently from the former. However, there is nothing known from North America comparable to the microtine-like cricetid *Microtodon*, which is very similar to what I would expect for a microtine ancestor. There are, however, true microtines known from North America that are older than *Microtodon*, indicating that this genus is probably a sterile side branch (Repenning, 1968). If the microtines did originate in North America, I would expect to find their ancestry in the "*Copemys* type" cricetids of the Barstovian and Valentinian. However, *Copemys* is not particularly microtine like. It does have fairly simple teeth, which would seem to be a prerequisite for a microtine ancestor. The earliest known microtine that might be ancestral to later forms is *Promimomys minimus* (Shotwell).

Promimomys shows the development of increased hypsodonty on a simple cricetid dentition, in which the alternating triangles clearly correspond to cusps on the cricetine tooth. As the tooth becomes more hyposodont, the reentrant angles tend to grow closer together creating a pattern of closed alternating triangles, which tends towards greater complexity in M_1 and M^3. In M_1 this change centers around the anterior loop which includes the anteroconid and the associated anterior cingulum. Commonly in cricetines the anteroconid bifurcates, and a similar process takes place to form a complicated anterior loop in microtines. Eventually, the growth of reentrant angles into the anterior loop adds more alternating triangles to the tooth. In M^3 a similar process takes place with the posterior loop. This process suggests that microtines tend to progressively emphasize the importance of M_1 and M^3 in mastication; thus in the cricetine *Copemys* or in the primitive microtine *Promimomys minimus* the M_1 is only slightly longer than M_2, while in the advanced genus *Microtus* the M_1 may be almost twice the length of M_2. In young individuals of primitive microtines the edge of the anterior loop tends to be crenulated and an enamel islet is often found in the anterior loop. This enamel islet may form in at least two different ways: it may be formed by a depression on the anterior loop (cricetine islet of Repenning, 1968) or by pinching off the lingual fold of the anterior cingulum (Hinton, 1926). The latter origin seems to apply to all North American microtines except *Paramicrotoscoptes* and *Promimomys*, which have cricetine islets. Primitively the incisors of microtines were short and the capsular processes small and fairly anterior; however, in several lineages the incisors have increased in length. As the molars become more hypsodont, the more leverage they exert against their sockets in chewing, and the peridontal ligaments which anchor the tooth move up towards the occlusal surface. These ligaments anchor to the cementum and cause the formation of progressively higher "dentine tracts" in many lineages. In lineages where hypsodonty is very advanced, cement is added to the reentrant angles, probably to strengthen the tooth. As microtine molars become more hypsodont, the number of roots are reduced until the molars are rootless and evergrowing. Primitively two are found on the lower molars and three on the upper molars with four on the M^2 of the Microtoscoptini.

As Guthrie (1971) points out, the basic microtine adaptation was related to the change from a diet like that of *Peromyscus* of nuts and fruits to one of vegetative foods and ultimately grass. Vegetative foods are extremely abrasive because of the sand and silt that adhere to them and because grass contains biogenic silica; therefore, grassland animals almost invariably develop hypsodont teeth. The relative amounts of grazing and browsing affect both the degree of complexity and of hypsodonty in the teeth of various taxa, but the same general evolutionary trends are reflected in all microtines (Guthrie, 1971). This results in an unusual opportunity for parallelism in the teeth of microtine rodents, and the whole group is extremely homogeneous.

PHYLOGENY

Very good samples, often closely spaced chronologically, characterize the fossil history of microtine rodents. However, these samples usually consist of isolated teeth

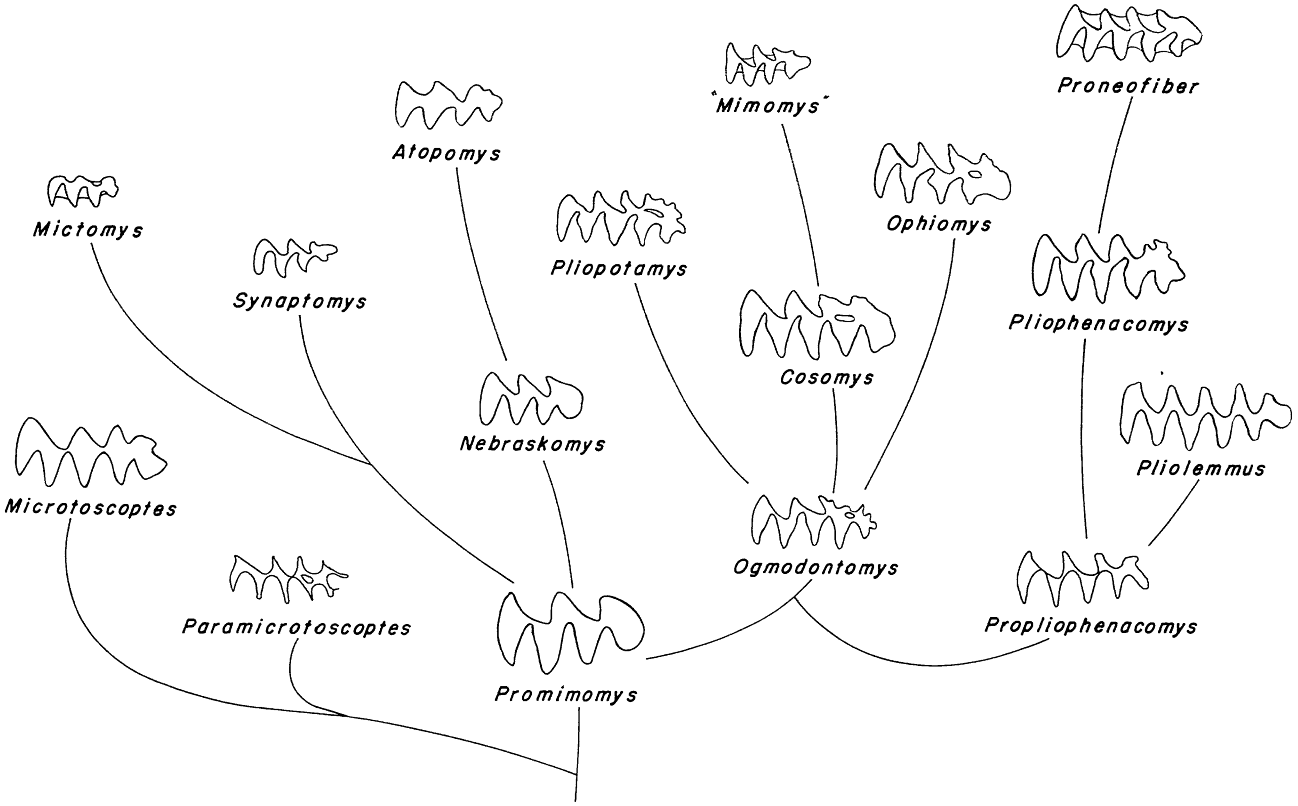

Fig. 7. Suggested phylogenetic relationships of early North American microtines with occlusal views of left lower first molars (not to scale).

and lower jaws, which are probably not the best evidence for reconstructing phylogenetic pathways.

The very simple dentition of *Promimomys* represents a possible starting point for the derivation of other microtines. By increasing the complexity of the anterior loop, the dental pattern of *Ogmodontomys* may be derived. *Ogmodontomys* has an anterior loop on M_1 with a prism fold and an enamel islet. These features also occur in *Ophiomys* and *Cosomys*, which may be derived from *Ogmodontomys* (Hibbard and Zakrzewski, 1967). *Mimomys monahani* from the late Blancan of Nebraska might be derived from *Cosomys* through the loss of the enamel pit on M_1 and the addition of cement to the reentrant angles (Schultz, Tanner, and Martin, 1972).

The ancestry of North American *Microtus* is presently unknown. I have previously suggested that *Mimomys monahani* might have given rise to *Microtus paroperarius* (Martin, 1970). That derivation was based on similarities between the lower first molars and might well be in error because it is possible that the ancestors of North American *Microtus* were Eurasian emigrants about 2 million years ago. The only other North American microtine that has the right dental patterns to be ancestral to *Microtus* is *Ophiomys*. To develop a dental pattern similar to that found in M_1 of *?Microtus llanensis* it is only necessary to increase hypsodonty, heighten dentine tracts, and add cement to that of *Ophiomys parvus*. Chaline (1966) derives the European *Microtus* from *Allophaiomys*, and this might also hold for North America if it can be shown that *Allophaiomys* occurs there.

The very simple dental pattern of M_1 in *Nebraskomys* would seem to require a very early derivation of that genus, perhaps directly from *Promimomys* as Hibbard (1970b) has suggested. *Nebraskomys* gave rise to *Atopomys* (Hibbard, 1972).

The genera *Pliophenacomys* and *Pliolemmus* appear to be related and might share a common ancestry in something like *Propliophenacomys*. Hibbard and Dalquest (1973) suggest *Pliophenacomys* as a possible ancestor for *Neofiber*. The origin of *Pliopotamys* is not clear, although it may ultimately be derived from *Ogmodontomys* (Zakrzewski, 1969); it certainly gives rise to *Ondatra*.

The lemmings of the genus *Synaptomys* also appear to have a North American origin and appear first with *Synaptomys vetus* in the late Blancan Grandview local fauna. The subgenera *Synaptomys* and *Mictomys* seem to have been already separate at this time, with *Synaptomys rinkeri* from the Dixon local fauna a possible ancestor for members of the subgenus *Synaptomys*, and *Synaptomys vetus* similar to members of the subgenus *Mictomys.* These lemmings are among the earliest microtines to develop cement in their reentrant angles and have simple dental patterns, which suggest a long separation from other microtines.

The Microtoscoptini are much different from other microtines, although the teeth of *Paramicrotoscoptes* suggest that they were also derived from a cricetine with alternating cusps. However, the separation of the Microtoscoptini from other microtines must have taken place before most of the unique features of the microtine ramus had become established, and eventually it may be shown that the Microtoscoptini are best regarded as a subfamily.

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PRELIMINARY CORRELATION OF NORTH AMERICAN LAND MAMMAL AGES AND GEOMAGNETIC CHRONOLOGY

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Abstract.— Sediments yielding vertebrate faunas from Arizona (Benson and Curtis Ranch faunas), Texas (Coffee Ranch, Axtel, Red Corral, Cita Canyon, and Mt. Blanco faunas), California (Irvington fauna), and Kansas (Fox Canyon, Rexroad, Bender, Sanders, Borchers, Cudahy, and Butler Spring faunas) were sampled for magnetic polarity. Type sections for Hemphillian (Coffee Ranch), Blancan (Mt. Blanco), and Irvingtonian (Irvington) Land Mammal Ages were compared with the magnetic-polarity sequence of sediments in the San Pedro Valley and the magnetic polarity of similar sediments in the Great Plains area. Radiometric data, magnetic polarity of the fossiliferous sediments, and faunal change were used to correlate the above faunas with geomagnetic chronology. Correlation of these faunas with the geomagnetic time scale indicates Hemphillian faunas occur in magnetic epoch 5 and most of the Gilbert magnetic epoch; Blancan faunas occur in the Gauss magnetic epoch, as well as the upper Gilbert and lower Matuyama magnetic epochs; and Irvingtonian faunas occur in the middle and upper Matuyama plus lower Brunhes magnetic epochs. Rancholabrean faunas span most of the Brunhes magnetic epoch.

