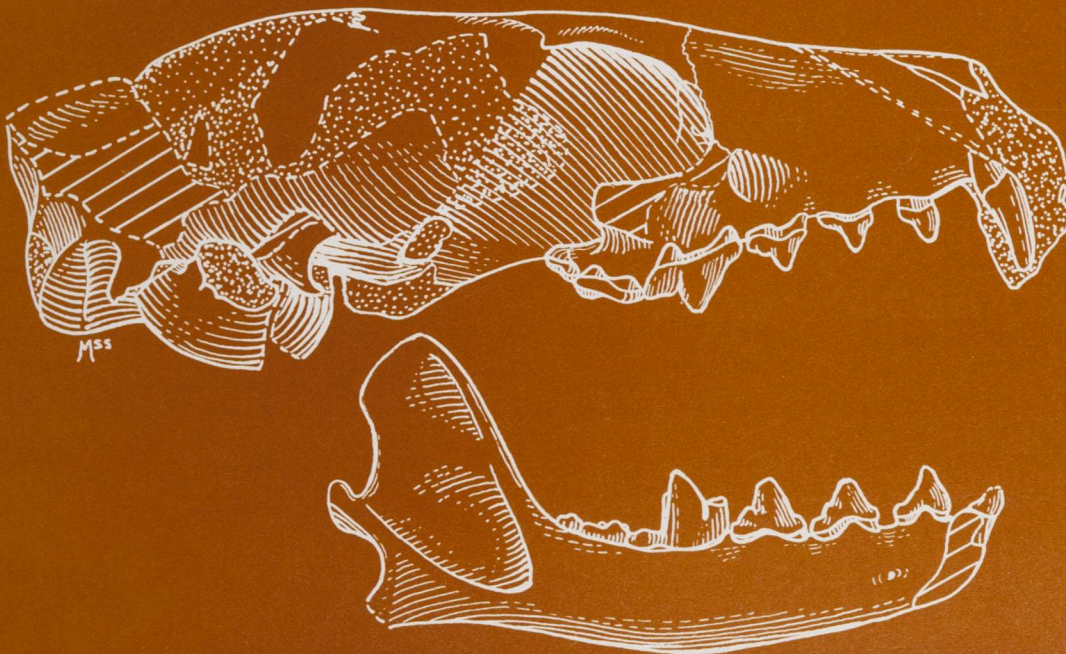


Texas Memorial Museum
Bulletin 33

CARNIVOROUS MAMMALS OF THE LATE EOCENE
AND EARLY OLIGOCENE
OF TRANS-PECOS TEXAS

Eric Paul Gustafson

The University of Texas at Austin
December 15, 1986



Texas Memorial Museum Bulletin 33

CARNIVOROUS MAMMALS OF THE LATE EOCENE AND EARLY OLIGOCENE OF TRANS-PECOS TEXAS

Eric Paul Gustafson



The University of Texas at Austin • 2400 Trinity • Austin, TX 78705

© 1986 by Texas Memorial Museum
The University of Texas at Austin
All rights reserved
Published December 15, 1986
Printed in the United States of America

ISSN 0082-3074-33

The Bulletin is an irregularly published series of
technical monographs deriving primarily from
research done on Texas Memorial Museum
collections and projects.

CONTENTS

LIST OF FIGURES.....	iv
LIST OF TABLES.....	v
ABSTRACT.....	1
INTRODUCTION.....	1
ACKNOWLEDGEMENTS.....	2
TERMINOLOGY.....	3
GEOGRAPHIC SETTING.....	3
PREVIOUS WORK.....	4
STRATIGRAPHY.....	4
CLASSIFICATION.....	7
SYSTEMATIC PALEONTOLOGY.....	8
ORDER CONDYLARTHRA.....	8
ORDER CREODONTA.....	14
ORDER CARNIVORA.....	36
CORRELATIONS.....	58
SUMMARY AND CONCLUSIONS.....	61
BIBLIOGRAPHY.....	63

FIGURES

1.	Dental terminology	3
2.	Dental terminology	3
3.	Map of Brewster and Presidio Counties, showing fossil localities	5
4.	Diagrammatic stratigraphic section of the Buck Hill Group	6
5.	<i>Harpagolestes</i> cf. <i>H. uintensis</i> , mandible	10
6.	<i>Harpagolestes</i> sp., maxilla and upper dentition	11
7.	<i>Hessolestes</i> sp., mandible and partial P ⁴ -M ¹	13
8.	? <i>Proviverra major</i> , mandible	15
9.	<i>Hemipsalodon viejaensis</i> n. sp., skull	17
10.	<i>Hemipsalodon viejaensis</i> n. sp., skull and mandible, lateral view	17
11.	<i>Hemipsalodon viejaensis</i> n. sp., skull, posterior view	18
12.	<i>Hemipsalodon viejaensis</i> n. sp., skull, ventral view	21
13.	<i>Hemipsalodon viejaensis</i> n. sp., interpretation of bones and foramina of orbit and lateral braincase	21
14.	<i>Hemipsalodon viejaensis</i> n. sp., stereophotos of dentition	22
15.	<i>Ischognathus savagei</i> , anterior mandible	26
16.	<i>Hyaenodon</i> cf. <i>H. vetus</i> , mandible	27
17.	<i>Hyaenodon</i> cf. <i>H. vetus</i> , stereophotos of skull	28
18.	<i>Hyaenodon montanus</i> , stereophotos of dentition	30
19.	<i>Hyaenodon montanus</i> , photo of mandible	31
20.	<i>Hyaenodon crucians</i> , stereophotos of skull and M ₂	32
21.	<i>Hyaenodon raineyi</i> n. sp., skull	34
22.	<i>Hyaenodon raineyi</i> n. sp., skull and mandible	35
23.	<i>Miacis cognitus</i> n. sp., skull, lateral view and reconstruction	36
24.	<i>Miacis cognitus</i> n. sp., skull, ventral view and reconstruction	37
25.	<i>Miacis cognitus</i> n. sp., skull, dorsal view and reconstruction	38
26.	<i>Miacis cognitus</i> , stereophotos of dentition and basicranium	39
27.	<i>Miacis cognitus</i> , features of endocast	40
28.	<i>Miacis cognitus</i> , photo of skull	42
29.	<i>Miacis australis</i> n. sp., dentition	43
30.	<i>Uintacyon scotti</i> , skull and mandible	45
31.	<i>Uintacyon scotti</i> , right upper dentition	46
32.	<i>Daphoenocyon dodgei</i> , <i>Daphoenus lambei</i> , and <i>Daphoeninae</i> indet.	49
33.	<i>Hesperocyon wilsoni</i> n. sp., skull and mandible	52
34.	<i>Hesperocyon wilsoni</i> n. sp., upper and lower dentitions	53
35.	?felid indet., rostrum	57
36.	Stratigraphic ranges of Uintan-Chadronian carnivorous mammal genera	59

TABLES

1.	Museum abbreviations	2
2.	Anatomical, statistical, and other abbreviations	2
3.	<i>Harpagolestes</i> measurements, lower teeth	9
4.	<i>Harpagolestes</i> measurements, upper teeth	10
5.	<i>Hessolestes</i> measurements	14
6.	? <i>Proviverra</i> measurements	16
7.	<i>Hemipsalodon</i> measurements	18
8.	<i>Hyaenodon</i> measurements, upper teeth	29
9.	<i>Hyaenodon</i> measurements, lower teeth	29
10.	<i>Miacis</i> measurements	41
11.	<i>Uintacyon</i> measurements	47
12.	Daphoeninae, measurements of upper teeth	50
13.	Daphoeninae, measurements of lower teeth	50
14.	<i>Hesperocyon</i> measurements, upper teeth.....	54
15.	<i>Hesperocyon</i> statistics, upper teeth	54
16.	<i>Hesperocyon</i> measurements, lower teeth.....	55
17.	<i>Hesperocyon</i> statistics, lower teeth	55

Carnivorous Mammals of the Late Eocene
and Early Oligocene
of Trans-Pecos Texas

By Eric Paul Gustafson

ABSTRACT

The fossil carnivore fauna of the late Eocene (Bridgerian-Uintan) and early Oligocene (Chadronian) of Trans-Pecos Texas includes specimens from stratigraphically superimposed faunas of three areas: the Sierra Vieja (Vieja Group), the badlands near Agua Fria Mountain (Buck Hill Group), and near Castolon in southern Big Bend National Park (Chisos Formation). Members of the mammalian orders Condylarthra, Creodonta, and Carnivora are included in this study. The fossils occur in volcanoclastic continental sediments, interbedded with lava flows and ignimbrites. The Cenozoic rocks unconformably overlie Cretaceous sedimentary rocks in all three areas. Radiometric dates from several stratigraphic levels allow the calibration of biostratigraphic data.

The Chisos Formation near Castolon has yielded one specimen, a partial skeleton of *Uintacyon scotti*. The specimen came from about 185 meters below the Bee Mountain Basalt and above the Alamo Creek Basalt (about 42-44.5 million years).

In the Agua Fria section, carnivores come from several levels between the post-Cretaceous unconformity and the Mitchell Mesa Ignimbrite (32.28* m.y.). The lowest level, the Whistler Squat local fauna (48.6 m.y.), includes *?Proviverra major*, *Uintacyon* sp., *Hessolestes* sp., a possible limnocyonine, and *Simidectes magnus*. This assemblage shows affinities to both Bridgerian and Uintan faunas but is probably Uintan. Much higher, in the Skyline gravels, *Simidectes magnus*, *Harpagolestes* sp., and *Hyaenodon* cf. *H. vetus* are found. This association is not seen in the Utah sections (where *Simidectes* appears much lower than *Hyaenodon*), but a similar joint occurrence of *Simidectes* and *Hyaenodon* is seen in the Pearson Ranch local fauna of the Sespe Formation, California.

Of the several superimposed local faunas in the Sierra Vieja, the lowest (Candelaria local fauna) includes only *Harpagolestes* cf. *H. uintensis*. It is Uintan on the basis of the fauna and of its position below the Buckshot Ignimbrite (38.6 m.y.). The stratigraphically higher faunas (Porvenir, Little Egypt, and Airstrip) are Chadronian, and include a new species of *Hemiposalodon*, four species of *Hyaenodon*, *Ischnognathus savagei* (an enigmatic form), two new species of *Miacis*, daphoenine amphicyonids, a new *Hesperocyon*, and an unidentified felid-like form.

INTRODUCTION

Skeletal remains of numerous animals of late Eocene and early Oligocene age are found in thick sequences of sedimentary rock in West Texas. Interbedded with the volcanoclastic sediments are lava flows, ignimbrites, and air-fall tuffs. The certain relationship of superimposed mammalian faunas and widespread volcanic rock units provides a combination of stratigraphic control with radiometric dates which furnishes exceptional geochronologic documentation of the fossil faunas of the area. The study presented here is one of a series which will eventually include all of the fossil mammal taxa of the area.

Fossil carnivores are scarce in comparison to herbivores at all of the West Texas localities. Of the approximately 50 specimens on which this report is based, only a few consist of more than a few teeth or skull fragments. However, the total assemblage is one of the best collections of carnivores from stratigraphically superimposed rock units of late Eocene and early Oligocene age in North America.

The time period spanned by these faunas covers a crucial change in the composition of carnivore faunas. It was in the late Eocene that members of the modern Order Carnivora began their major increase in diversity, while members of other orders, for example the Order Creodonta, became greatly reduced in diversity by the beginning of the Oligocene.

The purpose of this paper is to identify and describe the available specimens of carnivorous mammals from the Eocene and Oligocene rocks of Trans-Pecos Texas, to place them in the documented stratigraphic sequence, and to analyze their biostratigraphic and evolutionary significance. With these data and previous studies, it is possible to analyze the creodont-carnivore faunal replacement in more detail than has hitherto been done.

The completion of the final draft has taken several years. Only minor additions have been made since the last revision, made in 1981.

My practice of making comparisons between the Texas fossils and similar sized modern species raised some questions among reviewers. These comparisons are not intended to imply any taxonomic affinities, but simply to give a basis for comparison with taxa which are familiar to most readers, which are likely to be represented by skeletal material in most modest sized museum collections, and whose soft anatomy is known.

* The K-Ar dates given in this paper are not corrected to the IUGS Subcommission on Geochronology.

Table 1.—Museum abbreviations used in the text. Other abbreviations are given in figure captions.

AMNH	American Museum of Natural History, New York
CIT	California Institute of Technology (collections now at LACM)
CM	Carnegie Museum, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
KU	University of Kansas Museum, Lawrence
LACM	Natural History Museum of Los Angeles County
NMC	National Museum of Canada
OMSI	Oregon Museum of Science and Industry
OU	Stovall Museum, University of Oklahoma, Norman
PU	Princeton University, Philadelphia
ROM	Royal Ontario Museum, Toronto
TMM	Texas Memorial Museum, Austin
USNM	United States National Museum, Washington, D.C.
YPM	Yale Peapody Museum, New Haven

Table 2.—Anatomical, statistical, and other abbreviations used in the text. Additional abbreviations are given in figure captions.

a	measurement taken at inside rim of alveolus
AP	maximum anteroposterior diameter
C	canine
Co.	County
d	deciduous tooth
e	estimated measurement
Fm.	Formation
I	incisor
l.f.	local fauna
M	molar
m.y.	million years before present
N	number of specimens measured
n. sp.	new species
OR	observed range of variation
P	premolar
s	standard deviation
sp.	species
T	maximum transverse diameter
V	coefficient of variation
\bar{X}	sample mean

Specimen numbers cited without prefixes belong to the Vertebrate Paleontology Laboratory of the Texas Memorial Museum, which has detailed descriptions of their localities on file. All TMM numbers consist of a five digit locality number followed by a hyphen and an individual specimen number. In specimen lists numbers have been abbreviated by giving only the hyphen and the specimen number for second and subsequent numbers from the same locality (e.g., 41372-1, -2).

ACKNOWLEDGEMENTS

This project was suggested by Dr. John A. Wilson, who until his retirement was its supervisor. Indeed, without Dr. Wilson's energetic and patient collecting over many

years, such a project would not have been possible. I also benefitted from his direction and instruction in the field in West Texas and from his editing of the various drafts of this work. Dr. Ernest L. Lundelius, Jr., has been most patient and helpful in finishing the final drafts of the dissertation and in lending support during my stay at The University of Texas. I am indebted to Dr. Don Baird of Princeton University, Dr. Mary Dawson of the Carnegie Museum, Pittsburgh, Dr. C. Lewis Gazin, Dr. Clayton Ray, and Mr. Robert Purdy of the National Museum of Natural History, Dr. Robert Hunt of the University of Nebraska, and members of the staff of the American Museum of Natural History, New York, and Field Museum of Natural History, Chicago, for providing specimens, casts, and access to collections. Dr. James Mellett gave me much information on *Hyaenodon* and allowed me to use his casts of *Hyaenodon* types. Dr. Leonard Radinsky and Dr. Harry Jerison examined the brain casts of *Miacis* and other skulls and discussed their ideas with me. Many others have given their time to discuss various aspects of this project. The Vertebrate Paleontology Laboratory of the Texas Memorial Museum has given me its full support and use of its facilities. Parts of my work were supported financially by the Geology Foundation of the Department of Geological Sciences, The University of Texas at Austin.

All drawings not the work of the author were made by Margaret Skeels Stevens, and are identified by her initials. Mrs. Stevens also collected many of the specimens.

My wife Jessie has given me her wholehearted support during all of my work, under conditions which have sometimes been very difficult. For this support which no one else could give, I am extremely grateful.

This publication is a contribution of the Vertebrate Paleontology Laboratory, Texas Memorial Museum, The University of Texas at Austin.

TERMINOLOGY

Dental terminology (Fig. 1, 2) is taken from MacIntyre (1966), whose terms were developed for a generalized miacid dentition, but which also apply to other carnivorous mammals. Although names of major cusps and other features are standard terms, in some cases this terminology differs somewhat from that of Van Valen (1966) and Szalay (1969a), and terms for minor features often are not the same.

Skeletal and other anatomical terminology, particularly names of foramina and muscles, was taken from Romer (1970), Miller, Christensen and Evans (1964), and Davis (1964).

GEOGRAPHIC SETTING

The described specimens come from three areas within Presidio and Brewster Counties, Texas (Fig. 3). From northwest to southeast, these are: 1) the rugged and poorly accessible area between the high rim rock of the Sierra Vieja and the Rio Grande in Presidio County, 2) the badlands north and west of Agua Fria Mountain in southern Brewster County, and 3) an area southwest of the Chisos Mountains in Big Bend National Park near Castolon, also in Brewster County. Exposures are along the major tributaries of the Rio Grande.

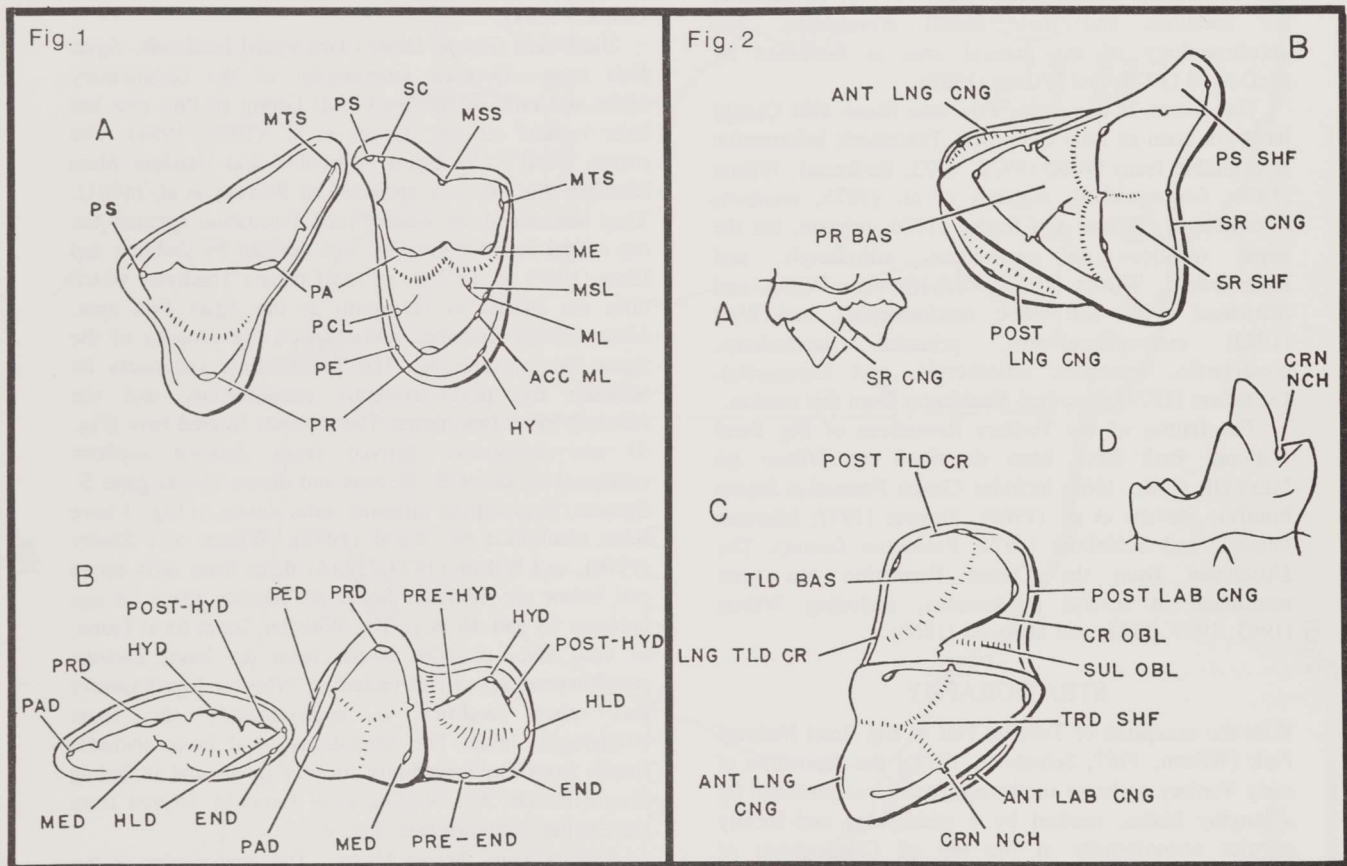


Figure 1.—Diagrammatic occlusal views of generalized miacid dentition, illustrating cusp terminology. A. Left upper teeth. B. Right lower teeth. From MacIntyre (1966, Fig. 1).

Abbreviations: ACC ML, accessory metaconule; END, entoconid; HLD, hypoconulid; HY, hypocone; HYD, hypoconid; ME, metacone; MED, metaconid; ML, metaconule; MSL, mesoconule; MSS, mesostyle; MTS, metastyle; PA, paracone; PAD, paraconid; PCL, paraconule; PE, pericone; PED, periconid; POST-HYD, post-hypoconid; PR, protocone; PRD, protoconid; PRE-END, per-entoconid; PRE-HYD, pre-hypoconid; PS, parastyle; SC, stylocone.

Figure 2.—Diagrams of generalized miacid molars, illustrating crest terminology. A. Labial view of upper molar. B. Occlusal view of upper molar. C. Occlusal view of lower molar. D. Lingual view of lower molar. From MacIntyre (1966, Fig. 2).

Abbreviations: ANT LAB CNG, anterior labial cingulum; ANT LNG CNG, anterior lingual cingulum; CRN NCH, carnassial notch; CR OBL, crista obliqua; LNG TLD CR, lingual talonid crest; POST LAB CNG, posterior labial cingulum; POST LNG CNG, posterior lingual cingulum; POST TLD CR, posterior talonid crest; PR BAS, protocone basin; PS SHF, parastyle shelf; SR CNG, stylar cingulum; SR SHF, stylar shelf; SUL OBL, sulcus oblique; TLD BAS, talonid basin; TRD SHF, trigonid shelf.

PREVIOUS WORK

Of the three fossiliferous sections mentioned in this report, the Vieja Group has received the most attention. Various taxa from the Vieja Group are discussed by Stovall (1948; the fauna including some carnivores), McGrew (1953; Equidae), Wilson (1966; primate), Harris (1967; rhinocerotoid), Harris and Wood (1969; eomyid rodent), Wilson (1971a; Entelodontidae, and 1971b; Agriochoeridae and Merycoidodontidae), Forsten (1971a and b; Equidae), McGrew (1971; Equidae), Wood (1974; Rodentia), Wilson (1974; Protoceratidae, Camelidae, and Hypertragulidae), Novacek (1976; Insectivora), Wilson (1977a; Brontotheriidae), and Wilson and Schiebout (1981 and 1984; Ceratomorpha). Wilson et al. (1968) present preliminary faunal lists (including carnivores) for the Vieja faunas together with stratigraphic information and radiometric dates, and Wilson (1977b) summarizes the localities and their faunal correlations. The geochronology of the general area is discussed by McDowell (1979) and Wilson (1980).

The faunas of the Agua Fria area (Buck Hill Group) have not been as fully described. Taxonomic information is available from Wood (1972, 1973; Rodentia), Wilson (1974; *Leptoreodon*), Stevens et al. (1975; mentions *Hyaenodon*), Wilson and Szalay (1976; primate, but the paper mentions an amynodont, artiodactyls, and *Hyaenodon*), Wilson (1977a; titanotheres). Wilson and Schiebout (1981 and 1984; ceratomorphs), and West (1982; marsupicarnivores, primates, taeniodonts, condylarths, bunodont artiodactyls, and Dinocerata). Gustafson (1979) described *Simidectes* from this section.

The faunas of the Tertiary formations of Big Bend National Park have been described by Wilson (in Maxwell, et al., 1967; includes Chisos Formation faunas briefly), Stevens et al. (1969), Stevens (1977; Miocene faunas), and Schiebout (1974; Paleocene faunas). The *Uintacyon* from the Chisos Formation has been mentioned in several publications, including Wilson (1965, 1967, 1972) and Maxwell (1968).

STRATIGRAPHY

With the exception of Tornillo Flat in Big Bend National Park (Wilson, 1967; Schiebout, 1974), the deposition of early Tertiary rocks in southwest Texas was preceded by a lengthy hiatus, marked by a widespread and locally angular unconformity at the top of Comanchean or Gulfian (Cretaceous) sediments which were folded during the Laramide orogeny. In many places the first Tertiary sediments are limestone-quartzite conglomerates (Jeff Conglomerate of DeFord, 1958), but these are generally thin and are buried under very thick deposits of tuffaceous sediment and volcanic flows (basalt, rhyolite, ignimbrites, and lahars). Tertiary volcanic activity seems to have begun in the Big Bend area in the mid to late Eocene (Stevens, 1969; Fig. 4) and continued intermittently through much of the Tertiary. Major normal faulting began in the early Miocene (Arikareean) and has combined with numerous igneous intrusions to make the geology highly complex.

Chisos Formation, Castolon area, Big Bend National Park.—The geology of Big Bend National Park was described by Maxwell et al. (1967), and the Castolon area was examined in detail by Stevens (1969). The only significant carnivore specimen, the skeleton of *Uintacyon scotti*, was found in the lower part of the Chisos Formation, which overlies Cretaceous rocks in this area and is unconformably overlain by the South Rim Formation, of Oligocene age. This stratigraphic section was given by Maxwell et al. (1967, p. 132, and Plate X, sec. 36). The *Uintacyon* skeleton was found in a tuffaceous mudstone between 20.7 and 27.4 m (68 and 90 feet) above the Alamo Creek Basalt. Maxwell et al. (1967) give K/Ar dates for the Alamo Creek of 38.7 m.y., 40.1 m.y., 42.7 m.y., and 44.3 m.y.*. Information from dates and faunas elsewhere suggests that the oldest date is nearest correct (Wilson, pers. comm., 1981).

Buck Hill Group, Devil's Graveyard badlands, Agua Fria area.—Detailed stratigraphy of the sedimentary rocks and tuffs of the Buck Hill Group in this area has been worked out by Stevens et al. (1975, 1984). The names Devil's Graveyard Formation and Bandera Mesa Member (Fig. 4) were proposed by Stevens et al. (1984). They abandoned the name Pruett Formation because the top of the Pruett Formation was defined by Goldich and Elms (1949) as the base of the Crossen Trachyte, which does not extend as far south as the Agua Fria area. Moon (1953) described and mapped the geology of the Agua Fria quadrangle. The fossiliferous sediments lie between the post-Cretaceous unconformity and the Mitchell Mesa Ignimbrite. The sections figured here (Fig. 4) are composites derived from detailed sections measured by James B. Stevens and drawn by Margaret S. Stevens. Some of the informal units shown in Fig. 4 have been mentioned by Wood (1973), Wilson and Szalay (1976), and Wilson (1977). K/Ar dates from tuffs above and below the Whistler Squat #2 locality place its age between 43 and 46 m.y. The Whistler Squat local fauna, as used here, includes faunas from the basal Tertiary conglomerate up to and including Whistler Squat Quarry and other localities at approximately the same stratigraphic level. The Serendipity local fauna includes fossils from the Serendipity locality up to and including Purple Bench. The Skyline local fauna is derived from the Skyline conglomerate (Fig. 4).

Vieja Group, Sierra Vieja.—The stratigraphy of the Vieja Group was worked out by R. K. DeFord and numerous graduate students and was summarized by DeFord (1958). The stratigraphic positions of faunas and radiometric dates of the igneous rocks were presented by Wilson et al. (1968) and by Wilson (1977b). Walton (1972, 1977) described the sedimentary petrology of the Vieja Group. The Group includes the following formations, from oldest to youngest:

* Radiometric dates are given as they originally appear in publications. I recognize that these dates, given accurately, should include some indication of error. It is unfortunate that these often are not available, and where error figures are given the nature of the indicated error range often is left unclear. For corrected dates see Stevens, Stevens, and Wilson (1984).

