SMITHSONIAN CONTRIBUTIONS TO PALEOBIOLOGY • NUMBER 54

The Carnivora of the Edson Local Fauna (Late Hemphillian), Kansas

Jessica A. Harrison

SMITHSONIAN INSTITUTION PRESS
City of Washington
1983

ABSTRACT

Harrison, Jessica A. The Carnivora of the Edson Local Fauna (Late Hemphillian), Kansas. *Smithsonian Contributions to Paleobiology*, number 54, 42 pages, 18 figures, 1983.—The late Hemphillian Edson Quarry Local Fauna contains 36 species of amphibians, reptiles, birds, and mammals. The eight species of carnivorans are *Canis davisi*, a primitive dog; *Osteoborus cyonoides*, a large borophagine; *Agriotherium* species, a long-limbed bear; *Plesiogulo marshalli*, a wolverine; *Pliotaxidea nevadensis*, a badger; *Martinogale alveodens*, a skunk; *Adelphailurus kansensis*, a metailurine felid; and *Machairodus coloradensis*, a machairodontine felid. Edson is one of several fossil localities in Sherman County, Kansas, and was deposited in a series of fine sands within the Ogallala Formation. A secondary channel in a braided stream system is proposed as the environment of deposition. The high percentage of juveniles, as well as the vast numbers of the salamander *Ambystoma kansensis*, indicate accumulation during the spring of the year. The Edson Quarry Local Fauna compares very well with such typically late Hemphillian faunas as Coffee Ranch, Texas, and Optima, Oklahoma. Although only the carnivorans have been treated in depth, a listing of the vertebrate taxa is offered as well.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The trilobite *Phacops rana* Green.

Library of Congress Cataloging in Publication Data
Harrison, Jessica A.
The Carnivora of the Edson local fauna (late Hemphillian), Kansas.
(Smithsonian contributions to paleobiology ; no. 54)
Bibliography: p.
Supt. of Docs. no.: SI 1.30:54
1. Carnivora, Fossil. 2. Paleontology—Pliocene. 3. Paleontology—Kansas—Sherman County. I. Title. II. Series.
QE701.S56 no. 54 [QE882.C15] 560s [569'.74] 83-600029

Contents

The Carnivora of the Edson Local Fauna (Late Hemphillian), Kansas

Jessica A. Harrison

Introduction

Edson Quarry, Kansas, has produced one of the largest and most diverse faunas from the late Hemphillian of North America. As such, it provides an unusually detailed glimpse into this interval during which the flora was completing a transition from woodland savanna to grassland, the climate was becoming more xeric, and faunal interchange with Europe, Asia, and South America was increasing.

Some 36 taxa of vertebrates representing amphibians, reptiles, birds, and mammals are known from the locality. Eight genera of carnivorans are present in the fauna. Although a complete systematic revision of the Edson Local Fauna is beyond the scope of this paper, a revised faunal list has been compiled.

PREVIOUS WORK.—The fossil concentration was discovered in 1924 by H. T. Martin of the University of Kansas Museum of Natural History and was subsequently worked by university field parties under the direction of Martin or Claude W. Hibbard into the 1930s. George Sternberg, a professional fossil collector, periodically excavated large amounts of material, approximately 80% of the total Edson sample, during the interval from 1933 to 1942. This material was sold to Childs Frick, a Trustee of the American Museum of Natural History, and following his death was bequeathed to that museum and eventually incorporated along with the rest of the Frick Collection into the holdings of the Department of Vertebrate Paleontology. A small number of specimens, notably the types of *Perognathus dunklei* and ?*Oryzomys pliocaenicus*, were collected in 1935 by David Dunkle for the Museum of Comparative Zoology at Harvard University.

Several authors have studied various components of the Edson fauna. Adams and Martin (1929, 1930) and Taylor (1936, 1941) described the Edson herpetofauna. Tihen (1958, 1962) revised much of this early work. The avifauna was dealt with by Wetmore (1937) and Wetmore and Martin (1930). Martin (1928) and Hibbard (1934, 1937, 1939) described several of the smaller mammals and published the first faunal lists. *Martinogale*, a mephitine mustelid, was named by Hall (1930), and Dunkle (1938) later referred additional material to this genus. Wood (1936) named the rodent, *Kansasimys*, and recently Wahlert (1978) has explored its systematic relationships. Harrison (1979) named a new lamine camel, *Alforjas*, and reviewed the wolverine material (1981, 1982). Prescott (1953) investigated the geology and groundwater resources of Sherman County.

Jessica A. Harrison, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

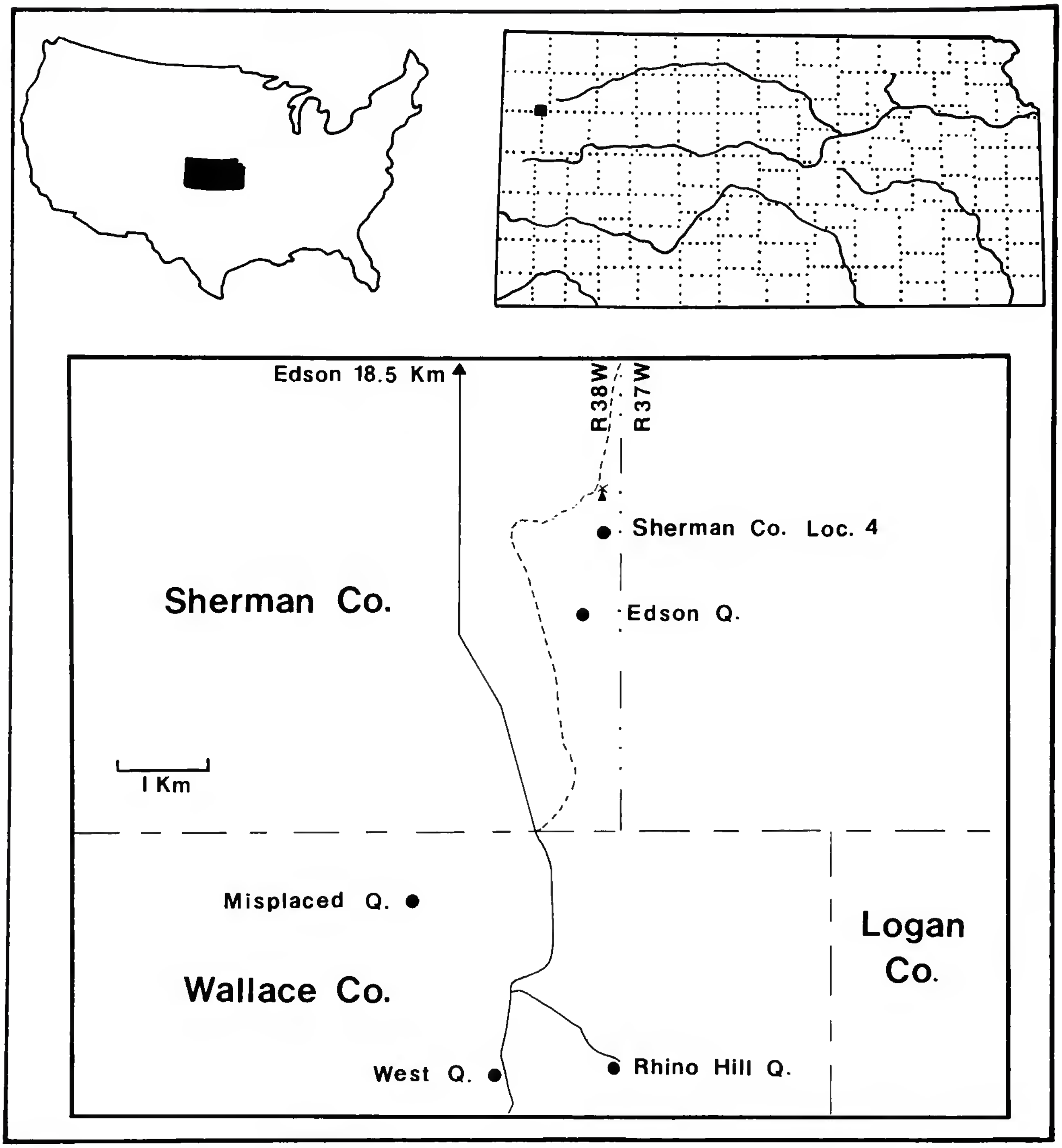

FIGURE 1.—Geographic location of Edson Quarry and adjacent fossil localities.

ABBREVIATIONS.—The following abbreviations are used in this study:

F:AM	Frick Collection, American Museum of Natural History, New York, New York
KUVP	University of Kansas Museum of Natural History, Lawrence, Kansas
SMM	Sternberg Memorial Museum
USNM	Former United States National Museum, collections now in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

ACKNOWLEDGMENTS.—I am grateful to Richard H. Tedford, Department of Vertebrate Paleontology, American Museum of Natural History, to Hans-Peter Schultze and Larry Martin, University of Kansas Museum of Natural History, and to Richard Zakrzewski, Sternberg Memorial Museum, for the loan of specimens. John Chorn unearthed the negative for Figure 2*a* from the KUVP archives. Debra K. Bennett took the photograph in Figure 3. Earl Manning identified the peccary from Edson Quarry. Henry Galiano was very generous with his knowledge of the metailurine felids. Richard Tedford offered several useful comments pertaining to *Canis davisi*. Sue Voss was very helpful in translating the work of French paleontologists. This paper represents part of a dissertation submitted to the University of Kansas. The project was supported in part by grants from the National Science Foundation and the Geological Society of America. I would especially like to thank Robert J. Emry, Ralph E. Eshelman, Earl E. Manning, and Henry Galiano for the considerable time and thought they expended in the review of this paper.

Location and Stratigraphy

Edson Quarry is located in the NW 1/4 of the SE 1/4 of Section 25, T 10 S, R 38 W, Sherman County, Kansas (Figure 1). It is one of several fossil localities (Rhino Hill Quarry, West Quarry, Sherman County Locality 4, and Misplaced Quarry) in southwest Sherman County and northeast Wallace County that have produced smaller collections of similar age and composition.

Edson Quarry is contained in the Ogallala Formation, which, throughout Sherman County, rests unconformably on the undulatory surface of the Pierre shale. The late Cretaceous Pierre shale, ranging in thickness from 180–275 meters, contains numerous thin beds of bentonitic clay representing altered deposits of volcanic ash (Prescott, 1953:25, 64).

The Ogallala Formation has been completely eroded in a few small areas of Sherman County, but attains a thickness of up to 90 meters in others. It is composed of a wide variety of fluvial sediments, including gravel, sand, silt, and clay, deposited by streams draining the Rocky Mountains. A very hard limestone layer capping the Ogallala sediments in many areas was described by Elias (1931:138, 139) as the "*Chlorellopsis* limestone" or the "Algal limestone." Because the limestone contains a high percentage of a fossil alga, *Chlorellopsis bradleyi*, Elias inferred the presence of a large, shallow lake or system of smaller lakes to provide the lacustrine environment requisite for its deposition.

The Ogallala Formation is overlain by a Pleistocene loess, the Sanborn Formation, which ranges up to 15 meters (about 50 feet) in thickness. Along valley and arroyo floors, Pleistocene alluvial sands and gravels may be found. The nature of the Ogallala deposits in neighboring Decatur, Wallace, Rawlins, and Thomas counties has been described by Elias, 1931 and 1937, Frye, 1945, and Hodson, 1963.

Edson Quarry is located in an arroyo draining into the North Fork of the Smoky Hill River. It was last worked by George Sternberg in 1942. The location was reestablished in 1973 through the use of field notes and photographs from the archives of the University of Kansas Museum of Natural History. Legend has it that Sternberg completely excavated the single, large, lenticular bone bed at Edson Quarry (Figure 2*a*). The approximate extent of the original excavations and the disposition of the backdirt mounds were still discernable in 1978 (Figure 2*b*); indeed, bone fragments continue to weather from the 40-year-old spoil heaps.

Adams and Martin (1929:504) stated that the fossil deposit was "about 20 feet below the level of the prairie." In order to expose a stratigraphic section of the enclosing sediments and to verify, if possible, the vertical position of the fossiliferous layer, two bulldozer trenches were dug, beginning on the arroyo floor that lies some 4 meters (13 feet) below the level of the prairie and continuing down another 4.5 meters. No remains of the original fossil concentration were found, a tribute

FIGURE 2.—*a*, Edson Quarry in late 1920's during excavation by H.T Martin and C.J. Hesse; *b*, Edson Quarry in 1977.

to the thoroughness of Sternberg's excavation; however, a few bone fragments were recovered from Trench II at a depth of about 2.2 meters (about 7 feet) or about 6.1 meters (20 feet) below the level of the prairie (Figure 3).

The two trenches were about 2.4 meters (8 feet) wide and from 9 to 12 meters (30 to 40 feet) long, with the maximum depth occurring at about midpoint. Trench I was oriented almost N-S, while Trench II ran about N 65° W Stratigraphic sections of both trenches are presented in Figure 4. The sediments are predominantly fine- to medium-grained sands that vary in color from light buff to yellow. With the exception of a few relatively thin layers, the sands are generally loose and friable. Calcium carbonate impregnated roots and patches of caliche are scattered liberally throughout the section (Figure 5). Primary sedimentary structures are of a very small scale and subtle nature. Two sequences in the Trench II section show sedimentary structures that enlarge in scale and increase in grain size toward the top. Very small, shallow ripples are overlain by fine laminae and then slightly larger ripples in coarser sand. This sequence is succeeded by another that repeats the progression of small ripples to fine laminae but culminates in festoon cross beds.

Miall (1977:1) defines a braided river as "a series of broad, shallow channels and bars, with elevated areas active only during floods, and dry islands." Although in some systems a single, dominant channel can be recognized, in others there are several main channels (Rust, 1972:223); moreover, there are several distinct topographic levels. These topographically high channels experience only ephemeral flow at flood stages and are frequently heavily vegetated. They are also characterized by small grain size and repetitive vertical sequences of structures that coarsen upwards in section. These upward coarsening cycles have been interpreted as due to channel re-occupation following avulsion (Eynon and Walker, 1974:67).

Bennett (1978) proposed a widespread, braided stream system as part of a depositional model for the strata containing the Rhinoceros Hill Local Fauna (see Figure 1). The sediments at Rhinoceros Hill are, with the exception of the diatomaceous marl, generally coarser and the primary sedimentary structures are of a much larger scale than those at Edson Quarry. The relatively fine sediments and small-scale primary sedimentary structures at Edson, indicative of a low energy flow regime, could represent a series of deposits in a topographically high channel within the main system of anastomosing channels. The minor amounts of mud renders an overbank or levee interpretation less likely; however, the absence of mud could also be due to scarcity in the source area.

Taphonomy

"The greatest riddle . . . is when, why, and how did all these assorted creatures, and in such absolutely countless numbers, get killed . . . and mashed up into this horrific indecency," Sanderson observed (1960:82). The discipline of taphonomy, through studying the effects of post-mortem and post-depositional events upon skeletal material, may provide some insight into the problem so melodramatically set forth by Sanderson.

FIGURE 3.—View along Trench II looking WNW.

Sternberg, who was by far the most active excavator at Edson Quarry, did not record detailed field notes or maps. Consequently, no data are available on the orientation of the hundreds of skeletal elements that were recovered. Such data would have been very informative on such subjects as major current direction and flow strength.

Very few of the fossil bones were found in articulation with other elements, although size, stage of wear, and ontogenetic age permit several

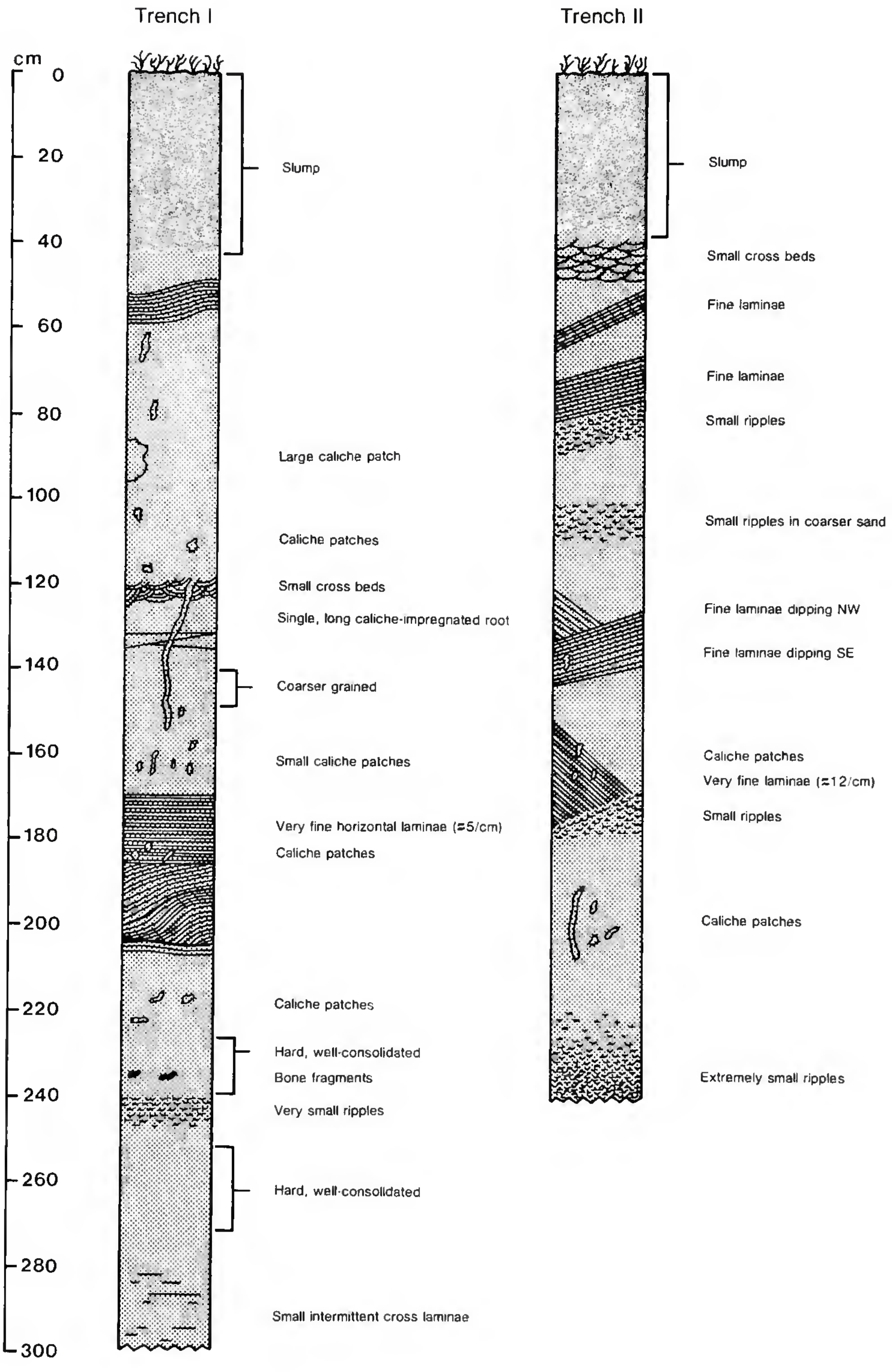

FIGURE 4.—Stratigraphic sections of Trenches I and II. Note occurrence of bone fragments at 235 cm in Trench I section.