A number of late Cenozoic vertebrate localities in Arizona, California, Texas, and Kansas have been sampled and measured for magnetic polarity. Faunas from these sites are placed in Hemphillian (early Pliocene), Blancan (late Pliocene), Irvingtonian (early Pleistocene), and Rancholabrean (late Pleistocene) Land Mammal Ages. The purpose of this paper is to describe magnetic polarity zones in the sampled fossiliferous deposits and to discuss how those deposits fit into the late Cenozoic magnetic-reversal chronology. Specifically, we shall compare the magnetic polarity zonation of several vertebrate localities in Texas and Kansas with fossiliferous deposits in the San Pedro Valley of Arizona.

A good magnetic sample in sedimentary rocks should be fine grained, strongly magnetized, free from secondary mineralization or weathering, and unlikely to have a history of lightning strikes. Fine grained rocks are essential because minute grains of ferromagnetic minerals in the sediment must be oriented by the earth's magnetic field rather than the geologic agent that transported the minerals to the site of deposition. Magnetization resulting from these oriented mineral grains is called detrital remanent magnetization; it purports to record the earth's magnetic field at the time of deposition. Secondary mineralization and weathering weaken or destroy the detrital remanent magnetization, and lightning produces changes in the magnetic vector in rocks surrounding the lightning strike. The sample selected for paleomagnetic study is routinely treated in alternating magnetic fields to try to remove unwanted secondary magnetizations acquired after the sample was deposited. The secondary magnetization could be viscous remanent magnetization (VRM) or chemical remanent magnetization (CRM). The residual detrital remanent magnetization (DRM) must be strong enough to measure, and replicate samples must give consistent results. For more details on sampling sediments for magnetic polarity determination and a.f. demagnetization, refer to Opdyke (1972) and Johnson et al. (1975).

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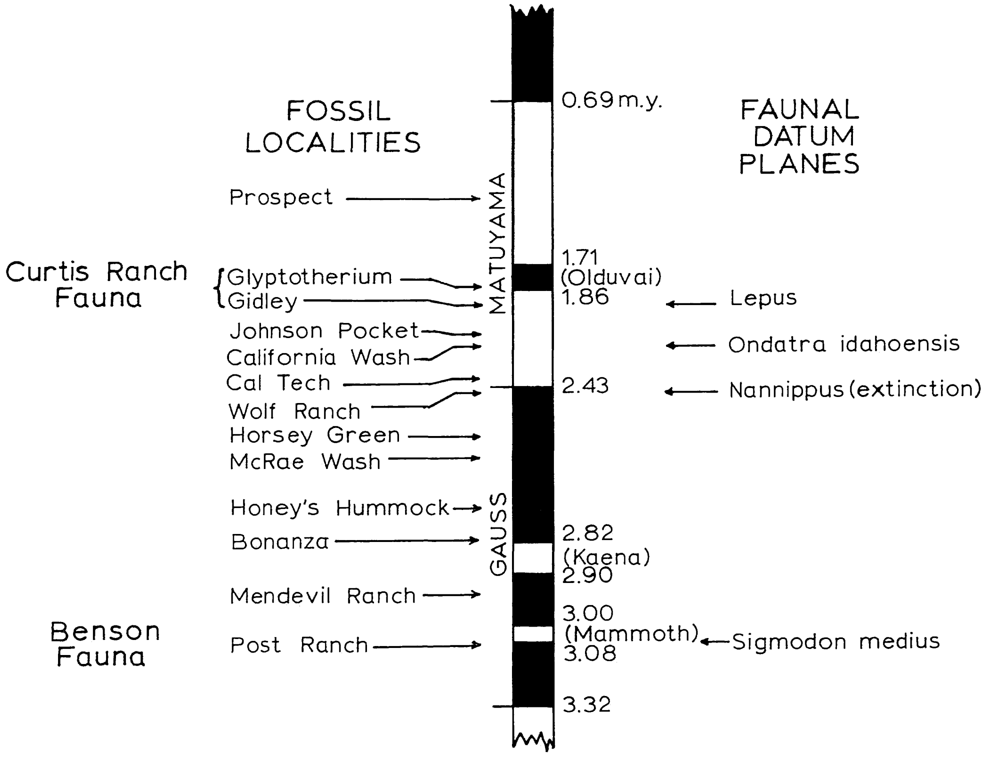

Fig. 1. Magnetic sequence of vertebrate fossil localities in the upper San Pedro Valley, Arizona (after Johnson et al., 1975). On this and later figures black segments of the vertical section are normally magnetized, and white segments are reversely magnetized.

SAN PEDRO VALLEY SEQUENCE

We started in 1970 to study the magnetic properties of terrestrial sediments in the San Pedro Valley of Arizona. Fortunately, we found that these sediments are strongly magnetized and the magnetic directions represent the magnetic field at the time of deposition. Fig. 1 summarizes our results in the San Pedro Valley. This is our major frame of reference for correlating North American Land Mammal Ages with the geomagnetic chronology. Thirteen fossil sites are placed in chronologic sequence, spanning most of the Gauss and Matuyama magnetic epochs. Calibration of the magnetic sequence follows Opdyke (1972). Chronologic-stratigraphic correlation of isolated sections, e.g. Post Ranch section, in the San Pedro Valley is based on recognition of magnetic reversals at the top or bottom of the Gauss magnetic epoch. The isolated section was then placed with the reversal equivalent to the corresponding boundary in the Curtis Ranch section. On Fig. 1, the positions of the 13 fossil localities relative to the magnetic sequence in the Curtis Ranch section are shown.

Within this sequence we recognize four faunal datum planes, the *Sigmodon, Nannippus* (extinction), *Ondatra,* and *Lepus* datum planes. These are significant faunal changes that occur within the San Pedro Valley sequence. We emphasize that these faunal datum planes are applicable only in the San Pedro Valley. The same faunal changes may occur at slightly different times in other areas of North America. For example, we record the three-toed horse, *Nannippus*, about half a million years later in Texas than the latest record for *Nannippus* in the San Pedro Valley. Faunal datum planes are useful in vertebrate chronology, as they indicate directions of dispersal and centers of radiation or refuge.

The best known faunas in the San Pedro Valley sequence are the Benson and Curtis Ranch faunas of Gidley (1922, 1926) and Gazin (1942). The Post Ranch locality is the restricted Benson fauna of Gidley and Gazin. The Gidley and Glyptotherium localities are the restricted Curtis Ranch fauna of those authors. Eight of the 13 fossil localities occur in one stratigraphic section, the Curtis Ranch section. Fig. 2 shows that section, along with the Post Ranch and Mendevil Ranch sections. The sequence of fossil sites in the Curtis Ranch section, starting from the bottom, is: Bonanza, Honey's Hummock, Horsey Green bed, Cal Tech, Johnson Pocket, Gidley level, Glyptotherium, Tusk site, and Prospect site. All of the superposed localities except the highest (Prospect site) occur in the middle member of the St. David Formation,

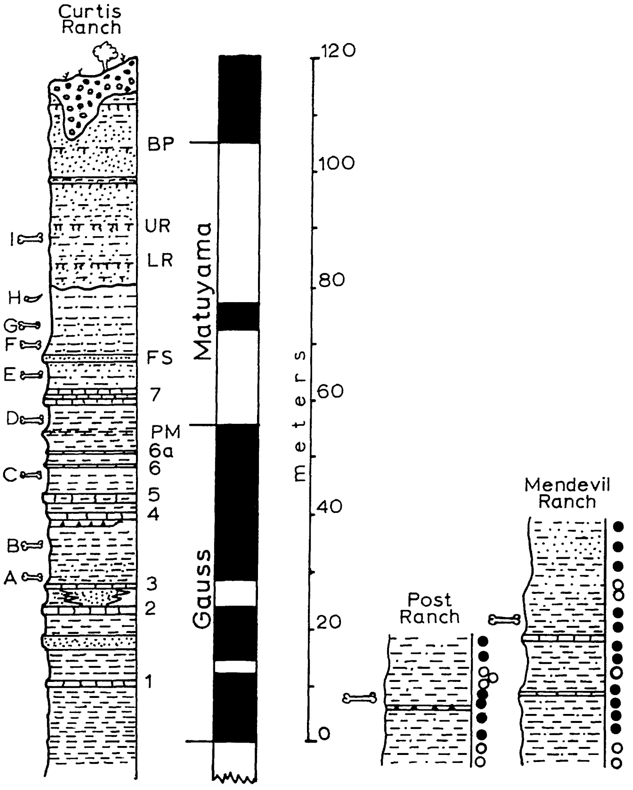

Fig. 2. Stratigraphic sequence of the Benson and Curtis Ranch faunas, San Pedro Valley, Arizona. The Curtis Ranch fauna of Gidley and Gazin is the fossiliferous level in the Curtis Ranch section. Benson fauna of Gidley and Gazin is the fossil level in the Post Ranch section. Fossil levels designated by letter in the Curtis Ranch section are: A, Bonanza; B, Honey's Hummock; C, Horsey green bed; D, Cal Tech site; E, Johnson Pocket; F, Gidley level; G, Glyptotherium; H, Tusk site; I, Prospect.

as defined by Gray (1967). Fossils in the Post Ranch and Mendevil Ranch sections also occur in the middle member of the St. David Formation, which is characterized by claystones, mudstones, and intermittent marls. Fossils at Post Ranch and Mendevil Ranch are comparable to the fossils at Honey's Hummock in the Curtis Ranch section. Each of these sections (Curtis Ranch, Post Ranch, and Mendevil Ranch) are underlain by a thick section of reversely magnetized sediment that we identify as the Gilbert magnetic epoch. We have not found the Jarmillo event in the Curtis Ranch section, primarily because our sampling is not dense enough to identify such a short magnetic reversal interval (50,000 years). The frequency of magnetic samples is greatest in the interval of fossil sites (upper Gauss and lower Matuyama magnetic polarity epochs) in the Curtis Ranch section.

Fig. 3 shows the faunal correlation of isolated fossiliferous sections in the San Pedro Valley. These correlations are based on similarities of the faunas and associated magnetic polarity zones. Scale on this and the following figures are identical. The reversed magnetic polarity zone that overlies the Post Ranch locality is correlated as the Mammoth event. An ash that underlies the Post Ranch fossil bed has been dated by Rashid Tahirkheli (pers. comm.) at 3.1 ± 0.7 million years. Another ash that underlies the California Wash fossil locality has been dated by Bob Scarborough (pers. comm.) at 2.1 ± 0.4 million years. The Post Ranch ash was dated by fission tracks in zircons and the California Wash ash was dated by potassium-argon on glass. Composition of the California Wash and Wolf Ranch faunas is similar to the Cal Tech fauna in the Curtis Ranch section. The magnetic reversal that underlies the Cal Tech and California Wash localities and overlies the Wolf Ranch locality is correlated as the Gauss-Matuyama reversal. The McRae Wash section is relatively thick, but our sampling frequency there is too low to detect the events in the Gauss magnetic epoch. We have only eight paleomagnetic sites in the McRae Wash section, compared to about 100 paleomagnetic sites in the Curtis Ranch section. Composition of the McRae Wash fauna is similar to the Post Ranch and Mendevil Ranch faunas.