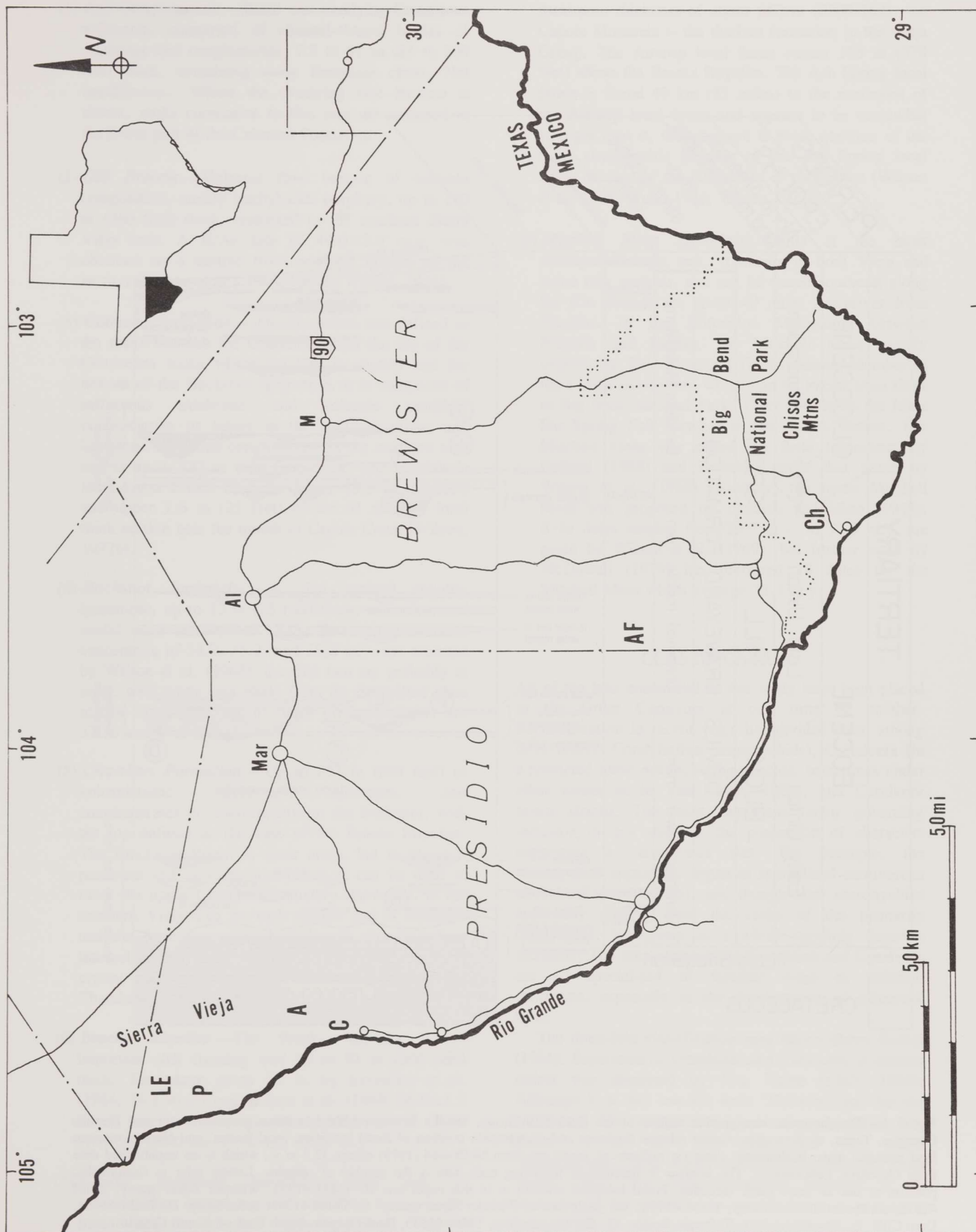


Figure 3.—Map of Brewster and Presidio Counties, Texas, showing fossil localities. **Abbreviations:** A, Agua Fria area; Al, Alpine; C, Candelaria l.f.; Ch, Chisos Formation, *Utiacynon* locality; LE, Little Egypt l.f.; M, Marathon; Mar, Marfa; P, Porvenir l.f.

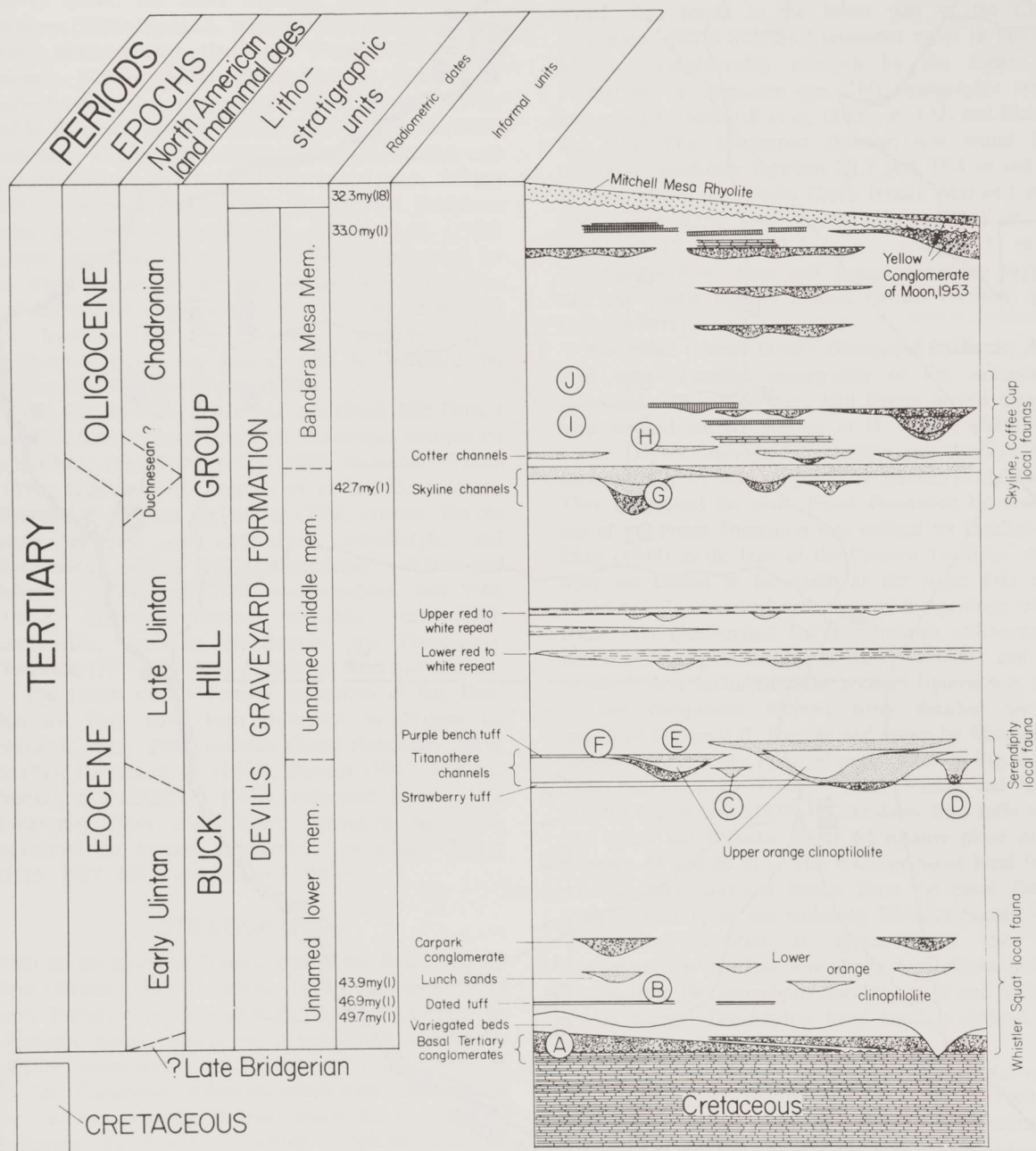


Figure 4.—Diagrammatic stratigraphic section of the Buck Hill Group, Devil's Graveyard-Bandera Mesa area, Brewster and Presidio Counties, Texas, to show approximate relative thickness and stratigraphic position of fossil localities, local faunas, and North American land mammal ages. Radiometric dates (in millions of years) are from McDowell (1979) except 32.3 m.y., which is an unpublished date from Geochron Laboratories. The number in parentheses following each data is the number of samples. Letters refer to stratigraphic position of one or more fossil localities. Fossil localities referred to in this paper are: B. TMM 41372, Whistler Squat quarry; TMM 41576, southwest of Wax Camp; TMM 41466, 300 yards east of Whistler Squat quarry. C. TMM 41745, Serendipity. D. TMM 41784, Unio Cliff. E. Titanotheres Hill. F. Purple Bench. G. Skyline channels; TMM 41535, Boot Canyon; North Fork of Alamo Cesario.

- (1) **Jeff Conglomerate.**—Basal unit overlying Cretaceous sediments, composed of channel-shaped bodies of sandstone and conglomerate, 7.3 to 91 m (24 to 300 feet) thick, containing many limestone clasts. Not fossiliferous. Where the overlying Gill Breccia is absent, rocks correlative to this unit are assigned to the lower part of the Colmena Formation.
- (2) **Gill Breccia.**—Volcanic flow breccia of variable composition, mostly trachybasalt porphyry, up to 110 m (360 feet) thick, restricted to the southern Sierra Vieja area. A K/Ar date of 40.0 ± 2.0 m.y. was obtained on a sample from near the bottom of the section (Wilson et al., 1968; but see Wilson, 1984).
- (3) **Colmena Formation.**—This formation was defined as the rocks between the Gill Breccia (or the top of the Cretaceous rocks where the Gill is absent) and the bottom of the Buckshot Ignimbrite. It is composed of tuffaceous sandstone and volcanic mudflow conglomerate or lahars in the southern areas, and limestone-sandstone conglomerate in the northern area and is up to 137 m (450 feet) thick. The Candelaria local fauna comes from the lower 15.2 m (50 feet) and upper 7.6 m (25 feet) of the 61 m (200 foot) thick section near the mouth of Capote Creek (Wilson, 1977b).
- (4) **Buckshot Ignimbrite.**—A fine grained rhyolite ignimbrite, up to 23 m (75 feet) thick, extensive, and useful as a marker bed. K/Ar dates on a sanidine concentrate of 34.7, 35.2, and 38.6 m.y. are reported by Wilson et al. (1968); the first two are probably in error, with argon loss likely from the devitrified glass matrix. The most recent dates (Wilson, 1984) are 37.30 and 37.0 m.y.
- (5) **Chambers Formation.**—Up to 257 m (844 feet) of volcanoclastic sandstones, siltstones, and conglomerates lie conformably on the Buckshot, with the top defined as the base of the Bracks Rhyolite. The Bracks is absent in some areas, but in places a persistent red siltstone just below it can be used to mark the upper Chambers boundary. However, in the southern Vieja area no such marker bed is available and the formation upper boundary is obscure. Two internal marker beds, a white ash flow tuff and a red crystal tuff, can be used for control within the Chambers (Walton, 1972).
- (6) **Bracks Rhyolite.**—The Bracks Rhyolite is an important cliff forming unit up to 91 m (300 feet) thick. Two dates given for it, by Evernden et al. (1964; 36.8 m.y.) and Wilson et al. (1968; 36.5 ± 1.2 m.y.), are in close agreement. More recent dates (Wilson, 1984) are 37.40 and 37.70 m.y.
- (7) **Capote Mountain Formation.**—This unit of volcanoclastic sediments and tuff lies between the Bracks and the Mitchell Mesa Ignimbrite. With a

maximum thickness of about 640 m (2100 feet), the Capote Mountain is the thickest formation in the Vieja Group. The Airstrip local fauna occurs 173 m (570 feet) above the Bracks Rhyolite. The Ash Spring local fauna is found 40 km (25 miles) to the northwest of the Airstrip local fauna and appears to be somewhat younger than it, though there is some question of the exact stratigraphic position of the Ash Spring local fauna because of the difficulties of correlation (Wilson et al. 1968; Wood 1974; Wilson 1977b).

- (8) **Mitchell Mesa Ignimbrite.**—This is the most widespread single unit. It occurs in both Vieja and Agua Fria sections, and can be traced southeast along the Rio Grande for about 40 miles downriver from Presidio. In the Bofecillos Mountains, between Presidio and Lajitas, the Mitchell Mesa closely overlies the Tule Mountain Trachyandesite Member of the Chisos Formation, which can be traced from there to Big Bend National Park. There it overlies the Mule Ear Spring Tuff Member in the Chisos section. The Mitchell Mesa was called the Brite Ignimbrite by DeFord (1958) and is listed under that name by Wilson et al. (1968); however, the name Mitchell Mesa was proposed by Goldich and Elms (1949). K/Ar dates ranging from 29.7 m.y. to 33.9 m.y. are given by Wilson et al. (1968), but further work by McDowell (1979) has produced 18 dates for the Mitchell Mesa which average 32.3 m.y.

CLASSIFICATION

All of the taxa considered in this study have been placed in the Order Carnivora at one time or another. Reclassification in recent years has divided them among three orders: Condylarthra (mesonychids), Creodonta (in a restricted sense not including miacids, sometimes under other names as in Van Valen, 1966), and Carnivora *sensu stricto*. The most important factor governing inclusion in this study is the possession of characters suggesting a carnivorous diet. For example, the mesonychids apparently began as specialized carnivorous animals (Szalay, 1969b), and though later mesonychids apparently strayed from the ranks of the primarily carnivorous, the group as a whole certainly deserves inclusion. The taxa representing Creodonta and Carnivora are all specialized in familiar ways as efficient carnivores, especially in the development of carnassial teeth.

The three-fold classification used here follows Romer (1966). Separation of Creodonta and Carnivora as distinct orders was discussed by Van Valen (1965, 1966). Although I do not use his term "Deltatheridia" for the creodonts, this arrangement is natural and useful. Van Valen (1974) has also abandoned the name "Deltatheridia", and would prefer "Hyaenodonta" (Van Valen, 1967). The name Creodonta, however, is not confusing if its contents are specified and is preferable because it is an older and well established name.

SYSTEMATIC PALEONTOLOGY

Order Condylarthra Cope, 1881

Family Mesonychidae Cope, 1875

Subfamily Mesonychinae Wortman, 1901

Genus *Harpagolestes* Wortman, 1901

Harpagolestes cf. *H. uintensis* (Scott, 1888)

Candelaria local fauna

Figure 5, Table 3

Type.—PU11659, isolated P_{3-4} , M_1 , M_3 , and another questionably associated premolar, Uinta Formation, Utah.

Referred material.—TMM 40498-3, right ramus with I_{2-3} , C, P_1 , P_{3-4} , and left P_4 .

Stratigraphic position.—Within the lower 15.2 m (50 feet) (lower sedimentary unit of Wilson, 1977b) of the Colmena Formation, Vieja Group, Presidio County, Texas.

Age.—Uintan (late Eocene).

Description.—This specimen (Fig. 5) falls within or near the known range of variation of *Harpagolestes uintensis* in all measurements (Table 3). There are two incisors, of which the lateral incisor (I_3) is somewhat the larger. The canine is very large at the base of the enamel but tapers rapidly toward the tip. P_1 is set close behind the canine. It is single cusped and single rooted, and is widest below the enamel, about 5 mm above the alveolar rim. P_2 is missing. Its smaller anterior alveolus is set partly medial to the P_1 alveolus. There are no diastemata such as are seen in some specimens of *H. uintensis*, particularly AMNH 1878 (Szalay and Gould, 1966, Fig. 4). This feature seems to be variable in *Harpagolestes*, as is also the depth of the mandible. The anterior basal cusp (paraconid) of P_3 is larger and much more distinctly cusped than in the type (PU 11659). The same is true of P_4 ; however, a referred specimen from Utah (CM 2961) has a paraconid nearly as large as the Texas specimen (Peterson, 1931a, plate 17). P_3 and P_4 are more robust than those of the type. There are two mental foramina, a larger foramen beneath the anterior root of P_2 and a smaller beneath the anterior root of P_3 .

Relationships.—The genus *Harpagolestes* is in need of revision. Except for a few specimens referred to *H. uintensis*, each new specimen has been given a new name. Furthermore, an attempt to designate AMNH 1892 as a neotype for *H. uintensis* (Szalay and Gould, 1966, p. 142) is not valid because the first and only specimen (PU 11659) placed in the species by Scott (automatically the holotype by Article 73a of the International Code of Zoological Nomenclature) has been consistently accepted as the type by various authors (Osborn, 1895; Peterson, 1919, 1931a; Thorpe, 1923). Some of the species described later (for instance *H. leontensis* Peterson, 1931a, and *H. immanis* Matthew, 1909) show little difference in the teeth from *H. uintensis* and may be synonyms. However, the variation in some features,

particularly in the depth of the mandible shown by specimens from the Uinta Formation (for instance, YPM 10072 and AMNH 1878) is more extreme than might be expected in a single species.

Harpagolestes uintensis is probably descended from *H. macrocephalus* from the Bridger Formation, providing that the loss of P^2 in *H. macrocephalus* is an individual variation of the type and only known specimen.

The ramus (40498-3) is broken posterior to M_1 , of which only the roots are preserved. A second fragment bearing what appear to be the roots of M_2 has a subsurface fit and the grain on the lateral side of the ramus matches perfectly. The more posterior of these roots of M_2 projects backwards at an angle which approaches the horizontal, suggesting that there may not have been any additional teeth behind it. In most mammals this would probably be the case. However, the lower margin of the mandible of *Harpagolestes uintensis* (which has P_1 - M_3 , [Peterson, 1931, Fig. 1]) is strongly arcuate, so that the roots of the posterior cheek teeth are not parallel but rather are radial about a point above the upper cheek teeth. If such strong curvature occurred in this specimen, there could well have been adequate room for a small M_3 .

Harpagolestes sp.

Skyline conglomerate

Figure 6, Table 4

Referred material.—TMM 41715-8, anterior partial rostrum, with alveoli for right canine and P^1 , complete P^2 - M^2 .

Stratigraphic position.—Skyline channels, base of Bandera Mesa Member, Devil's Graveyard Formation, North fork of Alamo de Cesario, Brewster Co., Texas.

Age.—late Uintan, early Duchesnean subage.

Description.—The specimen (Fig. 6) consists of the maxillary, lacrimal, jugal, and palatine bones of the right side, apparently separated from surrounding bones along the sutures. This separation and the lack of heavy wear on the dentition indicate this was an immature individual. Mesonychids commonly show substantial tooth wear, and most specimens of *Harpagolestes* have at least the tips of the cusps worn flat. The teeth in TMM 41715-8 show wear facets on the medial side of the paracones and metacones, and on the lateral sides of the protocones.

The side of the rostrum is relatively short and high, and the dorsal half of the maxilla is concave. Because of this, the dorsal surface of the snout, capped by the nasals, must have been high and narrow, as in *?Harpagolestes orientalis* Szalay and Gould. In the skulls of *H. uintensis*, *H. macrocephalus*, and *?H. orientalis* the anterior border of the orbit is over the center of M^2 . In the Texas specimen, however, the orbit is further forward, over the center of M^1 . As in other mesonychids, the lacrimal spreads over the anterior border of the orbit onto the side of the face. There are two openings for the lacrimal duct separated by a bony septum. Immediately dorsal to these on the anterior

Table 3.—Measurements of upper dentition of *Harpagolestes* (TMM 41715-8).

		<i>H. cf. H. uintensis</i> TMM 40498-3	<i>H. uintensis</i> PU 11659	<i>H. uintensis</i> YPM 10072	<i>H. uintensis</i> CM 2961	<i>H. uintensis</i> AMNH 1878	<i>H. brevipes</i> YPM 13098	<i>H. leotensis</i> CM 11778	<i>H. immanis</i> AMNH 13143
		right	left	type			type	type	type
I ₂	AP	10.4							
	T	6.9							
I ₃	AP	11.0							
	T	9.6							
C	AP	31.8							28.2
	T	22.0							19.3
P ₁	AP	11.3							
	T	8.4							
P ₂	AP	23.7a		20.7	21	16.7	23	20.2e	21.7
	T				13		15.5	11.5	10.8
P ₃	AP	29.4		28	26	28.3	32.2		30.4
	T	15.5	28.0		15		16		15.1
P ₄	AP	31.5	31.7	27.5	30	30	36	29.4	32.8
	T	16.9	14.7		16.5		19	15.1	16.3
M ₁	AP	28.7a	28.8	31.5	29	24.3	37a	30.6	30.2
	T		15.0		15.5			14.0	15.8
P ₁ -P ₄		94e			100	103		97	
Jaw depth, posterior M ₁		51		47	66	73	52	68	

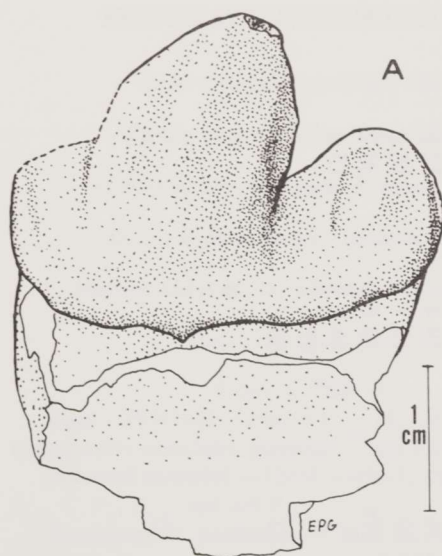


Table 4.—Measurements of upper dentition of *Harpagolestes* (TMM 41715-8).

	AP	T
Canine alveolus	29.8	17.7
P ¹ alveolus	13.9	9.6
P ² crown	18.9	10.5
P ³ crown	23.0	12.4
P ⁴ crown	23.0	20.5
M ¹ crown	23.3	24.3
M ² crown	15.0	18.0

Distance from anterior P¹ alveolus to posterior M³: 126.5

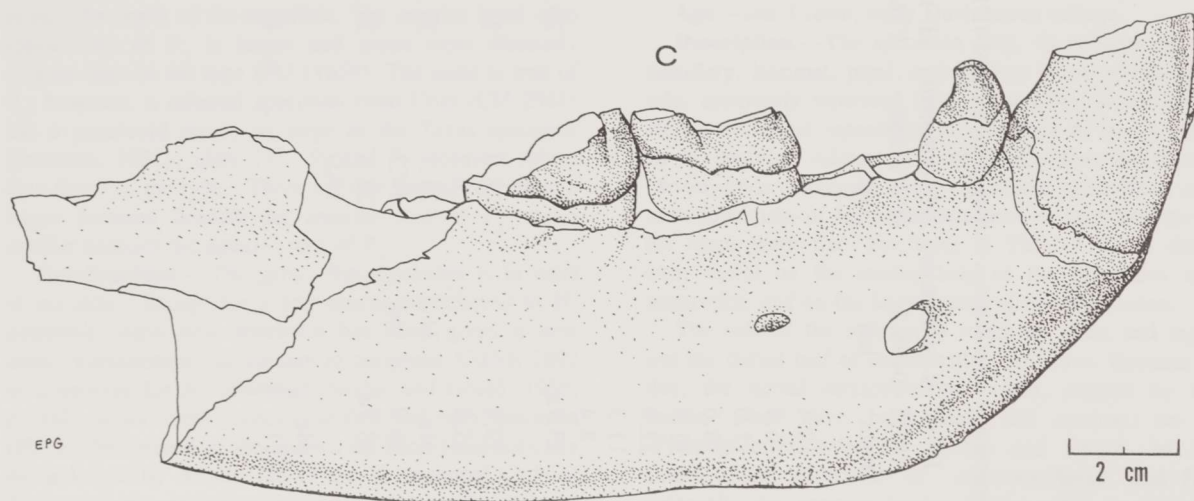
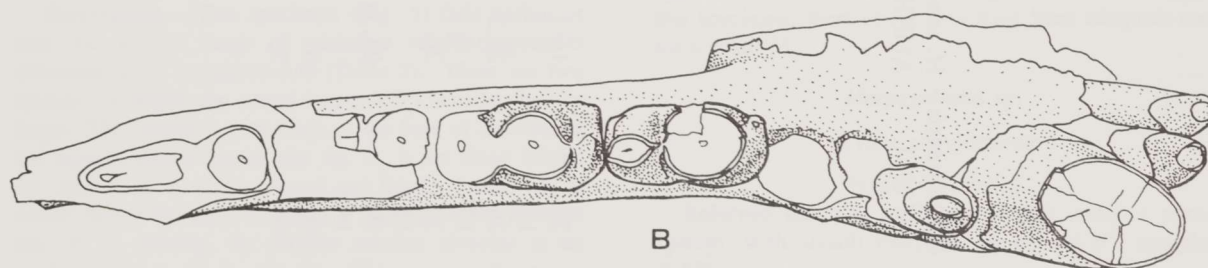


Figure 5.—*Harpagolestes* cf. *H. uintensis*, TMM 40498-3, Candelaria local fauna. A. Left P₄, lateral view. B-C. Right anterior ramus of mandible with incisors, canine, P₁, broken P₃ and P₄, dorsal (B) and lateral (C) views. Matrix and broken bone or tooth surfaces not shaded.

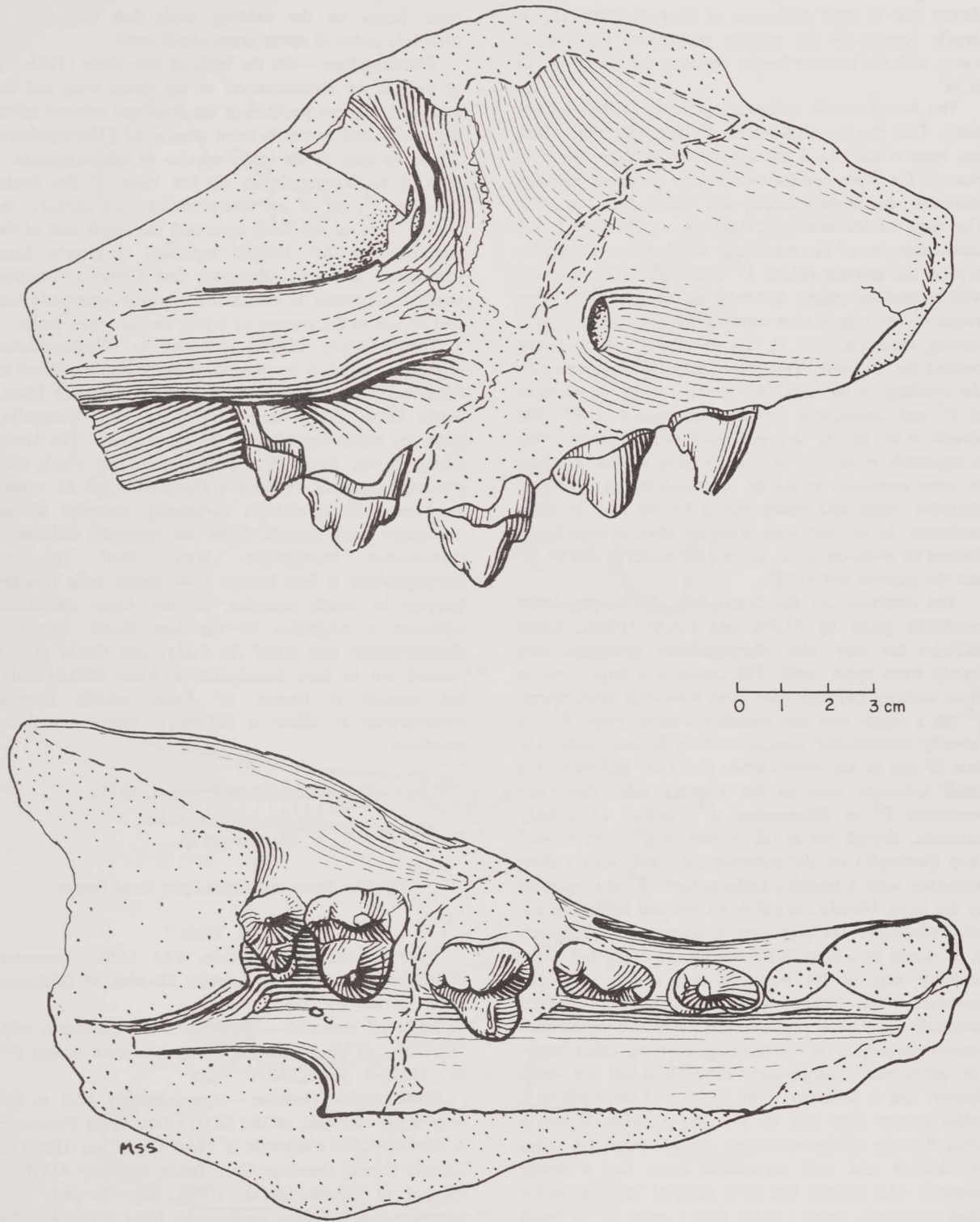


Figure 6.—*Harpagolestes* sp. TMM 41715-8, Skyline channels. Lateral and occlusal views.

orbital border is an oval knob of bone. The infraorbital foramen opens above the posterior root of P^3 at the narrowest part of the snout.