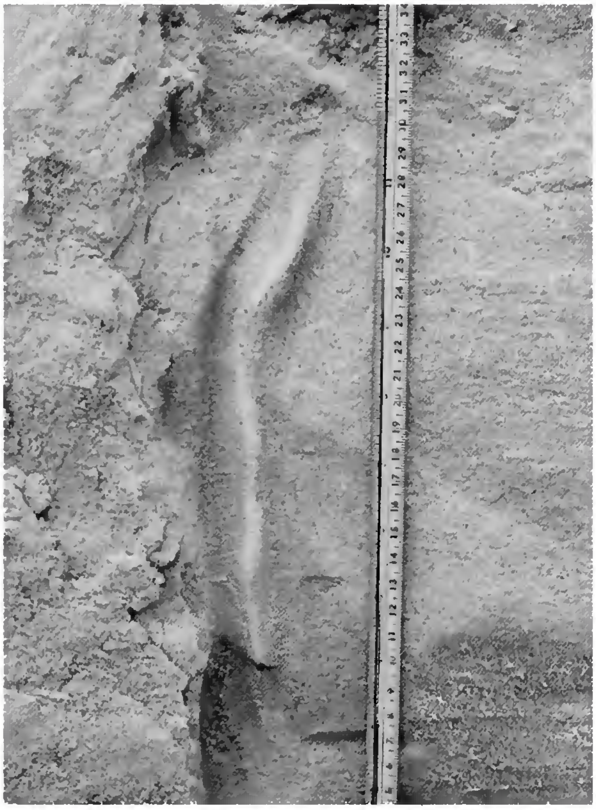

FIGURE 5.—One of many calcified roots occurring in Edson Quarry sediments.

tentative associations. Two factors that could be responsible for such a high incidence of disarticulation are a high energy depositional environment or the activity of scavengers. Neither factor is very well supported, since the grain size of the enclosing sediments and the very small scale primary sedimentary structures indicate a low energy environment and very few of the fossil bones exhibit traces of gnawing.

A third hypothesis, which accounts for both the low energy depositional environment and the largely dissociated nature of the fossil material, is as follows. A flood, even one of modest proportions, would garner the carcasses of animals having died in the vicinity. Such carcasses, many already partially decayed and disarticulated, could be transported in a stream of fairly low carrying capacity. Transport must have been relatively brief since the bones do not appear to be water-worn or tumbled. Narrow, shallow channels would favor the accumulation of skeletal material, whereas the high energy regime of larger channels would result in scattering.

Spring is the most common season for flooding in the Great Plains. Ambystomatid salamanders, especially *Ambystoma tigrinum mavortium* (barred tiger salamander), whose range extends over the central and southern Great Plains (Conant, 1975:256), only congregate to breed in ephemeral pools formed by spring rains. The vast numbers of *A. kansensis* present in the Edson Local Fauna, in addition to the high percentage of mammalian juveniles, as determined by deciduous dentitions and unfused epiphyses, further support the suggestion of a spring flood as the concentrating mechanism for the Edson Quarry fossil deposit.

Faunal List

The following is a list of the 36 vertebrate taxa represented in the Edson Local Fauna. Several discrepancies are apparent between it and the last faunal list to have been published (Hibbard, 1939:460, 461). Within the Amphibia, Tihen (1958:37;1962:26) synonymized *Plioambystoma* with *Ambystoma* and *Bufo arenarius* with *B. hibbardi.* Hibbard's faunal lists (1934, 1939) contain the taxon *Chelonia*, the sea turtle; this has been changed in favor of an undetermined chelydrid. An unidentified snake, represented by two articulated vertebrae, has been added to the Reptilia. Most of the changes have centered around the mammalian taxa. Additions include a talpid, a lagomorph, *Agriotherium* species, *Pliotaxidea nevadensis*, a lamine camel, and *Texoceras* cf. *guymonensis.* The degree of retraction in the nasals of a skull of *Aphelops* from Edson suggests that *A.* cf. *malachorhinus* may be more appropriate than *A.* cf. *mutilus.* The equids are represented by *Dinohippus interpolatus* and a small, very hypsodont, *Nannippus*-like form. Changes involving the Carnivora are discussed in detail within the systematics section of this paper.

AMPHIBIA
 AMBYSTOMIDAE
  Ambystoma kansensis (Adams, 1929)

- PELOBATIDAE
  - *Scaphiopus pliobatrachus* Taylor, 1936
- BUFONIDAE
  - *Bufo hibbardi* Taylor, 1936

REPTILIA
- CHELYDRIDAE
  - Genus and species indet.
- TESTUDINAE
  - *Geochelone* species
- COLUBRIDAE
  - Genus and species indet.

AVES
- COLYMBIDAE
  - *Colymbus nigricollis* Wetmore, 1937
- GRUIDAE
  - *Grus nannodes* Wetmore and Martin, 1930
- SCOLOPACIDAE
  - Genus and species indet.
- CORVIDAE
  - Genus and species indet.

MAMMALIA
- INSECTIVORA
  - TALPIDAE
    - Genus and species indet.
- LAGOMORPHA
  - Genus and species indet.
- RODENTIA
  - MYLAGAULIDAE
    - *Mylagaulus monodon* Cope, 1881
  - EOMYIDAE
    - *Kansasimys dubius* Wood, 1936
  - HETEROMYIDAE
    - *Perognathus dunklei* Hibbard, 1939
    - *Prodipodomys kansensis* (Hibbard, 1939)
  - CRICETIDAE
    - ?*Oryzomys pliocaenicus* Hibbard, 1939
    - *Peromyscus martini* Hibbard, 1937
- CARNIVORA
  - CANIDAE
    - *Canis davisi* Merriam, 1911
    - *Osteoborus cyonoides* (Martin, 1928)
  - URSIDAE
    - *Agriotherium* species
  - MUSTELIDAE
    - *Plesiogulo marshalli* (Martin, 1928)
    - *Pliotaxidea nevadensis* (Butterworth, 1916)
    - *Martinogale alveodens* Hall, 1930
  - FELIDAE
    - *Adelphailurus kansensis* Hibbard, 1934
    - *Machairodus coloradensis* Cook, 1922
- PERISSODACTYLA
  - EQUIDAE
    - *Dinohippus interpolatus* (Cope, 1893)
    - *Neohipparion* cf. *eurystyle*
    - *Nannippus* species
  - RHINOCEROTIDAE
    - *Aphelops* cf. *malachorhinus* Cope, 1878
    - *Teleoceras fossiger*
- ARTIODACTYLA
  - TAYASSUIDAE
    - *Platygonus rex*
  - CAMELIDAE
    - *Hemiauchenia vera* (Matthew, 1924)
    - *Alforjas taylori* Harrison, 1979
    - *Megatylopus gigas* Matthew and Cook, 1909
  - ANTILOCAPRIDAE
    - *Texoceras* cf. *guymonensis* Frick, 1937

Biochronology

The age of the Edson Local Fauna has of necessity been determined primarily on the basis of faunal parameters. Throughout the late Neogene, the biota of western Kansas was several times disturbed by the deposition of volcanic ash layers. Unfortunately for the paleobiologist, although perhaps not so for the then resident biota, no ash falls are recorded in the strata containing Edson Quarry. Hence, its age must rest upon criteria other than radiometric dating. The potential contributions of palynology and paleobotany are forestalled by the dearth of fossil plant material, although a fossil flora has been described from nearby Logan County (Chaney and Elias, 1936:23).

The Edson Local Fauna has long been held to be a principal correlative of the Coffee Ranch (Hemphill) Local Fauna of Texas (Wood et al., 1941:12). The Coffee Ranch Local Fauna is the principal fauna of the late Hemphillian North American Provincial Age that extends from late Miocene through early Pliocene, about 10 m.y. to 4 m.y. BP (Berggren and Van Couvering, 1974). Boellstorff (1976, fig. 8) has fission-track dated (glass) a volcanic ash that overlies the Coffee Ranch Local Fauna at 5.3±0.4 m.y. BP. For the same ash Izett (1975:202) has obtained fission-track dates of 4.7±0.8 m.y. BP (glass) and 6.6±0.8 m.y. BP (zircon).

Wood et al. (1941:12) recognized the Hemphillian by "the first appearance of ground sloths, *Lutravus*, *Machairodus*, and *Taxidea*; the last appearance of *Aphelops*, *Blastomeryx*, *Mylagaulus*, *Os-*

teoborus, *Pliauchenia*, *Pliohippus*, *Prosthennops*, rhinoceroses, *Sphenophalos*, and *Teleoceras*." They listed *Hypolagus*, *Megatylopus*, *Nannippus*, and *Neohipparion* as "characteristic fossils" and *Agriotherium*, *Dipoides*, *Illingoceros*, and *Plesiogulo* as "index fossils." Late Hemphillian faunas, such as Coffee Ranch, Edson Quarry, and Optima (Guymon), may be distinguished from early Hemphillian faunas, such as the *Amebelodon fricki* Quarry in Nebraska and the Box T Quarry in Texas, by a reduction in ungulate diversity, by the presence of *Pediomeryx*, and by the first appearance of such immigrant taxa as *Plesiogulo*, *Agriotherium*, *Ochotona*, and *Promimomys* (R.H. Tedford, pers. comm., 1976). Although the *Amebelodon fricki* Quarry was originally described as "Kimballian" in age, I herein follow Breyer (1981:1215).

In Table 1 the mammalian taxa of the Edson Local Fauna are compared with those of two other late Hemphillian local faunas, the Rhinoceros Hill Quarry, which is located in Wallace County about 4 kilometers (2.5 miles) south of Edson Quarry, and the type Coffee Ranch. A high degree of faunal similarity is immediately apparent, especially within the larger mammals. Within the Rodentia *Mylagaulus monodon* and *Kansasimys dubius* are present at both Edson and Coffee Ranch. It is unfortunate that no insectivores, lagomorphs, or rodents have yet been recovered from Rhinoceros Hill Quarry, because it is these smaller animals that are particularly useful in biostratigraphic correlation, especially among neighboring localities.

Three, possibly four, of the carnivoran genera are common to all three faunas. *Canis davisi* was originally described as *Leptocyon shermanensis* from

TABLE 1.—Comparison of mammalian faunas (* = holotype; X = occurrence in fauna)

Taxon	Edson Quarry	Coffee Ranch	Rhino Hill
Soricid gen. and sp. indet.		X	
Talpid gen. and sp. indet.	X		
Hypolagus sp.		X	
Lagomorph gen. and sp. indet.	X		
?Mylodontid gen. and sp. indet.		X	
Mylagaulus monodon	X	X	
Kansasimys dubius	*	X	
Spermophilus? sp.		X	
Geomyid gen. and sp. indet.		X	
Perognathus dunklei	*		
Prodipodomys kansensis	*		
Heteromyid gen. and sp. indet.		X	
Copemys sp.		X	
?*Oryzomys pliocaenicus*	*		
Peromyscus martini	*		
Canis davisi	*	X	X
Osteoborus cyonoides	*	X	X
Vulpes stenognathus		X	
Canid gen. and sp. indet.		X	
Agriotherium schneideri		X	
Agriotherium sp.	X		
Ursid gen. and sp. indet.			X
Plesiogulo marshalli	*	X	
Pliotaxidea nevadensis	X	X	
Martinogale alveodens	*		
Pseudaelurus hibbardi		*	
Adelphailurus kansensis	*		
Machairodus coloradensis	X	X	X
Platybelodon sp.			X
Rhynchotherium sp.		X	
Dinohippus interpolatus	X	X	X
Astrohippus ansae		*	X
Neohipparion cf. *eurystyle*	X	X	X
Nannippus cf. *lenticulare*		X	X
Nannippus sp.	X		
Aphelops mutilus		X	X
Aphelops malachorhinus	X		
Teleoceras fossiger	X	X	X
Platygonus rex	X		
Prosthennops sp.		X	X
Hemiauchenia vera	X	X	X
Alforjas taylori	*		X
Alforjas sp.		X	
Megatylopus gigas	X		
Megatylopus matthewi		*	X
?*Titanotylopus* sp.			X
Pediomeryx hemphillensis		*	X
Texoceras cf. *guymonensis*	X		
Texoceras altidens		X	
Texoceras sp.			X

Edson. It is listed as *Vulpes* cf. *V. shermanensis* at Coffee Ranch (Dalquest, 1969:4, 5) and at Rhinoceros Hill (Bennett, 1978:15). *Osteoborus cyonoides*, in addition to *Machairodus coloradensis* (listed as *M. catocopis* by Dalquest (1969:13)), also occur at all three localities. The ursid material from Edson and especially Rhinoceros Hill is fragmentary and only marginally diagnostic. Dalquest (1969:9) identified the Coffee Ranch ursid as *Indarctos oregonensis*, but Schultz and Martin (1975:50) have subsequently referred this material to *Agriotherium* species and indicate that it is probably conspecific with the *Agriotherium* that they described from University of Nebraska State Museum Collecting Locality Sm-101, Sherman County, Nebraska. However, Schultz (1977:75) in a faunal list of Coffee Ranch identifies the ursid as *A. schneideri*.

With regard to the Perissodactyla, Coffee Ranch more closely resembles Rhinoceros Hill Quarry than it does Edson; however, this is probably a reflection of the need for revision in the Edson horses. *Dinohippus interpolatus*, *Neohipparion* cf. *eurystyle*, and *Nannippus* are common to all three faunas. The two different species of rhinoceros, *Aphelops mutilus* at Coffee Ranch and Rhinoceros Hill and *A. malachorhinus* at Edson, may be resolved at a systematic level.

An age assignment of late Hemphillian for the Edson Local Fauna is substantiated by its high degree of faunal similarity to the type Coffee Ranch Local Fauna. The temporal relationship of the Edson Local Fauna to that of Rhinoceros Hill has long been uncertain. Due to the discontinuous nature of the enclosing Ogallala sediments and the lack of radiometrically datable strata (i.e., volcanic ashes), the sole basis for determining the relative ages of the two faunas has devolved upon a comparison of the mammalian components. This problem is compounded by the paucity of small mammals in the Rhinoceros Hill fauna. The overall similarity of the larger mammalian taxa supports the hypothesis that Edson and Rhinoceros Hill are more or less contemporaneous. The presence of a more derived species of *Megatylopus*, *M. matthewi*, and the possible presence of *Titanotylopus* suggest that Rhinoceros Hill is slightly later Hemphillian than is Edson. However, the occurrence of the Eurasian allochthons, *Plesiogulo* and *Agriotherium*, suggests that Edson may be the younger of the two faunas. A more conclusive assessment of the temporal relationship of Edson Quarry and Rhinoceros Hill must await the recovery of small mammals from the latter locality.

Paleoecology

During the late Clarendonian to late Hemphillian interval, the flora of the High Plains was evolving from open woodland savanna to predominantly treeless steppe or grassland (Webb, 1977). The Edson Local Fauna is characteristic of the climax of this period. No plant macrofossils or pollen have been recovered from Edson, but Chaney and Elias (1936:23) described a late Miocene flora from a diatomaceous marl in nearby Logan County. The Logan County flora is xeric in nature and consists of *Celtis kansana*, *Populus lamottei*, *Salix coalingensis*, *Typha lesquereuxi*, *Ulmus moorei*, and *Cyperacites* species. The elm, *U. moorei*, most closely resembles *U. parvifolia* of Asia, which inhabits areas of low rainfall. Chaney and Elias (1936:32) suggest that late Miocene conditions in western Kansas were similar to those of today, and that the mean annual precipitation was approximately 25 inches, some 5 inches more than at present.

The fauna of the High Plains was profoundly affected by the transition from savanna to grassland. A marked decrease in diversity is apparent in Hemphillian faunas as opposed to Barstovian-Clarendonian faunas; most obvious is the paucity of arboreal and browsing species (Gregory, 1971:70). By late Hemphillian time almost all of the large herbivores possessed high-crowned teeth, and a trend for increased hypsodonty may be observed even in the rodents (Webb, 1977; Wilson, 1960).

Of the nine ungulate herbivores in the Edson Local Fauna, all but two, *Platygonus* and *Megatylopus*, are hypsodont. The remaining seven (three horses, one rhinoceros, two camels, and one antilocaprid) range from moderately (*Alforjas*) to extremely (*Nannippus* and *Texoceras*) hypsodont. Of the ungulates, all but *Teleoceras* are cursorial forms. Among the Carnivora, even the bear (*Agriotherium*) and the two felids (*Adelphailurus* and *Machairodus*) are noted for their exceptionally long limbs.

The Edson Local Fauna is typical of an open grassland community dominated by hypsodont, cursorial herbivores, and pursuit-oriented predators. Narrow belts of open forest, consisting mainly of cottonwood, willow, and scrub elm, probably flourished along drainages. These tracts of riparian woodland provided browse and cover for the few brachydont herbivores and those carnivores commonly associated with forests.

The climate, as indicated by the flora and the extensive caliche deposits in the Edson sediments, was xeric although somewhat less so than at present. The only truly mesic elements in the fauna are the crane, *Grus nannodes*, and the grebe, *Colymbus nigricollis.* These birds may have been foraging in local pools or stream channels, but, as they are also the most vagile members of the fauna, it is likely that they nested around the fringes of the small lake located at Rhinoceros Hill (Bennett, 1978:46) some three miles (4.8 km) south of Edson Quarry. If the great abundance of the salamander, *Ambystoma kansensis*, does indeed represent a breeding congregation, it suggests that precipitation, then as now, was probably concentrated in the spring and secondarily in the early autumn.

Order CARNIVORA Bowdich, 1821

Family CANIDAE Gray, 1821

Subfamily CANINAE Gill, 1872

Canis davisi Merriam, 1911

FIGURES 6, 7

Canis davisi Merriam, 1911:242.
Leptocyon shermanensis Hibbard, 1937:460

REFERRED SPECIMENS.—KUVP 3608, right ramus; KUVP 3280, left P_4; KUVP 3281, canine; KUVP 3282, right M^1; F:AM 49464, partial palate; F:AM 49470, partial palate, axis, and cervical vertebra; F:AM 49458, left maxilla fragment; F:AM 49456, partial skeleton including right and left rami, atlas, axis, cervical vertebrae 3–6, 4 caudal vertebrae, left and right femora, left and right tibiae, left and right fibulae, left and right calcanea, left and right astragali, left and right cuboids, left ectocuneiform, right navicular, left and right metatarsi II–V, 6 first phalanges, 3 second phalanges, and 3 third phalanges; F:AM 49461, right ramus, right calcaneum, partial right scapula, right metatarsi III–V, left metatarsi II–III, partial left metatarsus IV; F:AM 49466, right and left rami; F:AM 49462, left ramus; F:AM 49465, right and left rami; F:AM 49463, partial right ramus; F:AM 49469, partial right ramus; F:AM 49457, right ramal fragment; F:AM 63178, left C^1; F:AM 63184, right C_1; F:AM 72826, left radius, distal ulna, right metacarpi II–V, 1 sesamoid, 4 first phalanges, 4 second phalanges, 3 third phalanges; F:AM 72827, left distal humerus; F:AM 63188, left distal radius; F:AM 63185, left metacarpus II; F:AM 72829, left metacarpus V; F:AM 72728, right distal tibia; F:AM 72728A, left distal tibia; F:AM 63177A, left calcaneum; F:AM 72832, right calcaneum; F:AM 72832A, left astragalus; F:AM 63187, right metatarsus II; F:AM 63189, right metatarsus IV; F:AM 72830, right metatarsus IV; F:AM 63177, right proximal metatarsus IV; F:AM 63186, right metatarsus V; F:AM 72831, right metatarsus V; F:AM 63176, 1 first phalanx, 2 second phalanges, 1 third phalanx; F:AM 63177B, first phalanx; F:AM 63179, first phalanx; F:AM 63181, first phalanx; F:AM 63190, first phalanx.