TYPE AREAS OF LATE CENOZOIC LAND MAMMAL AGES

When we began our study of the magnetic-faunal sequence in the San Pedro Valley we planned to visit the type areas of the late Cenozoic land mammal ages to establish the polarity sequence and fit the San Pedro Valley sequence into that of the type areas. Two problems counteracted this strategy. First, sediments in the type sequences in the Texas Panhandle were weakly magnetized and only partially stable to alternating fields. Second, sequences in the type areas were too short for recognition of distinctive magnetic polarity zones.

Fig. 4 shows the observed magnetic sequence in the stratotypes of Hemphillian, Blancan, and Irvingtonian faunas. Remanent magnetization of specimens from Texas and Kansas are very weak and only partially stable. For example, natural remanent magnetization of samples from Texas and Kansas averaged about 5 x 10^{-7} emu/g; it averaged 8 x 10^{-6} emu/g in San Pedro Valley sediments. The Texas and Kansas samples were demagnetized in an a.f. field of 100 to 150 oersteds to remove low coercivity viscous remanent magnetization. The within-site dispersions are large and the data is not of as high reliability as the results from Arizona. We believe our results from the

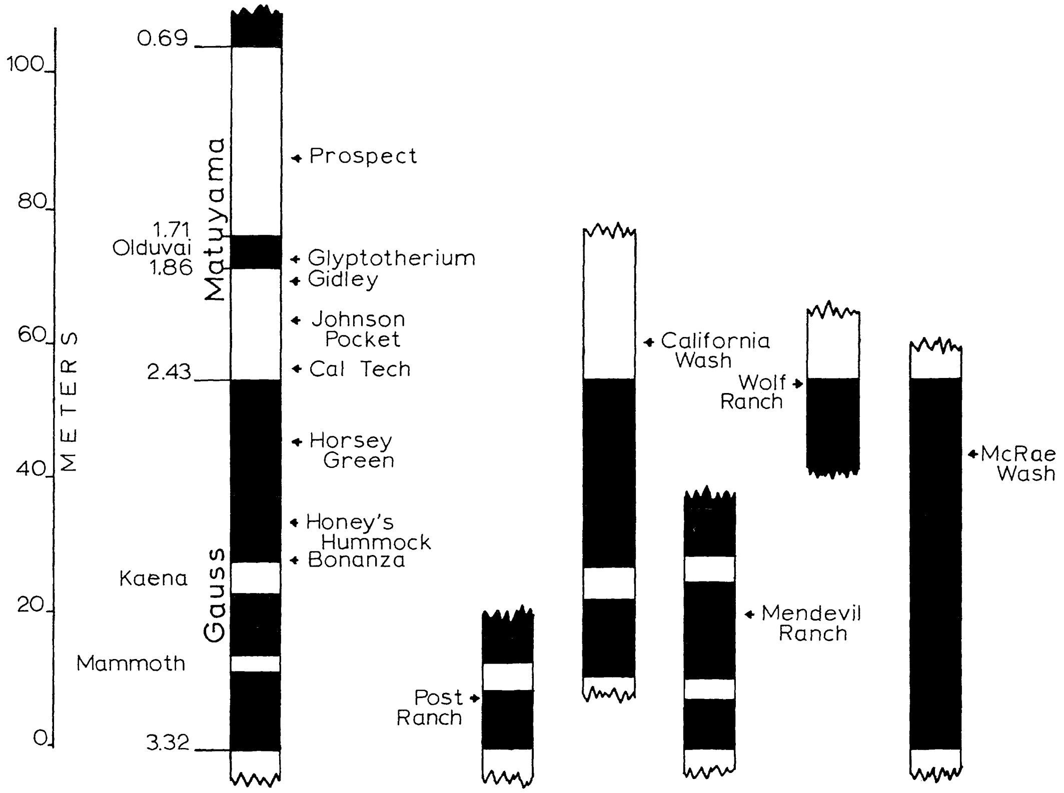

Fig. 3. Correlation of isolated section in the upper San Pedro Valley with the Curtis Ranch section.

Great Plains are not adequate to identify individual events since these sediments have large secondary magnetization and upon demagnetization they do not reach stable end points before acquiring significant magnetic components from the a.f. demagnetization apparatus. Samples from the Irvington area of California were fairly strongly magnetized and stable, being similar in magnetic properties to the San Pedro Valley samples.

The Hemphillian Land Mammal Age was defined primarily on the fauna from the Coffee Ranch Quarry in Hemphill County, Texas (Reed and Longnecker, 1932; Stirton, 1936). The Coffee Ranch fauna is overlain by an ash which has been dated by Izett and Naeser of the U.S. Geological Survey in Denver at 6.6 ± 0.8 m.y. based on fission tracks in zircons from the ash (G.A. Izett, in press). Fossils and ash in the Coffee Ranch section occur in a thick normally magnetized polarity zone. This normal polarity zone probably represents the lower part of magnetic epoch 5 because the ash date indicates it is older than the Gauss epoch (2.4 to 3.3 m.y.).

Type of Blancan Land Mammal Age is the fauna from Mount Blanco in Crosby County, Texas (Evans and Meade, 1945; Evans, 1948; Johnston and Savage, 1955). Mount Blanco fossils are overlain by an ash correlated with the Guaje pumice bed of the Jemez Mountains, New Mexico, by Izett et al. (1972). Age of the Guaje pumice bed is 1.4 m.y., based on fission tracks in glass shards. Another unnamed ash occurs below the Guaje ash bed in the Mount Blanco section. The entire Mount Blanco section is reversely magnetized. We sampled the Mount Blanco section at two different times to increase the frequency of magnetic data points. We had hoped to find a normal magnetic polarity zone in the Mount Blanco section, which would more precisely correlate the Mount Blanco and San Pedro sections. The 1.4 m.y. ash and absence of a normal magnetic polarity zone beneath the ash in the Mount Blanco section indicate the Mount Blanco fossils occur in the lower Matuyama magnetic interval, between 1.4 and 2.4 m.y. in age.

The Irvingtonian Land Mammal Age is based on the fauna from gravel pits southeast of Irvington, Alameda County, California (Stirton, 1939; Savage, 1951). The gravel pits that yielded the Irvington fauna are now abandoned, and are partly overlain by Interstate 680. Strata adjacent to the pits and at a level where fossils were collected are reversely magnetized. Irvington fossils are younger than Mount Blanco fossils, but are still in the Matuyama magnetic epoch. Therefore, the Irvington

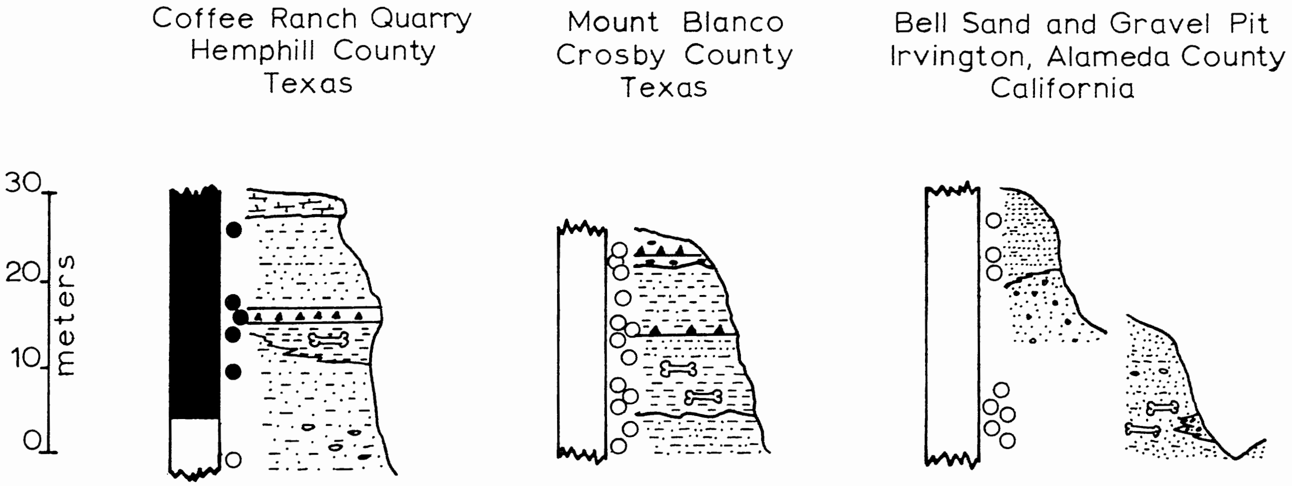

Fig. 4. Magnetic-stratigraphic profiles for Hemphillian, Blancan, and Irvingtonian type sections.

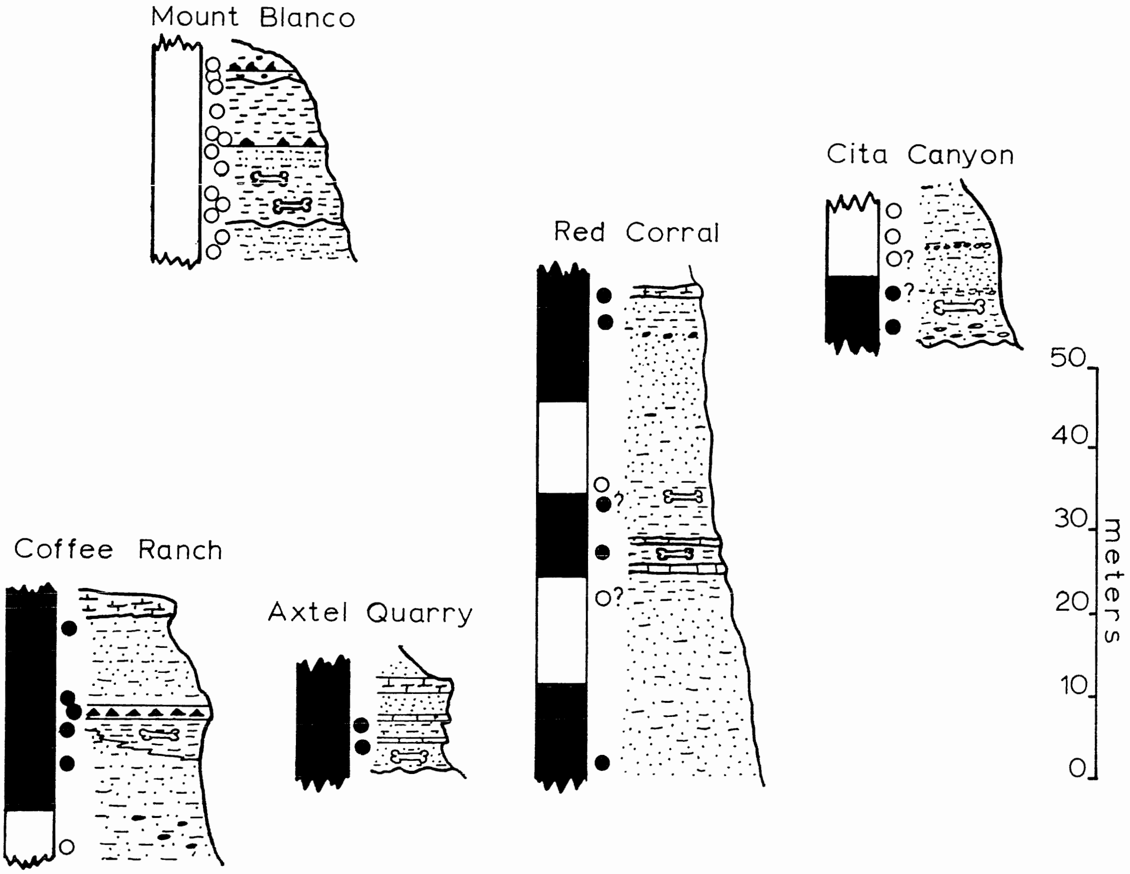

Fig. 5. Correlation of several Texas faunas.