The palate is relatively narrow and is anteroposteriorly shorter than in other specimens of *Harpagolestes*. This is largely because of the anterior position of the internal nares, with the anterior border opposite the posterior root of M^1 .

The dental arcade is strongly arcuate in the vertical plane. This is a common feature in *Harpagolestes*, which has been related to a mechanism for holding bones in place in the lower jaw for crushing by the upper posterior premolars and molars (Szalay and Gould, 1966, p. 160). The roots of the anterior premolars are enclosed in the lateral margins of the maxillary, which projects ventrally beyond the anterior palate. P^1 likewise extends ventrally well beyond the palate; however, the bony borders of the alveoli do not extend over much of the roots of this tooth, leaving them (at least in this individual) exposed well beyond the alveolus. This effect may be exaggerated by the crushing of the maxillary in the vicinity of the roots of P^4 and consequent ventral displacement of P^4 . The alveoli of M^1 and M^2 are recessed above the palate. This is especially evident in M^2 , which is in a position which in most mammals might be occupied by an unerupted posterior molar and which would be too high to allow occlusion. In this specimen there are obvious wear facets formed by abrasion of M_2 against the posterior end of M^2 and the anterior end of M^3 .

The dentition fits the description of *?Harpagolestes orientalis* given by Szalay and Gould (1966), which includes the only other *Harpagolestes* specimens with lightly worn upper teeth. The canine was large, oval in cross section, and may have been somewhat procumbent. P^1 has a single root and probably a single cusp. P^2 is a laterally compressed conical tooth with two roots. The axis of one of the roots curves posterad, and there is a small accessory cusp on the posterior side. This tooth resembles P^2 of *Hyaenodon*. P^3 consists of a large paracone, though not as tall as that on P^2 , with a small cusp (parastyle) on the anteromedial corner and a short metacone with a laterally bulbous base. P^4 is dominated by the large, bluntly conical protocone and by the slightly taller paracone. The protocone is separated from the rest of the tooth by a deep V-shaped valley. Appressed to the posterior side of the paracone is a poorly developed metacone. The buccal side of the tooth is flanked anteriorly by a small parastyle and posteriorly by an even smaller metastyle. M^1 is the largest of the cheek teeth. The protocone is surprisingly large. It is tall and bullet shaped, and is separated from the rest of the tooth by a valley deeper than that on P^4 . The paracone is nearly twice the size of the metacone, though these two cusps are distinct and well separated. There was a strong parastyle (the enamel has been chipped from it) and a small metastyle, more a bulge than a cusp. M^2 is much smaller than M^1 . The protocone is small and low, and is connected to the medial side of the paracone by a small ridge, with no intervening valley. The paracone dominates the tooth, but is not particularly large. The

metacone is a tiny cusp appressed to the posterior side of the paracone near its base. This M^1 is more reduced than that of any other specimen of *Harpagolestes*.

No lower dentition was found, but it appears from the wear facets on the existing teeth that there was a complete series of seven lower cheek teeth.

Relationships.—On the basis of size alone (Table 4), as well as the measurements of the cheek teeth and the relatively anterior position of the orbit and internal nares, this individual is much more similar to *?Harpagolestes orientalis* than to the larger species of *Harpagolestes*. I refer it to *Harpagolestes* on the basis of the dental formula (P^4, M^3 if my interpretations are correct), the arcuate form of the tooth row, and the small size of the metacone on M^2 (which separates it clearly from *Mesonyx*). The only other very late Uintan (=Duchesnean) mesonychid is *Hessolestes*, which apparently had lost or was in the process of losing its last lower molar.

The similarity of this specimen to *?Harpagolestes orientalis*, which is known only from specimens found in the late Eocene Ulan Shireh deposits at Chimney Butte, North Mesa, Shara Murun region of Inner Mongolia, poses an interesting biogeographical problem. The Texas specimen was found at a stratigraphic level which also produced the earliest record of *Hyaenodon* (cf. *H. vetus*) in Texas. *Hyaenodon* is commonly accepted as an immigrant from Eurasia. Does this specimen indicate a coincidental immigration from Asia? Or, as *Harpagolestes* is best known from earlier beds (middle Eocene) in North America, do the Asian specimens represent a migration of the last North American *Harpagolestes* into Asia? As Szalay and Gould (1966) pointed out in their description of Asian mesonychids, not enough is known of Asian middle Eocene mesonychids to allow a definitive answer to these questions.

Genus *Hessolestes* Peterson, 1931a

Hessolestes sp.

Whistler Squat and Serendipity local faunas

Figure 7, Table 5

Type.—*Hessolestes ultimus*, CM 11763, posterior right mandible with $?M_2$, Lapoint Member of Duchesne River Formation, Utah.

Referred material.—TMM 41784-1, left ramus with $?P_2, ?M_2$; 41723-1, maxillary fragment with partial P^4-M^3 ; 41576-6, partial $?M^2$.

Stratigraphic position.—Approximately 12.1 m (40 feet) above the base of the Devil's Graveyard Formation at locality 41576 southwest of "Wax Camp" on Alamo de Cesario Creek, Brewster Co., Texas. Locality 41576 is mapped in Stevens et al. (1984, Fig. 7) and is at approximately the same stratigraphic level as the Whistler Squat quarry. Localities 41723 and 41784 are in the titanotherine channels shown in Stevens et al. (1984, Fig. 5E and D). Locality 41723 is near the top of Titanotherine Hill which is approximately 200 feet (60.9 m) above the

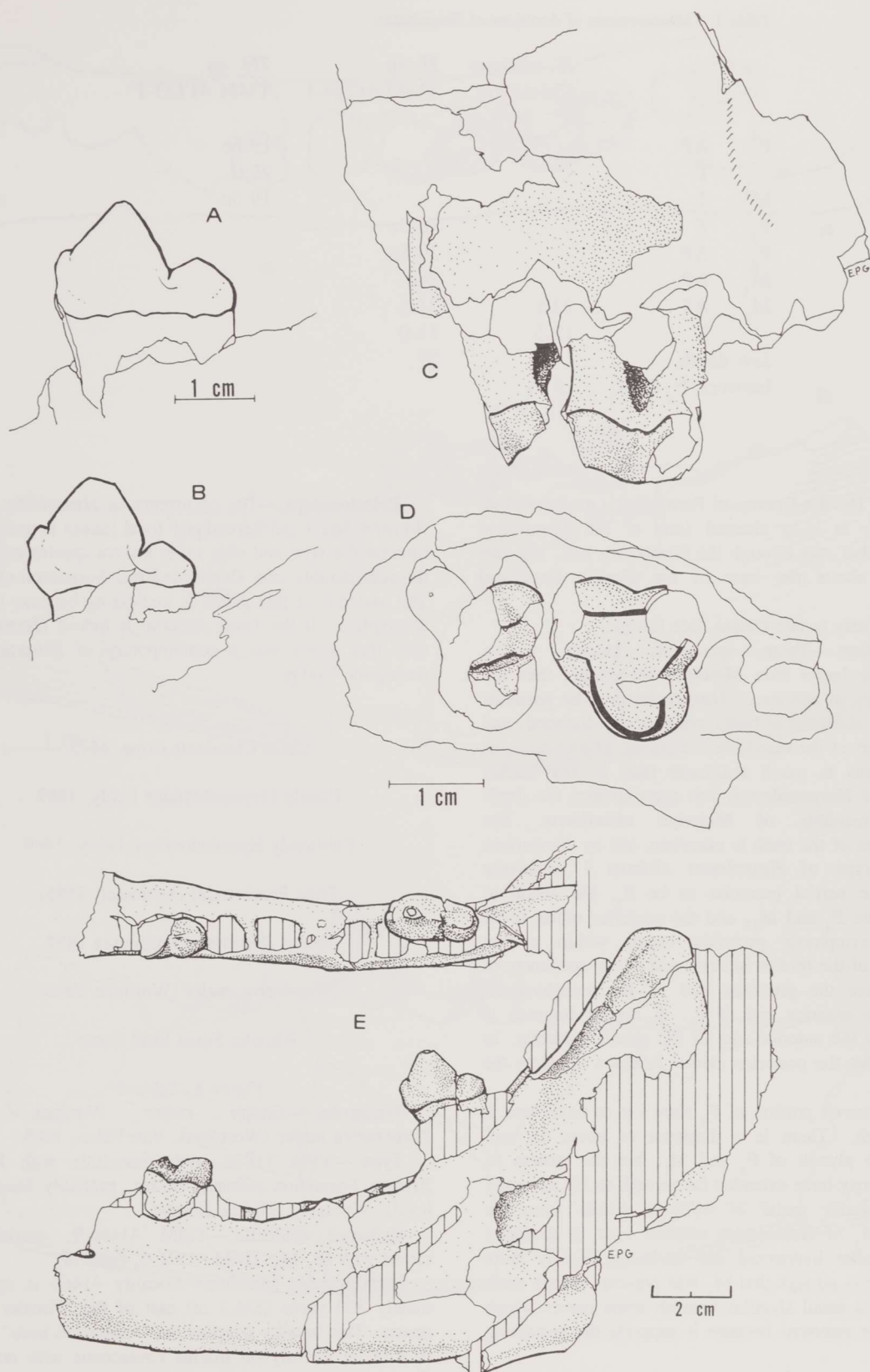


Figure 7.—*Hessolestes* sp. A. CM 11763, ?M₂ of type of *Hessolestes ultimus*, medial view. B. TMM 41784-1, ?M₂, medial view, reversed. C-D. TMM 41723-1, P³-M¹, lateral (C) and ventral (occlusal) (D) views, anterior to right, matrix and broken surfaces unshaded; short diagonal lines in lateral view indicate position of infraorbital foramen. E. TMM 41784-1, ramus of mandible with presumed P₃ and M₂, dorsal and lateral views; vertical lines indicate matrix.

Table 5.—Measurements of dentitions of *Hessolestes*.

		<i>H. ultimus</i> CM 11763	<i>H. sp.</i> TMM 41784-1	? <i>H. sp.</i> TMM 41723-1
P ⁴	AP			19.6e
	T			20.0
M ¹	T			19.5e
P ₃	T		10.5e	
P ₄	AP		20.8a	
M ₁	AP		24a	
M ₂	AP	22.8	21.8	
	T	11.5	11.0	
Jaw depth between P ₄ & M ₁			37	

base of the Devil's Graveyard Formation. Locality 41784, Unio Cliff, is in a channel (one of the Titanotheres Channels) that cuts through the Strawberry tuff, 152 feet (46.3 m) above the base of the Devil's Graveyard Formation.

Age.—Early to late Uintan, late Eocene.

Description.—These specimens belong to a mesonychine larger than *Mesonyx* but smaller than the North American species of *Harpagolestes*. The posterior part of the mandible is badly crushed and distorted, and the front part of the mandible is missing. The central part of the ramus is much shallower than in any known specimen of *Harpagolestes*, but approximates the depth of the mandible of *Mesonyx obtusidens*. The identification of the teeth is uncertain, but by comparison with the type of *Hessolestes ultimus* I tentatively consider the partial premolar to be P₃, the alveoli to accommodate P₄ and M₁, and the posterior molar to be M₂. The symphysis probably began within a few millimeters of the broken anterior end of the specimen; in *Harpagolestes* the posterior end of the symphysis is opposite the anterior end of P₃. A mental foramen is present near the anterior root of the partial premolar. In *Harpagolestes* the posterior mental foramen is below the anterior P₃.

The preserved portion of P₃ shows it to have been a narrow tooth. There is a diastema of about 10 mm between the alveoli of P₄ and M₁, but the crowns of these teeth may have extended far enough to fill this gap.

The posterior molar of 41784-1 differs from the presumed M₂ of *Hessolestes ultimus* only in having a slightly smaller hypoconid and in being slightly more worn. There is no sign that M₃ was present, though there is room for a small alveolus beneath some matrix which could not be removed because it supports the remaining tooth.

The upper tooth fragments are too worn and broken for firm identification. I very tentatively assign them to *Hessolestes* because they appear to be the proper size to match the Unio Cliff jaw.

Relationships.—The occurrence of *Hessolestes* in the Whistler Squat and Serendipity local faunas is unexpected because the type and only other known specimen is from the considerably later Duchesne River Formation of Utah. The material of this genus is tantalizing because it is so incomplete. If the Texas material is indeed *Hessolestes*, then that genus was a contemporary of *Harpagolestes* during the Uintan.

Order Creodonta Cope, 1875

Family Hyaenodontidae Leidy, 1869

Subfamily Hyaenodontinae Leidy, 1869

Tribe Proviverrini (Schlosser, 1886)

Genus *Proviverra* Rutimeyer 1862

?*Proviverra major* (Wortman 1902)

Whistler Squat local fauna

Figure 8, Table 6

Synonyms.—*Sinopa major* Wortman 1902; ?*Proviverra major* (Wortman), Van Valen, 1965.

Type.—YPM 11878, right mandible with P₃-M₃, Bridger Formation (Church Buttes, probably Bridger B level), Wyoming, Middle Eocene.

Referred material.—TMM 41466-9, partial left ramus with M₁-M₂; TMM 41576-5, right M₂.

Stratigraphic position.—Locality 41466 is approximately 300 yards (274.3 m) east of the Whistler Squat quarry. This locality overlies the "variegated beds" which in turn lie directly on marine Cretaceous with no basal Tertiary conglomerate present. TMM 41466 is approximately 30.4 m (100 feet) above the base of the Devil's Graveyard Formation and at approximately the same stratigraphic level as the Whistler Squat quarry. The strati-

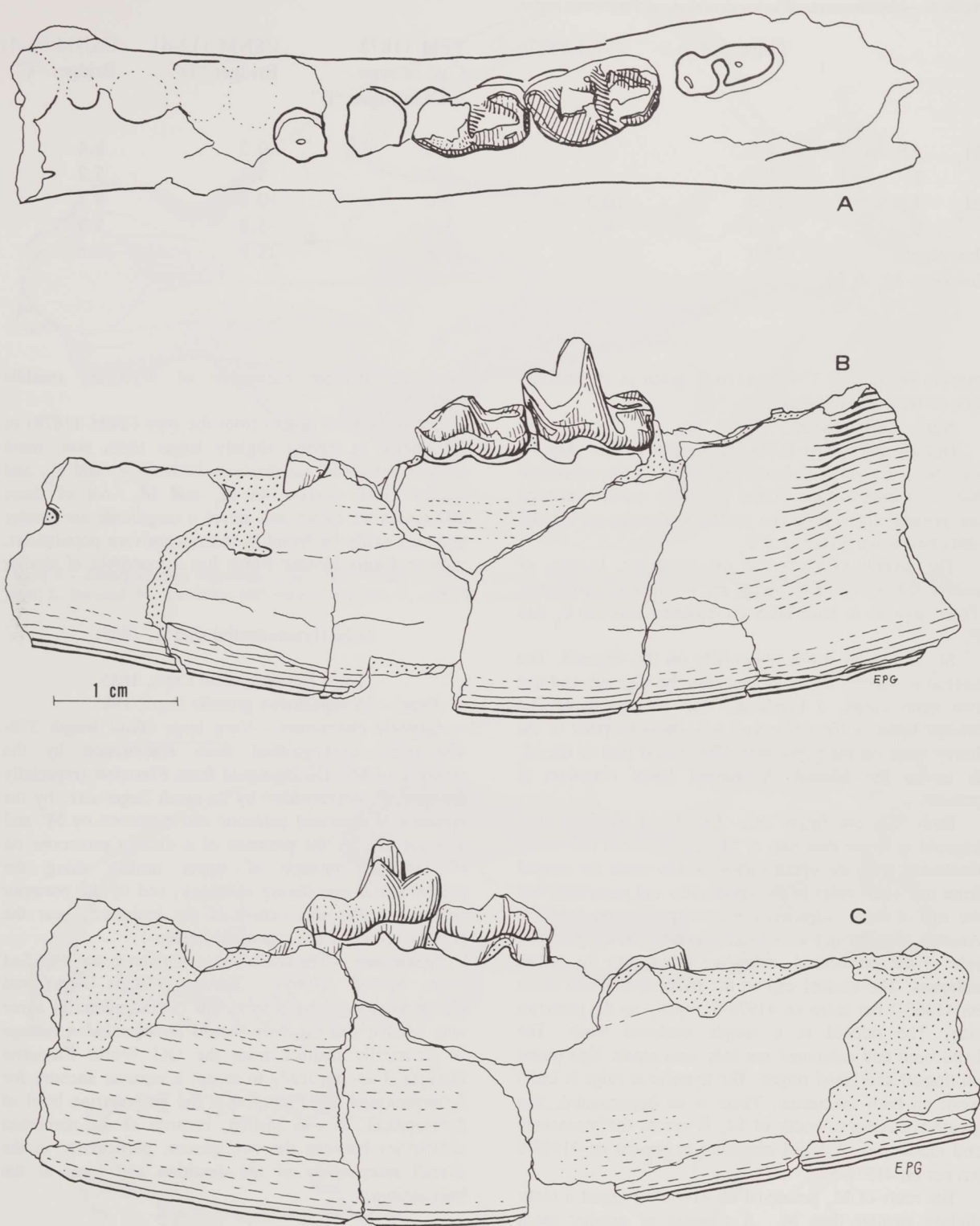


Figure 8.—*Proviverra major* (Wortman). TMM 41466-9, Whistler Squat local fauna. Mandible fragment with M_1 - M_2 . A. Occlusal view. B. External view. C. Internal view.

Table 6.—Measurements of lower dentitions of *Proviverra major*.

		TMM 41466-9	TMM 41576-5	YPM 11878 Cast of type, from Bridger "B"	USNM 112-41 Bridger "D"	USNM 98-41 Bridger "C"
M ₁	AP	9.7		8.8	9.5	8.4
	T	5.5		4.8	5.4	5.2
M ₂	AP	11.4	10.3	9.4	10.6	9.1
	T	6.5	6.1	5.5	5.8	5.9
Jaw depth between M ₁ & M ₂		23.1		19.8	18.8	18.8

graphic position of TMM 41576 is given in the description of *Hessolestes*, above.

Age.—Early Uintan.

Description.—The badly fractured mandible (Fig. 8) has about the same thickness and depth as the equivalent bone in *Canis latrans* (Table 6). Two mental foramina are present, one below the posterior alveolus of P₃, the other below the alveolus of P₁.

The alveoli of P₁-P₄ are preserved but, because of matrix fillings and fracturing, are not clearly delineated. There appears to have been no diastema between P₁ and P₂.

M₁ is heavily worn, especially on the trigonid. The talonid is slightly larger in area than the trigonid, and had two main cusps, a hypoconid and an entoconid. The talonid basin is triangular and was enclosed prior to the heavy wear on the hypoconid. The widest part of the M₃ is across the talonid. A distinct labial cingulum is present.

Both M₂s are larger than the M₁ of 41466-9. The trigonid is larger than that of M₁, and is much less worn. Occlusion with the upper carnassial has worn the enamel from the labial sides of the protoconid and paraconid, but the tips of these cusps are not heavily worn on 41466-9. Another less distinct wear facet is present on the posterior side of the protoconid, extending down into the *sulcus obliquus*. The enamel cap on the metaconid is still intact on 41466-9 but worn on 41576-5, mostly on the posterior side. The talonid is a simple enclosed basin. The hypoconid and entoconid are only noncuspsate high points on lingual and labial ridges. The hypoconid ridge is badly worn on both specimens. There is no hypoconulid. The greatest transverse width of M₂ is across the protoconid and metaconid. A labial cingulum is present on 41466-9 but not on 41576-5.

The roots of M₃ preserved on 41466-9 suggest a tooth slightly smaller than M₂. A trigonid of another tooth from this locality, lacking the talonid or any definite contact with the broken roots on the mandible, may be the M₃ of this individual.

Discussion.—I follow Van Valen (1965) in referring Wortman's *Sinopa major* to *Proviverra* with a query. There is little to distinguish these Texas specimens from the type and referred specimens of *Proviverra major*

from the Bridger Formation of Wyoming (middle Eocene).

TMM 41466-9 differs from the type (YPM 11878) of *?P. major* in having slightly larger tooth size, more massive mandible, no diastema between P₁ and P₂, and weaker labial cingula on M₁ and M₂. All of these differences are minor and are of a magnitude not greater than can easily be found in recent carnivore populations, such as *Canis latrans* which has a mandible of similar size.

Tribe Hyaenodontini (Leidy, 1869)

Genus *Hemipsalodon* Cope, 1885

Type.—*Hemipsalodon grandis* Cope, 1885

Generic characters.—Very large (skull length 370-450 mm). Distinguished from *Hyaenodon* by the presence of M³. Distinguished from *Pterodon* (especially the type, *P. dasyuroides*) by its much larger size, by the presence of separated paracone and metacone on M² and a larger M³, by the presence of a distinct protocone on P⁴, by the rotation of upper molars along the proximodistal axis during ontogeny, and by the posterior position of the constriction of the braincase, near the posterior roots of the zygomatic arches.

Discussion.—The characters given above are modified from Mellett (1969). Savage (1965) considered *Hemipsalodon* to be a synonym of *Pterodon*. I agree with Mellett that the New World *Hemipsalodon* lineage is generically distinct from the Old World *Pterodon* lineages. I am not ready to accept a separate ancestry for *Hemipsalodon* and *Pterodon* at the proviverrine level of development, as was Mellett, because of the numerous similarities between the two genera, particularly in the overall morphology of the dentition and form of the basicranium.

Hemipsalodon viejaensis n. sp.

Porvenir local fauna

Figs. 9-14, Table 7

Type.—TMM 40263-1, skull.

Referred material.—TMM 40688-50, maxillary

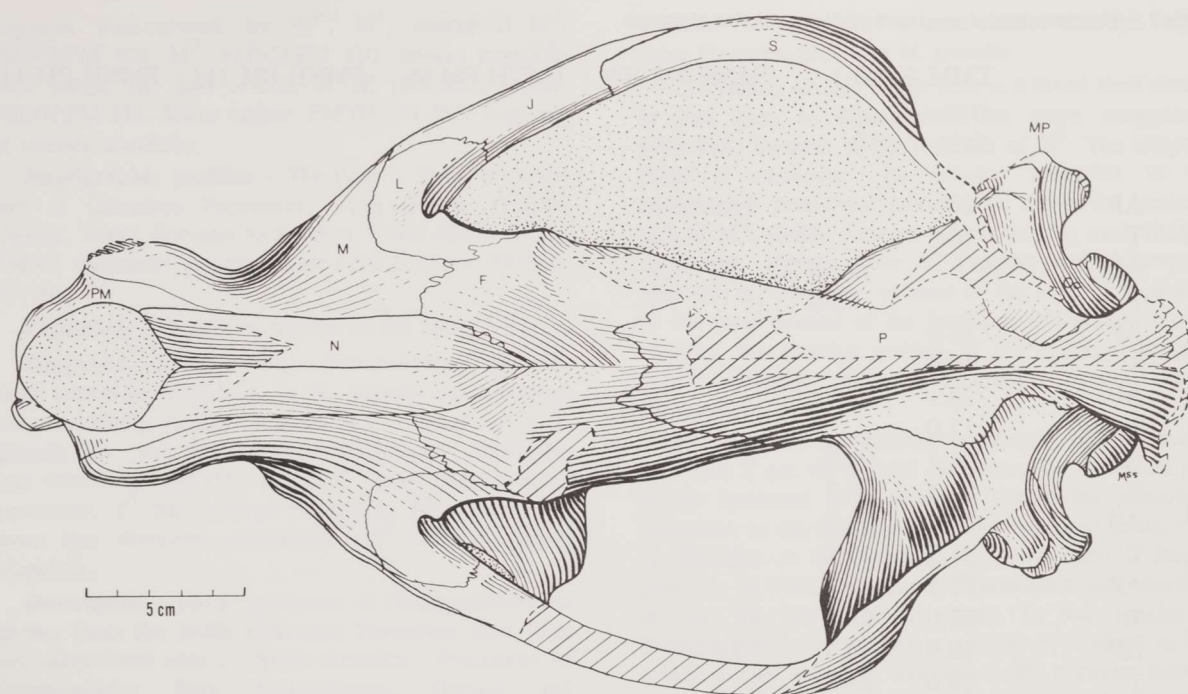


Figure 9.—*Hemipsalodon viejaensis* n. sp., type, TMM 40263-1, Porvenir local fauna. Skull, dorsal view. **Abbreviations:** F, frontal; J, jugal; L, lacrimal; M, maxillary; MP, mastoid process; N, nasal; P, parietal; PM, premaxillary

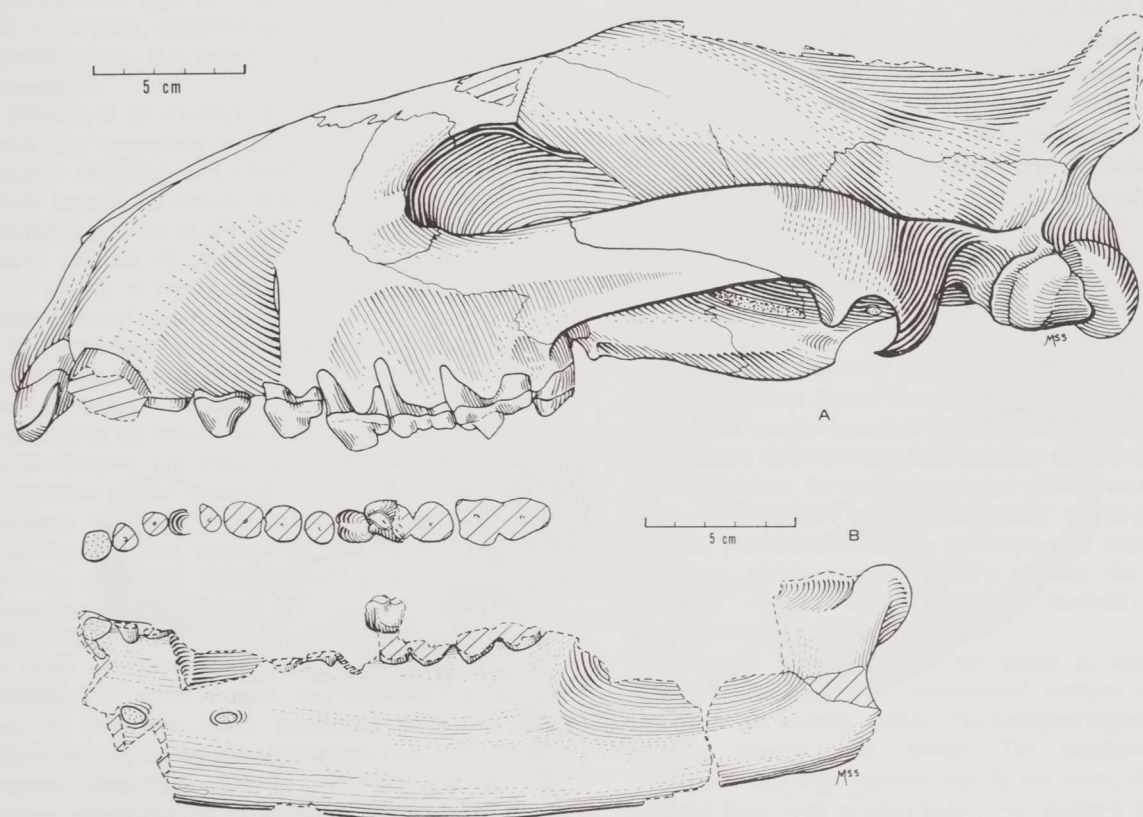


Figure 10.—*Hemipsalodon viejaensis* n. sp., Porvenir local fauna. A. TMM 40263-1, type, skull, lateral view (zygomatic arch restored from right side). B. FMNH PM 110, partial left ramus of mandible with alveoli and anterior M^1 .