DESCRIPTION.—Hibbard (1937:460) designated a small, slender ramus (KUVP 3608) from Edson Quarry as the type of *Leptocyon shermanensis.* Additional material from Edson, a few specimens in the University of Kansas collections, and several more in the Frick Collection (F:AM), considerably expand the topotypic sample. Of particular interest is a lower jaw (F:AM 49456) and an associated pair of hindlimbs. The ramus is slightly larger than Hibbard's type, but still slender and

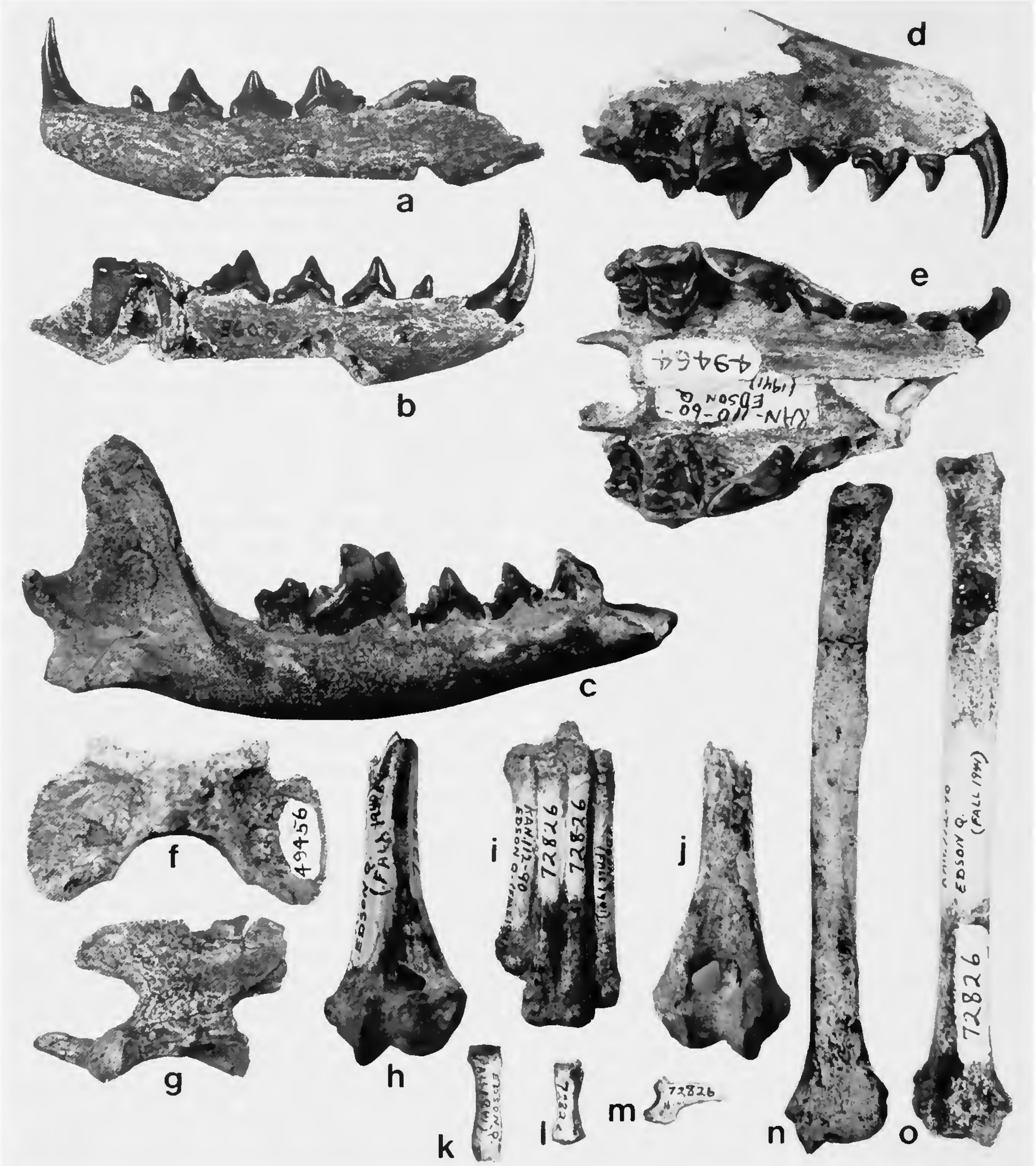

FIGURE 6.—*Canis davisi*: *a,b*, holotype, KUVP 3608, right ramus, lingual and lateral views; *c*, F:AM 49456, right ramus, lateral view; *d,e*, F:AM 49464, partial palate, right lateral and occlusal views; *f*, F:AM 49456, atlas, dorsal view; *g*, F:AM 49456, axis, lateral view; *h,j*, F:AM 27827, distal left humerus, anterior and posterior views; *i*, F:AM 72826, right metacarpus II–V, anterior view; *k*, F:AM 72826, first phalanx, anterior view; *l*, F:AM 72826, second phalanx, anterior view; *m*, F:AM 72826, third phalanx, lateral view; *n,o*, F:AM 72826, left radius, posterior and anterior views (× 1.0).

FIGURE 7.—*Canis davisi*: *a,b*, F:AM 49456, left tibia, anterior and lateral views; *c*, F:AM 49456, left fibula, lateral view; *d,e*, F:AM 63177A, left calcaneum, anterior and medial views; *f,g*, F:AM 72832A, left astragalus, anterior and lateral views; *h,i*, F:AM 49456, right cuboid, anterior and lateral views; *j*, F:AM 49456, right navicular, proximal view; *k*, F:AM 49456, right metatarsus II–V, anterior view; *l*, F:AM 49456, first phalanx, anterior view; *m*, F:AM 49456, second phalanx, anterior view; *n*, F:AM 49456, third phalanx, lateral views (× 1.0).

tapering toward the symphysis with a gently curved ventral border. The tooth row is uncrowded, as in the type, with a generous C_1-P_1 diastema. The posterior accessory cusps of P_{3-4} are somewhat stronger in the less worn F:AM 49456. The crown of M_1 in the type is badly broken. In other Edson specimens M_1 bears a large protoconid separated from the smaller paraconid by a deep, open notch. The metaconid is well developed. The talonid consists of an ento-

TABLE 2.—Measurements (cm) of dentition of *Canis davisi* (O.R. = observed range, $\bar{X}$ = sample mean, s.d. = standard deviation)

Element		No.	O.R.	$\bar{X}$	s.d.
C^1	length	2	0.57–0.61	0.59	
	width	2	0.37–0.46	0.41	
P^1	length	1	0.44		
	width	1	0.26		
P^2	length	1	0.88		
	width	1	0.28		
P^3	length	2	0.95–1.00	0.97	
	width	2	0.31–0.33	0.32	
P^4	length	3	1.62–1.71	1.67	
	width at protocone	3	0.70–0.73	0.71	
M^1	length	1	1.15		
	width	1	1.36		
M^2	length	1	0.66		
	width	1	1.01		
P^1-M^2	length	1	5.93		
dP^3	length	1	0.92		
	width at protocone	1	0.55		
dP^4	length	1	0.71		
	width	1	0.70		
C_1	length	2	0.59–0.64	0.61	
	width	2	0.44–0.51	0.47	
P_1	length	3	0.37–0.41	0.39	
	width	3	0.20–0.25	0.22	
P_2	length	3	0.84–0.88	0.86	
	width	3	0.29–0.31	0.30	
P_3	length	4	0.95–1.03	1.01	0.02
	width	5	0.30–0.35	0.31	0.02
P_4	length	4	1.03–1.12	1.07	0.04
	width	4	0.38–0.49	0.42	0.04
M_1	length	6	1.66–1.79	1.69	0.04
	width	6	0.60–0.67	0.65	0.02
M_2	length	5	0.80–0.90	0.84	0.04
	width	6	0.54–0.58	0.55	0.01
M_3	length	1	0.35		
	width	1	0.34		
dP_2	length	1	0.51		
	width	1	0.14		
dP_3	length	1	0.66		
	width	1	0.19		
dP_4	length	1	1.08		
	width	1	0.41		

conid and a slightly larger hypoconid with no connecting crest. A small accessory cusp occurs anterior to the entoconid. The M_2 bears a strong anterointernal cingulum. Only one M_3 is present in the sample; it is small, single-rooted, and positioned at the base of the ascending ramus.

TABLE 3.—Measurements (cm) of postcrania of *Canis davisi* (O.R. = observed range, $\bar{X}$ = sample mean)

Element		No.	O.R.	$\bar{X}$
Atlas	length	1	2.63	
	width	1	4.80	
	height	1	1.69	
Axis	width at anterior condyles	1	2.07	
	height	1	2.53	
Humerus	distal width	1	2.35	
Radius	length	1	11.64	
	distal width	1	1.78	
Metacarpus II	length	1	4.45	
Metacarpus III	length	1	4.83	
Metacarpus IV	length	1	4.75	
Metacarpus V	length	2	3.91–3.98	3.94
First phalanx	length	2	2.02–2.07	2.04
Second phalanx	length	2	1.41–1.43	1.42
Third phalanx	length	2	1.25–1.30	1.27
Tibia	distal width	2	1.66–1.72	1.69
Calcaneum	proximodistal	4	3.37–3.68	3.52
Astragalus	proximodistal	2	2.13–2.16	2.14
Cuboid	proximodistal	1	1.40	
Metatarsus II	length	2	5.73–6.16	5.94
Metatarsus III	length	2	6.32–6.87	6.59
Metatarsus IV	length	2	6.46–6.51	6.48
Metatarsus V	length	3	5.79–6.10	5.99
First phalanx	length	2	2.41–2.42	2.41
Second phalanx	length	1	1.74	
Third phalanx	length	2	1.07–1.19	1.13

A partial palate (F:AM 49464), bearing right C^1-M^2 and left P^3-M^2, is not directly associated with a lower jaw, but it so obviously complements the lower dentition in size and morphology that there can be little doubt of its belonging to the same species. The canine is long, curved, and sharply pointed. The upper premolars are slender, like the lowers, but without as many accessory cusps. P^1 is small and single-rooted and bears a shallow posterior heel. Diastemata, fore and aft, isolate P^2, which is larger than P^1 and bears a stronger posterior heel. The primary cusp of P^3 is slightly higher than that of P^2 and its larger posterior heel is in contact with P^4. The high paracone and shorter metacone form the slender cutting edge of the upper carnassial. The protocone is reduced and anteriorly positioned about level with the low, sharp parastyle. The paracone of M^1 is larger than the metacone but the discrepancy is not so marked as in *Vulpes*. These cusps are laterally compressed and together form a sharp crest that roughly parallels the external cingulum. Both upper molars bear a marked parastyle, a strong protocone, and a smaller metaconule. The posterior placement of the broad hypocone results in the curved anterior and posterior borders of the crown. M^2 is more strongly curved than M^1.

The limb elements are long, straight, and slender. Their morphology is typically canid and suggests an animal of small coyote size.

DISCUSSION.—Merriam (1906:5, 6; 1911:242) described *Canis davisi* from the John Day basin of Oregon. The type specimen, a maxilla fragment bearing right M^{1-2}, was found as float on the Mascall Formation immediately below the Rattlesnake Formation. Thus, the type horizon is in doubt, although Shotwell (1970:73) assigned it definitely to the Rattlesnake. The material of *Leptocyon shermanensis* from Edson is referrable to *Canis davisi* (R.H. Tedford and B.E. Taylor, pers. comm., 1977). The upper molars from Edson are very slightly larger than the type of *C. davisi*, but correspond closely in all other characters. The material from the Hemphillian Little Valley fauna of Oregon, which Shotwell (1970:73) referred to *C. davisi*, is slightly larger than that from Edson. The proportions and curvature of the ramus, as well as the general morphology of the dentition, are similar in the two samples. However, the tooth row is more open, P^4 is more slender and blade-like and bears a small parastyle, and the metaconid of M_1 is not so strong in the Edson specimens.

Subfamily BOROPHAGINAE Simpson, 1945

Osteoborus cyonoides (Martin, 1928)

FIGURES 8, 9

Hyaenognathus cyonoides Martin, 1928:235.
Borophagus cyonoides.—Matthew and Stirton, 1930:173.
Osteoborus cyonoides.—Stirton and VanderHoof, 1933;177.

HOLOTYPE.—KUVP 3468, right ramus bearing I_{1-3}, C_1, P_2 alveolus, P_{3-4}, M_{1-2}, and M_3 alveolus.

TYPE-LOCALITY.—Edson Quarry, Sherman County, Kansas.

REFERRED SPECIMENS.—KUVP 3470, right partial ramus; F:AM 61640, skull and mandible; F:AM 61641, skull and mandible; F:AM 61642, palate and mandible; F:AM 61643, right maxilla; F:AM 61644, left maxilla; F:AM 61645, partial palate; F:AM 61646, right maxilla; F:AM 61647, left maxilla; F:AM 61648, right partial maxilla; F:AM 61649, partial braincase; F:AM 61650, partial palate; F:AM 61651, right partial ramus; F:AM 61652, right and left rami; F:AM 61653, right and left rami; F:AM 61654, right partial ramus; F:AM 61655, right ramus; F:AM 61656, left M_1; F:AM 61657, left ramus; F:AM 61658, right partial ramus; F:AM 98088, right and left partial rami; F:AM 104719, right M^2; F:AM 67646, associated radius, ulna, fibula, partial tibia, lumbar vertebra, first phalanx, and third phalanx; F:AM 67647, associated humerus, partial ulna, and partial radius; F:AM 67648, humerus and partial tibia; F:AM 67649, associated femur head, partial fibula, calcaneum, metapodial fragments, 4 first phalanges, and a second phalanx; F:AM 67650, partial humerus; F:AM 67650-A, partial humerus; F:AM 67650-B, partial ulna; F:AM 67651, femur; F:AM 67652, metacarpal IV; F:AM 67653, metacarpal IV; F:AM 67654, metatarsal II; F:AM 67656, metacarpal IV: F:AM 67656-A, metacarpal IV; F:AM 67657, calcaneum; F:AM 67657-A, astragalus; F:AM 67657-B, cuboid; F:AM 67657-C, 2 first phalanges; F:AM 67657-D, first phalanx; F:AM 67658, articulated vertebrae and ribs, including atlas and axis; F:AM 104716, lumbar vertebra; F:AM 104717, partial radius; F:AM 104718, axis.

DESCRIPTION.—Although the type of *Osteoborus cyonoides*, KUVP 3468, is the only member of the hypodigm to have appeared in the literature (Martin, 1928:235), there are also two excellent skulls with associated rami, several unassociated maxillae and rami, and a considerable number of postcranial elements in the American Museum Frick Collections from Edson. Matthew and Stir-

FIGURE 8—*Osteoborus cyonoides*, F:AM 61640: *a–c*, skull, dorsal, lateral, and occlusal views; *d,e*, rami, lateral and occlusal views (× 0.5).

ton (1930:173–178) and Dalquest (1969:5–8) have described in detail the osteology of *O. cyonoides* based upon the large sample of referred material from the Coffee Ranch Local Fauna in Texas. The following description augments the work of Matthew and Stirton, and Dalquest with data on material from the type-locality, in addition to providing a populational framework against which to compare the type ramus.

F:AM 61640 is the skull of a fully mature individual, probably a female. The M^2 is in place and exhibits moderate wear. Both zygomatic arches are incomplete and the sagittal crest, the nasals, and a few of the anterior teeth are broken. With these exceptions, the skull is undamaged and undistorted. The remaining skull, F:AM 61641, is from a very old individual, probably a male. It also is missing portions of the zygomatic arches and the sagittal and lambdoidal crests, and several anterior teeth. The tympanic bullae are broken and the skull has been crushed laterally, thereby exaggerating the frontal bulge characteristic of *Osteoborus* and *Borophagus*.

Both crania agree with the descriptions of Matthew and Stirton (1930:174, 175) and Dalquest (1969:5–7), but the Edson Quarry material is slightly smaller than that of Coffee Ranch. The Edson and Coffee Ranch skulls of *Osteoborus* share the following features: a shortened muzzle; bulging frontals; broad palate; narrow occipital region; well-rounded, prominent tympanic bullae; strong, sharply pointed postorbital processes; and large, wide glenoid fossae.

The high degree of individual variation observed in the Coffee Ranch *Osteoborus* is also quite evident in the Edson Quarry material. The upper premolars are particularly variable, not only in size and shape, but also in position. In F:AM 61641 the left P^{1-4} are all in alignment, but the right P^3 is twisted out of line. In F:AM 61640 P^{2-3} are so twisted that their long axes are almost perpendicular to that of P^1 or P^4. All of the 11 P^4's retaining a sufficiently unworn or undamaged antero-external corner bear a distinct parastyle. The protocone is very reduced, even in unworn teeth, and is rapidly obliterated with little wear. A prominent cingulum is present on the internal side of the carnassial blade, posterior to the protocone. M^1 is very large and robust with heavy, blunt cusps. M^2 is reduced in size, but still fully functional.

TABLE 4.—Measurements (cm) of skull and upper dentition of *Osteoborus cyonoides* (O.R. = observed range, $\bar{X}$ = sample mean, s.d. = standard deviation)

Element	No.	O.R.	$\bar{X}$	s.d.
Occipital condyle to anterior incisor alveolus	2	18.26–21.14	19.70	
Posterior palatine process to anterior incisor alveolus	1	10.05		
Minimum interorbital constriction	2	4.68–5.21	4.49	
Width across C^1	3	7.50–7.85	7.62	
Width across M^2	1	5.67		
Width across occipital condyles	3	3.63–4.16	3.86	
I^2 length	3	0.63–0.66	0.65	
width	3	0.57–0.61	0.59	
I^3 length	2	0.77–0.82	0.79	
width	2	0.78–0.84	0.81	
C^1 length	4	1.11–0.132	1.23	0.09
width	4	0.81–0.92	0.85	0.05
P^1 length	3	0.56–0.66	0.61	
width	3	0.41–0.46	0.43	
P^2 length	7	0.84–1.00	0.90	0.06
width	7	0.42–0.60	0.50	0.06
P^3 length	6	1.06–1.27	1.21	0.07
width	6	0.56–0.75	0.62	0.07
P^4 length	6	2.19–2.75	2.40	0.20
width at protocone	4	1.18–1.43	1.26	0.11
M^1 length	7	1.39–1.61	1.52	0.08
width	7	1.76–2.10	1.85	0.11
M^2 length	5	0.83–1.02	0.91	0.07
width	5	1.29–1.42	1.35	0.05
P^2-M^1 length	6	5.08–6.20	5.50	0.37
P^2-M^2 length	4	5.58–5.97	5.85	0.18
P^4-M^1 length	7	3.55–4.16	3.72	0.20
P^4-M^2 length	4	4.42–4.61	4.49	0.08

The type of *O. cyonoides* is from a very young adult exhibiting little wear on P_4. M_{1-2} are in place and followed by the M_3 alveolus. It is one of the smaller individuals in the Edson sample. The premolars are well spaced and in alignment, as opposed to some other Edson specimens in which the premolars are severely twisted (F:AM 61640). A ramal fragment (F:AM 61654) bearing C_1 (broken), P_2, M_1 very closely approximates the type for size, stage of wear, and arrangement of cusps.