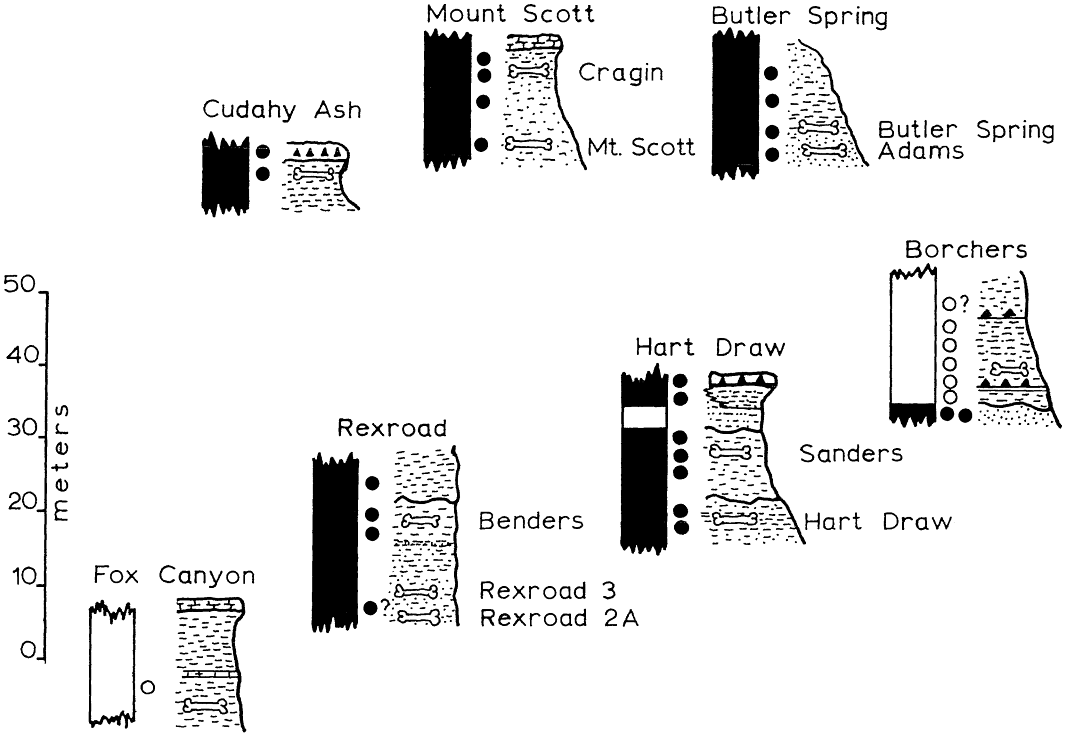

Fig. 6. Correlation of several Kansas faunas.

stratotype probably represents a portion of the upper Matuyama magnetic interval.

Each of these stratotypes, if taken separately, would not resolve magnetic correlations. A reference section with a sequence of magnetic polarity reversals, e.g. the Curtis Ranch section, is essential for precise correlations. Correlation of the weakly magnetized sediments at Coffee Ranch and Mount Blanco is supported by radiometrically dated ashes that overlie the faunas. Similarly, a thick section of reversed polarity, as at Mount Blanco, gives confidence that we are accurately measuring polarity of the magnetic field that prevailed when those deposits were laid down. Sediments that were remagnetized, or that are magnetically unstable, will usually give a normal polarity direction, not a reversed direction. The stratotypes shown here, and the Curtis Ranch section, provide a paleontologic-paleomagnetic frame of reference for correlation of other late Cenozoic vertebrate faunas in North America.

VERTEBRATE FAUNAS IN THE GREAT PLAINS AREA

Fig. 5 shows the correlation of some other faunas in Texas. The Axtel Quarry has yielded a Hemphillian fauna, slightly younger than the Coffee Ranch fauna. Faunal similarity between Coffee Ranch and the Axtel faunas and the same magnetic polarity suggest they are probably both in magnetic epoch 5. The Red Corral section is relatively thick, but unfortunately our sampling frequency was unavoidably low. Fossils at Red Corral are Blancan, and they occur in a normal magnetic polarity zone, most probably the Gauss magnetic epoch. More magnetic samples and/or more fossils are needed to determine the magnetic polarity limits of the Red Corral section. The Cita Canyon section contains a lower normal magnetic polarity zone and an upper reversed magnetic polarity zone. Cita Canyon fossils are considered Blancan Land Mammal Age, similar to the Mount Blanco fauna. We believe the Cita Canyon fauna occurs in the upper part of the Gauss epoch, and is therefore slightly older than the Mount Blanco fauna.

Fig. 6 shows magnetic sections of vertebrate faunas in Meade County, Kansas. These faunas were reviewed by Hibbard (1970) and Skinner and Hibbard (1972). The Fox Canyon, Rexroad, Benders, Hart Draw, Sanders, and Borchers faunas are all Blancan Land Mammal Age. The Borchers fauna overlies an ash, Pearlette type "B", dated 1.9 m.y. by Izett et al. (1971). The Borchers ash and fauna occur in the Crooked Creek Formation, which is reversely magnetized. This places the Borchers fauna in the lower Matuyama epoch. The Sanders fauna is from

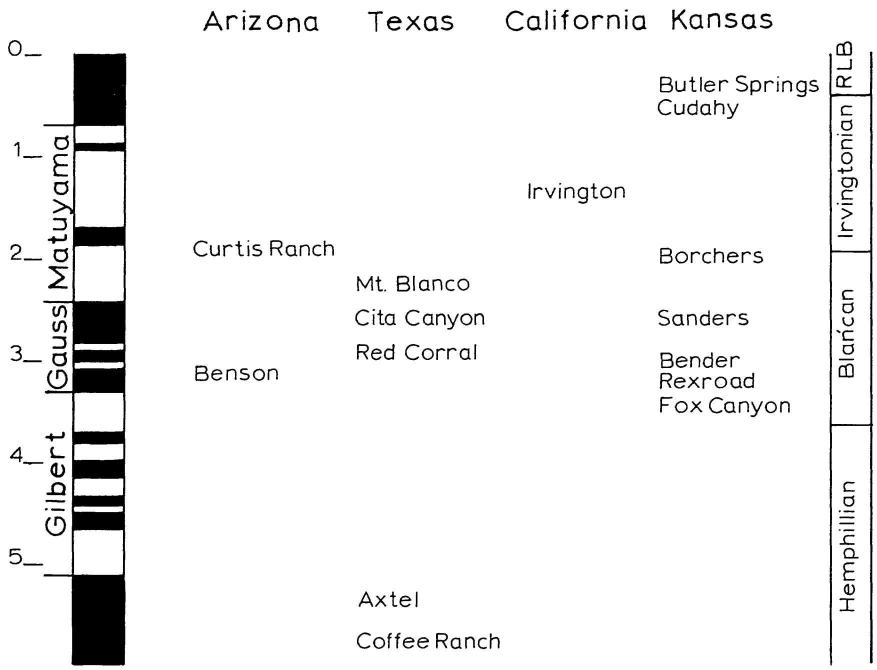

Fig. 7. Correlation of faunas in Arizona, Texas, California, and Kansas with the magnetic time scale.

the Ballard Formation, which underlies the Crooked Creek Formation. The Ballard Formation and the subjacent Rexroad Formation that has yielded the Benders, Rexroad, and Fox Canyon faunas is dominantly normally magnetized. These normally magnetized sections probably represent the Gauss epoch. We have a single, reversely magnetized sample site from the Fox Canyon section. Because the Fox Canyon fauna is considered older than the other Blancan faunas in the Rexroad Formation, we believe that the Fox Canyon fauna was deposited during the latter part of the Gilbert epoch. Another possibility is that the Fox Canyon fauna was deposited during the Mammoth or Kaena event of the Gauss epoch.

The Cudahy fauna is overlain by the Cudahy ash, correlated as Pearlette type "O" ash by Izett et al. (1971). The Pearlette type "O" ash is dated 0.6 m.y., which places it in the Brunhes magnetic epoch. We sampled the Cudahy ash and its correlatives wherever possible in Kansas and Texas to test the validity of those correlations. We reasoned that the Cudahy fauna should be very close, temporally, to the Brunhes-Matuyama boundary; therefore, any fauna equivalent to or younger than the Cudahy fauna should be in a normal magnetic polarity zone. In each case, we found this to be true. The top of the Hart Draw section is representative in this regard. The Cudahy fauna is Irvingtonian, indicating the Irvingtonian Land Mammal Age includes the Brunhes-Matuyama boundary. The Mount Scott, Cragin, Butler Spring, and Adams faunas are Rancholabrean Land Mammal Age. They occur in normally magnetized sediments which presumably represent the Brunhes magnetic epoch.

LATE CENOZOIC LAND MAMMAL AGES AND GEOMAGNETIC CHRONOLOGY

Fig. 7 is a synthesis of all our data, and fits the late Cenozoic land mammal ages into the perspective of the geomagnetic chronology. In summary, the Axtel and Coffee Ranch faunas are correlated with magnetic epoch 5. The Fox Canyon fauna probably correlates with the top of the Gilbert epoch. The Rexroad, Bender, Benson, Red Corral, Cita Canyon, and Sanders faunas most probably correlate with the Gauss epoch. The Borchers and Mount Blanco faunas correlate with the lower Matuyama epoch. The Curtis Ranch fauna correlates with the Olduvai event within the Matuyama epoch. Cudahy and younger faunas correlate with the Brunhes epoch.

The Hemphillian Land Mammal Age appears to be equivalent to most of the Gilbert and epoch 5. The Blancan Land Mammal Age includes all the Gauss plus the upper Gilbert and lower Matuyama epochs. The Irvingtonian Land Mammal age includes the middle and upper Matuyama and lower Brunhes epochs. The Rancholabrean Land Mammal Age includes most of the Brunhes epoch.

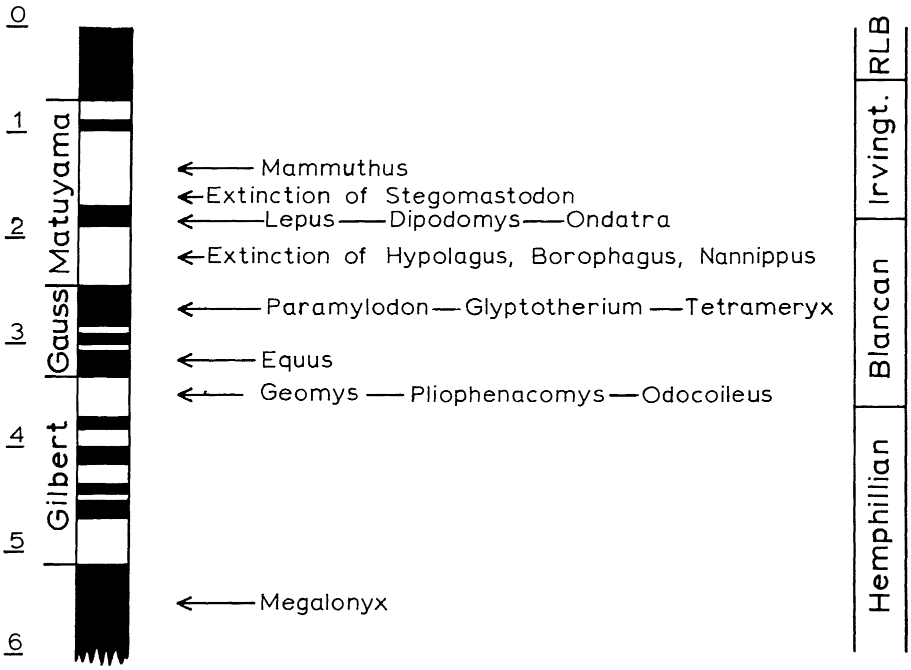

Fig. 8. Some North American Mammalian Datum Planes. These datum planes are based on the faunas correlated in Fig. 7.