Table 7.—Measurements of specimens of *Hemipsalodon viejaensis*.

		TMM 40263-1	FMNH PM 109	FMNH PM 96	FMNH PM 111	FMNH PM 110
		type				
		right	left			
C/	AP	23e				
	T	16e				
P ¹	AP		15.5e			
	T		8.0e			
P ²	AP	18.9				
	T	10.0				
P ³	AP	23.1				
	T	17.0				
P ⁴	AP	24.3	22.2			
	T	20.5	20.2			
M ¹	AP	20.2	21.2			
	T	17.7	18.0			
M ²	AP	27.3	25.9			
	T	22.0	22.0			
M ³	AP	10.0	10.3	10.2		
	T	23.6	23.5	25.1		
/C	AP			30.0		
	T			21.5		
M ¹ -M ³		60.0	60.5		61e	
P ¹ -M ³		142e	146.0			
P ₁ -M ₃						154a
Total skull length		378				
Maximum width		225				
across zygomas						
Maximum width		138				
across mastoids						
Maximum length of jaw						290a
Jaw depth at M ₁						50

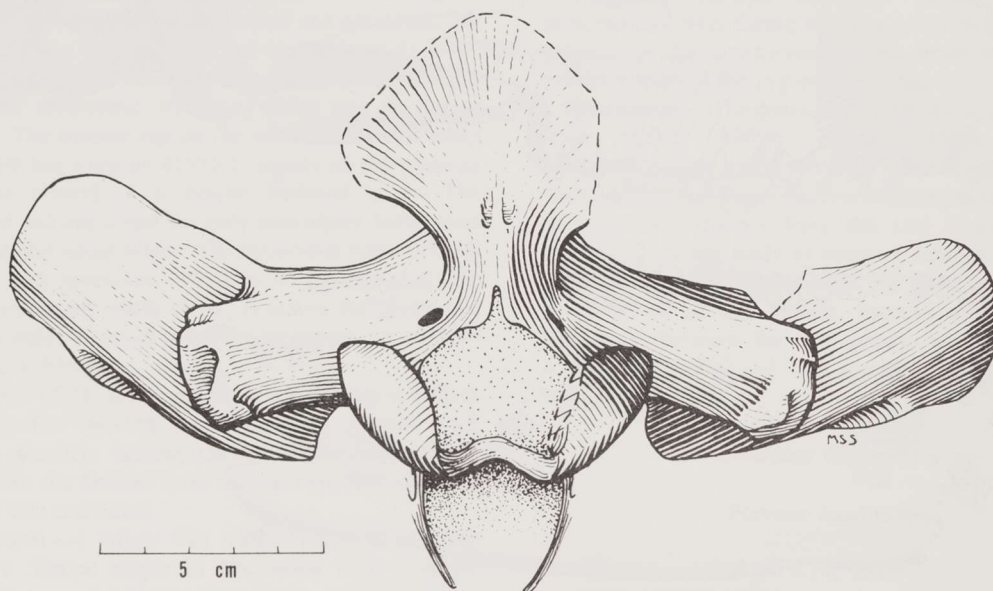


Figure 11.—*Hemipsalodon viejaensis* n. sp., type, TMM 40263-1, Porvenir local fauna. Skull, posterior view.

fragment with alveoli for dP^4 , M^1 , unerupted M^2 . FMNH:PM 109, M^3 . FMNH:PM 110, broken mandible with partial M^1 and alveoli of all postcanine teeth. FMNH:PM 111, lower canine. FMNH:PM 451, fragment of anterior mandible.

Stratigraphic position.—The type is from the lower part of Chambers Formation, Vieja Group, Presidio County, Texas, Porvenir local fauna, TMM 40688-50 and FMNH specimens are from Blue Cliff Horizon (Wilson, 1977b).

Etymology.—Native or resident of the Sierra Vieja.

Diagnosis.—Smaller than *Hemipsalodon grandis*, skull narrower. Nasals as in *H. grandis* but narrower, snout relatively slender, frontals not as broad as in *H. grandis* but more anteroposteriorly elongate. Premolars less crowded, relatively larger. P^3 may have a small protocone. P^4 has a large protocone. Maxillary tooth rows less divergent posteriorly. M^3 without lingual cingulum.

Description.—More specimens of *Hemipsalodon* are known from the lower Chambers Formation than from any other local area in North America. Specimens of *Hemipsalodon* from Saskatchewan, Oregon and Wyoming are consistently larger and closely match the excellent skull of *H. grandis* from Clarno, Oregon (Mellett, 1969). The specimens from the Chambers Formation are also consistent in size (Table 7), and there is little overlap between specimens of *H. grandis* and *H. viejaensis*. The type skull of *H. viejaensis* is an adult with worn teeth, complete except for sagittal crest, left zygomatic arch, and portions of the teeth, and is almost undistorted.

Because of the excellent preservation of this specimen I include a description of each of the skull bones, where possible. Crushing and cracking of the bones in the orbital region and fusion of bones in the posterior and basicranial portions of the skull make delineation of some sutures difficult or impossible, but in general, fusion along sutures is less than is present in living bears of similar size and maturity.

In dorsal view (Fig. 9) the dominant features of the skull are: the massive facial region, including a powerful snout expanded anteriorly for the large canines and posteriorly in the broad antorbital region; wide and strong but not massive zygomatic arches; small braincase with an hourglass outline in dorsal view; small and incomplete transverse occipital crests; and very large and laterally projecting conjoined mastoid and paroccipital processes. The long zygomatic arches, widest posteriorly, give a triangular shape to the outline of the skull. The skull is approximately the size of that of *Ursus arctos*. However, the skull of *Hemipsalodon* gives much less of the impression of great strength suggested by the grizzly skull. It lacks the heavy postorbital processes, well defined and rugose muscle attachments especially for the temporal, pterygoid, and masseter musculature, and compact appearance of the grizzly. It is likewise much less massive than either the Clarno (OMSI 619) or Cypress Hills, Saskatchewan, (NMC 8791) skulls of *H.*

grandis. The Texas skull is more slender although robust, more *Pterodon*-like, than *H. grandis*.

The ventral surface of the orbit is a broad shelf similar to that seen in *Hyaenodon*, but more exaggerated posteriorly because of the presence of M^3 . The temporal fossa is enormous. Its anterior extension to the rudimentary postorbital process lies above the posterior part of M^2 , farther forward than is seen in most fissiped carnivores, though those of *Procyon* and *Ailuropoda* approach it. However, because of the anterior expansion of the nasal portion of the braincase and posterior nasal cavities, the anterior portion of the temporal fossa is convex laterally, rather than strongly concave as in *Hyaenodon*.

The shape of the braincase is unusual. In *Hyaenodon* and most if not all fissiped carnivores the narrowest part of the braincase is immediately behind the postorbital processes, in the frontal bones. This seems to be the case in *Pterodon* as well, though the constriction is further posterior in *Pterodon* than in *Hyaenodon* and seems to be near the frontal-parietal suture. In both species of *Hemipsalodon* the greatest constriction is about at the middle of the parietals, adjacent to the posterior root of the zygomatic arches, and involves the dorsal portion of the squamosals.

In lateral view (Fig. 10) the skull is very bear-like, though with a more dorsally convex snout and more ventrally placed orbits. The face is long and deep. There is no postorbital projection on the jugal and only a small one on the frontal.

In posterior view (Fig. 11) the skull is dominated by the peculiarly restricted form of the transverse occipital crests, the very large combined mastoid-paroccipital processes, the large occipital condyles and foramen magnum, and the lateral extension of the posterior zygomatic arches.

The distribution of muscles supporting the head must have been considerably different from that in living large bears. Instead of attaching to a broad surface rimmed dorsally by the transverse occipital crests, the neck muscles attached to two very distinct areas, with apparently much less total surface area than on a grizzly of equivalent size. Part of the difference may be ascribed to the much smaller braincase in *Hemipsalodon*, and part to a greater differentiation between the muscles which attach just below the external occipital protuberance, and which raise the head (probably especially *rectus capitis dorsalis*, *semispinalis capitis*, *splenius*, and *trapezius*) and those which attach laterally, to turn the head (*obliquus capitis*, *rectus capitis lateralis*, and *sternomastoideus*).

In ventral view (Fig. 12) the palate is long and posteriorly widened. The ventrolateral surfaces of the maxillaries are broadly visible. The nasopharyngeal fossa is long, narrow, and tubular. The palatines and ?pterygoids converge ventrally but do not meet, forming a partial floor with parallel sides, and descend slightly posterad. There are no bullae. The posterior root of the zygomatic arch is much less expanded on the posterior

side than is that of *Ursus*, and the entire basicranial region is small.

Supraoccipital, exoccipital, and basioccipital bones are all thoroughly fused to each other and to the surrounding parietal, basisphenoid and squamosal. The peculiarly shaped posterodorsal portion of the occipitals presumably makes up the posterior surface of the sagittal and transverse occipital crests (though sutures are absent). The transverse occipital crests are incomplete. Instead of continuing laterally as sharp ridges which connect to the dorsal surface of the mastoid process, as in *Hyaenodon* and *Canis*, they converge ventrally, forming a concave, oval posterior surface above the foramen magnum. This condition is also seen in *Pterodon*, but the lateral compression above the foramen magnum is relatively greater in *Hemipsalodon viejaensis*.

The postero-lateral sutural contact of the occipital with the mastoid portion of the petiotic is clearly visible. The paroccipital process projects horizontally laterad with a distal posterad hook and is concave on the posterior side. The occipital condyles are shorter anteroposteriorly than in *Ursus*, and the foramen magnum is 25% wider and dorsoventrally slightly narrower. The hypoglossal foramina open directly ventrad. Mediad and anterad from the hypoglossal foramina are large depressed areas for attachment of the *rectus capitis ventralis* and *longus capitis* muscles. The occipital forms the posterior and medial walls of the posterior lacerate foramina.

The mastoid portion of the petiotic is large and forms a wedge between the squamosal and the paroccipital processes of the exoccipital. The mastoid processes face laterad and slightly ventrad and form the widest part of the basicranial region. The position of the stylomastoid foramen (for the facial nerve) is obscured by matrix, but a wide channel is present for this nerve on the ventromedial surface of the mastoid process, as in *Ursus*. The petrosal portion of the petiotic is visible only as a hemispherical projection in a deep, anteroposteriorly elongated fossa from which matrix has not yet been completely removed. The fossa is surrounded by the squamosal and basisphenoid-basioccipital bones. The *fenestrae rotundum* and *ovalis* are not visible.

The parietals form the roof of the posterior half of the skull, and appear to form the dorsal surface of the entire braincase. Anteriorly, the interparietal suture is unfused, and the dorsal edge of the parietals forms the high sagittal crest, which is broken for most of its length. Two lateral constrictions are visible in dorsal view. Both are overlapped by the dorsal edge of the squamosal. The swollen area between the constrictions indicates the position of the cerebral hemispheres. The peculiar posterior position of the narrowest part of the braincase makes interpretation of the form of the brain difficult. Compared to *Pterodon* (Piveteau, 1935), the cerebrum appears to have been shorter and broader, the cerebellum relatively smaller, and the olfactory lobes larger. However, there is altogether too much space in the postorbital portion of the skull within both parietals and frontals for even greatly expanded olfactory lobes. This

suggests that the nasal cavities probably extend back under the anterior parietals. The lateral edges of the anterior part of the parietals extend considerably ventrad just anterad from the constriction, presumably covering the sides of the olfactory lobes.

Although the frontals cover the anterodistal part of the brain in most mammals, this does not seem to have been true in *Hemipsalodon*, unless the frontal extends farther under the parietals than seems likely. The external frontal crest divides the dorsal part of the frontals into a concave anterior part which contacts the nasals and maxillaries, and a convex posterior part which makes up the anterior temporal fossa. The frontal contacts the lacrimal broadly on the side of the face and the medial wall of the orbit, then further posterad forms long sutural contacts (partly obscure) with the palatine and orbitosphenoid-alisphenoid complex. The sutural contact with the parietals extends far anterad dorsally, unlike fissiped carnivores in which this contact is nearly vertical as seen from the side. If ethmoid foramina are present, they must be small and hidden by cracking of the orbital wall.

The sphenoid complex, made up of the basisphenoid, alisphenoid and orbitosphenoid, is difficult to partition because of fusion of sutures between them and with the pterygoid and basioccipital.

There are three major foramina in the posterior orbital wall, all apparently within the sphenoid complex (Fig. 13). The anteriormost of these appears to be the optic foramen, for the optic nerve (II), if comparison to *Pterodon* is valid (Piveteau, 1935). However, I could not find an ethmoid foramen in the orbital wall at the frontal-sphenoid suture, nor am I positive that my reconstruction of the orbital sutures is correct. If I have placed this suture too far forward (Fig. 10), then the anteriormost large foramen might be the ethmoid, which is large and in this position in *Ursus* and *Ailuropoda*. I interpret the next most posterior foramen to be the orbital fissure (*fente sphenoidale* of Piveteau, 1935) for III, IV, the ophthalmic branch of V, and VI. Further posterad (38 mm behind the orbital fissure) is the *foramen rotundum*, which is somewhat larger than the other two foramina. In *Pterodon* (unlike *Hemipsalodon*) the *foramen rotundum* and orbital fissure are closely adjacent and equal in size, with the orbital fissure opening directly upon the dorsal marginal ridge of the *foramen rotundum*. There is no alisphenoid canal in *H. viejaensis*. Instead, a broad groove leading from the *foramen ovale* around the posterolateral wall of the alisphenoid carried the maxillary artery, which seems to have been quite large.

The contact of the alisphenoid and basisphenoid with the squamosal is clearly visible on the side of the cranium and can be followed posterad along the dorsal border of the *foramen ovale* to the position of the eustachian tube, where it becomes completely fused. The contact with the basioccipital and pterygoid bones is likewise invisible. Just ventrad from the groove of the maxillary artery, apparently in the pterygoid, is a small foramen, probably the posterior pterygoid foramen. The contact of the pterygoid-sphenoid complex with the palatine bones is very well marked.

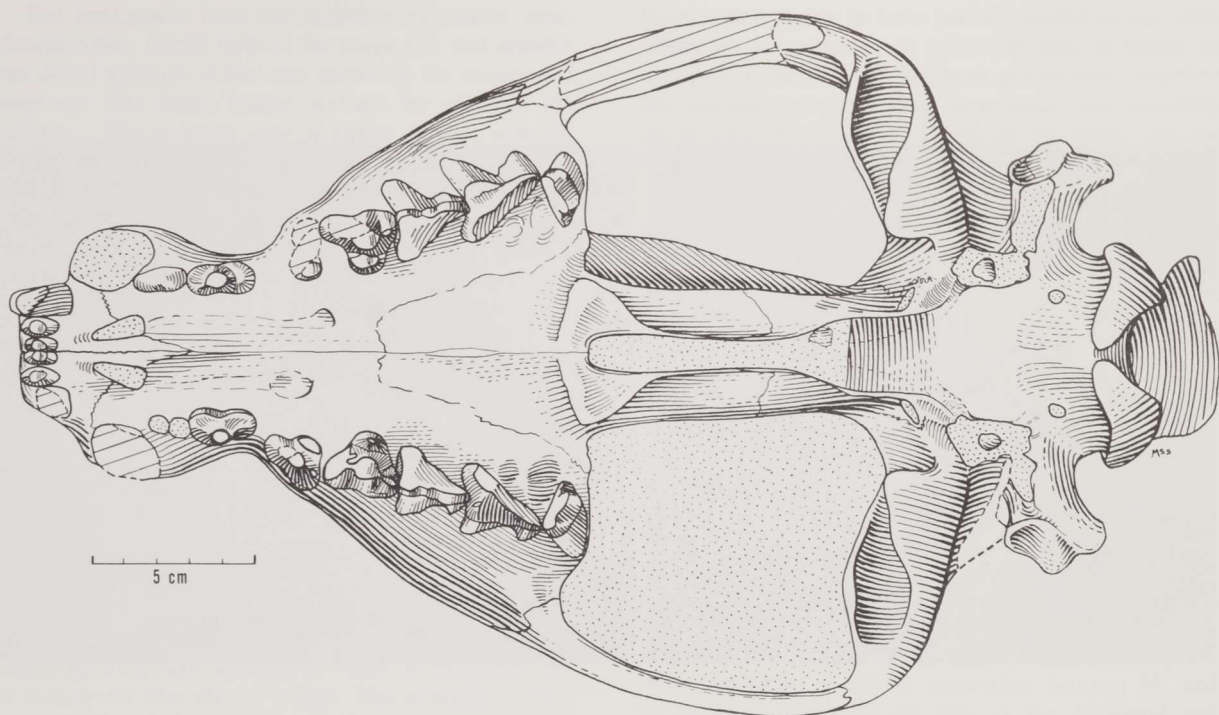


Figure 12.—*Hemipsalodon viejaensis* n. sp., type, TMM 40263-1, Porvenir local fauna. Skull, ventral view.

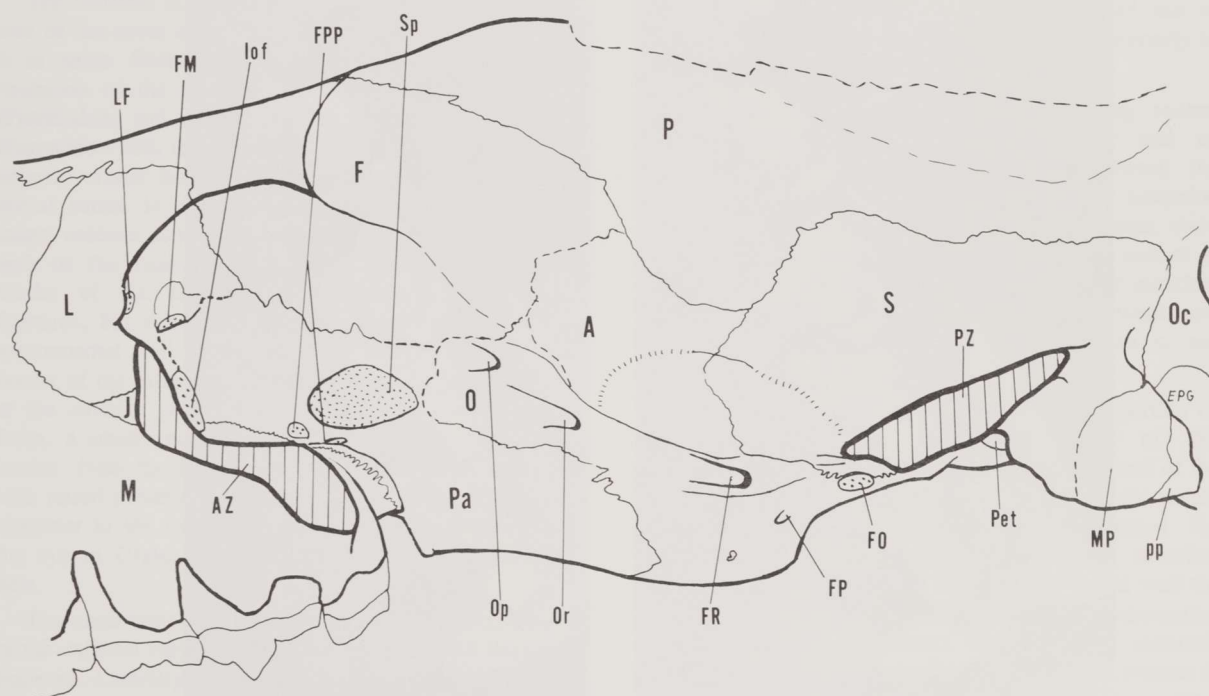


Figure 13.—*Hemipsalodon viejaensis* n. sp. Interpretation of bones and foramina of orbit and lateral braincase, based on details from both sides of the skull, TMM 40263-1.

Abbreviations: A, alisphenoid portion of sphenoid complex; AZ, anterior root of zygoma (cut); F, frontal; FM, fossa for inferior oblique muscle; FO, foramen ovale; FP, posterior pterygoid foramen; FPP, posterior palatine foramen; FR, foramen rotundum; Iof, infraorbital foramen; J, jugal; L, lacrimal; LF, lacrimal foramen; M, maxillary; MP, mastoid process of petiotic; O, orbitosphenoid portion of sphenoid complex; Oc, occipital; Op, optic foramen; Or, orbital fissure; P, parietal; Pa, palatine; Pet, petrosal portion of petiotic; PP, paroccipital process; PZ, posterior root of zygoma (cut); S, squamosal; Sp, sphenopalatine foramen.

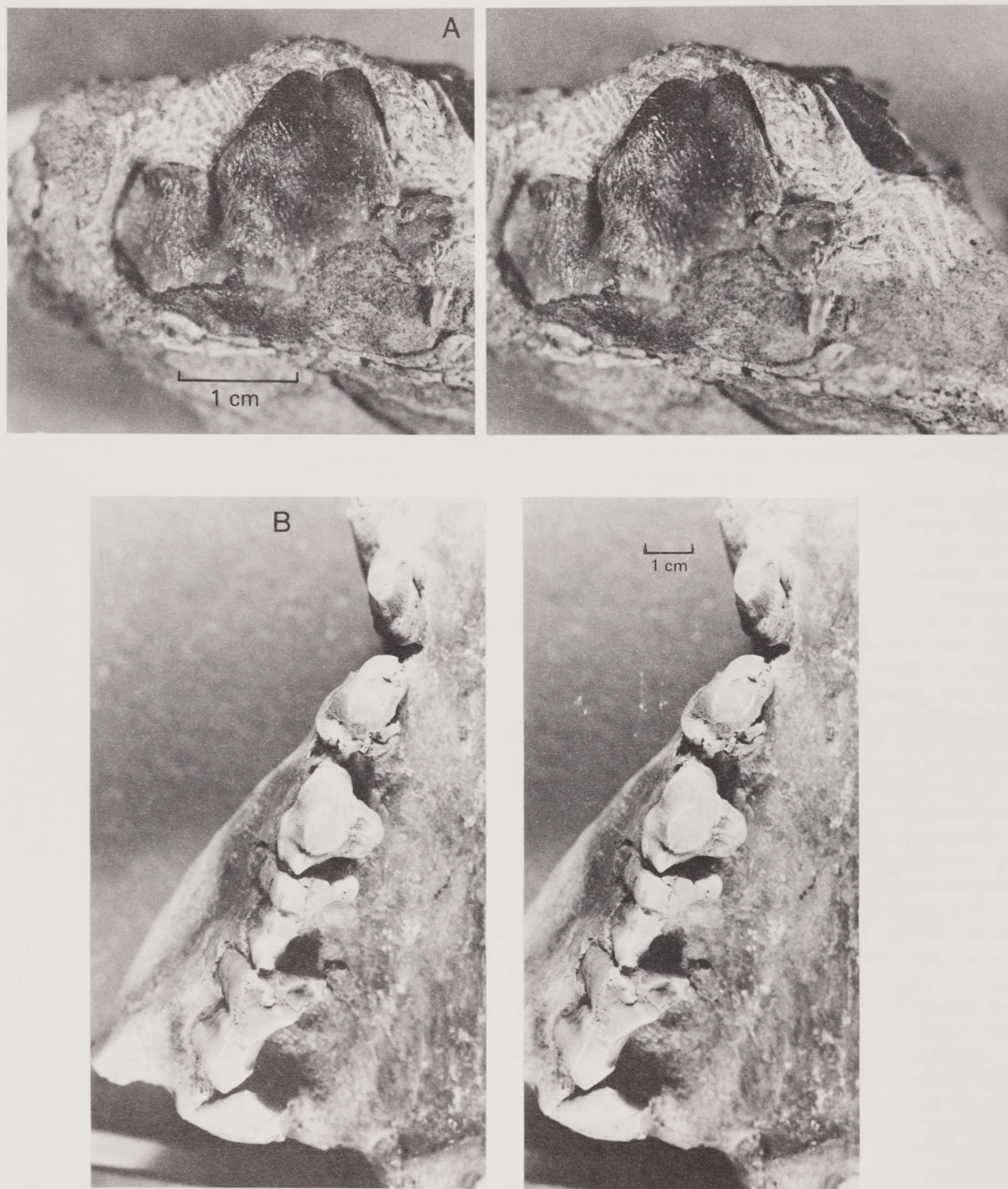


Figure 14.—*Hemipsalodon viejaensis*, Porvenir local fauna. A. TMM 40688-50, referred. Unworn M², showing paracone and metacone as distinct cusps. B. TMM 40263-1, type. Stereophotograph of right upper dentition (P²-M³).

The squamosals form the posterior zygomatic arch, glenoid fossa, lateral wall of the braincase, and anterior and dorsal portions of the area enclosing the middle and inner ear. The dorsal border overlaps the edges of the parietals. The posterior edge is saddle shaped, with the contact with the occipitals and mastoids on the posterad-facing surface. A broad lateral flange covers the anterodorsal surface of the mastoid process and makes up the posterior and dorsal sides of the external auditory meatus. The ventral contacts with the petiotic are obscure.

The broad spoutlike dorsal depression for the posterior portion of the temporal muscle is shorter anteroposteriorly than in *Ursus* and lacks the broad and well defined posterior shelf seen in *Ursus*. The entire posterior root of the zygomatic arch is narrower and apparently not as strong as in equivalent sized *Ursus*. The glenoid fossa is large, with a spiral shaped articulating surface. The condylar process of the mandible of a large *Ursus arctos* fits easily into the fossa with room to spare. The postglenoid process is large, with more ventral extension than in *Ursus*. The anterolateral glenoid process is large, producing a tubelike articulation which is more like that of a large cat than that of a bear. This evidently allows for strength and the precise occlusion necessary in some animals with specialized carnassial dentition. A similarly specialized glenoid fossa is found in larger mustelids (for example *Gulo* and *Taxidea*).