The majority of the *Osteoborus* mandibles are deeper and heavier than that of the type. All of the lower incisors in the Edson sample have been worn almost to the base of the crown, with the exception of the type and F:AM 61653, in which

TABLE 5.—Measurements (cm) of ramus and lower dentition of *Osteoborus cyonoides* (O.R. = observed range, $\bar{X}$ = sample mean, s.d. = standard deviation)

Element		No.	O.R.	$\bar{X}$	s.d.
Anterior incisor alveolus to mandibular condyle		2	13.06–14.42	13.74	
Width of ramus below protoconid of M_1		10	1.33–1.70	1.52	0.10
Width of mandibular condyle		3	2.98–4.06	3.40	0.57
I_1	length	2	0.48–0.49	0.48	
	width	2	0.31–0.36	0.33	
I_2	length	3	0.53–0.60	0.56	0.03
	width	3	0.41–0.45	0.34	
I_3	length	4	0.56–0.70	0.61	0.06
	width	4	0.49–0.55	0.52	0.03
C_1	length	4	1.04–1.17	1.11	0.06
	width	4	0.85–0.99	0.92	0.07
P_2	length	6	0.66–0.77	0.70	0.04
	width	6	0.45–0.58	0.51	0.04
P_3	length	8	0.74–1.07	0.92	0.10
	width	8	0.50–0.75	0.62	0.07
P_4	length	10	1.49–1.83	1.62	0.10
	width	9	0.97–1.20	1.06	0.08
M_1	length	10	2.45–2.76	2.67	0.09
	width at metaconid	10	1.05–1.25	1.15	0.07
M_2	length	8	1.05–1.23	1.15	0.06
	width	8	0.76–0.92	0.83	0.05
M_3	length	2	0.70–0.77	0.73	
	width	2	0.60–0.65	0.62	
C_1-M_2	length	5	8.00–8.57	8.26	0.24
P_4-M_1	length	9	3.87–4.51	4.21	0.20
P_4-M_2	length	6	4.92–5.42	5.20	0.18

they exhibit only moderate wear. The lower incisors increase in size from I_1 through I_3, and I_3 still bears traces of the lateral accessory cuspules present in the type. The lower premolars are variable in size, position, and alignment. Of the 14 P_4's present, all have a stepped posterior face. The M_1 is a strong tooth with a large, crushing talonid. Evidence of shear is present only in young individuals, such as the type and F:AM 61654. Of 13 M_1's having an unbroken or sufficiently unworn medial face, all bear a well-developed metaconid. M_2 was present in 15 out of 18 rami with wear ranging from slight to extreme. M_3 was more rarely retained in the socket, being present in only four rami. All M_3's, however, exhibited wear and, as indicated by the manipulation of associated skulls and mandibles, it is M_3 that produces a distinct thegosis on the posterior face of M^2. This facet is large and concave posteriorly in the right M^2 of F:AM 61641.

As in the Coffee Ranch sample of *Osteoborus*, the Edson postcranial material is disproportionately low in relation to cranial remains. In the following paragraphs the Edson *Osteoborus* postcrania are compared with a sample of Pleistocene *Canis lupus* from the Frick Collection. Of the few vertebrae represented, only F:AM 104718, an axis, can be identified with confidence. The dorsal spinous process does not project so far anteriorly in *Osteoborus* as in *Canis*, but rather it projects further posteriorly in *Osteoborus*, well beyond the posterior zygopophyses. The width of the atlanto-articular condyles is comparable, but the centrum is much shorter in *Osteoborus*.

The humerus is represented by one almost complete specimen (F:AM 67647) and three distal halves. A humerus of *Canis*, with a head of comparable size, is longer and slimmer. The greater tuberculum of *Osteoborus* is not so large as in *Canis*, but the deltoid crest and the sigmoid curvature of the shaft are more pronounced. The medial epicondyle and, to a lesser extent, the lateral epicondyle are expanded, thus increasing the transverse width greatly over *Canis*. The olecranon fossa is not so deeply pocketed as in *Canis*, and a well-developed entepicondylar foramen is present.

FIGURE 9.—*Osteoborus cyonoides*: *a,b*, F:AM 67647, left humerus, anterior and posterior views; *c,d*, F:AM 67646, left ulna, anterolateral and posteromedial views; *e,f*, F:AM 67646, left radius, anterior and posterior views; *g*, F:AM 104718, axis, lateral view; *h*, F:AM 67652, metacarpus IV, anterior view; *i,j*, F:AM 67651, right femur, anterior and posterior views; *k,l*, F:AM 67648, left tibia, anterior and posterior views; *m*, F:AM 67646, fibula, medial view; *n*, F:AM 67649, right calcaneum, medial view; *o*, F:AM 67657A, right astragalus, anterior view; *p*, F:AM 67649, metatarsus II, anterior view; *q*, F:AM 67655A, metatarsus III, anterior view; *r*, F:AM 67656A, metatarsus IV, anterior view (× 0.5).

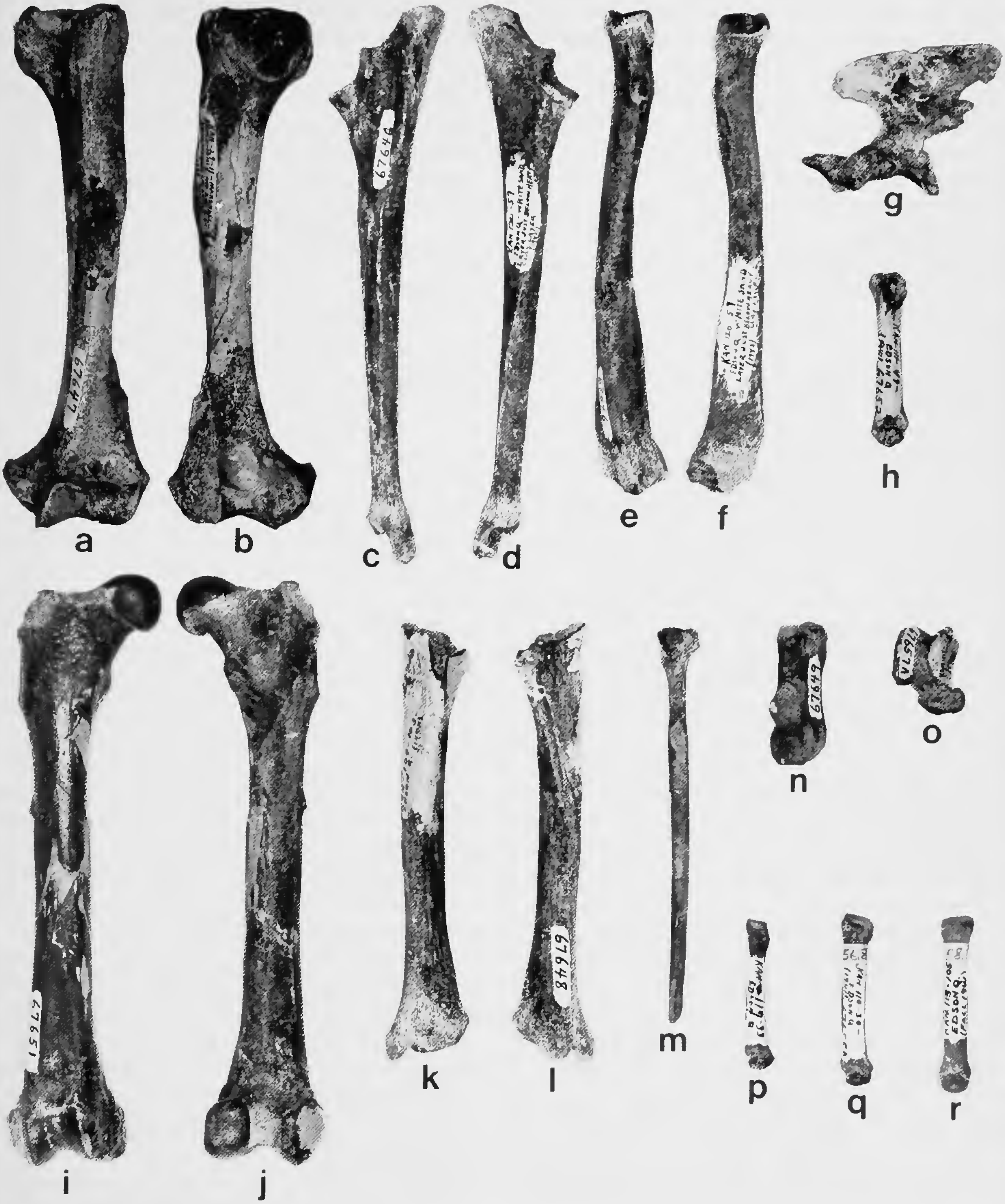
a
67647
b
c
67646
d
e
f
g
h
i
67651
j
k
l
67648
m
n
67649
o
p
q
r

TABLE 6.—Measurements (cm) of postcrania of *Osteoborus cyonoides* (O.R. = observed range, $\bar{X}$ = sample mean, s.d. = standard deviation)

Element	No.	O.R.	$\bar{X}$	s.d.
Axis				
tip of odontoid process to posterior surface of centrum	1	4.55		
antero-posterior of dorsal spinous process	1	5.50		
width at anterior condyles	1	3.50		
width at posterior zygopophyses	1	3.17		
Humerus				
length	1	17.18		
proximal end antero-posterior	1	4.61		
transverse	1	3.55		
distal end antero-posterior	4	1.35–1.60	1.46	0.12
transverse	2	4.72–4.93	4.82	
Radius				
length	1	15.92		
proximal end antero-posterior	2	1.55–1.56	1.55	
transverse	2	2.03–2.06	2.04	
distal end antero-posterior	1	2.69		
transverse	1	1.72		
Ulna				
antero-posterior of proximal surface of olecranon	1	3.06		
minimum antero-posterior of trochlear notch	1	2.26		
width below trochlear notch	2	0.95–1.03	0.99	
antero-posterior of shaft above lateral styloid process	2	1.41–1.50	1.45	
width of shaft above lateral styloid process	2	0.82–0.96	0.89	
Metacarpus IV				
length	2	5.15–5.77	5.46	
proximal end antero-posterior	2	1.16–1.17	1.16	
transverse	1	0.96		
distal end transverse at condyles	2	0.91–1.06	0.98	

Element	No.	O.R.	$\bar{X}$	s.d.
Femur				
head to distal condyles	1	19.48		
distal end antero-posterior	1	3.67		
transverse	1	3.95		
transverse of patellar surface	1	1.84		
Tibia				
distal end antero-posterior	2	1.73–1.80	1.76	
transverse	2	2.61–3.05	2.83	
Fibula				
distal end antero-posterior	1	1.30		
transverse	1	0.87		
Astragalus				
length	1	2.83		
transverse at tibial condyles	1	1.68		
minimum transverse constriction at neck	1	1.11		
Calcaneum				
length	1	4.75		
distal end antero-posterior	2	1.64–1.70	1.67	
transverse	2	1.34–1.49	1.41	
Metatarsus II				
length	2	4.70–4.98	4.84	
proximal end antero-posterior	2	1.26–1.28	1.27	
transverse	2	0.73–0.78	0.75	
distal end transverse at condyles	2	0.88–0.91	0.89	
Metatarsus III				
length	2	5.50–5.65	5.57	
proximal end antero-posterior	2	1.38–1.40	1.39	
transverse	2	0.99	0.99	
distal end transverse at condyles	2	0.85–0.89	0.87	
Metatarsus IV				
length	3	5.78–5.97	5.86	
proximal end antero-posterior	1	1.33		
transverse	1	0.84		
distal end transverse at condyles	2	0.90–0.94	0.92	

The ulna is represented by one proximal half, one distal half, and one specimen complete but for the olecranon. This element is much longer and thinner in *Canis*. The rugose fossa just distal to the radial notch is not so deep, and the lateral malleolus is much less elongated in *Osteoborus*.

The radius is represented by one proximal half, one distal half, and one specimen complete but for the disto-medial portion. The proximal outline of the head is more circular in *Osteoborus*, and the neck is more constricted. The radial tuberosity is larger, the shaft is shorter and more curved, and the distal articular surface is less transversely elongated than in *Canis*.

The metacarpus is represented by two metacarpi IV. For elements with distal condyles of comparable size, the shaft is much shorter in *Osteoborus*, but of approximately equal girth. The proximal articular surface is squarish, not antero-posteriorly elongated as in *Canis*.

The femur is represented by one fairly complete specimen. The neck is more constricted than in *Canis*, and the greater trochanter is not so high. The distal condyles are not so antero-posteriorly expanded as in *Canis*, and the patellar surface does not extend so far up the shaft. As in most postcranial elements, the shaft is proportionately shorter and heavier in *Osteoborus*.

The tibia is represented by two specimens that are missing the proximal end. The distal articular surface is transversely elongated in *Osteoborus*, particularly on the lateral side. The fibula is represented by a single specimen also missing the proximal end. The two small tubercles on the distal end are less distinct and more divergent than in *Canis*.

The astragalus is represented by only one specimen. The head is less laterally elongated, more rounded than in *Canis*, and the neck is shorter. Two calcanea are present, but both lack the sustentaculum. The distal end is elongated antero-posteriorly in *Osteoborus*, rather than transversely as in *Canis*.

The metatarsus is represented by one metatarsal II, two metatarsi III, and two metatarsi IV. The proximal articular surface of metatarsal II is not so antero-posteriorly elongated as in *Canis*, and the posterior end is not so sharply pointed. The lateral side of the proximal end is more deeply concave for articulation with metatarsal III in *Osteoborus*. The proximal articular surface of metatarsal IV is also not as antero-posteriorly elongated as in *Canis*, nor is the lateral side so deeply excavated.

Comparison of *Osteoborus cyonoides* with a late Pleistocene sample of *Canis lupus* indicates that the limbs of *Osteoborus* were shorter than those of a wolf, but were proportionately heavier and more robust. The distal limb elements were not as elongated as in *Canis lupus* or *C. latrans*. In *Canis* the olecranon fossa on the humerus is deeper, permitting greater extension of the elbow joint and hence, the entire forelimb. Moreover, in *Canis* the patellar surface extends further up the femoral shaft and the distal condyles are expanded antero-posteriorly, permitting greater flexion and extension at the knee. These modifications for increased length of stride are absent in *Osteoborus*, suggesting a less cursorial lifestyle for this genus. No articulated vertebral series or associated fore- and hindlimbs are known for *Osteoborus*; consequently, one can only speculate as to the degree of slope along the spine or the relative lengths of fore- and hindlimbs. However tempting it may be to project the hyaenoid parallels observed in the skull, jaws, and dentition onto the body proportions, Munthe (1979:33) maintained that the ratio of functional forelimb to hindlimb length in other borophagines was not indicative of a sloping back.

DISCUSSION.—*Hyaenognathus pachyodon* was described by Merriam (1903:278) from Kern County, California. Martin (1928:235) referred the Edson Quarry borophagine dog to this genus and erected a new species, *H. cyonoides*. Two years later Matthew and Stirton (1930:173) transferred it to the genus *Borophagus* and referred to it the material from Coffee Ranch. Later, Stirton and VanderHoof (1933:175) erected a new genus, *Osteoborus*, designating *O. cyonoides* as the genotypic species.

The systematic history of the Borophaginae in general and of *Osteoborus* in particular has been rendered complex to the point of confusion by numerous synonymies and revisions. Richey (1979:107) offers a most helpful synopsis of published borophagine species, their previous taxonomic history, and holotypic provenience. Many of the species of *Osteoborus* are based upon single specimens or very small hypodigms. The Edson Quarry material of *O. cyonoides*, together with that of Coffee Ranch, forms one of the largest and most complete samples of any of the species of *Osteoborus*. The postcrania, unknown for many species, are particularly well represented. As Richey (1979) has demonstrated, many of the species of *Osteoborus* are separated by little more than temporal/geographic differences. Future investigation may well indicate that at least *O. secundus*, *O. direptor*, and *O. cyonoides* are conspecific.

Family URSIDAE Gray, 1825

Subfamily AGRIOTHERIINAE

Agriotherium species

FIGURES 10, 11

REFERRED SPECIMENS.—KUPV 3603, femur; F:AM 104723, partial C^1; F:AM 68229, partial humerus; F:AM 68230, partial radius; F:AM 49477, partial ulna; F:AM 68231, partial ulna; F:AM 68233, partial metacarpus III; F:AM 104720, partial metacarpus IV; F:AM 104721, partial metapodial.

DESCRIPTION.—C^1 is large and robust. The root is missing as is a fragment from the postero-internal quadrant near the base of the crown. An antero-internal ridge extends from the base of the crown halfway to the tip. In *Agriotherium* and *Indarctos* a second ridge is present on the middle of the posterior face of the crown. *Ailuropoda* also has two ridges, although the anterior one is much more centrally positioned. If the posterior ridge was ever present in the Edson C^1, it was obliterated by wear, but in all else the tooth compares well with canines in the sample of *Agriotherium* from the late Hemphillian Old Cabin Quarry, Quiburis Formation, Arizona. No ridges are present in *Arctodus* or *Ursus*.

The humerus lacks the proximal third and the internal half of the distal articular surface. The posterior surface of the lateral epicondyle is broad in the Edson Quarry specimen, as in *Agriotherium* and *Ailuropoda*. Primitively it is narrower, as in *Ursus*, *Hemicyon*, and *Ursavus*.

The radius is missing the distal third. As in *Agriotherium*, *Indarctos*, *Arctodus*, *Hemicyon*, and possibly *Ursavus*, the proximal surface is not expanded to greatly overhang the shaft, as in *Ursus* and *Ailuropoda*. The shaft exhibits relatively little curvature. The tuberosity on the posterior face of the proximal end is enlarged, as in *Ailuropoda* and *Agriotherium*. Primitively it is small, as in *Hemicyon* and *Ursus*, and possibly *Ursavus*. Even in such a large form as *Arctodus*, the tuberosity is smaller in relation to the shaft. The radius appears comparable to, but slightly smaller than, the radius from Sherman County, Nebraska, which was referred to *Agriotherium* by Schultz and Martin (1975:50).