The Irvingtonian Land Mammal Age is characterized by the presence of *Mammuthus*, a Eurasian immigrant, as well as other mammal genera, and by the absence of later Eurasian immigrants such as *Bison*. We place the Curtis Ranch fauna in the Irvingtonian Land Mammal Age even though *Mammuthus* is absent from the Curtis Ranch fauna. This age assignment is based on the appearance of two genera in the Curtis Ranch fauna that are characteristic of Irvingtonian and younger faunas. These genera are *Lepus* and *Dipodomys*. Genera probably ancestral to *Lepus* and *Dipodomys*, i.e. *Sylvilagus* and *Prodipodomys*, occur in older faunas of the San Pedro Valley. The genus *Mammuthus* appears to have arrived in North America some time after the Olduvai event, probably about 1.5 m.y. ago (Berggren and Van Couvering, 1974). *Mammuthus* is recorded from the Irvington fauna.

Fig. 8 illustrates some faunal changes recorded in the 15 localities arranged chronologically in the last figure. These faunal changes are presented as datum planes, based on the assumption that chronologic ordering of localities in the previous figure is valid.

Megalonyx is a South American immigrant. Apparently, sloths reached North America (Coffee Ranch) prior to 6.6 m.y. ago. *Geomys, Pliophenacomys*, and *Odocoileus* are not known in North America prior to Blancan Land Mammal Age. They appear at about the base of the Blancan. The horse, *Equus*, is a characteristic Blancan genus, but is apparently absent from the earliest Blancan faunas represented here. An earlier Blancan record of *Equus* may occur in the Hagerman fauna of Idaho. *Paramylodon* and *Glyptotherium* are two South American immigrants that failed to reach North America until late Blancan (Cita Canyon). Three genera that are well represented in Blancan faunas, namely *Hypolagus, Borophagus*, and *Nannippus*, became extinct at about the same time (Mount Blanco). Three small mammals, *Lepus, Dipodomys*, and *Ondatra*, appear about the same time, early Irvingtonian Land Mammal Age. The gomphothere, *Stegomastodon*, lingers into the early Irvingtonian (Curtis Ranch), and *Mammuthus* appears slightly later (Irvington).

Magnetic-ploarity stratigraphy affords a convenient and simple means to correlate and/or date late Cenozoic fossil deposits in terrestrial as well as marine sediments. This chronologic tool holds great promise for future application. One of the more exciting prospects emerging from such precise chronologic correlation is calibration of rates of evolution and direction of dispersal in restricted mammalian species. By such applications, magnetic polarity stratigraphy opens a new dimension to vertebrate paleontology.

ACKNOWLEDGMENTS

We are especially grateful to the late Claude Hibbard

and our colleagues Jerry Schultz and Don Savage for helping us collect these specimens. Each of those gentlemen took time from their busy schedules to point out the precise fossil concentrations at specific sites so we were able to collect magnetic samples tied directly to productive fossil levels. In reality, the results we present here are an extension of their work.

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PLEISTOCENE STRATIGRAPHY AND PALEONTOLOGY IN WESTERN KANSAS: THE STATE OF THE ART, 1974

Richard J. Zakrzewski

Abstract.– A brief review of the development of the stratigraphic sequence that Hibbard developed for the Pleistocene of southwestern Kansas is given. This sequence was established by attempting to correlate the data from southwestern Kansas with the classical sequence of four glacial and three interglacial stages in the glaciated region of midwestern United States. The correlation was based, in part, on the paleoclimatological implications of the sediments and/or their contained faunas, and the assumption that the Pearlette Ash represented one fall, and therefore, a synchronous event.

Recent work has shown that there are at least four Pearlette-like ashes on the Great Plains and that some of the sedimentary cycles correlated with continental glaciation actually reflect the effects of montanè glaciation and are pre-continental glaciation in age. These findings have necessitated a reevaluation of the stratigraphy and paleontology in the area.

One interpretation of the new findings would support a date of 1.8 to 1.9 m.y.a. for the Plio-Pleistocene boundary as suggested by studies of the type section of the Pleistocene in Europe. In this interpretation it would follow that the cyclic strata previously considered as early Pleistocene in the area are Pliocene in age. Faunal analysis suggests that the boundary between the Blancan and Irvingtonian land mammal ages is approximately coincidental with the Plio-Pleistocene boundary.

One of Claude W. Hibbard's major contributions to the earth sciences was the discovery and development of a stratigraphic succession of late Cenozoic faunas in southwestern Kansas and northwestern Oklahoma (summarized by Hibbard, 1970). Hibbard spent much of thirty-nine summers working in that region developing and refining his data until it became the best documented sequence yet available to demonstrate evolution, faunal migration, and climatic change for the late Cenozoic in North America (if not the world).

Recent work undertaken outside that region on faunas (Skinner and Hibbard, 1972) and on stratigraphic marker beds (Izett et al., 1970) has necessitated a reevaluation of the stratigraphic arrangement of the deposits and their contained faunas. This reevaluation was underway when Hibbard met his untimely end. Therefore, it seems appropriate that in this volume in honor of Professor Hibbard we should consider how the development of the sequence came about, the discoveries which necessitated a reevaluation of the sequence, and the present status of Pleistocene stratigraphy and paleontology in western Kansas based on the work of Hibbard and his students.

The fact that a sequence of faunas which spanned most of late Cenozoic time might be present in the Meade County area first presented itself to Hibbard while he was working on the late Pliocene Rexroad local fauna (Hibbard, 1938, 1941a, b, c). In 1936 he was shown an exposure of Pleistocene deposits from which the Jones local fauna (Hibbard, 1940) of Wisconsinan age was obtained. Hibbard recognized that this fauna was much younger than the Rexroad local fauna and that intermediate faunas should be present. Subsequent finds, such as the Borchers local fauna (Hibbard, 1941d) in stratigraphically intermediate strata supported his thesis, and the first summary for the Meade County area was published in 1944 (Hibbard, 1944). Much controversy surrounded the development of

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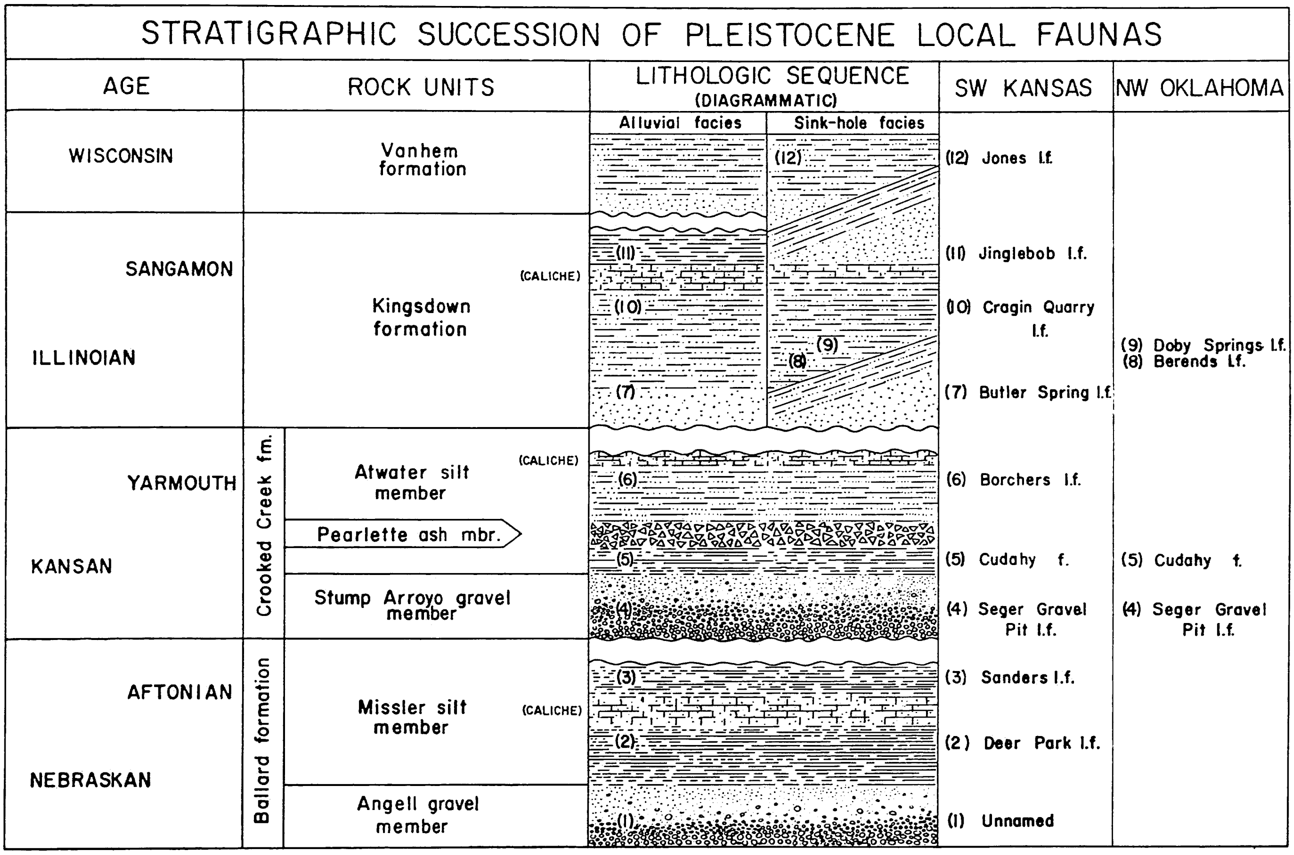

STRATIGRAPHIC SUCCESSION OF PLEISTOCENE LOCAL FAUNAS

AGE	ROCK UNITS		LITHOLOGIC SEQUENCE (DIAGRAMMATIC) Alluvial facies	Sink-hole facies	SW KANSAS	NW OKLAHOMA
WISCONSIN		Vanhem formation	(12)	(12)	(12) Jones l.f.	
SANGAMON		Kingsdown formation (CALICHE)	(11) (10)		(11) Jinglebob l.f. (10) Cragin Quarry l.f.	
ILLINOIAN			(7)	(9) (8)	(7) Butler Spring l.f.	(9) Doby Springs l.f. (8) Berends l.f.
YARMOUTH	Crooked Creek fm.	Atwater silt member (CALICHE)	(6)		(6) Borchers l.f.	
KANSAN	Crooked Creek fm.	Pearlette ash mbr. Stump Arroyo gravel member	(5) (4)		(5) Cudahy f. (4) Seger Gravel Pit l.f.	(5) Cudahy f. (4) Seger Gravel Pit l.f.
AFTONIAN	Ballard formation	Missler silt member (CALICHE)	(3) (2)		(3) Sanders l.f. (2) Deer Park l.f.	
NEBRASKAN	Ballard formation	Angell gravel member	(1)		(1) Unnamed	

Fig. 1. Stratigraphic succession of Pleistocene local faunas from southwestern Kansas and northwestern Oklahoma. (From Hibbard and Taylor, 1960)

the sequence, but some stability was achieved by the presumption that the deposits and the faunas could be tentatively correlated with the classical four glacial and three interglacial stages of the mid-continent region. Any parameter in the deposit or the fauna which would be suggestive of a cooler or more humid climate (for example, a gravel which would indicate an increase in the velocity of a stream, which might be suggestive of an increase in precipitation due to a pluvial situation, or taxa whose extant distribution is in a more northern or humid area) was used to place the deposit and/or fauna in a glacial stage. By the same token any parameter which might be suggestive of a similar or warmer climate was used to place the deposit and/or fauna in an interglacial stage. Relative age was based on the superposition of the strata and/or stage of evolution of the taxa in the fauna. As more of the sequence became known, empirical techniques were used.