The lacrimal is a large bone, expanded well onto the side of the snout as in many primitive mammals. In this it is more *Didelphis*-like than dog-like. The facial extension of the lacrimal is more pronounced than in *Hyaenodon*, and the lacrimal as a whole is larger. In *Hyaenodon* both the dorsal and ventral sutures are on the anterior orbital border. In *Hemipsalodon viejaensis* the dorsal suture is on the dorsal border and the ventral suture extends across the anterior base of the zygomatic arch on the ventral border of the orbit. The posterior border of the lacrimal is obscured by fusion and fractures, but this bone seems to make up most of the anteromedial wall of the orbit and may form the dorsal border of the infraorbital foramen. A rough knob of bone at the anterior point of the orbit protects the lacrimal fossa, a small opening about 11 mm inside the orbital border. Near the lacrimal-palatine contact is a large pit with raised posterior rim which is similar in position and character to the fossa for the inferior oblique muscle of the eye in *Ursus* and *Ailuropoda*, and is so identified here.

The nasal bones are long and broad. The dorsal border of the external narial opening is V-shaped, with the point posterad. Laterally, the nasals have a short contact with the premaxillaries, a long straight contact with the dorsal border of the maxillaries, and slightly shorter, posteriorly converging sutures with the frontals. The forehead is concave, with the posterior part of the nasals forming the anterior part of the shallow concavity. The nasals are convex between the maxillaries. The anterior nasals have a peculiar V-shaped concavity partly rimmed with frac-

tures, which appear to have partially healed in one area. There are no separated or offset fractures as would be expected if the damage had been postmortem; therefore this individual probably had been struck very forcefully on its nose, breaking and deforming the nasals, and the break at least partly healed before death.

The dorsal edges of the premaxillary bones are short, forming the lateral walls of the nasal opening and extending to a point above P¹. Ventrally, the premaxillaries form the alveoli for the incisors, the anteromedial wall of the canine alveolus, and the anterior and medial sides of the anterior palatine foramina. The premaxillary-maxillary sutures converge at an acute angle just posterior to those foramina.

The maxillary bones are large, forming most of the side of the snout the anterior base of the zygomatic arch, the alveoli for canines and cheek teeth, and much of the palate. Suture contacts with the premaxillaries, nasals, lacrimals and jugal bones are clear and incompletely fused despite the maturity of the animal, but the ventral contact with the palatines is fused and is obscure in places. Large palatine foramina are present between the third premolars. A double excavation between M² and M³ allowed space for the tips of the paraconid and protoconid of M₃. The lateral surface of the maxillary just dorsal from the roots of M¹⁻² is concave. The anterior opening of the infraorbital foramen is vertical and oval, placed above and between the roots of P³. The sides of the snout are strongly pinched inward just in front of the infraorbital foramen, then widen anteriorly to allow room for the very large canine roots.

Anteriorly, the jugal bones have a strong ventral buttress contacting the posterior maxillary and an elongated dorsal process which wedges between the lacrimal and maxillary. The posterior ventral extension tapers to an end at the widest point of the zygoma, close to the posterior end of the arch. The ventral surface is scarred by the attachment of powerful masseter muscles. The raised rim of the scarred area extends forward onto the lateral surface of the maxillary, but most of the attachment area was on the jugal.

The palatines make up the postero-ventral portion of the palate and the antero-lateral walls of the nasopharyngeal fossa. Surrounding the anterior end of the nasopharyngeal fossa and marking the end of the palate are two triangular raised areas which formed the anteromedial attachment for the pterygoid muscles. Dorsally, the palatines form a lateral and dorsal wall for the tube-like nasopharyngeal fossa and the ventromedial wall of the orbit, contacting the maxillary, lacrimal, frontal and sphenoid bones. Three foramina are present in this bone on the ventral and medial posterior orbital walls: two small posterior palatine foramina, and a very large oval hole, presumably the sphenopalatine foramen (*foramen palatin* of Piveteau, 1935, in *Pterodon*, in which it is relatively much smaller).

The upper dentition is well preserved except for the canines and P¹ (Fig. 14). All teeth show wear, but the

teeth of the left side of the type skull are more worn than those of the right side.

I¹ and I² are similar, relatively small single cusped teeth. I² is slightly larger than I¹ and possesses a small lateral cingulum. I³ is much larger, semicaniniform tooth, which wore laterally against the medial side of the lower canine. The incisors are more tightly packed together and more anteroposteriorly elongated than in *Ursus*. The central incisor cusps form an arc which is concave anteriorly.

The crowns of the canines are not preserved. The roots indicate that these teeth were about the same size as in *Ursus arctos horribilis*. The canines in *H. viejaensis* were considerably smaller than in *H. grandis*, and may have been smaller in relative as well as absolute terms.

The premolars increase in size from front to back. Only the left P¹ is preserved in the type skull, and its crown has been completely worn off. As in *H. grandis*, P¹ has two roots, with the anterior root turned slightly to the medial side of the canine. Judging from the preserved roots and alveoli, P¹ in *H. grandis* was almost as big as P², whereas in *H. viejaensis* it is somewhat smaller (alveoli just over half the length of those of P²). P² in *H. viejaensis* is very close in size to the P² of the Cypress Hills skull of *H. grandis*, and has the anterior root directly posterad to the posterior root of P¹, rather than being set mediad as in *H. grandis*. The crown of P² is relatively simple, consisting of a single main cusp (paracone) with anteromedial and posterior ridges, a slight medial and a large posterior cingulum. P² is separated from P³ by a small gap. P³ has a large posteromedial lobe which if cusped, could be called a protocone. Supporting this is an enlargement of the posterior root, though it is impossible to tell whether the posterior root is divided. A distinct metastyle is present posterad from the much larger paracone. As in the other cheek teeth, the enamel surface is finely crenulated.

P⁴ is relatively large. It is about the same length as P³ but much broader, taller and more massive. The protocone is quite large and is supported by a separate medial root. The metastyle is a distinct cusp but much smaller than the paracone. The tooth is worn mainly on the tips of the cusps and on the anterior surface. This is the first specimen of *Hemipsalodon* in which P⁴ is complete; however, Mellett (1969) deduced the presence of a large protocone on the Clarno specimens from the size of the medial root. The protocone of P⁴ in *Pterodon dasyuroides* is very small, only about the relative size of the protocone of P³ in *Hemipsalodon*.

M¹ is badly worn on both right and left. The protocone and metastyle were both large, and the tooth was certainly carnassial, as in *H. grandis*, but no details of the cusps are visible. M¹ is similar in size to P⁴, and a weakly developed labial cingulum is present, as on P⁴.

M² can be more completely described, thanks to the presence of a partial unerupted M² in TMM 40688-50, as well as the worn teeth on the type. It is similar in shape to M¹, but larger. The protocone is a large crescentic cusp set linguad and anterad from the paracone and

connected to it by low anterior and posterior crests. A small parastyle is present. The paracone and metacone are closely appressed and equal in height, but separated by a notch. The metacone-metastyle crest is long and deeply notched, forming a highly developed blade, which is honed to a sharp edge on the type specimen. A distinct cingulum is present along the entire labial margin of the tooth.

M³ has its long axis transverse to the rest of the tooth row, and wears mostly on its anterior surface and the tip of the highest cusp. It is relatively larger in *Hemipsalodon* than in *Pterodon*, and is larger in its transverse dimension than M¹ is in the anteroposterior dimension. The protocone of M³ projects much further mediad than in *Pterodon*. The paracone and metacone are not seen as distinct cusps on the type of *H. viejaensis* or on an isolated M³ (FMNH:PM 109). The parastyle is large, apparently relatively larger in *H. viejaensis* than in *H. grandis*. The protocone is crescentic, with distinct paraconules and metaconules on the type specimen, though these accessory cusps are small on FMNH:PM 109. The posterior crest connecting the protocone and metaconule is deeply notched and is lower than the anterior crest. A well defined posterolabial cingulum is present.

The mandible (FMNH:PM 110) is only slightly curved along its lower margin. In this and most other characters it is similar to the mandible of *Pterodon dasyuroides*, though much larger. The symphysis is not fused in either adult specimen of *H. viejaensis* or in specimens of *H. grandis*. There are two major mental foramina, the anterior and larger being beneath P₃ and the posterior beneath a point between P₃ and P₄. These are essentially the positions of these foramina in *Pterodon*. The mandible is much shallower in *H. viejaensis* than in the type specimen of *H. grandis* (NMC 6497), and is less strongly curved on the ventral margin. The coronoid process is not preserved, but judging from the preserved ventral part of the posterior mandible, it was probably broad and rounded, as in *Pterodon* and some other creodonts. The angular process was small and hooked slightly dorsad. The condyloid process is large, with the articulation surface carried farther anterodorsally, especially on the lateral side, than in *Ursus arctos*. The masseteric fossa is broad and deep, though there is no sharp ventral boundary ridge as in *Ursus arctos*. The lateral surface of the mandible just below M₃ is strongly swollen.

Alveoli are preserved for all the teeth except the incisors. An isolated canine (FMNH:PM 111) is of similar size and form to the canines of a specimen of *H. grandis* from Clarno (OMSI 619), though a little too large for the two available mandible fragments of *H. viejaensis*. It should be noted that the mandible (FMNH:PM 110) of *H. viejaensis* is a little too large to fit the skull (TMM 40263-1). Therefore, the canine FMNH:PM 111 appears to represent the largest known individual of *H. viejaensis*. P₁ had a single root, the alveolus for which is larger than either alveolus of P₂.

The alveolus was inclined from the vertical because of space limitations caused by the large canine root. The premolars are increased in size posterad to P_4 , which was somewhat larger than M_1 , as in *H. grandis*. Several fragments of teeth are present with FMNH:PM 110, but only the anterior part of M_2 could be fitted to the broken roots. The anterior surface of the paraconid of M_2 is bilobed, with a groove between the larger anteromedial and smaller anterolateral vertical ridges. The protoconid and paraconid appear to have been about the same height, though this is very uncertain because of breakage. This is unlike the M_2 of *Pterodon dasyuroides* in which the paraconid is relatively small. Wear on the lateral face of M_2 suggests a shearing function, though the tips of the paraconid and protoconid had been rounded sufficiently to greatly reduce the efficiency of shear by the time the animal died. M_3 was much larger than M_2 but only the roots are preserved.

Discussion.—Some comments on the validity of both the generic and specific names used for *Hemipsalodon viejaensis* are necessary. The differences between *H. grandis* and the proposed new species are largely matters of size and proportions. Because of this, one is compelled to consider the possibility of sexual dimorphism as being the cause of the differences. I have rejected this possibility because of the general consistency in size shown by specimens referred to *H. grandis*, though there probably is overlap in some dimensions between small individuals of *H. grandis* and large specimens of *H. viejaensis*. Neither sample shows dimorphism. If comparisons with size ranges in living bears are significant, it is notable that the skulls of *H. grandis* are about the size of skulls of the Kodiak bear (*Ursus middendorfi*) and the skull of *H. viejaensis* is similar in size to that of a grizzly (*Ursus arctos*). Those who would lump the grizzly with the Alaskan coastal brown bears might consider all specimens of *Hemipsalodon* to belong to a single species.

A similar problem of possibly marginal definitive criteria exists for the genus *Hemipsalodon*. I consider the differences in size, tooth proportions, and cranial structure discussed above and by Mellett (1969) to be sufficient for the generic distinction from *Pterodon*. Mellett emphasized the rotation of the upper tooth rows in *Hemipsalodon*, stating that the uppers were rotated mediad and the lowers laterad. He suggested no mechanism for this rotation, and indeed I can see no evidence for rotation of most of the teeth on the available specimens. An exception is the upper molars, which have strongly curved roots, convex laterally in M^1 and M^2 , posteriorly in M^3 . This curvature is strong enough that as the teeth wear down and are extruded from the alveoli the crowns will naturally be slightly rotated. There is no such mechanism in the lower molars since the roots are straight. However, it is possible that fairly constant pressures during chewing, or pressure when the jaws were closed and the teeth occluded, could cause a slight migration of the lower molars. However, the upper molars close covering the lateral surfaces of the lower

molars. Thus if occlusal pressures were present, one would expect a mediad rather than a lateral migration. Moreover, the M_3 's of *Pterodon dasyuroides* show a distinct lateral inclination (protoconids on opposite M_3 's strongly diverging dorsally, which is similar to the feature described as "rotation" described by Mellett in *Hemipsalodon*. It may be noted that in *Pterodon dasyuroides* the roots of the upper molars appear to be straight, so that the absence of molar rotation in *Pterodon* noted by Mellett is probably correct.

Discussion of the ancestry of *Hemipsalodon* is speculative, as morphologically convincing close "ancestors" are unknown. Certainly both *Hemipsalodon* and *Pterodon* shared a common ancestry, presumably in the Proviverrini, and the genus *Arfia* from the early Eocene of North America may be close to that common ancestor. In view of the generally close similarities among many European and North American mammalian faunas of Wasatchian-Spanacian age, it seems possible that the common ancestor of *Hemipsalodon* and *Pterodon* existed during the very early Eocene. This appears to be the view adopted by Mellett (1969) although he did not state it in this form.

Another possibility, essentially that suggested by Schlaikjer (1935), is that some species already at the stage of development of early *Pterodon* was the common ancestor of the known species of *Pterodon* and *Hemipsalodon*. The appearance of *Hyaenodon* in upper Eocene rocks just before the appearance of *Hemipsalodon* in both North America and Europe indicates that a migration route was available at this time (latest Eocene to earliest Oligocene). A closer common ancestry would more readily account for the close similarity, seen especially in the dentition and posterior cranium, than would parallel evolution over a period of 15 million years through the Eocene.

Ischnognathus savagei Stovall, 1948

Porvenir local fauna

Figure 15

Type.—OU 32-4-S1, symphyseal portion of mandible lacking crowns of teeth.

Stratigraphic position.—Chambers Formation, 4.6 to 6.1 m (15 to 20) feet below the lower marker bed, Vieja Group.

Age.—Early Chadronian, early Oligocene.

Description.—Stovall (1948) accurately describes the shape, particularly the deep, narrow ventral groove of the symphyseal region, which is apparently unique (Fig. 15a). The form and arrangement of the incisors is uncertain. At least two small incisors seem to have been present, with the medial incisor alveolus on the dorsal side of the lateral incisor alveolus (or alveoli). On the left side, two matrix-filled alveoli appear to be present. On the right side, the matrix has been excavated from the alveoli, and the ventral (lateral) alveolus appears to have

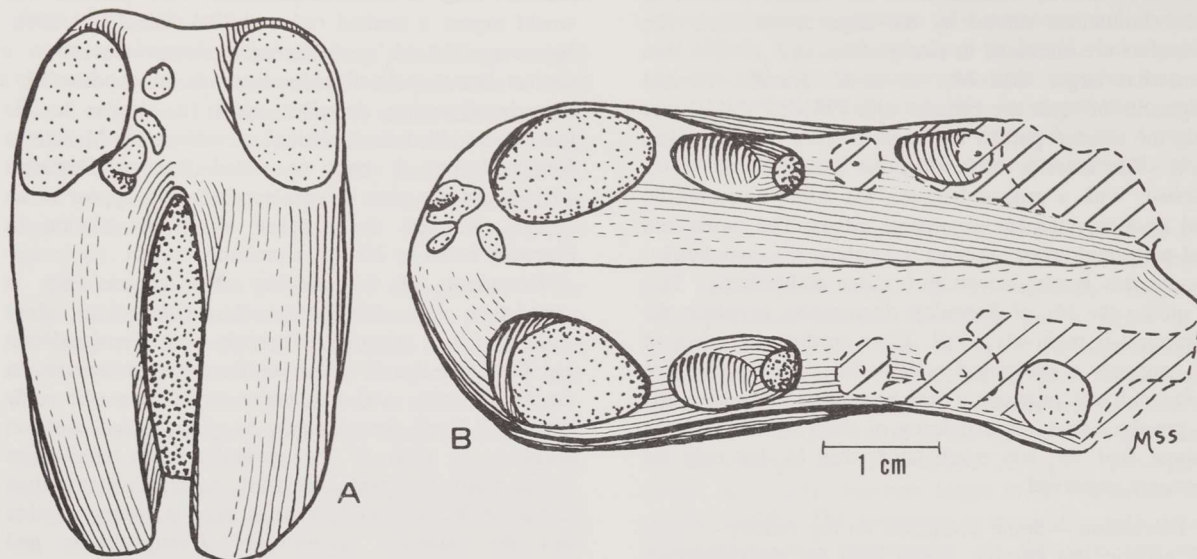


Figure 15.—*Ischnognathus sagagei* Stovall, type, OU 32-4-51. Mandibular symphysis. A. Anterior view. B. Dorsal view, anterior to left.

consisted of three holes. The area is sufficiently damaged to make interpretation of these holes uncertain.

There are six premolar alveoli on the left side. Stovall (1948, Fig. 2c) interpreted the anterior two to have been for a two rooted P_1 . By comparison with *Hyaenodon* and *Hemipsalodon*, I would interpret the first as the lodgement of a single rooted, anteriorly inclined premolar. The alveoli of P_1 , P_2 , P_3 and the anterior side of the P_4 alveolus are present. P_1 would have had to be relatively small and crowded between the canine and P_2 .

Relationships.—This specimen is as enigmatic now as when it was first described. The suggestion by Van Valen (1966; quoting a personal communication from Patterson) that “new material shows it to be a hyaenodontid” may have been initiated by the discovery of material assignable to *Hemipsalodon viejaensis*. The two taxa are almost certainly distinct, since the jaws of *Hemipsalodon* do not show the peculiar depth, narrowness and flanged form of *Ischnognathus*. It is unlikely that this specimen represents a juvenile *Hemipsalodon* because the two rami appear to have been firmly connected and probably partly fused, whereas the two mandibles of *H. viejaensis* (both probably from adult specimens) were unfused. Moreover, since the posterior root of P_3 of *I. sagagei* seems to have been broken and worn from use, this may have been a late adult individual.

Genus *Hyaenodon* Laizer and Parieu, 1838

Where possible I have followed Mellett's 1977 revision of the taxonomy of North American *Hyaenodon*, including his use of subgenera. Specimens reported here have generally been assigned to previously described species, although in some specimens characteristics which Mellett used for diagnosis either have not been preserved or are

contradictory. Comparisons have been made with original types or casts of the types of the species in question.

Hyaenodon (*Neohyaenodon*) cf. *H. vetus*, Stock, 1933a

Skyline local fauna

Figs. 16-17, Tables 8-9

Type.—CIT 1243, skull from “Sespe upper Eocene, North of Simi Valley, Ventura Co., California”.

Referred material.—TMM 41535-1, ramus with P_3 and M_3 ; 41715-4, skull with left M^{1-2} lacking snout.

Stratigraphic position.—Both 41535 and 41715 are from the Skyline channels, which are at the base of the Bandera Mesa Member approximately 213 m (700 feet) above the base of the Devil's Graveyard Formation, Brewster Co., Texas.

Age.—Late Uintan (early Duchesnean subage).

Description.—The anterior part of the skull (Fig. 17) with most of the dentition is missing. What remains is fractured but only slightly distorted and the bone is well preserved. The frontals and posterior nasals are broad and flattened, with a deep depression immediately anterior to the point where the sagittal crest divides. The postorbital processes are large, and the small conical braincase tapers rapidly to a strong constriction, surmounted by a very large sagittal crest which divides anteriorly just in front of the postorbital cranial constriction. The large lambdoidal crests form ridges that make up the dorsal surfaces of the mastoid processes. The orbit appears to be relatively small but this may be partly due to dorsoventral crushing. The zygomatic arch is slender, as is usual in *Hyaenodon*. The posterior point of the M^2 extends posteriorly just beyond the ventral orbital shelf. The posterior nasal opening is relatively larger, or less

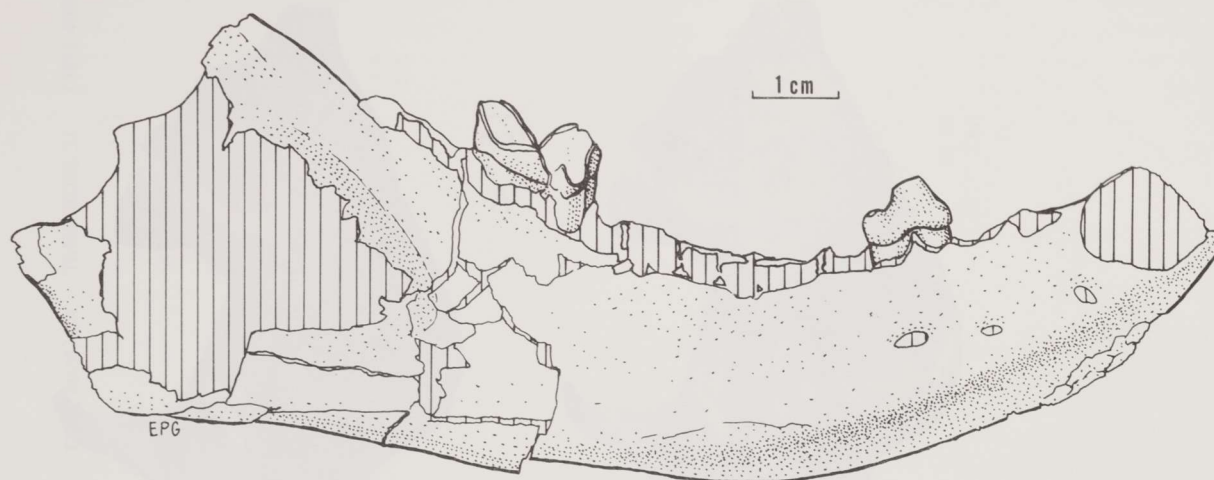


Figure 16.—*Hyaeonodon* cf. *H. vetus* Stock, TMM 41535-1, Skyline channels. Right ramus of mandible with P_3 - M_3 , lateral view.

enclosed ventrally by the palatine bones, than in *H. crucians*. Little can be said about the dentition except that M^1 and M^2 are smaller than in *H. montanus* and similar in shape to M^{1-2} of other North American species of *Hyaeonodon*.

The mandible (TMM 41535-1, Fig. 16) is moderate in depth but is considerably thickened just above its ventral margin. There are only two alveoli between P_3 and the canine alveolus, probably both for roots of P_2 . There apparently was no P_1 . P_3 has a large protoconid, a small paraconid, and a low but broad posterior cusp in the position of a hypoconulid. There are no cingula. M_3 is heavily worn. As is usual in *Hyaeonodon*, it carried anteroposteriorly elongated protoconid and paraconid, and the carnassial notch is centrally placed.

This mandible is from an older individual than the skull. The worn or missing parts of the dentition make a species identification even less certain than for the skull. Absence of a P_1 is unusual in *Hyaeonodon*, but with only a single specimen showing this character, it is probably best to interpret it as an individual anomaly.

Relationships.—Assignment of these two specimens to *Hyaeonodon* cf. *H. vetus* is tentative. I have assumed that the specimens represent only one species, because of similarities in size (Tables 8-9) and stratigraphic position. Both specimens are slightly smaller than other specimens of *H. vetus*, but considerably larger than *H. venturae* Mellett (1977), the other known late Eocene, "Duchesnean," species. There are several primitive characters. In the skull the most striking is the lack of closure of the palatine bones over the posterior narial opening. The right ramus was separated from the left along the median of the mental symphysis. Erosion of the bone prevents knowing for certain that an unfused symphyseal suture was present, but this seems likely. The

posterior molars strongly resemble those of *H. vetus*, and the upper molars are almost identical in both size and form to those on a maxillary fragment (CM 11770) from the Duchesne River Formation of Utah (Peterson, 1931b, Fig. 2) which Mellett (1977) has referred to *Hyaeonodon* cf. *H. vetus*.

Hyaeonodon (*Neohyaenodon*) *montanus* Douglass, 1901

Porvenir local fauna

Figs. 18-19, Tables 8-9

Type.—CM 764, skull and mandible "found northeast of Toston, Montana", Chadronian age.

Referred material.—FMNH:PM 82, ramus with P_3 and damaged P_4 and M_3 ; TMM 40203-17, P^4 ; 40203-334, M^2 ; 40206-24, M_3 ; 40206-31, maxilla fragment with P^3 - M^1 ; 40688-42, P_4^2 .

Stratigraphic position.—Localities for FMNH:PM 82 and 40203 and 40206 are in the lower 30.4 m (100 feet) of the Chambers Tuff below the lower marker bed (Wilson 1977b); 40688 is between 0 and 26.8 m (0 and 88 feet) above the lower marker bed (Wilson 1977b).

Age.—Early Chadronian.

Description.—A partial ramus, FMNH:PM 82 (Fig. 19) is similar in size and proportions to the mandible of *H. montanus*. P_3 is much lower crowned than in the type of *H. montanus*. P_4 is slightly larger than in the type. A second partial P_4 , TMM 40688-42, is similar to that of FMNH:PM 82 and is also a little larger than that of the type of *H. montanus*. An M_2 , 40206-24 (Fig. 18b) is relatively low and broad, with a strong talonid cusp (hypoconid). It is very close in form to that of the type of *H. montanus*.

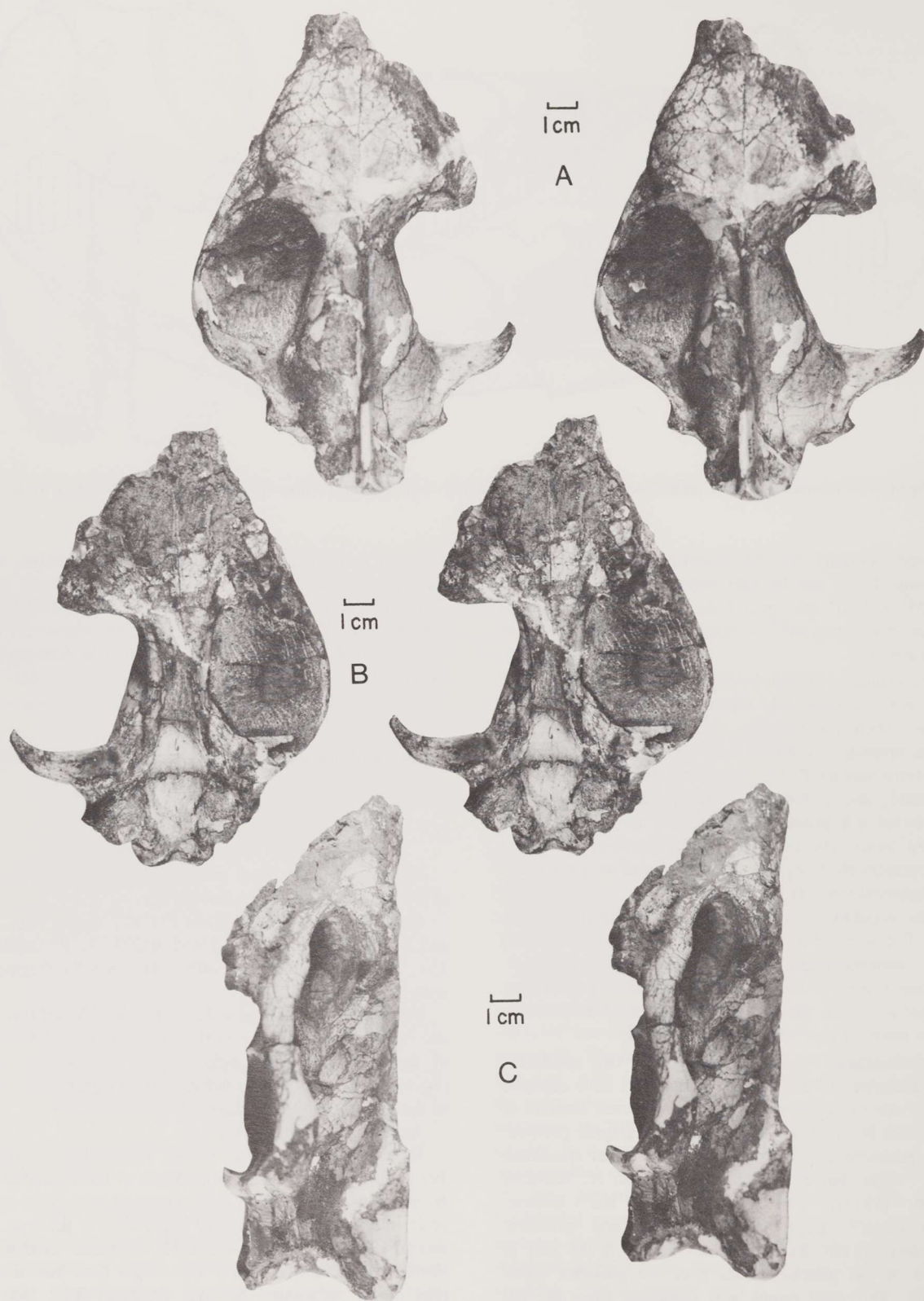


Figure 17.—*Hyaenodon* cf. *H. vetus* Stock, TMM 41535-4, Skyline channels. Stereophotographs of partial skull. A. dorsal view. B. Ventral view. C. Left lateral view.