Two ulnae of greatly disparate dimensions occur in the Edson Quarry sample. The smaller ulna consists of the central portion of the shaft. The distal end is missing entirely and only a small portion of the proximal articular surface remains. In size and proportions this ulna resembles that of *Machairodus*, also represented in the Edson Quarry Local Fauna. It may be separated from that of *Machairodus* by the shape of the shaft approximately one quarter of the length from the distal end. In the bear the shaft is rounded, whereas in the cat it is distinctly triangular in cross section. The larger ulna consists of the proximal two-thirds and is missing the coronoid process. The semilunar notch is shallow and wide.

Metacarpal III is missing the distal condyle. It is slender and exhibits little curvature. The proximal articular surface forms an elongated triangle. The internal and external surfaces are not deeply excavated.

Metacarpal IV also lacks the distal end. The shaft is heavy and elongated with many rugose areas for muscle attachment. The external surface is more deeply concave than the internal surface. The proximal articular surface is smoothly convex antero-posteriorly.

The femur is very long and slender. Only a small portion of the internal distal condyle is missing. The head does not extend far above the greater trochanter in *Agriotherium*, *Ailuropoda*, and *Hemicyon*, but does in *Arctodus* and *Ursus*. The femur of *Ursavus* is unknown. The lesser trochanter is large in *Agriotherium*, *Ailuropoda*, and *Hemicyon* and reduced in *Arctodus* and *Ursus*. The shaft is long, slender, and exhibits a slight sigmoid curvature, as in *Hemicyon*, rather than straight, as in *Ursus*, *Ailuropoda*, and *Arctodus*. This may be due to the greater degree of plantigrady present in the latter three genera. The femur, like the smaller of

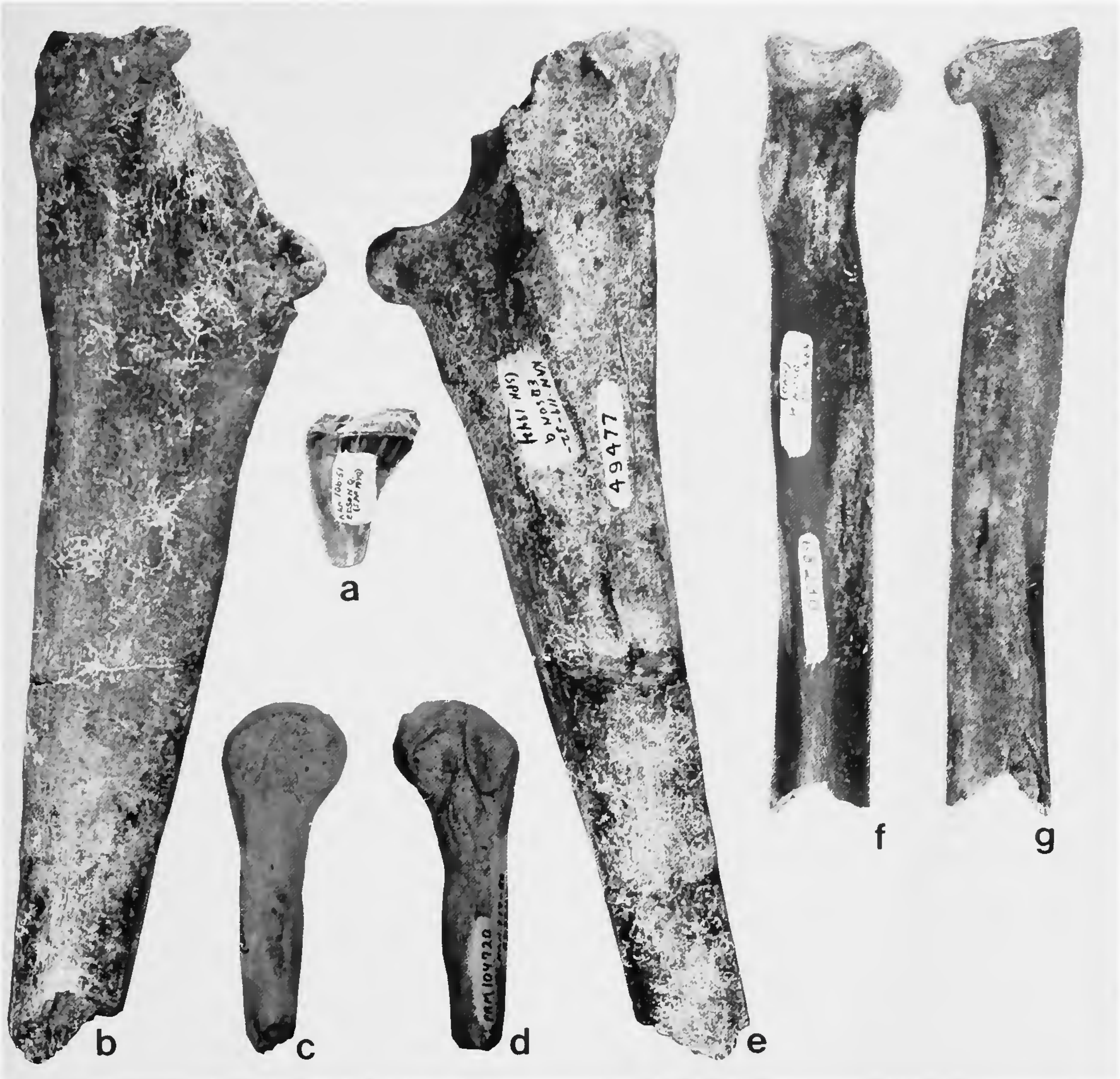

FIGURE 10.—*Agriotherium* species: *a*, F:AM 104723, left C^1, lateral view; *b,e*, F:AM 49477, right proximal ulna, posteromedial and anterolateral views; *c,d*, F:AM 104720, proximal metacarpus IV, lateral and medial views; *f,g*, F:AM 68230, right radius, anterior and posterior views (× 0.5).

the two ulnae, may be easily confused with the femur of *Machairodus*. The primary differences are (1) the head of the femur is approximately level with the greater trochanter in *Machairodus*, whereas in the bear, the head extends somewhat above it; (2) the patellar surface is wider in the bear and the proximal border is clearly defined and transverse to the long axis, whereas in *Machairodus* the patellar surface is narrower and has a poorly defined proximal border.

The extremely wide range of variation in size in the Edson ursid material may be attributed to

FIGURE 11.—*Agriotherium* species, KUVP 3603, left femur: *a*, anterior view; *b*, posterior view × 0.33.

sexual dimorphism. Such marked disparity in size between sexes is observable not only in most of the extant bears, but in such ursid fossil assemblages as those of the Redington locality, Quiburis Formation, and the Wikieup locality, Big Sandy Formation, Arizona. The humerus, the radius, the smaller ulna, the third metacarpus, and the femur form a homogenous size-grouping and are tentatively identified as female. The larger ulna, the fourth metacarpus, and the distal metapodial fragment may be labeled as male.

DISCUSSION.—In the late Miocene the hemicyonines, the giant bear-dogs of Eurasia and North America, were well on the way to extinction and were being replaced by members of the Ursidae. *Agriotherium* is one of the first ursid genera to appear in North America, and together with its contemporary, *Indarctos*, achieved a holarctic distribution during the Pliocene.

Agriotherium and *Indarctos* belong to a group of ursids characterized by a short, broad skull and long limbs. *Arctodus*, largest of the short-faced bears, became widespread in the North and South American Pleistocene, and is currently thought to be most closely related to the extant, South American spectacled bear, *Tremarctos*. If the premasseteric fossa is considered to be a derived character, its presence unites *Agriotherium*, *Arctodus*, and *Tremarctos*. The presence of a parastyle on P^4 is almost certainly apomorphic for ursids and if it has not been developed independently, its presence unites *Agriotherium*, *Indarctos*, and *Ailuropoda*. It is interesting to speculate upon the possibility of deriving both *Ailuropoda* and *Tremarctos* from a mid-Pliocene *Agriotherium/Indarctos* stock. This theory is partially supported by karyological studies (Wurster and Benirschke, 1968:373; Wurster, 1968, fig. 1; Todd and Pressman, 1968:105) that indicate that *Ailuropoda* and *Tremarctos*, two of the most aberrant and geographically disparate ursids, are closely related.

Indarctos may be separated from *Agriotherium* by virtue of the elongation of the talon on M^2 and absence of the premasseteric fossa. The Edson sample does not contain an M^2, let alone a ramus; therefore, an identification based upon these characters is not practicable. Size alone is a character of little value due to the considerable overlap between the two genera; however, metapodial proportions appear to be useful in separating them. *Agriotherium* is more digitigrade, with longer, more slender metapodials; whereas *Indarc-*

TABLE 7.—Measurements (cm) of *Agriotherium* species

Element		Measurements	
C^1		F:AM 104273	
length		3.25	
width		2.37	
Radius		F:AM 68230	
proximal articular surface	antero-posterior	3.43	
	transverse	4.40	
Ulna		F:AM 49477	F:AM 68231
antero-posterior at level of radial notch		5.10	
antero-posterior below radial notch		8.33	
width below radial notch		3.42	2.43
Metacarpus III		F:AM 68233	
proximal end	antero-posterior	3.06	
	transverse	1.80	
Metacarpus IV		F:AM 104720	
proximal end	antero-posterior	3.90	
	transverse	2.58	
Femur		KUVP 3603	
length		41.24	
proximal end	transverse	9.80	
distal end	transverse	8.07	
width at patellar surface		3.98	

tos is more plantigrade, with shorter, more massive metapodials. The Box T, Pit 1 locality, Higgins area, Lipscomb County, Texas, has produced, in addition to an *Indarctos* M^2 and assorted postcrania, a fourth metacarpus. The proximal end of this bone is very close in size to that of the Edson Quarry metacarpus IV; however, the Edson Quarry specimen is longer by the length of the distal condyle. Based upon the metapodial proportions and the considerable resemblance to the Redington, Arizona, material, I have referred the Edson ursid specimens to *Agriotherium*.

Family MUSTELIDAE Swainson, 1835

Subfamily GULONINAE Miller, 1912

Plesiogulo marshalli (Martin, 1928)

Brachypsalis marshalli Martin, 1928:233.
Plesiogulo marshalli.—Hibbard, 1934:247.

HOLOTYPE.—KUVP 3464, right ramus with P_{3-4}, M_1 and alveoli of I_1-P_2 and M_1, and skull fragments bearing the glenoid fossae.

TYPE-LOCALITY.—Edson Quarry, Sherman County, Kansas.

REFERRED SPECIMENS.—KUVP 3465, right P^4-M^1; KUVP 3467, right ramus with dP_{3-4}, M_{1-2}; KUVP 3606, right ramus with C_1, dP_4,M_1; F:AM 49479, mandible with right C_1-P_2, dP_4, P_4(germ), M_1 and left C_1-P_2, dP_3; F:AM 104724, left C_1; F:AM 67650-A, right partial humerus.

DISCUSSION.—In addition to the holotype of *P. marshalli*, Edson Quarry has produced three deciduous dentitions representing the only known juveniles of *Plesiogulo*. The very similar stage of wear in the immature râmi suggests that they were possible litter mates. Detailed description, discussion, and illustration of the Edson Quarry wolverine is contained in Harrison (1981) and so is not repeated herein.

Subfamily MELINAE Burmeister, 1850

Pliotaxidea nevadensis (Butterworth, 1916)

FIGURE 12*a*

Taxidea nevadensis Butterworth, 1916:21.
Pliotaxidea nevadensis.—Hall, 1944:11

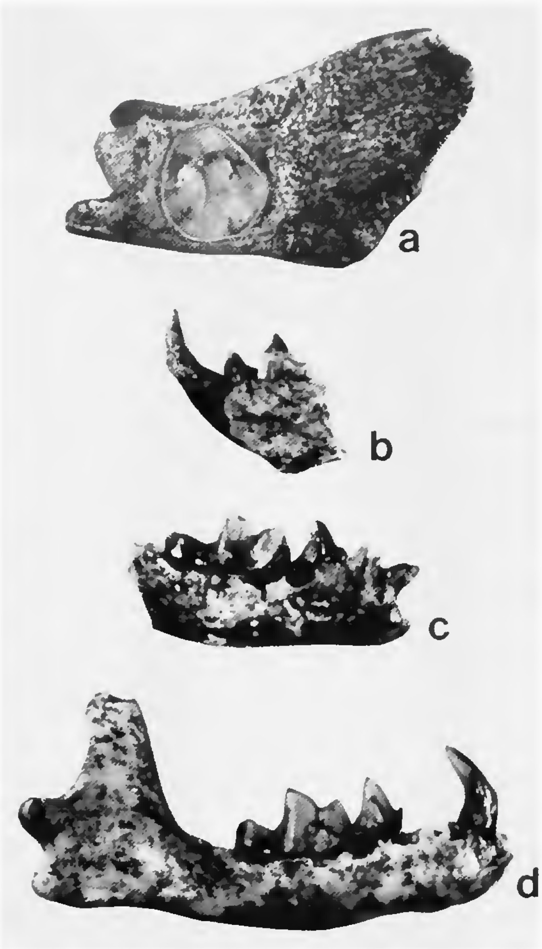

FIGURE 12.—*Pliotaxidea nevadensis*: *a*, SMM 13979-1, right ramal fragment bearing M_2, occlusal view. *Martinogale alveodens*: *b*, KUVP 3922, left ramal fragment bearing C_1,$P_{2,3}$, lateral view; *c*, holotype, KUVP 3473, right ramal fragment bearing P_3 (broken), P_4-M_1, lateral view; *d*, KUVP 3833, right ramus bearing C_1,P_4-M_1, lateral view (× 3.0).

REFERRED SPECIMENS.—SMM 13979-1, right M_2.

DESCRIPTION.—The single M_2 is in place in a fragment of the right dentary bearing the posterior portion of the alveolus of M_1 and a small piece of the coronoid process. The occlusal surface exhibits very little wear. The protoconid and hypoconid are the largest of the five cusps. The metaconid and entoconid are somewhat smaller and weakly separated. A small but distinct accessory cusp is present on the labial edge of the crown. Dimensions of the tooth are as follows: length = 4.8 mm; width = 5.2 mm.

DISCUSSION.—The M_2 in *Pliotaxidea* is far from diagnostic. However, the Edson Quarry specimen agrees more closely with the illustrations and description of *P. nevadensis* (Butterworth, 1916:21; Hall, 1944:11) than with those of *P. garberi* (Wagner, 1976:112). In particular, Wagner describes the M_2 of *P garberi* as bearing four tubercles, the largest being posterior and labial, as opposed to five in the Edson Quarry specimen, with the largest being lingual.

Subfamily MEPHITINAE Gill, 1872

Martinogale alveodens Hall, 1930

FIGURE 12*b*

Martinogale alveodens Hall, 1930:147.

HOLOTYPE.—KUVP 3473, right partial ramus bearing P_3 (broken), P_4-M_1.

TYPE-LOCALITY.—Edson Quarry, Sherman County, Kansas.

REFERRED SPECIMENS.—KUVP 3583, right P_3; KUVP 3833, right ramus bearing C_1, P_4-M_1; KUVP 3922, left partial ramus bearing C_1, P_{2-3}.

DESCRIPTION.—The type ramus and most of the referred specimens have been described in detail elsewhere (Hall, 1930:148; Dunkle, 1938:181–184). The sole undescribed specimen from Edson Quarry is a ramal fragment bearing C_1, P_{2-3} (KUVP 3922). This is the only known P_2 of *M. alveodens*. The tooth is very reduced and closely appressed to C_1. The long axis of P_2 diverges from the long axis of the tooth row by approximately 30°. There are no well-defined accessory cusps, although the antero-internal region of the cingulum is broadened slightly as in P_3 and P_4.

A derived feature of M_1 that was not discussed by either Hall or Dunkle is the presence of two slender accessory rootlets, one directly beneath the protoconid, the other beneath the metaconid.

DISCUSSION.—The type-locality of *M. alveodens* is listed by Hall (1930:147) as "eighteen miles southeast of Goodland, Sherman County, Kansas," the location of Edson Quarry. The locality listed by Dunkle (1938:181) is "the SW 1/4 of

TABLE 8.—Measurements (cm) of *Martinogale alveodens*

Element	Measurements	
Ramus	KUVP 3833	KUPV 3473
length	20.20	
depth at anterior base of M_1	3.20	3.50
P_2	KUVP 3922	
length	1.96	
width	1.04	
P_3	KUVP 3922	
length	2.06	
width	1.29	
P_4	KUVP 3833	KUVP 3473
length	2.90	2.90
width	1.67	1.45
M_1	KUVP 3833	KUVP 3473
length	5.27	5.72
width at metaconid	2.56	2.16

Sec. 26, T 10 S, R 38 W, Sherman County, Kansas," also Edson Quarry.

Hall (1930:147) considered *Martinogale* as a possible ancestor of *Mustela.* Dunkle (1938:181) indicated a greater similarity between *Martinogale* and *Spilogale.* I agree with Dunkle as regards the mephitine affinities of *Martinogale.* Such derived characters as the two accessory rootlets on M_1 and the enlarged metaconid support a close relationship of *Martinogale* to the extant mephitines, *Spilogale*, *Conepatus*, and *Mephitis.* These same two characters serve to differentiate *Martinogale* from *Pliogale*, which possesses only an external rootlet and a smaller, more posteriorly placed metaconid.

The only other species contained within *Martinogale* is *M. nambiana* from New Mexico (Hall, 1930:148). I have examined the type (USNM 1038), which consists of a ramal fragment bearing the posterior alveolus of P_2, both alveoli of P_3, P_4, and the anterior lobe of M_1. The posterior cingulum on P_4 is expanded into a shelf in *M. nambiana*, whereas in *M. alveodens* the posterior cingulum of P_4 is narrow. The overall structure of P_4 supports the referral of the Edson Quarry material and the New Mexico specimen to separate species. However, the limited data obtainable from the type of *M. nambiana* could as readily result in its referral to the genus *Pliogale.*

Family FELIDAE Gray, 1821

Subfamily MACHAIRODONTINAE Gill, 1872

Tribe METAILURINI Beaumont, 1964

Adelphailurus kansensis Hibbard, 1934

FIGURES 13, 14

Adelphailurus kansensis Hibbard, 1934:243.

HOLOTYPE.—KUVP 3462, anterior portion of skull with dentition missing only right M^1.

TYPE-LOCALITY.—Edson Quarry, Sherman County, Kansas.

REFERRED SPECIMENS.—F:AM 62224, partial humerus with associated radius and ulna; F:AM 62225, radius; F:AM 62230, partial radius; F:AM 104740, first phalanx; F:AM 104741, first phalanx.

DESCRIPTION.—The holotype of *Adelphailurus kansensis* was described in considerable detail by Hibbard (1934:243–246). For the most part I concur with Hibbard; however, I disagree with his description of the upper canine. He maintained that *Adelphailurus* possesses only a posterior cutting edge on C^1, whereas an anterior cutting edge is indeed present, albeit less pronounced distally than in the proximal half.

The referred postcrania were not found in direct association with the type dentition. They are distinctly felid in appearance, but fall well below the size range of *Machairodus*, the only other felid in the Edson Quarry fauna. No postcrania of *Adelphailurus* have been previously described in the literature. The material is compared to another felid of similar size, *Puma concolor.* Individuals whose $P^{3,4}$ were of comparable size to those of *Adelphailurus* were selected for comparison.