Another valuable stratigraphic indicator was the Pearlette ash bed (Cragin, 1896), which was thought to occur over wide areas of the Great Plains and Rocky Mountains on the basis of certain petrographic and chemical properties as defined by Swineford and Frye (1946). The Pearlette ash was thought to represent a single eruption and, therefore, to be a useful marker. Hibbard (1958) erected and/or redefined stratigraphic units in southwestern Kansas and considered the Pearlette ash to be late Kansan in age. When the Pearlette ash was present in a stratigraphic sequence, the units and faunas could be assigned an age based on their position above or below the ash. A good example is the placement of the Borchers local fauna (Hibbard, 1941d) recovered from deposits in the type area of the Crooked Creek Formation (Hibbard, 1958) overlying an ash with the petrographic characteristics assigned by Swineford and Frye (1946) to the Pearlette. The taxa found in the Borchers local fauna have southern affinities and include relicts from the Rexroad local fauna (Zakrzewski, 1972) and are therefore suggestive of an interglacial stage. Because the fauna was found above the ash and was suggestive of an interglacial stage, it was placed in the Yarmouth Stage. A summary of the stratigraphy and local faunas was given in Hibbard and Taylor (1960) and is reproduced here as Figure 1. With the exception of the addition of new late Pleistocene faunas

(Miller, 1966; Schultz, 1967) the relationships remained unchanged.

The first suggestion that Hibbard's sequence might need reevaluation came when Taylor (1966) suggested that there was no evidence of severe climatic deterioration in the Meade area until the time the Cudahy fauna lived. The molluscan faunas found in the Ballard Formation, assigned a Nebraskan-Aftonian age, were transitional with molluscan faunas in the Rexroad Formation, assigned a late Pliocene age, with no evidence for marked climatic change. Therefore, the Ballard Formation represented deposits which were laid down prior to extensive continental glaciation. The faunas from the Ballard Formation might possibly be related to alpine glaciation and should be considered pre-Nebraskan, but still Pleistocene in age. Additional support for Taylor's argument was the discovery in the Ballard Formation of the Spring Creek local fauna (Berry and Miller, 1966). This local fauna contains a preponderance of individuals of the molluscan genus *Biomphalaria*, which now reaches no farther north in North America than the southern extremities of the United States. While an earlier age for the formation was suggested, there were no changes in the sequential arrangement of the faunas.

Although Hibbard understood the implications of this suggestion, he made no public comment until he undertook the study of the Sand Draw local fauna in northern Nebraska. That he had been aware that problems existed with some relationships can be seen from his discussion in Skinner and Hibbard (1972). "Some local faunas of the Great Plains assigned to the Nebraskan, and especially those assigned to the Aftonian (Hibbard, 1970b), do not fit into conventional North American Pleistocene correlation charts. I have previously been at a loss to explain why certain mammalian taxa survived the Nebraskan glaciation and the Aftonian interglacial only to become extinct during the early part of the Kansan. How does one explain the dispersal northward of the large land tortoise (*Geochelone*) after the withdrawal of Nebraskan ice only to have it occur as a fossil early in the supposed Aftonian Sand Draw local fauna?" When the study of the Keim Formation, which contains the Sand Draw local fauna, was completed and it was shown that the Keim Formation was overlain by the Long Pine Formation (a fluvial gravel sheet correlative to outwash gravels to the east) the concept of pre-Nebraskan Pleistocene deposits was accepted by Hibbard (Skinner and Hibbard, 1972).

The second change came about when workers from the United States Geological Survey undertook a study of the extensive beds of light-colored rhyolitic ash found in upper Cenozoic deposits in western United States. The ash bed under consideration was the Bishop Tuff and its associated ash falls, which were found at 11 localities scattered from California to Nebraska (Izett et al., 1970). At six of the localities the Bishop ash is overlain by a "Pearlette-like" ash. At Cerro Summit in southwestern Colorado the Bishop ash is not found, and the "Pearlette-like" ash overlies another "Pearlette-like" ash with an intervening soil zone between. The younger "Pearlette-like" ash was named the type O for its occurrence at Onion Creek, Utah, whereas the underlying ash was named type S, for its occurrence at the type locality of the Sappa Formation in Nebraska (Izett et al., 1970). With the idea that there may be more than one "Pearlette-like" ash fairly engrained, samples were collected from the Meade County area because of the well-documented sequence available. The results of this study (Naeser et al., 1973) showed that the ash overlying the type Cudahy fauna, near the type locality of the Pearlette ash, dated 0.6 m.y. This ash is equivalent to the type O. The ash at the type locality of the Crooked Creek Formation which underlies the Borchers local fauna was dated at 2 m.y. and called the type B. No type S was found in Meade County. Boellstorff (1973) independently achieved the same results but provided formal names for the ashes; he restricted the name Pearlette to the type O, for type S he supplied the name Coleridge, and for the type B the name Borchers. Although the great disparity in ages between the Pearlette (restricted) and Borchers ash changed the sequence of the faunas somewhat, making the Borchers local fauna older than the Cudahy, it also improved the relationships by maintaining the continuity between the Ballard and Crooked Creek formations and by making it easier to explain the relicts from the Rexroad local fauna in the Borchers local fauna and the anomalously sized specimens in the ondatrine size chronocline obtained by Semken (1966). However, it leaves the Cudahy fauna and the Pearlette (restricted) ash in deposits that are as yet unnamed. The results of these new findings are summarized in Figure 2.

Southwestern Kansas was not the only area in the state that drew Hibbard's attention. Earlier in his career, while serving as a consultant for the Kansas Geological Survey, a number of faunal sites were discovered by him and his coworkers along the valleys of the Smoky Hill and Saline rivers (Frye et al., 1943) which resulted in preliminary studies by Hibbard (1943, 1952). He was not drawn back into this area until finds of fossil mammals by Mr. and Mrs. Clayton Griggs of McPherson, Kansas, were reported to him and he, in turn, interested his students in the area (Semken and Griggs, 1965; Semken, 1966). Subsequent field work by the Griggs resulted in the discovery of additional sites in Rice (Hall, 1972) and Ellsworth counties (Holman, 1972). It was this latter find at Kanopolis, Kansas, that drew most of Hibbard's interest in his final years.

A number of Hibbard's students have maintained an active interest in the stratigraphy and paleontology of

Fig. 2. Stratigraphic succession of Pleistocene local faunas from southwestern Kansas based on acceptance of a pre-Nebraskan Pleistocene and multiple Pearlette-like ashes.

Age	Rock Units		Local Faunas
Wisconsinan	Vanhem Formation		Robert Jones
Sangamon	Kingsdown Formation		Jinglebob Cragin Quarry
Illinoian			Mt. Scott Butler Spring Adams
Yarmouth	Unnamed formation Pearlette ash (res.)= Type O		
Kansan			Cudahy
Aftonian	Crooked Creek Fm.	Atwater Member Borchers ash=Type B	Borchers
Nebraskan		Stump Arroyo Member	Seger
pre-Nebraskan warm interval	Ballard Formation	Missler Member	Sanders Deer Park Spring Creek
pre-Nebraskan cold interval		Angell Member	Unnamed

western Kansas. This has resulted in the discovery of new sites (Zakrzewski and Maxfield, 1971), primarily in the Smoky Hill and Saline river valleys, and the refinement of certain parts of the section (Miller, this volume). The remainder of the paper summarizes how these new finds and refinements are related to the section in southwestern Kansas (Fig. 3) as conceived by Hibbard, and suggests some alternative interpretations of the relationships (Fig. 4).

The relationships of the pre-Wisconsinan local faunas in southwestern Kansas as depicted in Figure 3 are based on the ideas of Hibbard. The Wisconsinan sites with the radiometric dates are from Miller (this volume). The Keiger Creek local fauna is located in south-central Clark County, Kansas. This material taken from silts channeled into the Permian bedrock includes among the vertebrates snake, ground squirrel, and gopher and among the invertebrates such indicators of more humid and cooler conditions as *Pupilla muscorum* (K.K. Kolb, pers. comm.). This local fauna is considered Wisconsinan in age because of the climatic indicators and the topographic position of the locality.

The local faunas from the Saline and Smoky Hill river valleys are not as well known or understood. They are known from a wider geographic area, so there is less superposition of strata and it is more difficult to trace the stratigraphic units.

No pre-Kansan Pleistocene local faunas have been discovered in this area. The unnamed local fauna considered to be Kansan has been discovered relatively recently by me along the Smoky Hill River in eastern Trego County. This local fauna is found in silty clays which underlie a "Pearlette-like" ash. It is tentatively considered Kansan because of its presence below the ash and the topographic position of the ash. This local fauna is presently under study as a M.S. problem by K.K. Kolb at Fort Hays Kansas State College. Preliminary analysis of the molluscan taxa shows a strong resemblance to the type Cudahy molluscan fauna' from Meade County (Leonard, 1950). Fossil vertebrates are rare and none are diagnostic.

The Wilson Valley and Tobin local faunas had been considered Cudahy equivalents (Hibbard, 1944), as both sites are below a "Pearlette-like" ash. The stage of evolution of some of the taxa (such as *Geomys tobinensis*) at the localities suggested to Hibbard (pers. comm.) that these sites might be somewhat older than previously suspected. The arvicoline genus, *Phenacomys*, has been reported from the Wilson Valley site and from the County Line local fauna at Little Sioux, Iowa (Guilday and Parmalee, 1972), which was also considered a Cudahy equivalent. A radiometric date of 0.7 m.y. was obtained on the Hartford ash at the Iowa site (Boellstorff, 1973). Ash samples from the Tobin and Wilson Valley sites are presently under study by John Boellstorff of the Nebraska Geological Survey.