Table 8.—Measurements of upper dentitions of *Hyadenodon*.

		<i>H. (P.) raineyi</i> new species				<i>H. cf. H. vetus</i>		<i>H. crucians</i>		<i>H. montanus</i>			
		TMM 40504-125	TMM 40504-236	TMM 40504-294	TMM 41715-4	FMNH PM 403	TMM 40203-17	TMM 40203-34	TMM 40206-31	TMM 40688-17			
		right	left	right	left	right	left						
C	AP		4.8	5.4									
	T		3.8	3.9e	3.5e						14.2		
P ¹	AP		6.7	6.9	6.8						7.5		
	T		3.3	3.1	2.9						13.7		
P ²	AP		7.2	7.1	6.9						10.5		
	T		3.6	3.4	3.3						11.6		
P ³	AP	8.0	8.2	7.8	7.7						8.8		
	T		3.9	4.0	4.2			15e					
P ⁴	AP	8.5	7.7	7.2	7.8			8.3			8.5e		
	T		5.9	5.9	5.9							13.4	
M ¹	AP	8.0	6.9	8.1								6.5	
	T		4.5	5.7									
M ²	AP	9.5	8.7	8.1									
	T		4.7	5.6									
dp ⁴	AP												
	T												
M ¹ -M ²		16.0	15.0	14.9									
P ¹ -M ²			45.3	44.7	46.3								

Table 9.—Measurements of lower dentitions of *Hyaenodon*.[illegible]

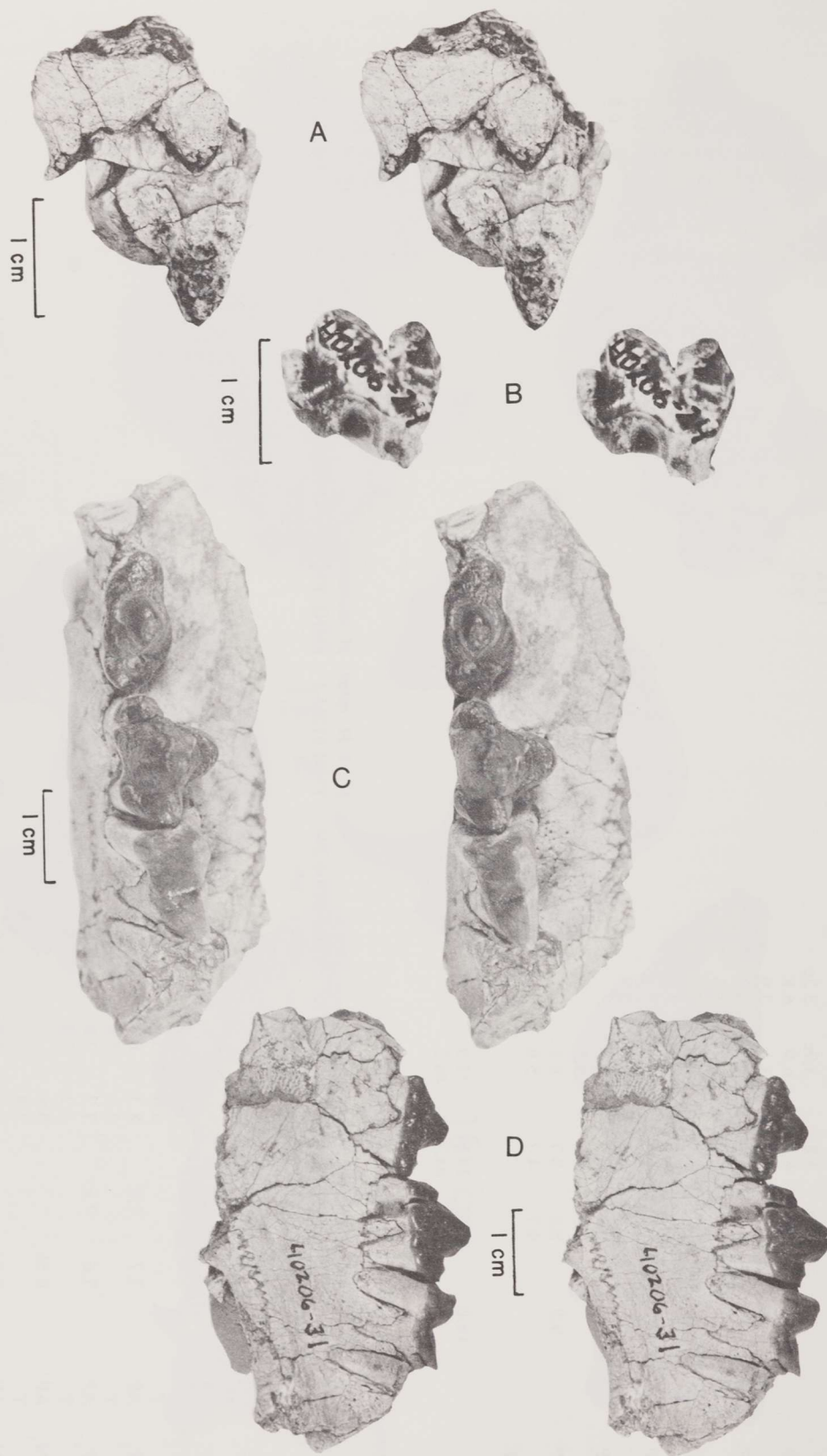


Figure 18.—*Hyaeonodon montanus*, Porvenir local fauna, stereophotographs. A. TMM 40203-34, M², lateral view. B. TMM 40206-24, M², lateral view. C-D. TMM 40206-31, maxillary with P³-M¹, lateral and occlusal views, anterior to top of page.

The referred upper teeth (Fig. 18a, c, d) also are similar in size and proportions to CM 764. P^3 preserved on 40206-31 appears to be abnormal, with a relatively short crown which was probably damaged during its development. There is a posterior lingual bulge on the crown enamel and a large metacone, as in *H. montanus*. P^4 is present on 40206-31 and in an isolated specimen, 40203-17. Both have a shelf-like protocone, a small parastyle, large paracone, and well developed but small metacone. M^1 is worn but complete. It bears a small parastyle, almost fused paracone and metacone, and enlarged metastyle. There is no protocone cusp on the lingual root. M^3 , 40203-34, is strongly convex on the labial side, has a distinct anterolabial ridge, and no protocone cusp.

Relationship.—Most if not all other occurrences of *Hyaenodon montanus* are Chadronian, from Montana and South Dakota. Specimens referred to this species are consistent in size and in the relative robustness of the teeth. If the identifications made here and by Clark et al. (1967) are correct, the species seems to span essentially all of Chadronian time. It may have been derived from *Hyaenodon vetus*, as Mellett (1977) has also suggested.

Hyaenodon (Neohyaenodon) cf. H. horridus Leidy, 1853

Little Egypt local fauna

Table 9

Referred material.—TMM 41025-3, mandible fragment with partly erupted P_3 .

Stratigraphic position.—Same level as Reeves bonebed, upper part of the Chambers Formation, Vieja Group, Presidio Co., Texas.

Age.—Chadronian, probably middle Chadronian.

Discussion.—The juvenile mandible fragment includes a partial unerupted lower canine and P_4 as well as the P_3 which is exposed but not worn. P_3 is almost identical in form to P_3 of FMNH:PM 82 from the Porvenir local fauna, but it is about the size of *H. cruentus* Leidy.

Mellett (1977) has synonymized *H. cruentus* with *Hyaenodon horridus*, stating that differences between these forms are likely the result of sexual dimorphism. This specimen is lower crowned than Leidy's type of *H. cruentus* (NMNH 134) and the posterior cusp is slightly larger, but it is closer to the *H. cruentus* than to other described species.

Hyaenodon (Protohyaenodon) crucians Leidy, 1853

Porvenir and ?Airstrip local faunas

Figure 20, Tables 8-9

Type.—ANSP 11046-7, skull and mandible "from the Mauvaises Terres of Nebraska".

Referred material.—FMNH:PM 403, skull with M^1 - M^2 , M_2 and part of P^4 ; TMM 40688-17 dP^4 . Questionably referred: TMM 40502-9, mandible fragment with $?P_{2-4}$.

Stratigraphic position.—The skull, FMNH PM 403 and 40688 are from 0 to 26.8 m (0 to 88 feet) above the lower marker bed, Chambers Tuff; 40502 is from approximately 173.7 m (570 feet) above the Bracks Rhyolite, Capote Mountain Formation

Age.—Chadronian (early Oligocene).

Description.—The most complete specimen, FMNH:PM 403 (Fig. 20), is a badly weathered and broken juvenile skull. What is preserved of the teeth is nearly identical to the teeth of *Hyaenodon crucians*. M_2 , in particular, is indistinguishable in size and shape from that of the type of *H. crucians*, by comparison to a cast of the type.

dP^4 has a large paracone as well as the metacone and metastyle. The protocone has been broken away. The paracone is a little larger than that shown on dP^4 of *H. crucians* by Scott and Jepsen (1936, Fig. 3) and the tooth is somewhat smaller, but it is otherwise similar.

The partial mandible, TMM 40502-9, includes 3 premolars. They are probably P_{2-4} because the roots of

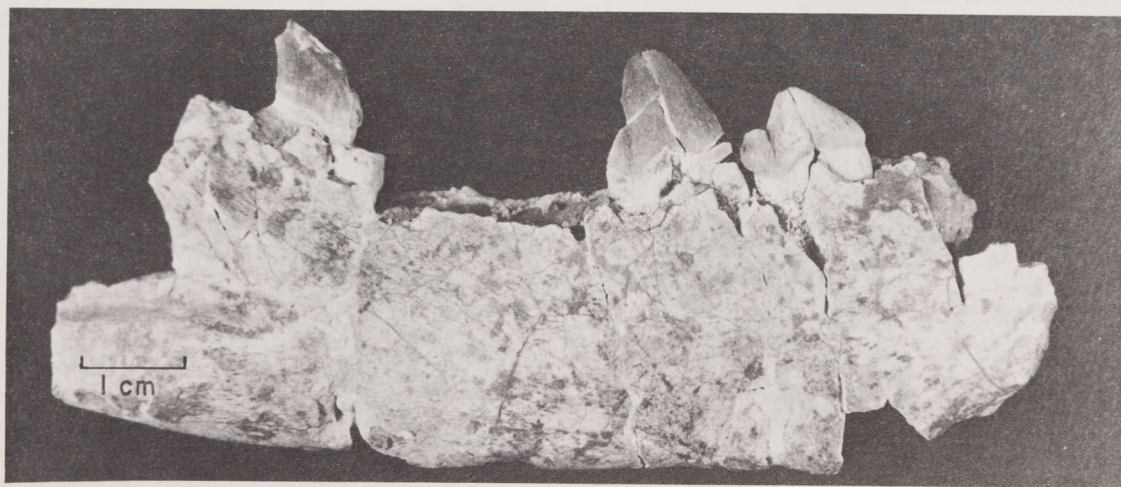


Figure 19.—*Hyaenodon montanus*, Porvenir local fauna. FMNH PM 82, ramus of mandible with P_3 , partial P_4 and M_3 , right lateral view.

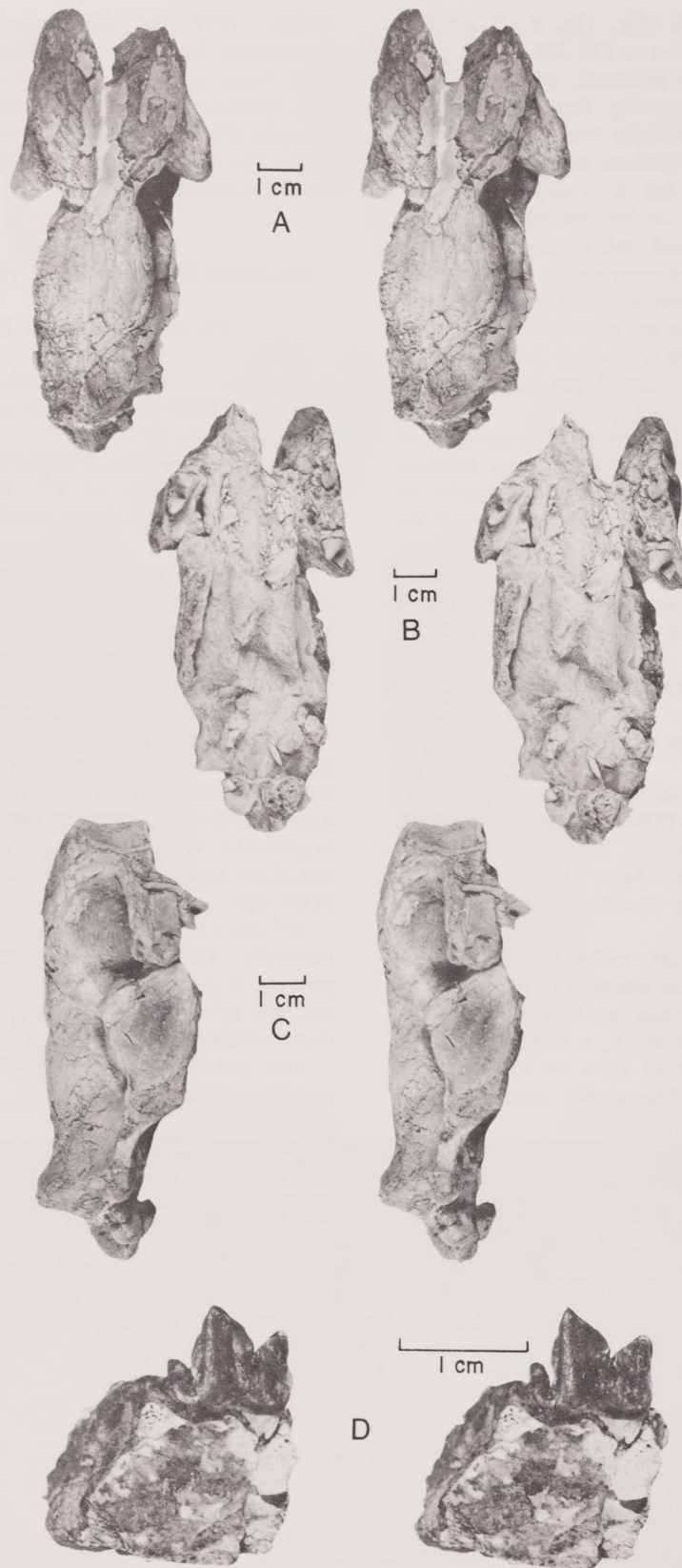


Figure 20.—*Hyaeonodon crucians*, Porvenir local fauna. FMNH PM 403, stereophotographs of skull with M^1 and part of mandible. A. Dorsal view. B. Ventral view. C. Lateral view. D. Right M_2 , lateral view.

the next posterior tooth are crowded as in M_1 of *Hyaenodon*. This specimen is questionably placed in *H. crucians* solely on the basis of size. *Hyaenodon crucians* apparently was a wide ranging and long lived species. Mellett (1977) reports it from the early Chadronian of Saskatchewan to the middle Orellan of Nebraska, and the present report extends the range to Texas in the early Chadronian.

Hyaenodon (Protohyaenodon) raineyi new species

Airstrip local fauna

Figures 21-22, Tables 8-9

Type.—TMM 40504-236, damaged skull and mandible including all teeth except incisors and P_1 .

Referred material.—TMM 40504-125, partial skull with mandible in occlusion; 40504-294, partial skull with right ramus.

Stratigraphic position.—Capote Mountain Formation approximately 174 m (570 feet) above Bracks Rhyolite.

Age.—Middle Chadronian (early Oligocene).

Etymology.—Named for R. H. (Bob) Rainey, Preparator, Vertebrate Paleontology Laboratory, Texas Memorial Museum.

Diagnosis.—A hyaenodont intermediate in size between *H. microdon* and *H. venturae*. P_1 with one root, posterior accessory cusp on P^3 very small, canines relatively small, lingual cingula on upper premolars weak or absent, skull narrows abruptly behind postorbital processes, brain relatively large.

Description.—Most of the external features of the rostrum can be seen on at least one of the three skulls, including well preserved dentitions except for incisors. The type skull (40504-236, Fig. 21b,c) has part of I^3 and alveoli for I^{1-2} . I^1 and I^2 were somewhat smaller than I^3 . The canines are relatively smaller than in large species of *Hyaenodon* (*H. horribilis*, for example), slightly curved, and somewhat procumbent. P^1 has two roots and is elongated with the single cusp relatively far forward. P^2 is tall crowned and bears a small posterior accessory cusp. P^3 is larger, broader, and shorter crowned than P^2 , as is usual in *Hyaenodon*, and has a weakly developed lingual cingulum. P^4 has three roots and a small protocone that is only a shelf of enamel capping the medial root. There is a small metacone. The parastyle is not distinctly cusped. The protocones on M^1 and M^2 are tiny cusps which wear down rapidly. Both molars are highly effective carnassials.

Portions of the lower incisors are visible on the type (Fig. 22c). There were three, increasing in size towards I_3 , but all small and simple. The lower canine is sharply recurved but more procumbent than in *Urocyon*. P_1 is missing on 40504-236 and damaged on both sides of 40504-294. It has only one root, which is inclined anteriorly, and the crown is elongated anteroposteriorly. P_2 is close to P_1 in size, and like P_1 carries its low single cusp far anterad. P_3 and P_4 are similar to each other

except that P_4 is slightly larger. Each bears a small hypoconid. M_1 is badly worn in adult specimens, and no details are visible except that a small but distinct talonid cusp is present. M_2 is larger, and like M_1 has a small talonid cusp. The metaconid is absent and the protoconid is the highest cusp. M_3 is the most specialized of the carnassials, entirely lacking a talonid and possessing a long cutting edge on the posterior side of the paraconid and the longer anterior side of the posterior-inclined protoconid. Like the upper premolars, the premolars are a little more widely spaced on 40504-294 than on 40504-236 but all other dental characters are consistent.

Sutures between skull bones are clearly visible. Most bones are similar to those of other species of *Hyaenodon* (Scott and Jepsen, 1936), except as noted below. In 40504-236 (Fig. 21a) the structure of the endocranium and dorsal skull cavities has been exposed by erosion. The brain is relatively large for *Hyaenodon* (as would be expected in a small mammal) and is about the equivalent in complexity of folding to its contemporary, the canid *Hesperocyon*, in which only the coronolateral and suprasylvian sulci are present. The olfactory lobes were large and were not covered by the anterior cerebrum. The space available for the turbinates, of which portions are visible, was much larger than in canids of similar size.

The shape of the central portion of the skull as seen in dorsal view is distinctive. In most *Hyaenodon* species this area is somewhat hourglass shaped; that is, the narrowest part of the skull is a short distance behind the postorbital processes, and the skull tapers posterad to the constriction. In *H. raineyi* this taper is very abrupt, and in 40504-236 the constriction is almost directly between the posterior projections of the postorbital processes. It is about 3 to 4 mm behind the postorbital processes in 40504-125. Behind the constriction the lateral walls of the braincase swell more abruptly than in other *Hyaenodon* species. Because of damage to the dorsal surface of the braincase in all three skulls, the size and form of the sagittal crest is not discernible, but it was probably relatively small. There is no crest on the dorsal posterior extension of the frontals in 40504-125, unlike specimens of other species which I have seen.

Referred skull 40504-125 is unusual in having the tympanic ring preserved (Fig. 22a,b). The tympanic is U-shaped, and broadest at the anteromedial corner. It is relatively larger than that pictured for *H. "cruentus"* (now *H. horribilis*) by Scott and Jepsen (1936, Plate 8, Fig. 3). There is no evidence for the existence of an ossified entotympanic such as has been found in *H. crucians* (van der Klaauw, 1931), and *H. brevirostris* (Mellett, 1977).

Relationships.—This species fits readily into Mellett's subgenus *Protohyaenodon* on the basis of the following characters: Small *Hyaenodon* in which M^2 length was about 19% of P^1 - M^2 length (actual figures for the two specimens in which this can be determined are 17.4% and 19.4%). Pediculate glenoids not developed. Anterior and posterior paracristid of M_3 subequal in length.

Mellett (1977, p. 7) recognized the existence of this species from measurements supplied to him by Wilson,

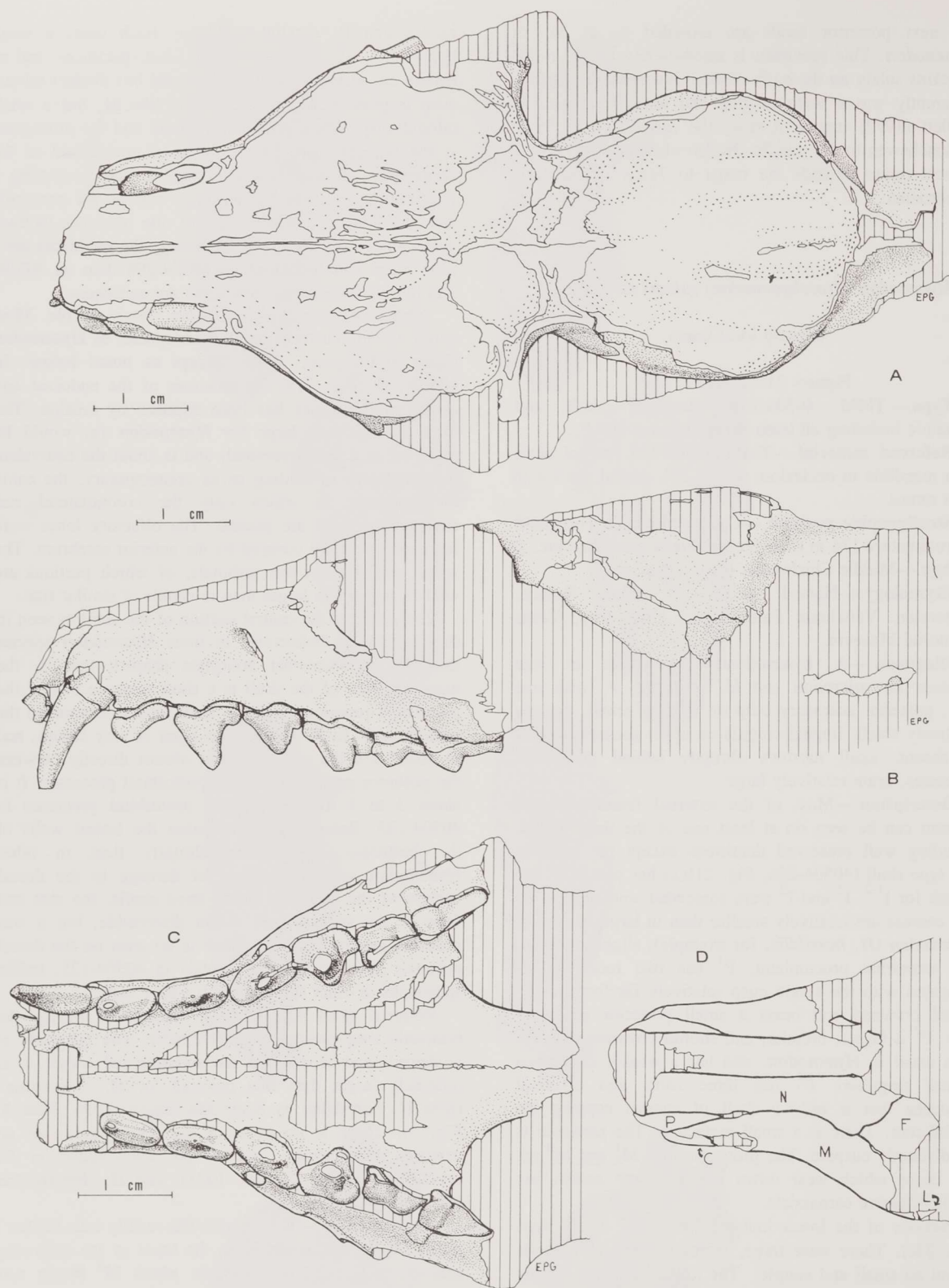


Figure 21.—*Hyænodon raineyi*, n. sp., Airstrip local fauna. A-C. TMM 40504-236, type skull, dorsal (A), lateral (B), and ventral (only palate and dentition) (C) views. Matrix fillings of skull cavities indicated by coarse stippling, matrix on external surfaces indicated by vertical lines, broken bone surfaces unshaded. D. TMM 40504-294, diagram of dorsal rostrum showing sutures. Matrix indicated by vertical lines.

Abbreviations: C, canine; F, frontal; L, lacrimal; M, maxillary; N, nasal; P, premaxillary.