The humerus is represented by one distal half. In *Adelphailurus* the distal end is more transversely expanded than in *Puma concolor.* The medial epicondyle is more expanded than the lateral epicondyle. The entepicondylar foramen is longer and wider in *P. concolor.*

Two complete radii and one partial radius are present in the sample. The head is set at a more

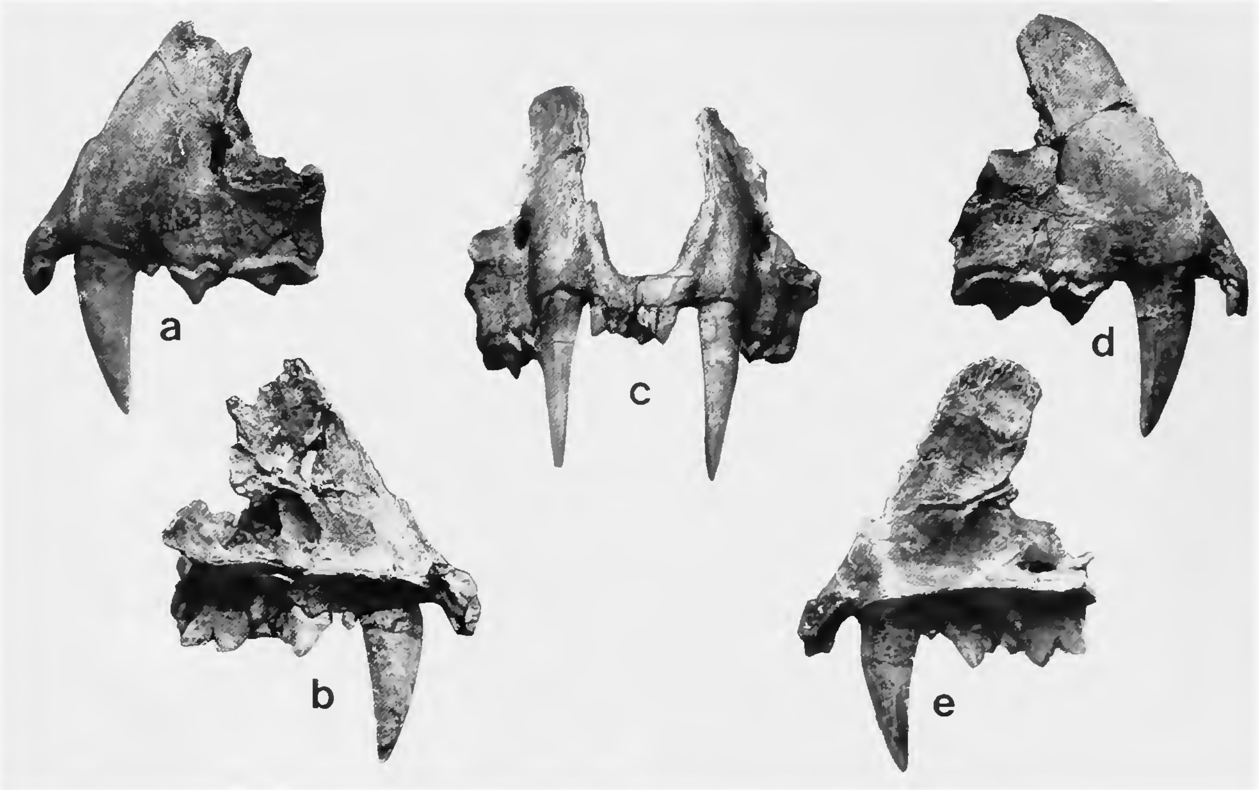

FIGURE 13.—*Adelphailurus kansensis*, holotype, KUVP 3462, right and left maxillae: *a,b*, left maxilla, lateral and lingual views; *c*, articulated maxillae, anterior view; *d,e*, right maxilla, lateral and lingual views (× 0.5).

acute angle in relation to the long axis of the shaft in *Adelphailurus.* The shaft is straighter in *Adelphailurus* with less transverse curvature. The distal ulnar articular surface is larger than in *P. concolor.*

The ulna is represented by a single specimen that is missing the distal end and part of the top of the olecranon process. The proximolateral portion of the trochlear notch extends further up onto the olecranon process in *Adelphailurus.* The interosseous crest is quite pronounced in *Adelphailurus.*

Several phalanges are present. The shaft is more curved in *Adelphailurus* than in the puma, and the distal condyles are longer antero-posteriorly and more deeply separated.

DISCUSSION.—Hibbard (1934:246) made note of some differences between *Metailurus* Zdansky from China and *Adelphailurus*. These two genera are, nevertheless, closely related and belong to a group of predominantly Eurasian felids that have been designated the Metailurini (Beaumont, 1964; Berta and Galiano, 1983) or the Metailurinae (Crusafont-Pairo and Aguirre, 1972) (Table 10). Beaumont placed the Metailurini within the Felinae, but Crusafont-Pairo and Aguirre felt that the group occupied a position intermediate between the Felinae and the Machairodontinae and, hence, warranted its own subfamily. Berta and Galiano placed the group within the Machairodontinae.

The Metailurini are the least specialized tribe of the Machairodontinae. The upper canine is long and laterally compressed, but not to the extent observed in the Machairodontini or the Smilodontini. The same relative degree of development applies to such characters as upper incisor enlargement, muzzle procumbency, accessory

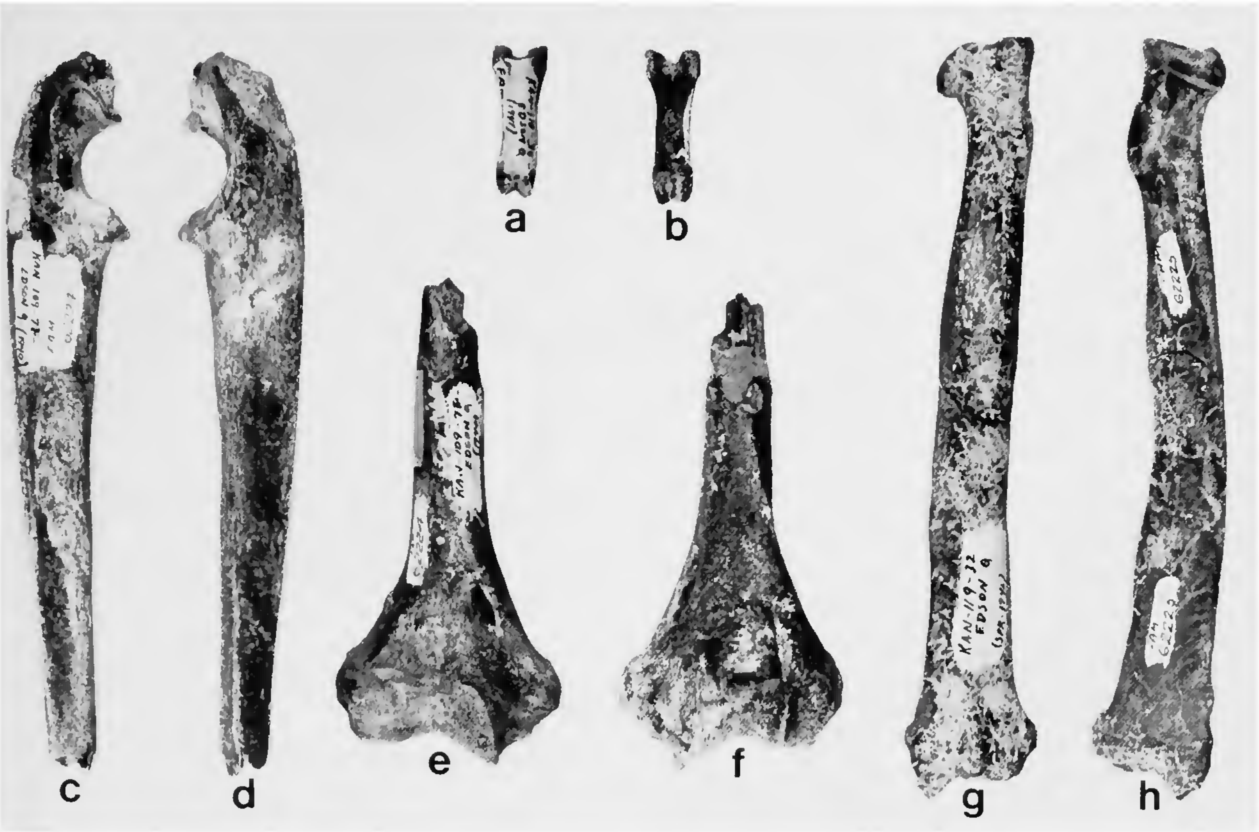

FIGURE 14.—*Adelphailurus kansensis*: *a,b*, F:AM 10741, first phalanx, anterior and posterior views; *c,d*, F:AM 62224, right ulna, anterolateral and posteromedial views; *e,f*, F:AM 62224, right distal humerus, anterior and posterior views; *g,h*, F:AM 62225, left radius, anterior and posterior views (× 0.5).

cusps on P^{3}_{3-4}, and coronoid process reduction. These primitive expressions of machairodontine characters in the Metailurini were misinterpreted as intermediate by Crusafont-Pairo and Aguirre and resulted in the invalid subfamily Metailurinae. Neither Beaumont nor Berta and Galiano offered a diagnosis for the Metailurini; however, two derived characters delineate this group. The upper canine of metailurines bears an anterointernal groove that ranges from fairly deep in *Adelphailurus* to shallow in *Therailurus piveteaui*. Contrary to Hibbard (1934:246), this groove is present in both *Metailurus major* and *M. minor*. The groove follows the contour of the anterior cutting edge and is quite distinct from the grooves observed in a feline C^1. The skull of metailurines lacks the massive occipital region of the machairodontine skull. The cranial profile of the metailurine skull is primitively rounded, curving gently through its apex in the frontals just dorsal to the orbits. In a more derived species of *Therailurus*, the skull assumes the more flattened profile and massive occiput typical of the Machairodontini.

Zdansky (1924:123, 131, 137) described three species from China, *Metailurus major*, *M. minor*, and *Dinofelis abeli*. Kretzoi (1929:1298) made *Machirodus orientalis* (Kittl, 1887:329) the type of *Pontosmilus*, described a new species, *P indicus*, and referred *Felis ogygia* (Kaup, 1832:156), *Machairodus hungaricus* (Kormos, 1911:182), and *Machairodus schlosseri* (Weithofer, 1888:233) to this genus. Piveteau (1948:104) designated *Felis diastemata* (Astre, 1929:203) as the type of *Therailurus*. Ewer (1955:588, 599) described *T. piveteaui* and transferred *Megantereon barlowi* (Broom, 1937:757) to *T. barlowi*. *Stenailurus teilhardi* was described by Crusafont-Pairo and Aguirre (1972:219).

The two species of *Metailurus* that Zdansky

TABLE 9.—Measurements (cm) of *Adelphailurus kansensis*

Element		Measurements		
Humerus		F:AM 62224		
distal end	minimum antero-posterior	1.72		
	transverse	6.05		
	maximum transverse of articular surface	3.98		
Radius		F:AM 62224	F:AM 62225	F:AM 62230
length		18.81	19.15	
proximal end	antero-posterior	1.87	2.00	1.85
	transverse	2.62	2.71	2.65
distal end	antero-posterior	2.35	2.26	
	transverse	3.28	3.32	
Ulna		F:AM 62224		
antero-posterior at middle of trochlear notch		1.92		
antero-posterior just distal to trochlear notch		2.69		
transverse just distal to trochlear notch		1.17		
First phalanx		F:AM 104740	F:AM 104741	
length		3.79	4.12	
proximal end	transverse	1.40	1.49	
distal end	transverse at condyles	1.10	1.10	

described probably represent two different lines within the metailurines, and *M. minor* may eventually be removed to a separate genus (H. Galiano, pers. comm., 1982). Subsequent workers have largely ignored the existence of the two species, indiscriminately ascribing to *M. major* characters peculiar to *M. minor. Adelphailurus* and *Stenailurus* retain P^2 and have not developed an anterior accessory cusp on P^3; however, they share very elongated upper canines that bear minute serrations. *Pontosmilus* most closely resembles *Adelphailurus* and *Stenailurus*, but has lost P^2 and has slightly larger upper incisors.

Viret (1951:89), Ewer (1955:594), and Piveteau (1961:795) were aware of the close relationship of *Metailurus* and *Therailurus. Metailurus major* and *T. diastemata* are very similar in size; both have lost P^2 and have a strong anterior accessory cusp on P^3. Their C^1 is not so elongated as in *Adelphailurus*, *Stenailurus*, or *Pontosmilus*, nor is it serrated. *Therailurus barlowi* from Sterkfontein and *T. piveteaui* from Kromdraai are among the youngest as well as the most derived of the metailurines; dates of 2.6 m.y. BP and 1.6 m.y. BP have been applied to their respective type-localities (Szalay and Delson, 1979:10). These species exhibit a trend toward a more typically machairodontine morphology: the upper incisor complex is increasingly enlarged and procumbent, the upper canines are long and finely serrated, the occipital region is enlarged, and P^3 accessory cusps are more robust.

Beaumont (1964, 1978), Crusafont-Pairo and Aguirre (1972), and Berta and Galiano (1983) have included *Dinofelis* with the metailurines. *Dinofelis* has moderately enlarged upper incisors, elongated C^1, and a low coronoid process reminiscent of machairodontines in general; however, its relationships within the group are uncertain. Thenius (1967:134) suggested that *Dinofelis* may be the senior synonym of *Therailurus.*

In the literature *Adelphailurus* has consisted solely of the type specimen. However, in addition to the referred material from the type locality, the Frick Collection at the American Museum

TABLE 10.—Previous classifications of the metailurines.

Beaumont, 1964	Crusafont-Pairo and Aguirre, 1972	Berta and Galiano, 1983
Family Felidae	Family Felidae	Family Felidae
Subfamily Felinae	Subfamily Metailurinae	Subfamily Machairodontinae
Tribe Metailurini	*Metailurus*	Tribe Metailurini
Metailurus	*Therailurus*	*Metailurus*
Therailurus	*Dinofelis*	*Therailurus*
Dinofelis?	*Stenailurus*	*Dinofelis*
		Stenailurus
		Adelphailurus
		Pontosmilus

also contains undescribed specimens from Optima, Oklahoma, Wikieup, Arizona, and Bone Valley, Florida. The material from Wikieup is particularly interesting in that there appear to be two species represented.

Tribe MACHAIRODONTINI Beaumont, 1964

Machairodus coloradensis Cook, 1922

FIGURES 15–18

Machairodus coloradensis Cook, 1922:7.

REFERRED SPECIMENS.—F:AM 104732, left premaxilla bearing I^{1-3}; F:AM 104731, partial left maxilla with P^3; F:AM 104728, left ramus bearing I_2-C_1, P_4; F:AM 104729, partial right ramus bearing P_4-M_1; F:AM 104730, right C_1; F:AM 104725, right radius, ulna, scapholunar, pisiform, magnum, metacarpi II–V, 5 first phalanges, 2 second phalanges, and 3 third phalanges; F:AM 104726, left tibia, fibula, calcaneum, astragalus, navicular, ectocuneiform, mesocuneiform, metatarsi II–V, 4 first phalanges, 2 second phalanges, and 2 third phalanges; F:AM 104727, femur; F:AM 104734, partial ulna; F:AM 104735, partial pelvis; F:AM 104736, partial pelvis; F:AM 104733, partial first phalange.

DESCRIPTION.—The skull and upper dentition of *Machairodus* is represented in the Edson Local Fauna only by a partial premaxilla bearing I^{1-3} and by a left maxilla fragment bearing P^3. The upper incisors are uncrowded; I^1 is slightly smaller than I^2 and both bear strong lingual cingula. The caniniform I^3 is larger still, and laterally compressed with serrated anterior and posterior ridges. The emerging P^3 is large with a high central cusp and a single anterior and two posterior accessory cusps.

The lower jaw and dentition are represented by an isolated C_1 and two partial rami, one bearing I_{2-3}, C_1, P_3 (broken), P_4 and the other bearing P_4-M_1. Both individuals are young adults as indicated by the barely emergent P_4. The lateral ramal flanges are smaller and more rounded than in *Dinobastis* (Meade, 1961, pls. 2, 3) or *Homotherium* (Ballesio, 1963, fig. 13; De Bonis, 1976:169). The lower incisors are slightly crowded and increase in size from I_1 (alveolus) through I_3. Only the tip of C_1 has erupted, and it is uncertain as to whether the tooth is rounded in cross section as stated by Cook (1922:8, 25) and by Dalquest (1969:16) or oval as illustrated in Burt (1931, Pl. 46) and Martin and Schultz (1975:57, fig. 4A). However, the isolated C_1 (F:AM 104730) is typically machairodontine, laterally compressed, and bearing strongly serrated anterolingual and posterior cutting edges. The double-rooted P_3 is broken at the level of the alveolus. In addition to a high central cusp and one anterior and one posterior accessory cusp, P_4 bears a very small cuspule on the midline of the strong posterior cingulum. M_1 is long and slender with well-developed shearing blades; no metaconid is present.