The Kentuck local fauna from McPherson County has always been problematical. The fossils are obtained from a deposit which is a channel fill in a "Pearlette-like" ash. Hibbard (1952) considered the Kentuck a mixed assemblage because of the presence of the lemming *Synaptomys (Mictomys)* and the cotton rat *Sigmodon*. Semken (1966) in restudying the Kentuck came to the same conclusion. More recently the finding of a Kentuck-like fauna, the Wathena, underneath a Kansan till in Doniphan County, Kansas (Einsohn, 1971) suggests that the Kentuck is not a mixture. This is supported in part by the equability model of glacial times recently suggested by Semken (in prep.). He now feels that the Kentuck is a typical glacial fauna. The stage of evolution of the taxa in the Kentuck local fauna suggests that it is Kansan in age.

The Kanopolis local fauna from Ellsworth County

Fig. 3. Stratigraphic succession of Pleistocene local faunas in western Kansas based on new evidence.

Age	Rock Units		Southwestern Kansas Local Faunas	Smoky Hill and Saline River Local Faunas
Wisconsinan	Vanhem Formation		Boyd 10,790±280 Robert 11,110±350 Classen 16,100±250 Jones 26,700±1500 Bird locality 29,300±1250 Keiger Creek ?	
Sangamon	Kingsdown Formation		Jinglebob Cragin Quarry	
Illinoian			Mt. Scott Butler Spring Adams	Duck Creek Williams Sandahl Unnamed 2 Unnamed 1
Yarmouth	Unnamed formation			Rezabek Kanopolis
Kansan	Pearlette ash (res.)= Type O		Cudahy	Kentuck Wilson Valley Tobin Unnamed
Aftonian	Crooked Creek Fm	Atwater Borchers ash =Type B	Borchers	
Nebraskan		Stump Arroyo Mbr	Seger	
pre-Nebraskan warm interval	Ballard Fm	Missler Member	Sanders Deer Park Spring Creek	
pre-Nebraskan cool interval		Angell Mbr	Unnamed	

(Holman, 1972) is considered Yarmouth in age based on the stage of evolution of the taxa in the fauna and the type of climate they indicate. Mammals present include the giant armadillo and the tapir.

The Rezabek local fauna (Hibbard, 1943) had long been considered Illinoian in age. Recently, Hibbard reevaluated this fauna and, based on the sympatric occurrence of *Ondatra* and *Neofiber*, suggested that it was Yarmouth in age (Hibbard and Dalquest, 1973).

The two unnamed Illinoian faunas were discovered by field parties from Fort Hays Kansas State College. One is in southeastern Gove County, the other in northwestern Ellis County. The former contains *Valvata tricarinata, Microtus pennsylvanicus,* and *Equus* among other taxa; the latter contains horse, camel, mammoth, and rodent. Both are tentatively considered Illinoian based on their topographic position.

The Duck Creek local fauna is located in extreme southeastern Ellis County and was also discovered by field parties from Fort Hays Kansas State College. The mammalian taxa from this site were described recently by McMullen (1974). Among the taxa are the first records of *Clethrionomys gapperi* (Zakrzewski and Maxfield, 1971) and *Synaptomys borealis* on the Plains. The molluscan taxa are presently under study (Kolb et al., 1974). Both groups of taxa suggest a period of time cooler than that which can be inferred from other Illinoian local faunas so far found in the Plains region.

The Sandahl and Williams local faunas were both discovered by Mr. and Mrs. Clayton Griggs. The former is located in McPherson County and was studied by Semken (1966). The Williams local fauna is located in northwestern Rice County. The molluscs were studied by Hall (1972) and he reported taxa which had previously not been found on the Plains. A study of the mammals is presently underway by McMullen. Preliminary analysis of the Williams local fauna in conjunction with his work on the Duck Creek local fauna enabled McMullen (1975) to name a new species of *Sorex*, found in both faunas.

Some Alternatives

Examination of Figures 1-3 shows that the stratigraphy and paleontology of western Kansas has undergone a drastic revision in the last few years. Further work will no doubt bring even more revision and refinement. These changes will come about as the poorly known sites are studied and new ones are found. Likewise, as more radiometric dates are obtained, revision and refinement will occur.

More immediate revision depends on approaches taken to climatological interpretations which define glacial stages and the beginning of the Pleistocene epoch. Semken (in prep) suggests that the climate during glacial stages was more equable than during the interglacials. The winters might not have been any more severe than at present but the summers would have been much cooler, thus allowing taxa with extant northern distributions (*Sorex, Thomomys*) to extend their range and become sympatric with taxa whose distribution is thought of primarily as southern, but whose northern limit is in the central Great Plains (such as *Sigmodon*). Previously these local faunas (such as the Kentuck) had been considered to be mixed assemblages (Hibbard, 1952; Semken, 1966) but, by the equability model, the Kentuck and Jinglebob would be considered glacial faunas. I have considered the Kentuck a Kansan fauna based on the stage of evolution of some contained taxa, but following Semken's model would place the Jinglebob in the Wisconsinan rather than the Sangamon, an alternative that had been considered by Hibbard(1955). Pollen data (Kapp, 1965) suggest cooler summers at the time the Jinglebob local fauna lived as well. Perhaps the sympatry of *Neofiber* and *Ondatra* indicates a similar climatic condition and the Rezabek local fauna should be retained in the Illinoian.

The position of the Plio-Pleistocene boundary has always been problematical. Cooke (1973) recently discussed the problem of a long versus a short chronology for the Pleistocene, and tentatively correlated events in North America with those in Europe. His Table 3 suggests that he favors a long chronology with the Pleistocene beginning approximately 2.5 to 3 m.y.a. He does state that the early glaciations were montane in nature and that problems exist in trying to place the Nebraskan (the first distinct continental glaciation) and the boundary between the Irvingtonian and Blancan land mammal ages. Cooke (1973) points out that if the date of 1.36 m.y. on the Bruneau Basalts in Idaho is not spurious then the Aftonian and Nebraskan should be older than the position he gives to them in his table. A small fauna is found between the basalts in the area which is Irvingtonian in aspect. This date would put the start of the Irvingtonian approximately 1.4 m.y.a. Recently, dates of 1.6 to 1.8 m.y.a. have been obtained on the same basalt (Armstrong et al., 1975) and, if correct, would push the Irvingtonian farther back in time.

If we consider the sequence in southwestern Kansas, it appears that a long chronology is favored. The Angell Gravel Member of the Ballard Formation is thought to suggest increased runoff from the mountains due to glaciation. However, as mentioned above, there is no evidence for severe climatic deterioration as might be associated with continental glaciation until the time of the Cudahy local fauna and its equivalents. The Cudahy local fauna is overlain by the Pearlette ash (restricted), which dates 0.6 m.y.a. This date coincides with the date for the Plio-Pleistocene boundary favored by those workers (Emiliani, 1966) who favor a short chronology for the Pleistocene. Other workers (Ericson and Wollin, 1968; Richmond, 1970) using the same data favor a date between 1.5 to 2.0 m.y.a. Bandy and Wilcoxon (1970) suggest a date of 1.8 m.y.a. as they have correlated a marine section in California with the type Calabrian in Italy on the basis of foraminiferal zones and in turn correlated these with the Gilsa paleomagnetic event of 1.79 m.y.a. However, even in these cases some type of climatic deterioration is suggested near the boundary.

Fig. 4. Stratigraphic succession of local faunas in western Kansas based on acceptance of equability model and date of 1.8 m.y.a. for Plio-Pleistocene boundary.

Age	Land Mammal Age	Rock Units		Southwestern Kansas Local Fauna	Smoky Hill and Saline River Local Faunas
Wisconsinan	Rancho la brean	Vanhem Formation		Boyd 10,790±280 Robert 11,110±350 Classen 16,100±250 Jones 26,700±1500 Bird locality 29,300±1250 Keiger Creek ? Jinglebob ?	
Sangamon				Cragin Quarry	
Illinoian		Kingsdown Formation		Mt. Scott Butler Spring Adams	Duck Creek Williams Sandahl Unnamed 2 Unnamed 1
Yarmouth	Irvingtonian	Unnamed formation			Rezabek ? Kanopolis
Kansan		Pearlette ash (r.) = Type O		Cudahy	Kentuck Wilson Valley Tobin Unnamed
Aftonian Nebraskan		missing ?			
Pliocene	Blancan	Crooked Creek Fm	Borchers ash = Type B Atwater Member	Borchers	
			Stump Arroyo Member	Seger	
		Ballard Fm	Missler Member	Sanders Deer Park Spring Creek	
			Angell Member	Unnamed	

In southwestern Kansas, the Borchers ash dates approximately 2.0 m.y.a. and is overlain by sediments which contain the Borchers local fauna. This local fauna is indicative of a warm period of time and, based on the stage of evolution of the taxa, has more in common with the Blancan than the Irvingtonian land mammal age. Although it is not impossible for a warm fauna to be present near the base of the Pleistocene, especially if the boundary is defined by criteria other than climatic deterioration, it would not seem reasonable to include the Borchers local fauna as part of the Aftonian Stage.

The Crooked Creek Formation that contains the Borchers local fauna is part of a sequence of cyclic deposition similar to the underlying Ballard Formation. Both of these formations are the result of deposition from the ancestral Arkansas River (Stevens, 1965). The Arkansas is the only stream in Kansas which heads in the mountains, and the gravel members of both formations are the result of increased runoff in the Arkansas because of meltwater from montane glaciation. Therefore, both formations are indicative of pre-Pleistocene continental glaciation. The Nebraskan-Aftonian sequence associated with continental glaciation is not represented by deposits in southwestern Kansas unless the ash which is located north of the Borchers site and is being studied by John Boellstorff turns out to be the Coleridge ash. The Coleridge ash dates 1.2 m.y.a. and has been found in eastern Nebraska overlain by a till and in western Nebraska at the type section of the Sappa Formation. At this latter locality, the ash is underlain by deposits that contain a fauna which was thought to be a Cudahy equivalent (Schultz and Martin, 1970). Even though this fauna is approximately 0.5 m.y. older than the Cudahy, it is still Irvingtonian in aspect and suggestive of climatic deterioration.

On the basis of the above information, I would suggest that the boundary of the Plio-Pleistocene be drawn at approximately 1.5 to 1.8 m.y.a. This date would coincide with the beginning of the Nebraskan as suggested by both Richmond (1970) and Bandy and Wilcoxon (1970) and the beginning of the Irvingtonian land mammal age as suggested by the aspect of the faunas associated with radiometric dates near this time. The local faunas assigned to the Blancan land mammal age should be considered Pliocene (Fig. 4).

Addendum

Since the submission of this manuscript two facts that have some bearing on the stratigraphic section in southwestern Kansas have come to my attention. The first is the occurrence of the Nash local fauna, which is found in deposits near the type area of the Crooked Creek Formation, stratigraphically above those which contain the Borchers local fauna (C.K. Bayne, pers. comm.). Although the fauna is predominantly warm, remains of *Synaptomys (Mictomys)*, the northern bog lemming, have been recovered. This taxon may be indicative of some climatic deterioration. The second fact is that the ash recovered north of the Borchers and Nash sites has been dated at 1.2 m.y.a. (J. Boellstorff, pers. comm.). This means that the Coleridge ash (type-S) is also present in Meade County.

The implications or questions raised by these facts are: (a) because the deposits that contain the Nash local fauna overlie those that contain the Borchers with little or no apparent unconformity, does the Nash represent an early Nebraskan fauna, or (b) are we missing the unconformity and is the Nash temporally associated with the Coleridge ash and therefore equivalent to the fauna reported under that ash in Nebraska? In either case it appears that at least two stadials are represented for one of the early glaciations in the stratigraphic record of the periglacial region of the Plains.