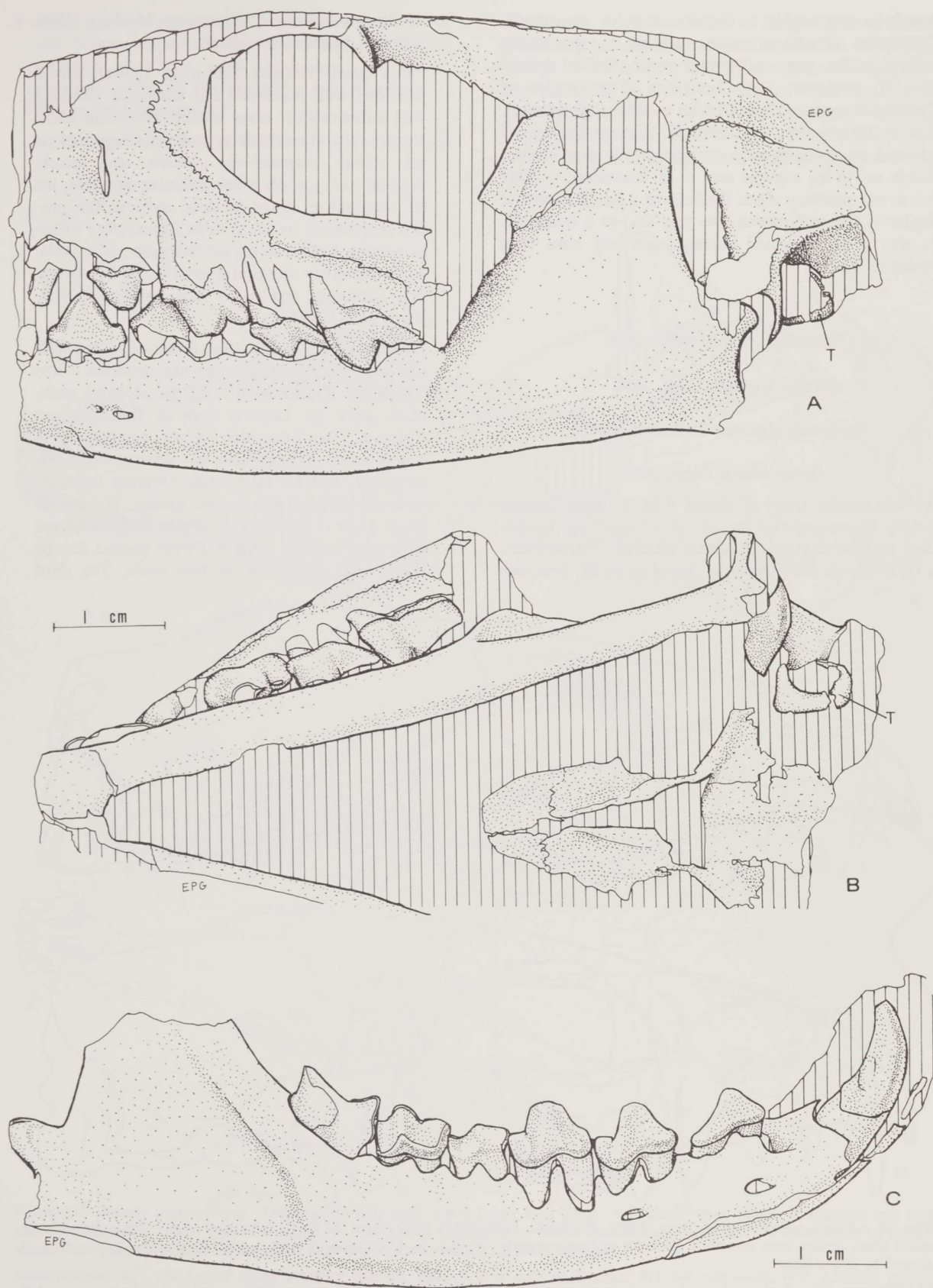


Figure 22.—*Hyenodon raineyi*, n.sp., Airstrip local fauna. A & B. TMM 40504-125, skull with jaws in occlusion, lateral (A) and ventral (B) views. C. TMM 40504-236, type, mandible, lateral view.

though he was unable to describe it in his monograph. *Hyaenodon* (*Protohyaenodon*) *raineyi* n. sp. clearly belongs in the group of species which Mellett derived from *H. venturae*. The Chadronian diversification of *Hyaenodon* produced species with a wide range of sizes. If it is derived from *H. venturae*, *Hyaenodon raineyi* achieved its distinctiveness through a reduction in size, though not to the extreme seen in *H. microdon*. In body size it was probably about the bulk of a fox (the skull is similar in size to *Urocyon*, the gray fox) or a house cat. Its prey preferences and hunting style may have been similar to these.

Order Carnivora Bowdich, 1821

Family Miacidae Cope, 1880

Subfamily Miacinae Trouessart, 1885

Genus *Miacis* Cope, 1872

The stratigraphic range of *Miacis* is broad (early Eocene to early Oligocene) and several (if not most) species are based on poor or poorly described material. This includes the type species, *M. parvivorus*, based on an M_2 from the

lower Bridger Formation, Wyoming. Matthew (1909, p. 362) gave a diagnosis for *Miacis*:

"This genus includes the more typical cynoid Miacidae with carnassial and tubercular dentition well differentiated, lower molars with basin heels, slender or moderately deep jaws with the symphyseal region comparatively shallow and loosely sutured, and typically a full eutherian dentition, but M^3 vestigial or absent in some species. The general proportions are much as in *Cynodictis* [= *Hesperocyon*], but the braincase is smaller. The skeleton is decidedly more primitive than in any Oligocene Carnivora, and agrees very closely with *Vulpavus* and *Oodectes*.

"The teeth are much like those of *Cynodictis* [= *Hesperocyon*] but the tubercular dentition is less completely differentiated from the sectorial teeth, much more so, however than in *Oodectes* and *Vulpavus*, the tubercular molars retaining to a certain extent the similarity of construction to the carnassial, and the subordinate shearing function, more obviously shown in these genera. The second lower molar is less elongate than in *Didymictis* and *Viveravus*, and the third is always present though small, with either one or two roots. The third

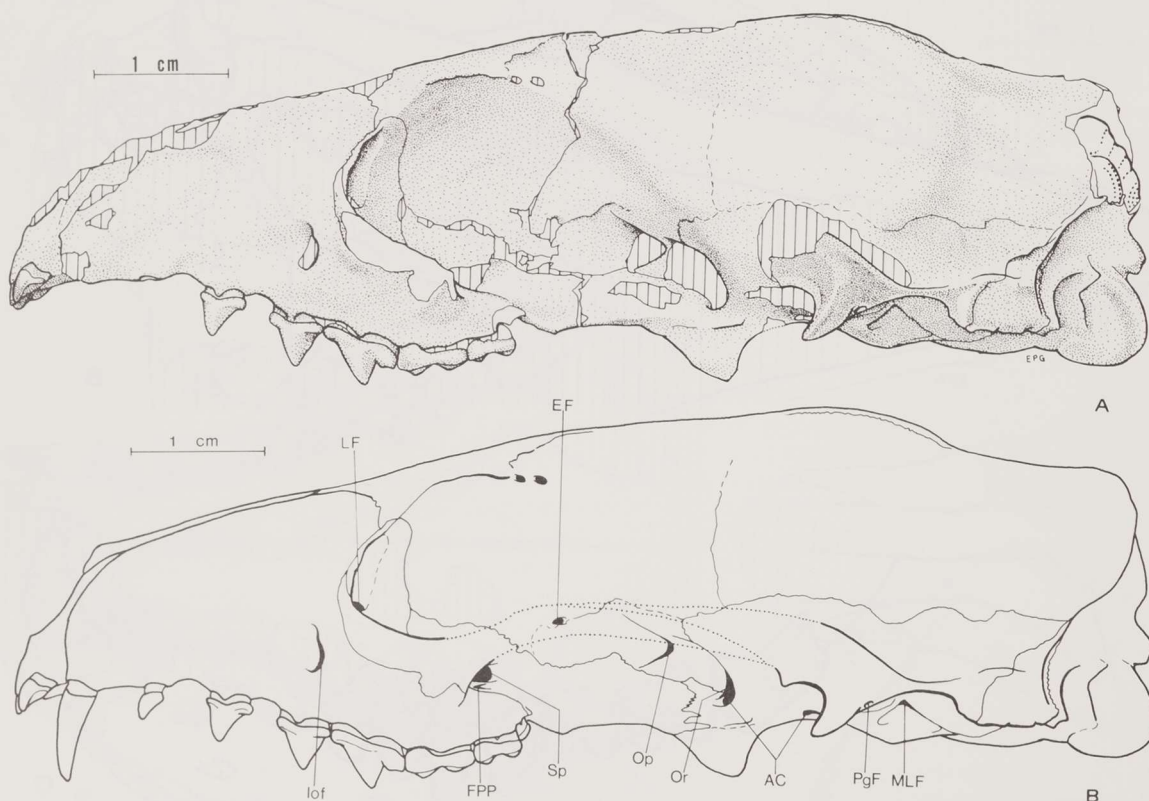


Figure 23.—*Miacis cognitus* n. sp., type. TMM 40209-200, Little Egypt local fauna. A. Skull, left lateral view. Matrix indicated by vertical lines, broken bone unshaded, posterior endocast coarsely stippled. B. Restoration of skull in left lateral view. Zygomatic arch indicated by dotted lines.

Abbreviations: AC, alisphenoid canal, anterior and posterior openings; EF, ethmoid foramen; FPP, posterior palatine foramen; Iof, infraorbital foramen; LF, lacrimal fossa; MLF, middle lacerate foramen; Op, optic foramen; Or, orbital fissure; PgF, postglenoid foramen; Sp, sphenopalatine foramen.

upper molar is always small, sometimes vestigial, and perhaps absent in the Uinta species. The parastyle of P^4 is small or minute, and the accessory cusps of the premolars less developed than in the Viverravinae."

In this paper comparisons will be primarily to the type

species, *M. parvivorus* and to *Hesperocyon gregarius*. No *Miacis* basicrania have been described in the literature except for the crushed skull of the type of *M. gracilis*. I am fortunate to have a referred specimen of *M. parvivorus* (USNM 214706, Bridgerian level B, Wyoming) in which parts of the auditory region as well as an excellent upper and lower dentition are preserved.

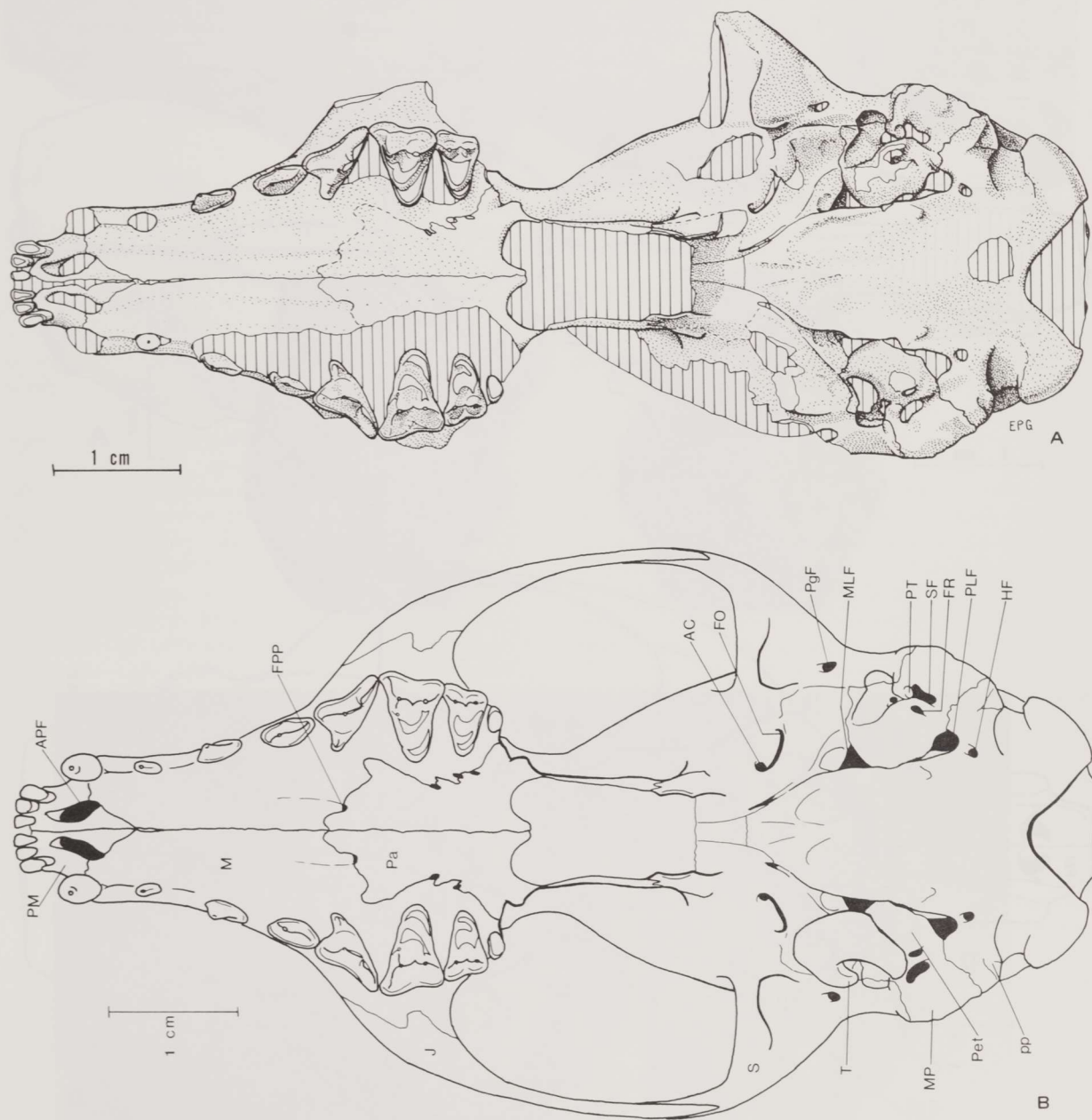


Figure 24.—*Miacis cognitus* type, TMM 40209-200, skull, Little Egypt local fauna. A. Ventral view. Matrix of endocast and nasal cavities indicated by coarse stipple, other matrix indicated by vertical lines, broken bone surfaces unshaded. B. Restoration of skull in ventral view. Right tympanic restored from bone contacts and comparison with *Nandinia*.

Abbreviations: AC, alisphenoid canal, posterior opening; APF, anterior palatine foramen; FO, foramen ovale; FPP, posterior palatine foramen; FR, fenestra rotundum; HF, hypoglossal foramen; J, jugal; M, maxillary; MLF, middle lacerate foramen; MP, mastoid portion of periotic; Pa, palatine; Pet, petrosal portion of periotic; PgF, postglenoid foramen; PLF, posterior lacerate foramen; PM, premaxillary; pp, paroccipital process; PT, posterior articulation for tympanic; S, squamosal; SF, stylomastoid foramen; T, tympanic.

Miacis cognitus new species

Little Egypt local fauna

Figures 23-28, Table 10

Type.—TMM 40209-200, uncrushed skull lacking zygomatic arches, canines, first premolars, left M^3 and portions of right frontal, right parietal, and nasals.

Stratigraphic position.—Above upper marker bed in upper Chambers Formation, Reeves Bone Bed locality, Presidio County, Texas (Wilson, 1977b, Fig. 9).

Age.—Chadronian (early Oligocene).

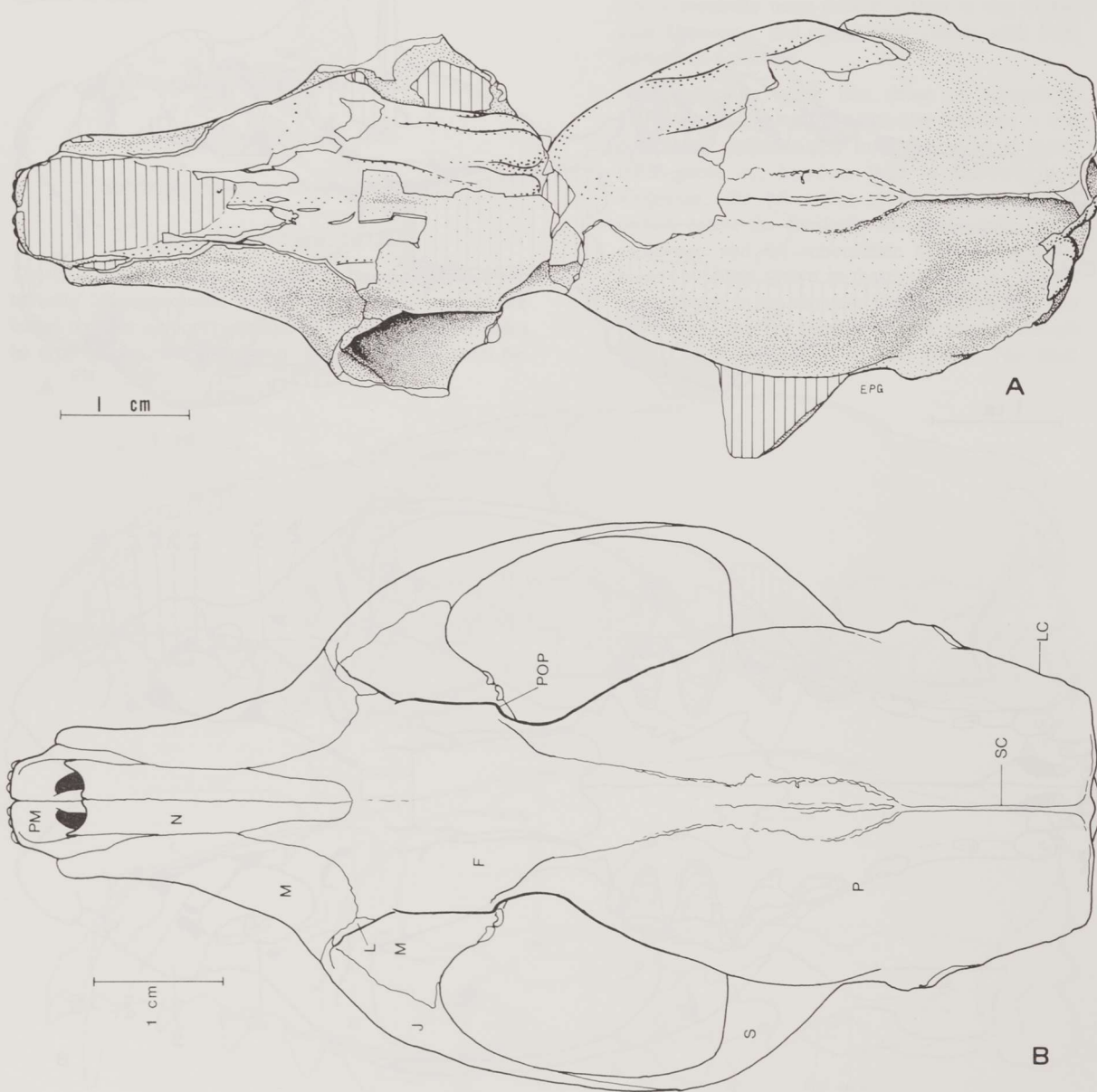


Figure 25.—*Miacis cognitus* type, TMM 40209-200, skull, Little Egypt local fauna. A. Dorsal view. Matrix of endocast and nasal cavities indicated by coarse stipple, other matrix indicated by vertical lines, broken bone surfaces unshaded. B. Restoration of skull in dorsal view.

Abbreviations: F, frontal; J, jugal; L, lacrimal; LC, lambdoidal crest; M, maxillary; N, nasal; P, parietal (boundaries obscure); PM, premaxillary; POP, postorbital process; S, squamosal; SC, sagittal crest.

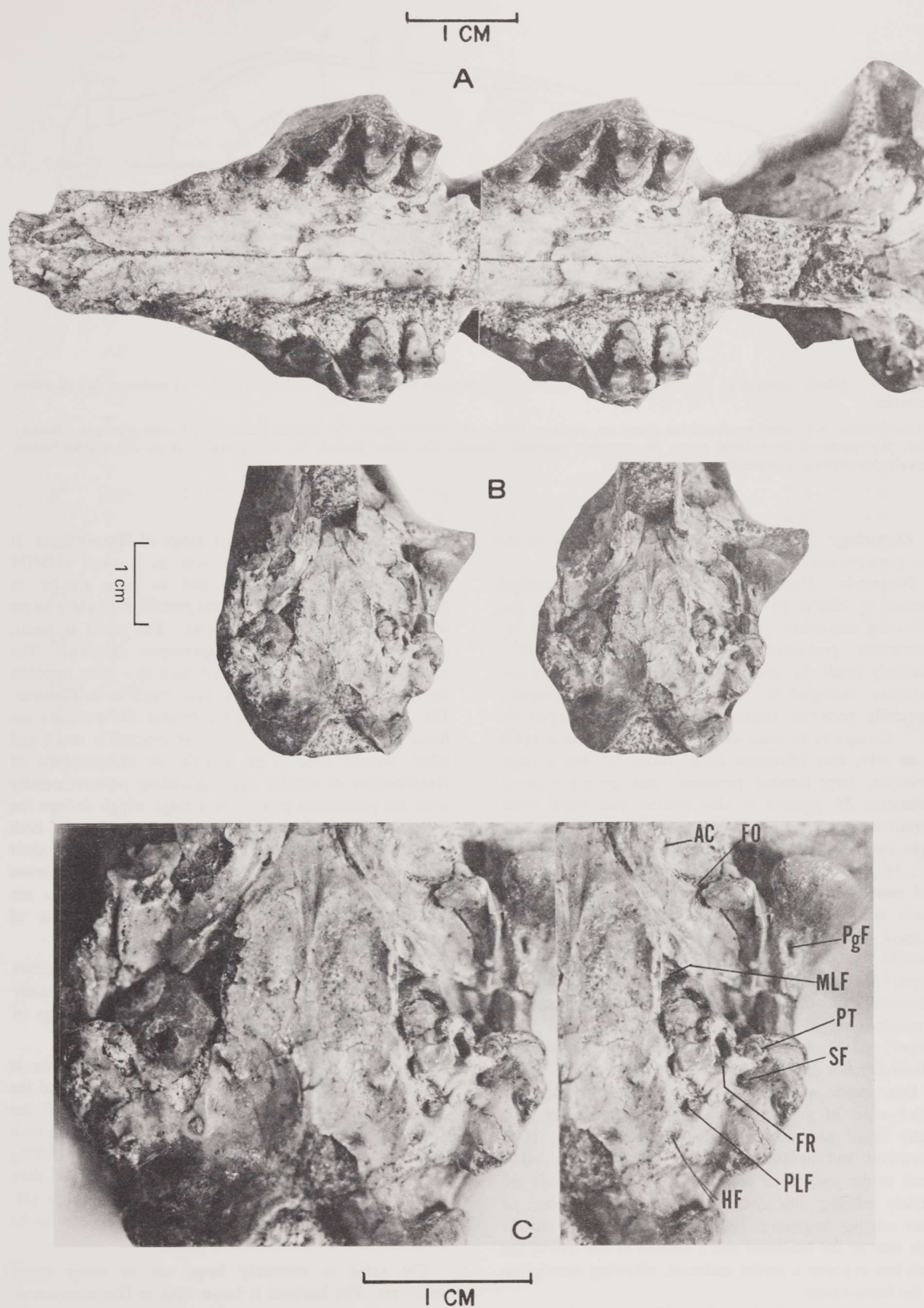


Figure 26.—*Miacis cognitus* n. sp., type, TMM 40209-200, Little Egypt local fauna. Stereophotos of skull. A. Dentition, ventral view. B. Basicranial region. C. Enlargement of ear region, abbreviations as in Figure 25.

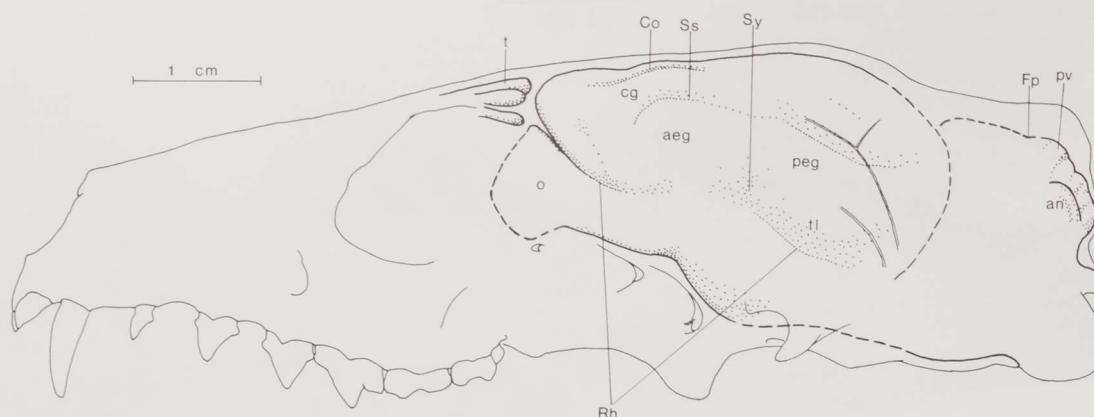


Figure 27.—*Miacis cognitus* n. sp., type, outline of skull showing position and features of endocast. Outline of endocast dashed where uncertain.

Abbreviations: aeg, anterior ectosylvian gyrus; an, ansiform lobule; cg, coronal gyrus; Co, coronal sulcus; Fp, fissura prima; o, olfactory lobe; peg, posterior ectosylvian gyrus; pv, posterior cerebellar vermis; Rh, rhinal fissure; Ss, suprasylvian sulcus; Sy, sylvian sulcus (poorly developed); t, turbinals; tl, temporal lobe.

Etymology.—Latin *cognitus*=known, referring to the fine preservation of the type specimen.

Diagnosis.—Distinguished from previously described species of *Miacis* by presence of one or more of the following characters: size of skull similar to that of *M. parvivorius*, protocone of P^4 and parastyles of M^{1-2} relatively small, M^3 present but very small, paracone and metacone subequal in size on M^{1-2} , lingual cingula, especially posterior lingual cingula, well developed on M^{1-2} . Compared to other described species: *Miacis exilis* is an odd, tiny European form whose M^1 has a large parastyle, large central paracone, and greatly reduced metacone; *M. jepseni* is also smaller and much more primitive; all of the other Eocene species have relatively large paracones and parastyles and small metacones on M^1 , M^2 , or both; *M. gracilis* had a M^1 with paracone and metacone of about equal size but an M^2 which is much reduced and almost lacking a metacone; *M. hargeri*, *M. latidens*, *M. medius*, *M. uintensis*, *M. gracilis*, *M. australis* n. sp. and *M.?* *macintyri* are all larger; *M. washakius*, *M. gracilis*, *M. jepseni*, *M. sylvestris*, *M. latidens*, *M. hargeri* all either have smaller hypocones on M^{1-2} or lack a hypocone on M^2 ; *M. hargeri* and *M. medius* have relatively large M^3 ; and *M. sylvestris* has a relatively larger P^4 .

Description.—The skull is from an adult individual in which most of the sutures of the cranium are at least partly fused and the molars considerably worn. It is uncrushed and undistorted except minimally around a break at the postorbital constriction. Only the nasals are entirely missing; this circumstance allows restoration of other missing fragments. Natural removal of bone on the right side of the braincase and a portion of the rear of the skull has exposed a partial endocast, allowing description of the brain cavity.

As seen in dorsal view (Fig. 25), the skull is very similar in size (Table 10) and proportions to that of

Genetta, and is within the size range of *Hesperocyon*. It is almost exactly the same size as a skull (USNM 214706) of *M. parvivorius* and is very similar in proportions to that skull. *Miacis gracilis* is slightly larger but also is similar in proportions. The snout is small, slightly narrower than in *Hesperocyon gregarius*. The nasals were narrow and extended back to a point opposite the anterior rim of the orbits, very much as in *Genetta*. The dorsal sutures between the frontal and parietals are fused and obscure. The postorbital process is small and blunt, smaller than in *M. gracilis* or in specimens of *Hesperocyon* of similar size. Extending posteromedially from the postorbital process is a ridge which defines the dorsal border of the temporal fossa. The ridges of both sides form a lyrate prominence, but join to form a short sagittal crest immediately posterior to the maximum swelling of the braincase. The lambdoidal crests are prominent, again similar in proportions to those of *Hesperocyon*, *Genetta*, and *M. gracilis*.

The braincase is slightly smaller than in either *Hesperocyon* or *Genetta*, differing from *Genetta* mainly in the lesser anterolateral and posterodorsal swellings of the bone covering the cerebrum.

In lateral view (Fig. 23) the dorsal facial outline is relatively straight. The maxillary forms nearly all of the side wall of the snout. The dorsal process of the relatively small premaxillary is much smaller than in such canids as *Canis latrans* and *Vulpes macrotis*, making contact with the nasals for less than a quarter of their length. The premaxillary in other species of *Miacis* (*M. gracilis*, *M. parvivorius*, *M. hargeri*) also appears to be small.

The orbit is relatively large, as in many small carnivores. The lacrimal is larger than in *Hesperocyon* or *Genetta*. It forms a sharp ridge on the anterior edge of the orbit, behind which is a pronounced pit, presumably

Table 10.—Measurements of specimens of *Miacis*.