In the following descriptions of the postcrania of *Machairodus*, comparisons were made primarily with material of *Nimravides* from the early Hemphillian Sebastin Place (Savage Ranch), Decatur

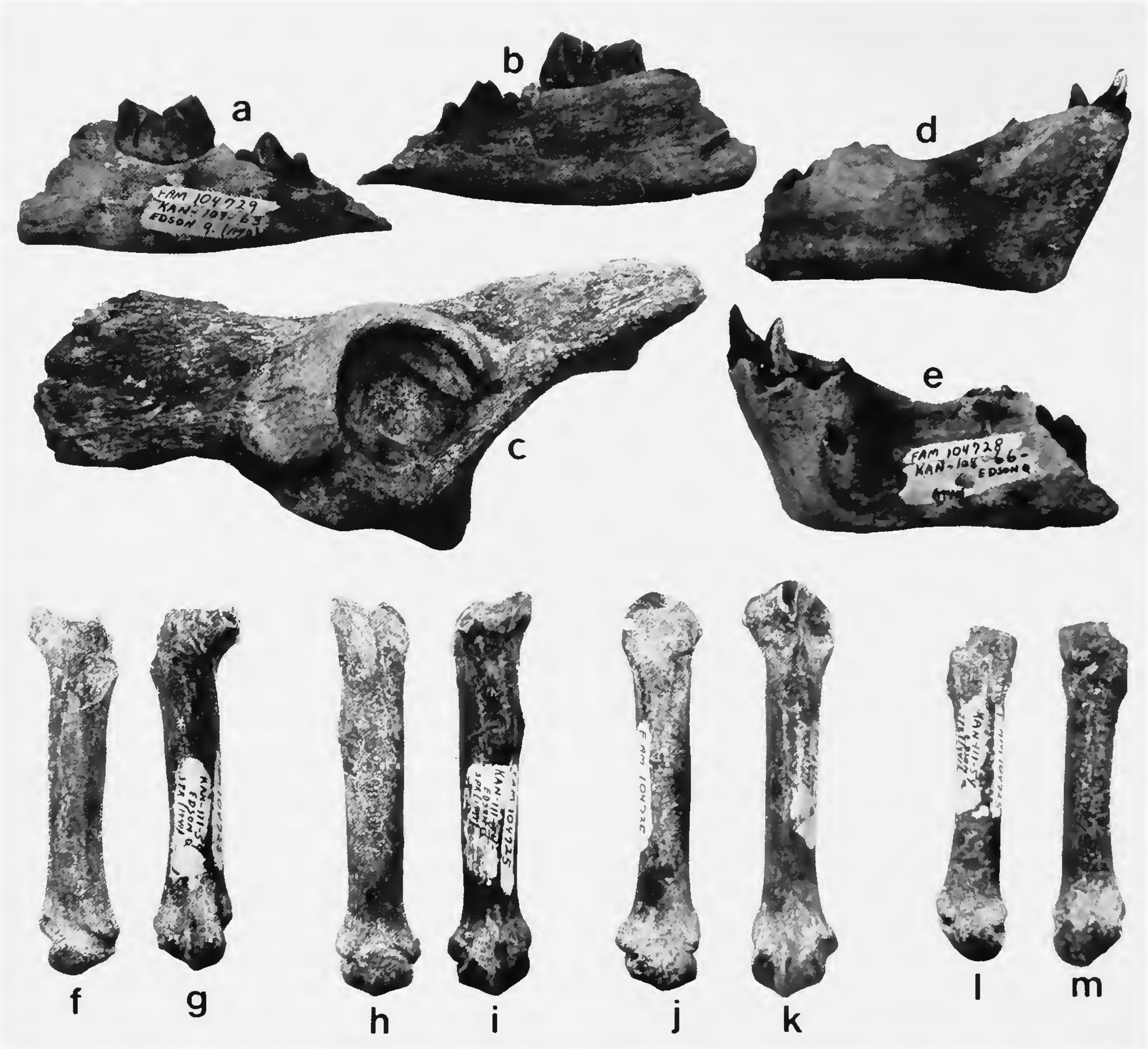

FIGURE 15.—*Machairodus coloradensis*: *a,b*, F:AM 104729, right ramal fragment bearing P_4-M_1, lateral and medial views; *c*, F:AM 104736, left innominate with acetabulum, lateral view; *d,e*, F:AM 104728, left ramal fragment bearing I_2-C_1, P_4 (emerging), medial and lateral views; *f,g*, F:AM 104725, right metacarpus II, anterior and posterior views; *h,i*, F:AM 104725, right metacarpus III, anterior and posterior views; *j,k*, F:AM 104725, right metacarpus IV, anterior and posterior views; *l,m*, F:AM 104725, right metacarpus V, anterior and posterior views (× 0.5).

County, Kansas, in the Frick Collection of the American Museum of Natural History. *Machairodus* and *Nimravides* have not been identified from the same fauna, but both are Hemphillian in age. Therefore, it is important to be able to differentiate between these two genera when confronted by remains of a large cat in a fauna that may be either early or late Hemphillian. This particular sample of *Nimravides* was selected because of its many associated cranial and postcranial elements including one almost complete skeleton (F:AM 104044).

TABLE 11.—Measurements (cm) of dentition and forelimb of *Machairodus coloradensis*

Element			Measurements
			F:AM 104732
I^1	length		0.89
	width		0.69
I^2	length		1.10
	width		0.89
I^3	length		1.30
			F:AM 104728
I$_2$	length		0.85
	width		0.76
I$_3$	length		1.08
			F:AM 104729
P$_4$	length		2.70
M$_1$	length		2.94
	width		1.27
Ramus thickness below M$_1$			1.74
Ulna			F:AM 104725
	distal end	antero-posterior	3.45
		transverse	3.25
Radius			F:AM 104725
	length		29.85
	proximal end	antero-posterior	3.20
		transverse	4.12
	distal end	antero-posterior	4.34
		transverse	6.10
	maximum midshaft diameter		2.97
	minimum midshaft diameter		2.37
Metacarpus II			F:AM 104725
	length		10.99
	proximal end	antero-posterior	2.93
		transverse	2.47
	distal end	antero-posterior	2.30
		transverse	2.46
Metacarpus III			F:AM 104725
	length		12.08
	proximal end	antero-posterior	2.68
		transverse	2.35
	distal end	antero-posterior	2.35
		transverse	2.55
Metacarpus IV			F:AM 104725
	length		11.80
	proximal end	antero-posterior	2.52
		transverse	2.18
	distal end	antero-posterior	2.29
		transverse	2.48
Metacarpus V			F:AM 104725
	length		9.76
	proximal end	antero-posterior	2.42
		transverse	1.86
	distal end	antero-posterior	2.13
		transverse	2.11

TABLE 12.—Measurements (cm) of hindlimb of *Machairodus coloradensis*

Element			Measurements
Femur			F:AM 104727
	length		33.80
	greater trochanter to head		8.45
	antero-posterior of head		3.89
	distal end	antero-posterior	7.12
		transverse	6.77
	transverse of intercondylar notch		1.74
Tibia			F:AM 104726
	length		29.50
	proximal end	transverse	7.07
	distal end	antero-posterior	3.31
		transverse	5.36
Calcaneum			F:AM 104726
	length		9.72
	maximum antero-posterior		4.37
	maximum transverse		4.00
Astragalus			F:AM 104726
	length		4.76
	maximum transverse		4.86
	minimum diameter of neck		2.62
	maximum diameter of head		3.13
Navicular			F:AM 104726
	maximum antero-posterior		3.73
	maximum transverse		2.95
Metatarsus II			F:AM 104726
	length		10.42
	proximal end	antero-posterior	2.86
		transverse	1.54
	distal end	antero-posterior	1.85
		transverse	1.84
Metarsus III			F:AM 104726
	length		11.85
	proximal end	antero-posterior	3.10
		transverse	2.26
	distal end	antero-posterior	1.89
		transverse	2.10
Metatarsus IV			F:AM 104726
	length		11.73
	proximal end	antero-posterior	2.52
		transverse	1.66
	distal end	antero-posterior	1.87
		transverse	1.78
Metatarsus V			F:AM 104726
	length		10.36
	proximal end	antero-posterior	1.57
		transverse	1.71
	distal end	antero-posterior	1.61
		transverse	1.64

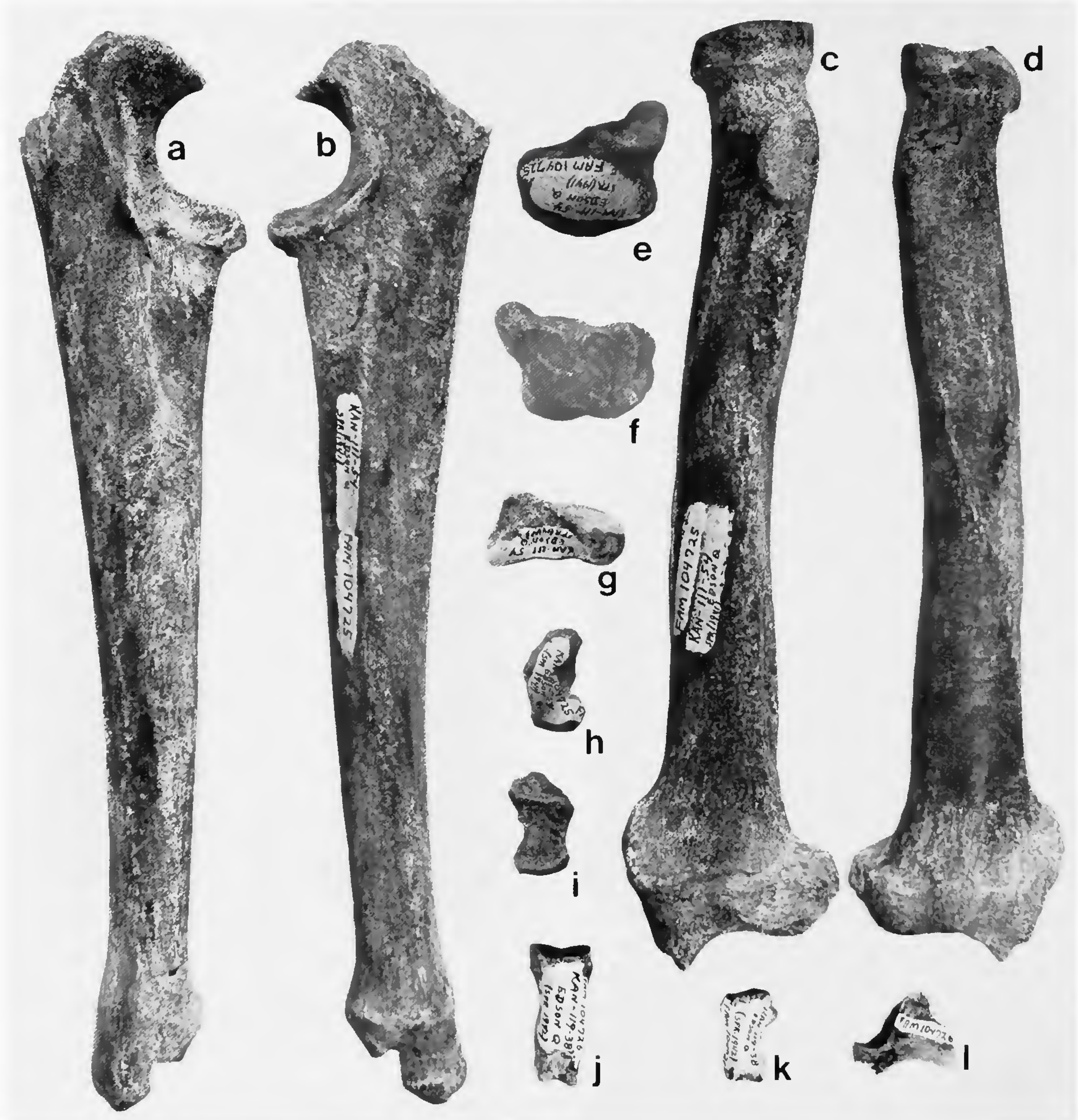

FIGURE 16.—*Machairodus coloradensis*: *a,b*, F:AM 104725, right ulna, anterolateral and posteromedial views; *c,d*, F:AM 104725, right radius, anterior and posterior views; *e,f*, F:AM 104725, right scapholunar, proximal and distal views; *g*, F:AM 104725, right pisiform, lateral view; *h,i*, F:AM 104725, right magnum, proximal and distal views; *j*, F:AM 104726, first phalanx, anterior view; *k*, F:AM 104726, second phalanx, anterior view; *l*, F:AM 104726, third phalanx, lateral view (× 0.5).

FIGURE 17.—*Machairodus coloradensis*: *a,b*, F:AM 104727, left femur, anterior and posterior views; *c,f*, F:AM 104726, left tibia, anterior and posterior views; *d,e*, F:AM 104726, left fibula, lateral and medial views (× 0.5).

The Edson Quarry sample contains many associated elements of a distal forelimb (F:AM 104725): a radius and ulna with scapholunar, cuneiform (triquetrum), pisiform, trapezium, magnum, metacarpi II–V, and a few phalanges. The shaft of the radius is more curved and the neck more constricted in *Machairodus* than in *Nimravides*. The attachment surface of the interosseous membrane is much more rugose and extensive in *Machairodus*. The proximal surface of the head of the radius is more circular in *Machairodus* and more oval in *Nimravides*. The two radii are of comparable length, but that of *Machairodus* is slightly heavier with larger proximal and distal ends. The Edson Quarry ulna is complete but for a portion of the olecranon. It is about the same length as that of *Nimravides*, but heavier and more triangular in cross section. The radial notch and the distal radial facet are larger in *Machairodus*, suggesting greater rotational mobility in the antebrachium. The styloid process is longer in *Machairodus*. The radial facet of the scapholunar extends further laterally, reflecting the larger size of the distal radius of *Machairodus*. The medial surface of the magnum is more deeply excavated in *Machairodus*. The remaining carpals and metacarpals are quite similar.

The pelvis is represented in the Edson Quarry sample of *Machairodus* by two left acetabula, each bearing portions of the three innominate bones. The acetabulum is hemispherical. The femora of *Nimravides* from the Sebastin Place were both longer than the femur of *Machairodus* from Edson Quarry, but other differences were subtle and somewhat equivocal. Several associated elements of a distal hindlimb (F:AM 104726) of *Machairodus* include tibia, fibula, calcaneum, astragalus, navicular, mesocuneiform, ectocuneiform, metatarsi II–V, and some phalanges. The elements of the hindlimb of *Machairodus* from Edson are consistently smaller than those of *Nimravides* from Sebastin Place, whereas the elements of the forelimb were of comparable size. The tibia is complete and bears a fragment of the proximal fibula on the lateral side of the proximal end. Even though the Edson tibia is shorter than that of *Nimravides*, the shafts are about equal in girth. The antero-lateral concavity at the proximal end, occupied largely by the *M. tibialis anterior*, is deeper in *Machairodus*. The lateral crest extends further distally in *Machairodus* and the medial malleolus is heavier. The anterior notch just lateral to the malleolus is deep in both genera. The fibula is missing all of the distal end; it is slender and straight in *Machairodus* as in *Nimravides*. The tarsals and metatarsals do not differ significantly from those of *Nimravides*.

DISCUSSION.—Cope (1887:1019) described the first North American species attributed to *Machairodus*, *M. catacopis*, based upon a partial mandibular symphysis. Cook (1922:7) later described material from Yuma County, Colorado, as *Machairodus* (*Heterofelis*) *coloradensis*. Specimens from the late Hemphillian Coffee Ranch Local Fauna were referred by Burt (1931:262) to *M. catocopis*. Dalquest (1969:13–25) made extensive comparisons of additional material from Coffee Ranch, including an almost complete skeleton, with specimens of *Smilodon californicus* Bovard, as well as illustrations from Merriam and Stock (1932). Matthew (1924:148) synonymized *M. coloradensis* with *M. catacopis*, but Martin and Schultz (1975:60) present evidence that the type of *M. catocopis* is referrable to *Nimravides*, thus resurrecting *M. coloradensis* as a valid species. They refer the material from Coffee Ranch to *M. coloradensis*, along with the type material from Colorado.

Kurten (1963:97) divided machairodontines into two tribes, the Homotheriini and the Smilodontini. Churcher (1968:272, 273) summarized the Smilodontini as having "more massive crania, relatively hypsodont and smooth-edged sabres of an oval cross-section, incisive teeth arranged in a transverse row, protoradix on the upper carnassial, and a heavier and more massive build," and the Homotheriini as having "lighter crania, less hypsodont and compressed sabres, incisive teeth separated from each other and arranged in an arc, no protoradix on the upper carnassial, both milk and permanent dentitions generally serrated when unworn, and a lighter and more lion-like skeleton." Berta and Galiano (1983) accepted Kurtén's Smilodontini, but enlarged the Machairodontini (Beaumont, 1964:840) to include *Ma-*

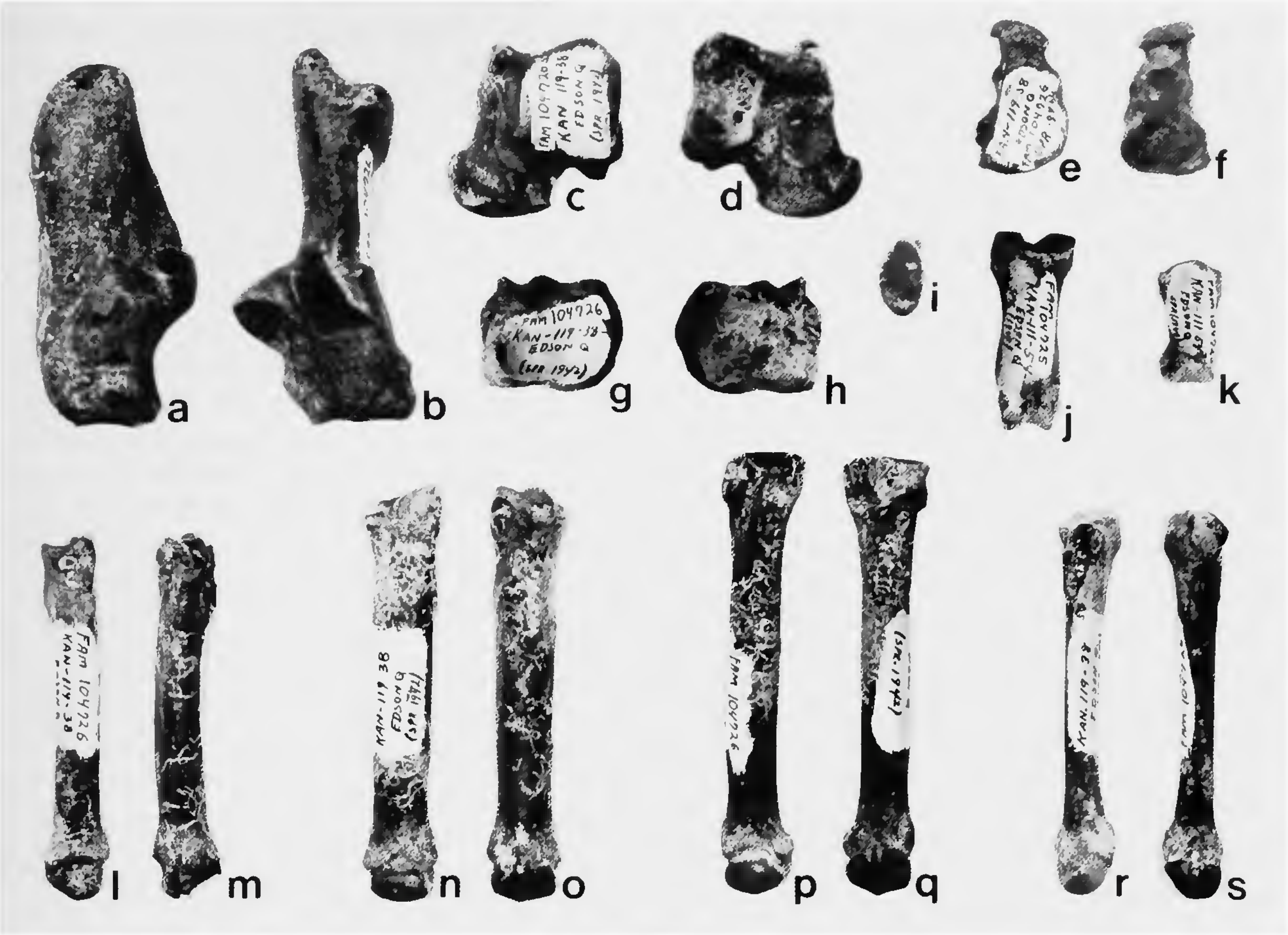

FIGURE 18.—*Machairodus coloradensis*, F:AM 104726, left tarsus: *a,b*, calcaneum, medial and anterior views; *c,d*, astragalus, anterior and posterior views; *e,f*, ectocuneiform, proximal and distal views; *g,h*, navicular, proximal and distal views; *i*, mesocuneiform, proximal view; *j*, first phalanx, anterior view; *k*, second phalanx, anterior view; *l,m*, metatarsus II, anterior and posterior views; *n,o*, metatarsus III, anterior and posterior views; *p,q*, metatarsus IV, anterior and posterior views; *r,s*, metatarsus V, anterior and posterior views (× 0.5).

chairodus, *Nimravides*, *Miomachairodus*, *Homotherium*, and *Dinobastis*. Based upon the almost complete skeleton from Coffee Ranch, Dalquest (1969:25) suggested that *Machairodus* would have had a large head and stout neck, a slender trunk, long, slender limbs, and relatively large feet and claws. The material from Edson Quarry does not contradict Dalquests's conception.