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LETTER FROM C. W. HIBBARD TO W. G. KÜHNE

Dear Professor Kühne: September 20, 1961

Please pardon the delay in answering your letter of July 23, that arrived while I was in the field. I returned last Wednesday (September 13) and have been working my way through three months' mail. Our classes started today in the University.

The washing method was a "brain child" of 1928. I originally included how the method was developed in my paper on the washing method, but Dr. Kellum, Director of the Museum, removed it from the article since he considered it was not scientific.

I was raised on a farm and greatly interested in natural history, also hunting and trapping. I made money to buy clothes while in grade school and high school by trapping fur-bearing mammals. To be a successful trapper or hunter one must study animals – their ways and habits. As a boy I always wanted to hunt large game in Africa; this was impossible.

I entered the University of Kansas in the fall of 1926. I learned that if I could get on as a member of the expedition to collect fossils, I could help find fossil rhinos, camels, etc. In the spring of 1928 I got my chance to go as cook for Mr. H.T. Martin, curator of vertebrate fossils at the Museum of Vertebrate Paleontology, University of Kansas.

One of the greatest days of my life was when we left Lawrence, early in June, 1928, for the Middle Pliocene Beds in northwestern Kansas. I had cooked in cafes since September, 1926, to earn money to go to the University. Cooking for the Professor and three students was of no concern. We were going to collect fossils.

Mr. Martin had located a quarry (Edson Quarry) in Sherman County, northwestern Kansas in 1924, and worked it again in 1926. The quarry was located in stream channel sand and sandy silt. Martin and Adams published a paper in 1929, "A new Urodele from the lower Pliocene of Kansas," (Amer. J. Sci., 5th ser., vol. 18, no. 102). The salamander was *Ambystoma kansensis.*

In those days the overburden (top soil and other matrix) above a fossil horizon was removed by a plow, scraper, and a team of horses. In 1926, when Martin returned to the locality, he found on the quarry dump from the fossil horizon (fine sand) many parts of a salamander skeleton. He picked some of these up, saved them, and took them back to the University. Dr. Adams' mother lived in Lawrence, where the University of Kansas is located. When Dr. Adams visited Lawrence to see his mother, he always came to the Museum, since he had worked his way through college in the building. He became interested in the small bones and studied the specimens. He also requested that Martin get more of the material in 1928.

When we arrived at the quarry in June, 1928, my job was to set up camp, arrange it, cook, and do dishes. Martin hired a rancher with a team to remove the overburden. I hurriedly set up camp and went to the fossil quarry. It turned out no student could drive a team or handle a plow or scraper. So I not only became cook but I ran the plow and scraper. We worked hard and got the overburden off. The next day I finished dishes and camp work and rushed to the quarry to find for myself a rhino and camel.

I was greeted by Martin with a pair of tweezers and told to carefully go over the quarry dump of 1926 and to pick up every piece of small bone. I worked about 1½ hours that forenoon and 2½ in the afternoon. There was no shade; one crawled around in the hot sand on his knees or lay on his belly picking up vertebrae, etc. By this time I was well acquainted with the rancher, so I asked him if he had any old pieces of screen wire. This is used on doors and windows to keep insects out of the house. He said he did and I asked him to bring 3 or 4 large pieces the next morning. I said nothing to anyone about my idea.

The next morning he drove past camp to get to the quarry and left the pieces of wire. That morning I did not go to the quarry but got everything in top shape at camp (a good dinner and supper organized). After dinner I rushed with the dishes and then took the camp truck with 4 or 5 gunny sacs (burlap bags) that hold from 100 to 150 pounds and went to the quarry to fill them with fossil-bearing sand. Mr. Martin saw the truck coming, got excited, and left the diggings to meet me and see what was wrong. I explained I was going to load up the sacs with sand, use the screen which I had shaped into baskets, take the sand to a buffalo-wallow about 2 miles away, and wash out the bones. Buffalo-wallows are places where the American *Bison* would dust in the dirt to get rid of flies. They developed holes from 12 inches to over 2 feet in depth and from the size for one *Bison* to larger ones that would hold a number. In the rainy season these holes filled with water. (A buffalo-wallow is a depression generally filled with dust but an excellent toad (*Bufo*) pool in the wet season).

I placed a shovel full of fine sand containing the fossils in the basket-like structures and set them in the water in the buffalo wallow. I then lifted and lowered the screen in the water. All of the fine sand passed through the screen leaving chiefly fossil bone. These were vertebrae and bones of salamander, frog, toad, bird, and rodent jaws. That afternoon I got enough small fossils to fill a kitchen match box (2½ by 2 by 5 inches in size). When Martin and the students returned from the quarry that evening, I had supper on time and had my whole summer laid out, planning to wash for fossils. That night Mr. Martin said, "What did you get?" I showed him. His eyes opened wide. He said, "My God!! You have enough small fossils for all of the museums in the world." My world of collecting small fossils vanished. The next day I began digging for three-toed horse, camel, and rhino.

I fully realized at that time that 50% or more of a fauna went into a quarry dump and vowed I would collect small fossils if I could ever get the chance.

In 1929 we worked all summer on part of a Columbian mastodon and spent over $2000 for lumber, freight, etc. In 1930 Curtis Hesse was in charge and we collected horses and camels. In 1931 I spent most of the summer collecting Recent vertebrates, but I got a month or better to collect fossils. We recovered snake, bird, rodent, and large mammals. Large vertebrates were a headache and expensive.

The University of Kansas ran no field trips in 1932, 1933, 1934, or 1935. I personally paid for the little field work done in 1932 and 1933 out of my own pocket by working at 35 cents an hour for the Museum. In 1934 and 1935 I worked for the United States National Park Service. I joined the staff of the University of Kansas in the fall of 1935. It was during the depression years. Instead of the $2000 for the summer field fund I got

$300 for field work. The University considered it so low that I would not go to the field. We left as soon as school was out in June of 1936 and returned late in August. We lived off the land. We shot or caught our fresh meat and bought only what we had to buy. I realized I could not collect large fossils or remove overburden, so we turned to hand labor of sifting for fossils.

My whole plan was to return to the Edson quarry of 1928. We did, but it was destroyed. [If you check the 1929 papers of Adams and Martin, also Wetmore and Martin, 1930, "A fossil crane from the Pliocene of Kansas," you will find that no locality nor county is given. When I was a student in 1929, I was present when Martin told George Sternberg, now alive and at Hays, Kansas, "George, I have known you and your father for years. You know as well as I do, blood is thicker than water. If you ever go into Edson and Rhino Hill quarries, I will shoot to kill." George said, "Now Martin, you know me. I will never go in." I, as a student, followed the advice of Alex Wetmore, who insisted that the Cope and Marsh days were over and I must publish with my master's thesis the location of Edson Quarry ("Two new genera of Felidae from the Middle Pliocene of Kansas," Trans. Kansas Acad. Sci., vol. 37, pp. 239-248, 1934). We arrived at Edson Quarry to find it gutted by George Sternberg for Childs Frick. Martin had died the spring of 1931. I at once took this up with Wetmore who hired Sternberg about six months each year to collect for the U.S. National Museum. Wetmore stopped Sternberg from working other quarries but his own. This had been the Sternberg practice for two generations up to this date.]

During the depression I turned entirely to sifting and washing for the smaller fauna associated with the larger vertebrates, since I had only from $300 to $350 for summer field funds. Much of the credit goes to Harry Jocob, an engineering student, who insisted on washing for the recovery of mollusks that I was trying to pick by hand. The washing of matrix containing mollusks also contained remains of fish, amphibians, snakes, lizards, birds, and mammalian jaws. We also recovered snail (molluscan) eggs and oogonia of chara.

In our collecting we never left fossils, but by the time all matrix around a large fossil was dried and washed, there was never enough time to remove too many yards of dirt a year by this practice.

I was always interested in the entire flora and fauna, also the conditions under which they lived. I had two questions I asked myself – what lived and how, and under what kind of climate?

I must admit much of my work has been entirely for my personal information. I have wanted to know what and why. My interest in the ostracods and mollusks was to get as complete a picture of the environment of the region as possible. Most of the vertebrate paleontologists consider my conclusions concerning past climates and habitats as guesses and not based on facts. They consider paleobotany as the only basis for constructing past climates and that it is impossible to do so from vertebrates.

My work has been ridiculed in the past. Some have often said it will only work locally in a certain part of Kansas, but not in Nebraska and the rest of North America. The American Museum, Harvard, Yale, and Princeton do not believe a new method or a new idea can be developed outside of their walls (e.g., see A.S. Romer, 1959, "Vertebrate paleontology, 1908-1958," J. Paleont., vol. 33, no. 5, pp. 915-925). We spread out about 300 hand towels to place the wet concentrate upon after washing—when dry, we pick off the fossil vertebrates with tweezers. I have showed slides of our work and the older vertebrate paleontologists stated, "What are the diapers for?"

Regardless, it has taken a new generation to recognize the value of washing for small vertebrates. The younger vertebrate paleontologists realize that more fossils were left in the old quarry dumps than were ever recovered. They also realize the value of micro – or small vertebrates – and the invertebrates; all of these help to complete the story of the past. Malcolm McKenna started in our fossil camp and washed fossils until he learned our process and method. Malcolm was a highschool classmate of Dwight W. Taylor. Dwight was a member of my field party in 1950 at the time McKenna visited our camp. Dwight Taylor (1960, "Late Cenozoic molluscan faunas from the High Plains," U.S. Geological Survey Professional Paper 337) states, "Fossils collected at this original locality and exploration of the Meade County region in general subsequently have produced almost an overabundance of paleontological riches." I just had a letter from Malcolm McKenna; during June and July this summer they washed 170 tons of Cretaceous matrix containing remains of mammals. He has had a most successful summer.

In the fall of 1943 Mr. Elmer S. Riggs, curator of vertebrates, Field Museum of Natural History, Chicago, Illinois, then retired but now living in Oklahoma with his son, went to western Kansas with me to collect fossils. We found the camel quarry (see Geol. Soc. Amer. Bull. vol. 60 "Upper Pliocene vertebrates from Keefe Canyon, Meade County, Kansas"). Riggs, an old dinosaur collector, was after large bone. We finally divided the quarry and when he finished gutting and chopping out his one-half, he went home to Lawrence. He chopped up all small bone and Manuel Maldonado made the statement that if a bone was not 18 inches long with teeth, it was not a fossil. This statement fits well the definition of a vertebrate fossil of the old-time collectors in this country. This fitted Rigg's definition perfectly.

I had two boys to help us part of one of the three summers we worked the quarry. We could not wash but we sifted the sand (about 10% of the throw-away matrix) and we doubled the fauna. Riggs got very angry; he said, "Hibbard, you are not a vertebrate paleontologist. No one knows about you. What you collect are small potatoes," in reference to the small fossils. The students had him in an uproar. One would shout, "I have a small potato with 3 teeth," another, "I have a small potato with one tooth." We doubled the fauna by sifting the sand from the quarry. What would it have been if we could have washed it?

Regardless, it has been a lot of hard work and a pleasure. We shall see a new generation of students with far more fields of interest to study and vertebrate paleontology shall begin to take its place in science.

Sincerely,

Claude W. Hibbard

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