Conclusions

The 36 taxa of amphibians, reptiles, birds, and mammals comprising the Edson Quarry Local Fauna represent one of the largest and most diverse vertebrate faunas in the North American Hemphillian. The fauna was deposited in a series of fine sands within the Ogallala Formation of Sherman County, Kansas. Analysis of grain size and primary sedimentary structures suggests a low energy environment of deposition, probably that of a high, secondary channel in a braided stream system. The deposit of fossil material may represent the remains of carcasses accumulated, but not necessarily killed, by a spring flood and concentrated in a small channel.

Eight carnivorans are present in the Edson

Quarry Local Fauna. *Canis davisi* is a primitive dog of medium size. *Osteoborus cyonoides*, a large borophagine canid, is the most abundant carnivoran in the fauna. One C^1 and a few postcrania are referrable to *Agriotherium* species. Three genera of mustelids are present. *Plesiogulo marshalli*, a wolverine, is represented by three deciduous dentitions, in addition to the mature type ramus and two almost complete bacula. The two remaining mustelids are *Pliotaxidea nevadensis*, the rarest mammal in the fauna, and *Martinogale alveodens*, a small skunk. The two felids at Edson are *Adelphailurus kansensis*, a New World member of the Metailurini, and *Machairodus coloradensis*. The Edson sample contains the only known postcranial elements referrable to *Adelphailurus*.

Due to the discontinuous nature of the enclosing sediments and the absence of radiometrically datable strata (i.e., volcanic ash layers) and paleobotanical material, the age of the Edson Local Fauna, Late Hemphillian, has been determined on the basis of vertebrate faunal parameters. Edson compares well with the Late Hemphillian Coffee Ranch Local Fauna of Texas and with the Optima Local Fauna, a principal correlative. The fauna contains such typically Hemphillian taxa as *Megatylopus*, *Hemiauchenia*, *Osteoborus*, and *Machairodus*, in addition to the Eurasian immigrants, *Plesiogulo* and *Agriotherium*. The Edson Local Fauna is probably contemporaneous with the nearby Rhinoceros Hill Local Fauna.

Literature Cited

Adams, L.A., and H.T. Martin

1929. A New Urodele from the Lower Pliocene of Kansas. *American Journal of Science*, 17(102):504–520, figures 1–32.

1930. An Addition to the Urodele Fauna of Kansas from the Lower Pliocene. *University of Kansas Science Bulletin*, 19(14):289–297, plates 30–32.

Astre, G.

1929. Sur un Félin à particularités Ursoïdes des limons Pliocènes du Rousillon. *Bulletin de la Société Géologique de France*, 29:199–204, figures 1–3.

Ballesio, R.

1963. Monographie d'un *Machairodus* du Gisement Villafranchien de Seneze: *Homotherium crenatidens* Fabrini. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, new series, 9:1–129, figures 1–57, plates 1–4.

Beaumont, G. de

1964. Remarques sur la classification des Felidae. *Eclogae Géologicae Helvetiae*, 57:837–845.

1978. Notes complémentaires sur quelques Félidés (Carnivores). *Archives des Sciences*, 31(3):219–222, figures 1–2.

Bennett, D.K.

1978. Paleontology, Paleoecology, and Biostratigraphy of the Rhinoceros Hill Fauna (Hemiphillian: Latest Miocene) and Sedimentology of the Enclosing Ogallala Formation, Ash Hollow Member, Wallace County, Kansas. Masters thesis, Department of Geology, University of Kansas, Lawrence, Kansas.

Berggren, W.A., and J. VanCouvering

1974. The Late Neogene Biostratigraphy, Geochronology, and Paleoclimatology of the Last 15 Million Years in Marine and Continental Sequences. *Palaeogeography, Palaeoclimatology, and Palaeoecology*, 16(1, 2):1–216, figures 1–15.

Berta, A., and H. Galiano

In press. *Megantereon hesperus* (Felidae) from the Late Hemphillian of Florida. *Journal of Paleontology*.

Boellstorff, J.

1976. The Succession of Late Cenozoic Ashes in the Great Plains: A Progress Report. In *Guidebook to the 24th Annual Meeting of the Midwestern Friends of the Pleistocene*, 37–71, figures 1–8.

Breyer, J.A.

1981. The Kimballian Land-Mammal Age: Mene, Mene, Tekel, Upharsin (Dan. 5:25). *Journal of Paleontology*, 55(6):1207–1216, figures 1–5.

Broom, R.

1937. On Some New Pleistocene Mammals from Limestone Caves of the Transvaal. *South African Journal of Science*, 33:750–768, figures 1–8.

Burt, W.H.

1931. *Machaerodus catacopis* Cope from the Pliocene of Texas. *University of California Publications, Bulletin of the Department of Geological Sciences*, 20(7):261–292, plates 43–50.

Butterworth, E.M.

1916. A New Mustelid from the Thousand Creek Pliocene of Nevada. *University of California Publications, Bulletin of the Department of Geological Sciences*, 10(2):21–24, 1 figure.

Chaney, R.W., and M.K. Elias

1936. Late Tertiary Floras from the High Plains, with a Chapter on the Lower Pliocene Vertebrate Fossils from the Ogallala Formation (Lavern Zone) of Beaver County, Oklahoma. *Carnegie Institution of Washington Publication*, 476(I):1–72, figures 1–10, plates 1–7.

Churcher, C.S.

1968. The Affinities of *Dinobastis serus* Cope, 1893. *Quaternaria*, 8:263–275, 1 figure.

Conant, R.

1975. *A Field Guide to Reptiles and Amphibians of Eastern and Central North America.* 429 pages. Boston: Houghton Mifflin Company.

Cook, H.J.

1922. A Pliocene Fauna from Yuma County, Colorado, with Notes on the Closely Related Snake Creek Beds of Nebraska. *Proceedings of the Colorado Museum of Natural History*, 4(2):3–15, plates 1–14.

Cope, E.D.

1887. A Saber-Tooth Tiger from the Loup Fork. *American Naturalist*, 21:1019–1020.

Crusafont-Pairo, M., and E. Aguirre

1972. *Stenailurus*, félidé nouveau, du Turolien d'Espagne. *Annales des Paléontologie (Vertebres)*, 58(2):211–223, figures 1, 2, plate 1.

Dalquest, W.W.

1969. Pliocene Carnivores of the Coffee Ranch (Type Hemphill) Local Fauna. *Bulletin of the Texas Memorial Museum*, 15:1–43, figures 1–11, plate 1.

De Bonis, L.

1976. Un Felide a longues canines de la colline de Perrier (Puy-De-Dome): Ses Rapport avec les felines Machairodontes. *Annales des Paléontologie (Vertebres)*, 62(2):159–198, figures 1–13, plate 1.

Dunkle, D.H.

1938. A Lower Jaw of *Martinogale alveodens* Hall. *University of Kansas Science Bulletin*, 15(8):181–185, plate 21.

Elias, M.K.

1931. The Geology of Wallace County, Kansas. *Bulletin of the Kansas Geological Survey*, 18:1–254, figures 1–7, plates 1–42.

1937. Geology of Rawlins and Decatur Counties, with Special Reference to Water Resources. *Mineral Resources Circular of the Kansas Geological Survey*, 7:1–25, figures 1–4.

Ewer, R.F.

1955. The Fossil Carnivores of the Transvaal Caves: Machairodontinae. *Proceedings of the Zoological Society of London*, 125(3, 4):587–615, figures 1–11, plates 1–3.

Eynon, G., and R.G. Walker

1974. Facies Relationships in Pleistocene Outwash Gravels, Southern Ontario: A Model for Bar Growth in Braided Rivers. *Sedimentology*, 21:43–70, figures 1–13.

Frye, J.C.

1945. Geology and Ground-Water Resources of Thomas County, Kansas. *Bulletin of the Kansas Geological Survey*, 59:1–110, figures 1–13, plates 1–6.

Gregory, J.T.

1971. Speculations on the Significance of Fossil Vertebrates for the Antiquity of the Great Plains of North America. *Abhandlungen Hessisches Landesamtes für Bodenforshungen*, 60:64–72, figure 1.

Hall, E.R.

1930. Three New Genera of Mustelidae from the Later Tertiary of North America. *Journal of Mammalogy*, 11:146–155, plates 7–8.

1944. A New Genus of American Pliocene Badger with Remarks on the Relationships of Badgers of the Northern Hemisphere. *Carnegie Institution of Washington Publication*, 551:9–23, figures 1, 2, plates 1, 2.

Harrison, J.A.

1979. Revision of the Camelinae (Artiodactyla, Tylopoda) and Description of the New Genus *Alforjas*. *University of Kansas Paleontological Contributions*, 95:1–28, figures 1–3, plates 1–7.

1981. A Review of the Extinct Wolverine, *Plesiogulo* (Carnivora: Mustelidae), from North America. *Smithsonian Contributions to Paleobiology*, 46:1–27, figures 1–16.

1982. The Baculum of *Plesiogulo* (Carnivora: Mustelidae). *Journal of Paleontology*, 56:1266–1273, plates 1–3.

Hibbard, C.W.

1934. Two New Genera of Felidae from the Middle Pliocene of Kansas. *Transactions of the Kansas Academy of Science*, 37:239–255, plates 4–6.

1937. Additional Fauna of Edson Quarry of the Middle Pliocene of Kansas. *American Midland Naturalist*, 18(3):460–464, figures 1–4.

1939. Notes on Additional Fauna of Edson Quarry of the Middle Pliocene of Kansas. *Transactions of the Kansas Academy of Science*, 42:457–462, figures 1–6.

Hodson, W.G.

1963. Geology and Ground-Water Resources of Wallace County, Kansas. *Bulletin of the Kansas Geological Survey*, 161:1–108, figures 1–22, plates 1–3.

Izett, G.A.

1975. Late Cenozoic Sedimentation and Deformation in Northern Colorado and Adjoining Areas. *In* B.M. Curtis, editor, Cenozoic History of the Southern Rocky Mountains. *Bulletin of the Geological Society of America*, 144:179–209.

Kaup, J.J.

1832. Description d'Ossments fossiles de Mammifères inconnus jusqu'a présent qui se trouvent au Muséum grand-ducal de Darmstadt. *Archiv für Mineralogie, Geognosie, Bergbau,und Huttenkunde*, 3:150–158.

Kittl, E.

1887. Beiträge zur Kenntniss der Fossilen Säugethiere von Maragha in Persien, I: Carnivoren. *Annalen des Naturhistorischen Hofmuseums*, 2:317–338, plates 14–18.

Kormos, T.

1911. Der Pliozäne Knochenfund bei Polgárdi. *Földtani Közlöny*, 41(1, 2):171–189, figures 11–19.

Kretzoi, N.

1929. Materialien zur Phylogenetischen Klassifikation der Aeluroïdeen. In *10th International Congress of Zoology, Budapest, (1927)*, part 2:1293–1355.

Kurtén, B.

1963. Notes on Some Pleistocene Mammal Migrations from the Palaearctic to the Nearctic. *Eiszeitalter und Gegenwart*, 14:96–103, figures 1–2.

Martin, H.T.

1928. Two New Carnivores from the Pliocene of Kansas. *Journal of Mammalogy*, 9:233–236, plates 20–21.

Martin, L.D., and C.B. Schultz

1975. Scimitar-toothed Cats, *Machairodus* and *Nimravides*, from the Pliocene of Kansas and Nebraska. *Bulletin of the University of Nebraska State Museum*, 10(1):55–63, figures 1–5.

Matthew, W.D.

1924. Third Contribution to the Snake Creek Fauna. *Bulletin of the American Museum of Natural History*, 50(2):59–210, figures 1–63.

Matthew, W.D., and R.A. Stirton

1930. Osteology and Affinities of *Borophagus*. *University of California Publications, Bulletin of the Department of Geological Sciences*, 19(7):71–126, figures 1, 2, plates 21–34.

Meade, G.E.

1961. The Saber-toothed Cat, *Dinobastis serus. Bulletin of the Texas Memorial Museum*, 2(2):23–60, figure 1, plates 1–9.

Merriam, J.C.

1903. The Pliocene and Quaternary Canidae of the Great Valley of California. *University of California Publications, Bulletin of the Department of Geological Sciences*, 3(14):277–290, plates 28–30.

1906. Carnivora from the Tertiary Formations of the John Day Region. *University of California Publications, Bulletin of the Department of Geology*, 5(1):1–64, plates 1–6.

1911. Tertiary Mammal Beds of Virgin Valley and Thousand Creek of Northwestern Nevada. *University of California Publications, Bulletin of the Department of Geology*, 6(11):199–304, plates 32–33.

Merriam, J.C., and C. Stock

1932. The Felidae of Rancho La Brea. *Carnegie Institution of Washington Publication*, 422:1–231, figures 1–152, plates 1–42.

Miall, A.D.

1977. A Review of the Braided-River Depositional Environment. *Earth-Science Review*, 13:1–62, figures 1–16.

Munthe, L.K.

1979. The Skeleton of the Borophaginae (Carnivora: Canidae): Morphology and Function. Doctoral Dissertation, Department of Paleontology, University of California, Berkeley, California.

Piveteau, J.

1948. Un Félidé du Pliocène du Roussillon. *Annales des Paléontologie (Vertébrés)*, 34:99–124, figures 1–14.

1961. *In* Felidae. *In* Piveteau, editor, *Traité de Paléontologie*, 1(6):769–797. Paris: Masson.

Prescott, G.C., Jr.

1953. Geology and Ground-Water Resources of Sherman County, Kansas. *Bulletin of the Kansas Geological Survey*, 105:1–130, figures 1–12, plates 1–11.

Richey, K.A.

1979. Variation and Evolution in the Premolar Teeth of *Osteoborus* and *Borophagus* (Canidae). *Transactions of the Nebraska Academy of Sciences*, 7:105–123, figures 1–11.

Rust, B.R.

1972. Structure and Process in a Braided River. *Sedimentology*, 18:221–246, figures 1–14.

Sanderson, I.T.

1960. Riddle of the Frozen Giants. *Saturday Evening Post*, January 16:39–83.

Schultz, C.B., and L.D. Martin

1975. Bears (Ursidae) from the Late Cenozoic of Nebraska. *Bulletin of the University of Nebraska State Museum*, 10(1):47–54, figures 1–3.

Schultz, G.E.

1977. Guidebook for Field Conference on Late Cenozoic Biostratigraphy of the Texas Panhandle and Adjacent Oklahoma. *Special Publication of the Kilgore Research Center, West Texas State University*, 1:1–160, figures 1–35.

Shotwell, J.A.

1970. Pliocene Mammals of Southeast Oregon and Adjacent Idaho. *Bulletin of the University of Oregon Museum of Natural Hisotry*, 17:1–103, figures 1–43.

Stirton, R.A., and V.L. VanderHoof

1933. *Osteoborus*, a New Genus of Dogs, and Its Relation to *Borophagus* Cope. *University of California Publications, Bulletin of the Department of Geological Sciences*, 23(4):175–182, figure 1–3.

Szalay, F.S., and E. Delson

1979. *Evolutionary History of the Primates*. 580 pages. New York: Academic Press.

Taylor, E.H.

1936. Una nueva fauna de Batrácios Anuros del Plioceno Medio de Kansas. *Anales del Institucion de Biología (México)*, 7(4):513–529, plates 1, 2.

1941. Extinct Toads and Salamanders from Middle Pliocene Beds of Wallace and Sherman Counties, Kansas. *Bulletin of the Kansas Geological Survey*, 38(6):177–196, figures 1–7.

Thenius, E.

1967. Zur Phylogenie der Feliden (Carnivora, Mammalia). *Zeitschrift fur Zoologische Systematik und Evolutionsforschung*, 5:129–143, figure 1.

Tihen, J.A.

1958. Comments on the Osteology and Phylogeny of Ambystomatid Salamanders. *Bulletin of the Florida State Museum*, 3:1–49, figures 1–11.

1962. The New World Bufonids. *American Midland Naturalist*, 68(1):1–50, figures 1–62.

Todd, N.B., and S.R. Pressman

1968. The Karyotype of the Lesser Panda (*Ailurus fulgens*) and General Remarks on the Phylogeny and Affinities of the Panda. *Carnivore Genetics Newsletter*, 5:105–108, figures 1, 2.

Viret, J.

1951. Catalogue critique de la faune des Mammifères Miocènes de la Grive Saint-Alban (Isère). *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon*, 3:1–104, figures 1–23, plates 1–4.

Wagner, H.M.

1976. A New Species of *Pliotaxidea* (Mustelidae: Carnivora) from California. *Journal of Paleontology*, 50(1):107–127, figures 1–19.

Wahlert, J.H.

1978. Cranial Foramina and Relationships of the Eomyoidea (Rodentia, Geomorpha): Skull and Upper Teeth of *Kansasimys. American Museum of Natural History Novitates*, 2645:1–16, figures 1–8.

Webb, S.D.
1977. A History of Savanna Vertebrates in the New World, Part I: North America. *Annual Review of Ecology and Systematics*, 8:355–380, figures 1, 2.

Weithofer, A.
1888. Beiträge zur Kenntniss der Fauna von Pikermi bei Athen. *Beiträge zur Paläontologie Oesterreich-Ungarischen*, 6(3):225–292, plates 10–19.

Wetmore, A.
1937. The Earred Grebe and Other Birds from the Pliocene of Kansas. *Condor*, 39:40.

Wetmore, A., and H.T. Martin
1930. A Fossil Crane from the Pliocene of Kansas. *Condor*, 32:62–63, figures 23–25.

Wilson, R.W.
1960. Early Miocene Rodents and Insectivores from Northeastern Colorado. *University of Kansas Paleontological Contributions, Vertebrata*, 7:1–92, figures 1–131.

Wood, A.E.
1936. A New Rodent from the Pliocene of Kansas. *Journal of Paleontology*, 10(5):392–394, figures 1, 2.

Wood, H.E., W. Chaney, J. Clark, E.H. Colbert, G.L. Jepsen, J.B. Reeside, Jr., and C. Stock
1941. Nomenclature and Correlation of the North American Continental Tertiary. *Bulletin of the Geological Society of America*, 52:1–48, plate 1.

Wurster, D.H.
1968. Cytogenetic and Phylogenetic Studies in Carnivora. *In* K. Benirschke, editor, *Conference on Comparative Mammalian Cytogenetics, Dartmouth Medical School, 1968*, pages 310–329. New York: Springer-Verlag Press.

Wurster, D.H., and K. Benirschke
1968. Comparative Cytogenetic Studies in the Order Carnivora. *Chromosoma*, 24:336–382, figures 1–34.

Zdansky, O.
1924. Jungertiäre Carnivoren Chinas. *Paleontologica sinica*, series C, 2(1):1–155.