		<i>M. cognitus</i> type TMM 40209-200		<i>M. australis</i> FMNH PM 423 (type)		<i>M. parvivorus</i> USNM 214706		
		right	left	right	left	TMM 41211-5 left	right	left
C/	AP	3.5e	3.5e		4.4e		4.1	
	T	2.3e	2.3e		2.5e		3.4	
P ¹	AP	2.6a	2.7a		2.6a		2.5	
	T	2.3a	1.9a		1.9a		1.4	
P ²	AP	4.2	4.0		4.8a		3.5	
	T	1.9	1.9				1.6	
P ³	AP	4.7	4.6		5.9		5.0	4.7
	T	2.3e	2.7				2.6	2.5
P ⁴	AP	6.7	6.9	7.9e	7.5e		7.3	7.6
	T	4.4	4.2	4.9	5.1		4.8	4.8
M ¹	AP	5.1	5.4	5.8e	6.7		5.9	5.8
	T	7.8	7.5	9.0e	9.7e		8.7	8.6
M ²	AP	3.8	3.8	4.5e	4.8e		3.7	3.7
	T	6.0	6.0	6.8e	6.7e		6.2	6.2
M ³	AP	1.6						
	T	2.3						
Post. C-M ²		32.4	32.5		37.3		29.3	
/C	AP				4.0			
	T				3.3			
P ₁	AP						2.0	
	T						1.3	
P ₂	AP						3.2e	
	T						1.3	
P ₃	AP			6.1	5.9		4.2	
	T			2.5			2.2	
P ₄	AP			6.5	6.7a		5.6	
	T			2.7			2.9	
M ₁	AP			7.5	7.8		7.1	6.9
	T			4.3	4.1		4.3	4.1
M ₂	AP			5.3	4.9a	5.6	4.5	4.6
	T			3.5		3.5	3.5	3.7
M ₃	AP				2.5a		2.3a	2.2
	T						1.9a	2.4
Post. C-M ₃				41.8e	41.5a		32.1a	
Jaw depth at M ₁				11.0	11.1	10.9	8.9	9.2
Length of skull		84.4						
Width at mastoids		29.2						
Width of condyles		21.0						



Figure 28.—*Miacis cognitus* n.sp., type, TMM 40206-200, Little Egypt local fauna. Posterior view showing cerebellar endocranium.

for a large lacrimal gland. A similar structure is seen in *Bassariscus*, but it is not present in *Genetta* and is much smaller in *Hesperocyon*. The lacrimal forms the dorsal border of the posterior opening of the infraorbital canal. The anterolateral border of the orbit was formed by the jugal, of which only the anteriormost part is preserved. There was a distinct maxillary process or ventral projection of the jugal overlapping the lateral surface of the maxillary, which is indicated by an articular surface in *M. cognitus*. This is present in *Miacis parvivorus*, all canids, and at least some procyonids (*Procyon*, *Nasua*), but not in viverrids, felids or mustelids. The dorsomedial wall of the orbit is formed by the frontal. Two small foramina are present immediately posterior to the postorbital process. The ethmoid foramen is a single oval opening at the contact of the frontal with the orbitosphenoid. The boundary of the orbitosphenoid is difficult to locate because of breakage of this delicate bone. However, it appears to have formed the optic foramen and the medial wall of the orbital fissure. An alisphenoid canal is present, apparently opening as in *Hesperocyon* within the foramen rotundum immediately lateral to the orbital fissure. The close association of the orbital fissure and anterior opening of the alisphenoid canal is similar to the structure found in *Nandinia* as well as in *Hesperocyon*. Boundaries between the alisphenoid and other bones are poorly marked on this specimen.

The ventromedial and ventral walls of the orbit are formed by the palatine and maxillary, respectively. The lateral wall of the palatine contains the sphenopalatine and posterior palatine foramina. The maxillary forms a flat floor for the orbit and encloses most of the infraorbital foramen, which is nearly circular at its anterior opening above P^3 .

The palate is composed of premaxillary, maxillary, and palatine bones. The premaxillaries contain the incisor alveoli, and form the anteromedial border of the canine alveoli and the anterior and medial borders of the anterior palatine foramina. The palatine foramina are slightly smaller than in *Genetta* and are concave laterally. The anterior border of the palatines lies between the protocones of P^4 . The contact between palatines and maxillaries is irregular, and the posterior palatine foramina and several minor foramina open along it.

The basicranial region is well preserved (Fig. 26b, c). The basioccipital and basisphenoid are broad and completely fused. There is no ossified bulla preserved, and there are no facets on the bones on the medial and posterior sides of the promontorium which would indicate the presence of an ossified caudal entotympanic. A small buttonlike process on the mastoid part of the petiotic, just anterior to the stylomastoid foramen, appears to be the articulation for the posterior limb of the tympanic, to which it apparently was attached by a small ligament. A similar articular process is seen in *Miacis parvivorus*, in Recent *Nandinia* (in which the tympanic does not fuse to other bones), and in juvenile carnivores before the tympanic fuses to other bones (Hunt, 1974a, Fig. 6 and 25). The articulation for the anterior limb of the tympanic, against the posterior side of the alisphenoid and squamosal, is less well defined, though it is broader and better defined than in *M. parvivorus*. It appears that this articular area was relatively smaller in *M. cognitus* than it is in *Nandinia*, and that the tympanic may have been less expanded than in *Nandinia* though more expanded than in *M. parvivorus*. I cannot distinguish articular surfaces for the rostral entotympanic, and this element, like the caudal entotympanic, may have been unossified.

The foramina of the skull are shown in Figure 23a and 24a. The hypoglossal foramen is round and separated from the posterior lacerate foramen. The posterior lacerate foramen is larger than the hypoglossal and is continuous in part with the inferior petrosal sinus. The inferior petrosal sinus is narrow and is roofed dorsally by portions of both the petrosal and basioccipital. The petrosal is similar to that of *Miacis parvivorus*. In both, the petrosals are rounded ventrally, with an anterior projection between the fossa for the *tensor tympani* muscle and the middle lacerate foramen. The *fenestra rotundum* faces more laterally than in *Hesperocyon*. In *M. cognitus* a small shelflike projection is present on the petrosal posterior to the *fenestra rotundum*. This shelf is absent in *M. parvivorus* (in which the *fenestra rotundum* is therefore closer to the posterior margin of the petrosal), but is present and broader in *Hesperocyon gregarius*. In *M. parvivorus* a small groove on the ventral surface of the promontorium may indicate the presence of a promontory branch of the carotid artery. No such groove is visible in *M. cognitus*, but a small foramen visible on the right side lateral to the middle lacerate foramen, situated on the contact between the alisphenoid and petrosal, may be a promontory foramen and may indicate

the presence of a promontory artery. In *M. cognitus* the ventral edge of the petrosal contacts the basioccipital along 3 mm of its edge. The extent of the dorsal contact is difficult to determine, but is probably substantially less than in *Hesperocyon*. The stylomastoid foramen is situated posterolateral to the *fenestra rotundum*. The middle lacerate foramen is a triangular opening on the anteromedial side of the petrosal. On the medial side of the middle lacerate foramen in the basisphenoid is a looped groove by which the medial branch of the internal carotid enters the cranial cavity (Hunt 1974a, p. 39). The postglenoid foramen, foramen ovale, and the posterior opening of the alisphenoid canal are present and virtually identical in *M. cognitus* and *M. parvivorus*.

The paroccipital and mastoid processes are small, and neither shows any sign of being involved in the formation of, or of being in contact with, a bulla.

A well preserved endocast (Figs. 27,28) is exposed on the right side of the cranium and in portions of the occipital region. This is the first known specimen referable to *Miacis* in which the endocast is preserved. The brain was notably primitive. It shows (as would be expected in a miacid) relatively little expansion of the neocortex or complication of the lobes and fissures. The endocast resembles those of the most primitive canid, *Hesperocyon* (early Oligocene; Radinsky, 1969), the late Eocene European miacid *Procynodictis* (= "*Viverravus*") *angustidens* (illustrated in Piveteau, 1962), and the late Oligocene viverrid *Herpestides antiquus* (illustrated in Radinsky, 1971) in the presence of only two well developed neocortical sulci, the coronolateral and

suprasylvian. The rhinal fissure, separating neocortex from paleocortex, is high and is indistinct except in the anteriormost portion and just anterad from the widest part of the endocast. The *fissura prima*, an important landmark, can only be located approximately, and the posterior cerebrum is covered. From the form of the parietals it appears that the posterior cerebrum overlaps the cerebellum to a slightly greater extent than in *P. angustidens*, but less than in *Hesperocyon gregarius*. The shape of the olfactory bulbs can be approximated from swellings on the medial orbital walls. These appear to be smaller and more overlapped by the anterior cerebrum than in *P. angustidens*. Compared to *P. angustidens*, the brain of *M. cognitus* is lower and flatter, particularly in the posterior half of the cerebrum, has a narrower gyrus between the posterior rhinal fissure and the posterior suprasylvian sulcus, and a more posteriorly located incipient sylvian notch.

Only the upper dentition is known (Fig. 26a). The incisors are small, simple, and closely packed, with I^3 slightly larger than the others. The canines and the first premolars are missing; these teeth were probably similar to those of *M. parvivorus*. The anterior premolars are widely spaced, more so than in *M. parvivorus*, in which P^2 and P^3 are not separated by a diastema. P^2 is a simple premolar lacking accessory cusps. P^3 also lacks accessory cusps but is larger and has a distinct lingual cingulum. P^4 differs from that of *M. parvivorus* in the much smaller protocone and slightly longer metastyle. The space between the lingual shearing surface of P^4 and the anterior side of M^1 is similar to that of *M. parvivorus*

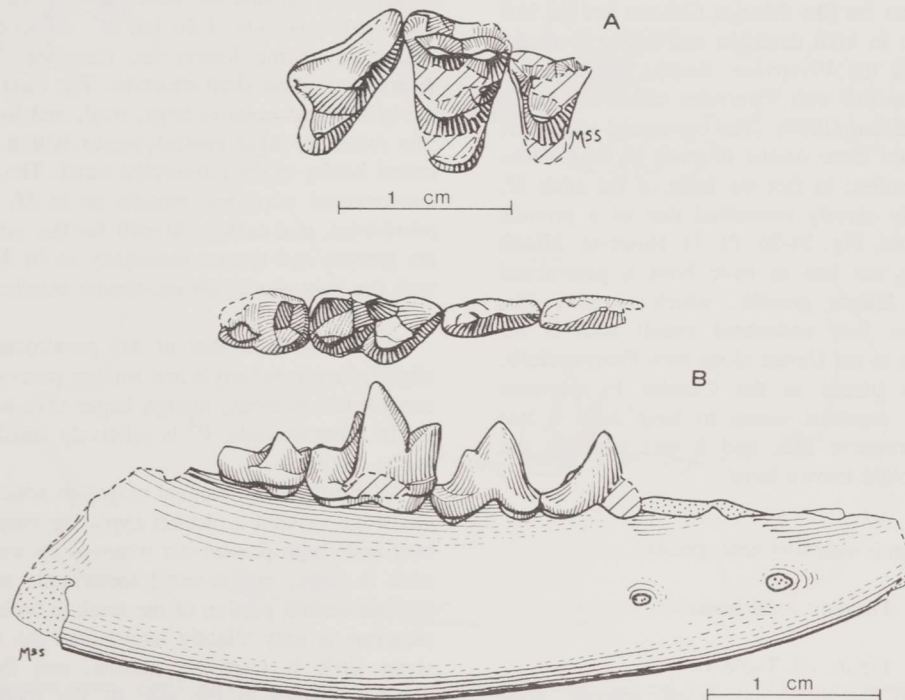


Figure 29.—*Miacis australis* n.sp., type, FMNH PM 423, Porvenir local fauna. A. Maxillary fragment with P^4 - M^2 (P^4 reversed from right side), occlusal view. B. Ramus of mandible with P^3 - M^2 , occlusal and outside views.

but is considerably smaller than in *Hesperocyon*. The M^1 of *M. cognitus* is much more symmetrical than that of *M. parvivor* or *Hesperocyon* because the parastyle is smaller than in either of these taxa. The metacone and paracone are subequal in size, and the hypocone, or widest part of the lingual cingulum, is situated in a more anterior and lingual position. The hypocone is larger than in *Uintacyon* and *Procynodictis* and resembles that on the M^1 of *Daphoenus*. The lingual cingulum does not extend as far around the anterior side of the tooth as in *M. parvivor* but it does extend farther than in some specimens of *Hesperocyon*. The distinguishing features of M^1 are repeated in M^2 . Although M^2 is smaller than M^1 it is not as small as in *Hesperocyon*. The posterior lingual cingulum is smaller in *M. cognitus* than in *M. parvivor*. M^3 is a small oval tooth with probably two roots in *M. cognitus*, and judging from the alveoli was smaller than in *M. parvivor*.

Relationships.—This skull shows a great many primitive features. It is perhaps more similar to *Miacis parvivor* of the Bridger Formation (middle Eocene) than to anything else which is adequately known, but differs from that species particularly in characters of the dentition. The dentition is complete and lacks such reduction as is seen in viverrids, canids, and other extant families. The teeth are perhaps more amphicyonid-like, particularly resembling *Daphoenus*, than like those of other families. The skull lacks the expansion of the inferior petrosal sinus which is characteristic of the Amphicyonidae (Hunt, 1974b). It also lacks the posterior expansion of the caudal entotympanic chamber which is seen in the Viverridae, including *Nandinia* in which the caudal entotympanic is not ossified. The skull proportions of *Miacis cognitus* are like those of *Genetta* but the lack of specializations in both dentition and bullae precludes classification with the Viverridae, despite the precedent of combining Miacidae with Viverridae which was set by Gregory and Hellman (1939). The basicranial characters of *M. cognitus* are more similar to those of the Canidae than to other families; in fact the bulla of the adult *M. cognitus* probably closely resembled that of a juvenile canid (Hunt, 1974a, Fig. 24-26, Pl. 7). However, *Miacis cognitus* appears too late to have been a generalized canid ancestor. *Miacis gracilis*, which is more like *Hesperocyon* (the first undoubted canid) than is *M. cognitus*, appears in the Uintan along with *Procynodictis*, which has been placed in the Canidae by previous workers. *Miacis cognitus* seems to have been a late survivor of a primitive line, and it was probably not ancestral to any other known form.

Miacis australis new species

Porvenir local fauna

Figure 29, Table 10

Type.—FMNH:PM 423, incomplete anterior skull including partial left P^4 - M^2 , right P^4 , mandibular rami with partial left canine and M_1 , right P_3 - M_2 .

Referred material.—TMM 41211-5, mandible fragment with M_2 .

Stratigraphic position.—The type is from the Chambers Formation, 0 to 26.8 m (0 to 88 feet) above lower marker bed and 41211 is near Adobe Springs (Wilson, 1977b, Fig. 8), 7.6 to 12.8 m (25 to 42 feet) above the Buckshot Ignimbrite, Presidio County, Texas.

Age.—Early Chadronian (early Oligocene).

Etymology.—Refers to the southern position among U. S. Chadronian fossil localities.

Diagnosis.—Protocone of P^4 large, parastyle of M^1 relatively small, paracone and metacone subequal in size on both M^1 and probably M^2 , lingual cingulum well developed on both M^1 and M^2 , protoconid-paraconid shearing blade on M_1 directed more anteroposteriorly than in *M. parvivor* but less so than in *Hesperocyon*.

Compared to other species of *Miacis*, *M. australis* is larger than *M. cognitus* n. sp. and *M. parvivor*, and much larger than *M. exilis* and *M. jepseni*. It differs from *M. gracilis* in having a relatively smaller P^4 , a large hypocone on M^1 , a relatively larger M_2 and a more anteroposteriorly oriented protoconid-paraconid blade on M_1 . It differs from all other species except *M. cognitus* in the relatively small size of the M^1 parastyle, but differs from that species in the relatively large size of the P^4 protocone. The form of the trigonid of M_1 also separates *M. australis* from all other *Miacis* species in which this structure is known.

Description.—The type specimen consists of fragments of the rostrum of a skull in a block and two associated partial mandibular rami. The skull has separated along the midline and the fragments have been rotated 180° so that the labial side of the right P^4 rests near the lingual side of the left M^1 . All of the upper teeth and most of the lowers are damaged. Little can be determined of the skull structure. The anterior opening of the infraorbital canal is large, oval, and located over P^3 . The maxillary-jugal contact passes within 1 mm of the lateral border of the infraorbital canal. The jugal bears an anteroventral maxillary process as in *M. cognitus*, *M. parvivor*, and canids. Alveoli for the canine and P^1 - P^3 are present and spaced essentially as in *M. parvivor*, with the only significant diastemata anterior and posterior to P^1 .

P^4 differs from that of *M. parvivor* in having a slightly larger metastyle and smaller parastyle. The protocone is less bulbous, though larger than in *M. cognitus*. As in other miacids, P^4 is relatively small in proportion to the molars.

M^1 bears a large lingual cingulum which is a continuous ridge without a distinct hypocone cusp. Such a cusp may have been present but removed by wear. The protocone is large, and a small metaconule is present. The anterior central portion of the tooth is broken away. The paracone is only slightly larger than the metacone. The stylar shelf is relatively narrow, and the parastyle is smaller relative to the size of the tooth than in *M. parvivor*.

The labial side of M^2 is badly damaged, but it appears

to be similar to though smaller than M^1 . A large lingual cingulum was present but is broken off. The protocone is low and broad. A tiny paraconule is present, but the metaconule is indistinct. The overall shape of both molars is similar to those of *M. cognitus*. No M^3 is preserved, though it may have been present. The bone posterior to M^2 is broken and covered by very hard matrix so that the presence or absence of alveoli for M^3 cannot be determined.

The mandible is gently curved on its ventral border. There are two mental foramina, one beneath P_1 and the other beneath anterior root of P_3 . The mandible tapers anteriorly. The canine was not large. P_3 is simple except for the presence of a very small metaconid on the lingual side of the posterior slope of the protoconid. P_4 has a distinct hypoconid and differs from P_4 of *M. parvivorus* in the absence of any paraconid and in the relatively narrow posterior portion of the tooth. M_1 resembles that of *M. gracilis* Clark in the shape of the trigonid, more

than that of *M. parvivorus*, because the paraconid-protoconid blade is turned to a more anteroposterior position in the former species and the paraconid is distinctly larger than the metaconid. The talonid is basin shaped, with equal sized hypoconid and entoconid. The hypoconid is placed closer to the labial margin of the tooth than in *M. parvivorus*. M_2 is relatively large (Table 10), similar to that of *M. parvivorus* and somewhat larger than that of *M. gracilis*. The trigonid is low but all three cusps are distinct. The hypoconid is placed close to the labial margin as in M_1 . M_3 had one root and was about the same size as in *M. parvivorus*. Its crown is not preserved.

Comments.—The molar structure of *M. australis* appears to be similar to that of *M. cognitus* in that both preserved upper molars in both species are substantially more symmetrical about a mediolateral axis than is usual in miacids, because the parastyle is small and the metacones and paracones are similar in size on each



Figure 30.—*Uintacyon scotti*, TMM 40165-4, Lower chisos Formation, Big Bend National Park. A. Skull, right lateral view. Skull is badly crushed and distorted; the undistorted distance from P^4 to the glenoid fossa would have been about 15% shorter than shown here. Broken surfaces and matrix unshaded. B. Right ramus of mandible, associated with skull. Top of coronoid process and P_3 - P_4 drawn from left mandible, P_1 drawn from isolated tooth.

molar. Neither has an anterior cingulum. *Miacis australis*, of Chadronian age, is more like the Bridgerian species of *Miacis* than some Uintan miacids, for example *Tapocyon* with its enlarged anterior M_1 and *Uintacyon scotti* with its broadened upper molars. Other than a slight reduction of the parastyle, the upper teeth are little more advanced than those of the Bridgerian *M. parvivorus*. The reduction in size of the M^2 which is seen in *M. gracilis* and *Procynodictis vulpiceps*, both of the Uinta Formation of Utah, is not apparent in *M. australis*. M_1 is slightly more advanced than in *M. gracilis*, but it is more primitive than in *Hesperocyon*. *Miacis australis* and *M. cognitus* are apparently relicts of the considerable radiation of miacine miacids which occurred in Bridgerian and Uintan time. In the Texas sections, *Hesperocyon* apparently does not appear until after the miacids are gone. Though the evidence is sparse and partly negative, this could well be interpreted as a replacement of a primitive southern miacid fauna by more advanced and adaptively similar canids which may have appeared earlier in the Cypress Hills to the north.

Genus *Uintacyon* Leidy, 1872

Uintacyon scotti (Wortman and Matthew, 1899)

Figs. 30-31, Table 11

Synonyms.—*Prodaphaenus scotti* Wortman and Matthew, 1899; *Uintacyon (Miocyon) scotti*, Matthew, 1909.

Type.—PU 11238, P^3 - M^2 , upper part of Wagonhound Member, (Uinta "B"), Uinta Formation, Utah.

Referred Material.—TMM 40165-4, skeleton with skull, left canine, P^3 - M^3 , right P^4 , M^2 - M^3 , mandible with canines, left P_3 - M_1 , right P_1 , M_1 , all or parts of 15 vertebrae and several ribs, all or parts of scapula, humerus, radius, ulna, femur, tibia, fibula, patella, tarsals, metatarsals, and phalanges. Questionably referred: TMM 41372-362, partial M^1 ; 41372-367, P_4 ; 41672-59, partial M_1 .

Stratigraphic position.—Lower part of Chisos Formation; probably Whistler Squat and Serendipity local faunas. The partial skeleton came from low in the Chisos Formation, about 20.7 to 27.4 m (68 to 90 feet) above

the Alamo Creek Basalt (locality T 14 of Plate II, Maxwell et al., 1967). The M^1 and P_4 are from the Whistler Squat local fauna, lower 15.2 m (50 feet) of the Devil's Graveyard Formation. The M_1 is from the Purple Bench locality, approximately 67 m (220 feet) stratigraphically higher in the Devil's Graveyard Formation, all from Brewster County, Texas.

Age.—Uintan (late Eocene).

Description.—The skeleton (40165-4) allows the first description of associated upper and lower dentitions of this species. The upper canine is straight and only slightly compressed. The posterior, medial and lateral surfaces are flattened, forming sharp ridges at their junctions. A low anteromedial ridge is also present. The alveolus for P^1 is closely appressed to the canine alveolus. It is slightly larger than either of the alveoli of P^2 . P^3 and P^4 are like those of the type. P^3 is short and wide, with a strong posterior cingulum raised at the rear into a small cusp. P^4 is also short anteroposteriorly, with a large protocone, central paracone, relatively small metastyle, and narrow labial cingulum. M^1 of the Texas specimen shows some minor differences from that of the type. The parastyle is smaller and the styler cingulum is not divided into two cusps as on PU 11238. M^2 is distinctive. It is long anteroposteriorly and is low crowned. The metacone is much larger than in *U. vorax* from the Bridgerian, and the tooth is almost completely rimmed by a broad cingulum which connects the indistinct protocone with the large parastyle, the styler cingulum, and the posterior side of the metacone. There is no trace of a hypocone on either M^1 or M^2 . M^3 is oval and small but functional. A low ridge parallels the rounded edges of the tooth, and the only discernible cusp is an indistinct paracone. The right M^3 has two roots, whereas the left has three.

An isolated lower incisor resembles an I^2 of *Canis*. The crown includes a main medial cusp and a small lateral cusp. The lower canines are tall and slightly recurved, and like the upper canines have a sharp posterior ridge and a less prominent anteromedial ridge. The lateral side is longitudinally grooved. An isolated P_1 is a simple tooth similar to, though smaller than, its equivalent in *Canis latrans*. The anterior mandible of ?*U. scotti* figured by Wortman (1901, Fig. 17), if it belongs with

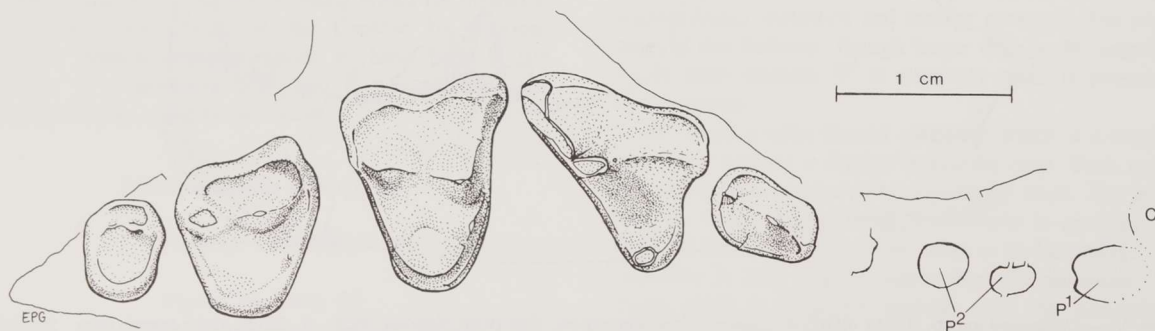


Figure 31.—*Uintacyon scotti*, TMM 40165-4, Lower Chisos Formation, Big Bend National Park. Right upper dentition, occlusal view, position of alveoli for C-P² shown in outline. Breakage has separated the teeth. M^2 drawn from left side.

Table 11.—Measurements of dentitions of *Uintacyon scotti*.

		<i>U. scotti</i>		<i>U. sp.</i>	<i>U. scotti</i> type
		TMM 40165-4		TMM 41372-367	PU 11238
		right	left		
C	AP		9.5		
	T		7.8		
P ³	AP	7.0			7.6
	T	4.5			5.1
P ⁴	AP	11.6	11.8		11.4
	T	9.4	9.2		10.5
M ¹	AP	9.7			10.9
	T	13.4			16.3
M ²	AP	9e	8.8		8.5
	T	12e	11.6		12.3e
M ³	AP	4.8	4.9		
	T	6.3	6.5		
C	AP	8.8	8.7		
	T	6.5	6.8		
P ₁	AP	3.2a	4.0		
	T		2.5		
P ₂	AP	6.2a	6.2a		
P ₃	AP	6.2a	5.4		
	T		3.5		
P ₄	AP	8.2a	8.7	7.9	
	T		4.6	4.8	
M ₁	AP	13.4	12.4		
	T	7.1	7.2		
M ₂	AP	10.3a	10.2a		
M ₃	AP	5.3a	4.5a		
M ₁ -M ₃		27.5a	27a		
P ₁ -M ₃		56a	60a		

this taxon, is abnormal in having two single rooted anterior premolars. As nearly as can be told from the alveoli, P₂ was about the same size as P₃. P₃ is small, with a distinct hypoconid and posterior lingual cingulum. P₄ is also relatively small, with the posterad-leaning main cusp that is typical of *Uintacyon*.

M₁ is tall, with a well developed protoconid-paraconid blade which is oriented more anteroposteriorly than in *U. bathygnathus*. The paraconid and metaconid are well separated and equal in size. The anterior labial cingulum is present but is not as large as on *U. bathygnathus*. The talonid is typical of *Uintacyon*, consisting mostly of a large centrally placed hypoconid, with a small marginal entoconid. The alveoli of M₂ show that, like M², the tooth was elongated anteroposteriorly and was almost as long as M₁. M₃ was also relatively large, though single rooted.

The mandible is almost identical in length to that of *Canis latrans*, but it is deeper, straighter along the ventral margin, and has a more abrupt and distinct chin.

The tooth row of *U. scotti* is relatively short (Table 11), and the coronoid process and masseteric fossa are very broad. The masseteric fossa is extremely deep and its margins are sharply delineated. The angular process is large and is set lower on the mandible than in *Canis*.

The skull is badly crushed, and the premaxillaries, part of the left maxillary, zygomatic arches, and the posterior part of the braincase are missing. The rostrum was relatively short and high, though somewhat less blunt than in the recent large cats. The length of the tooth row relative to the mandible length is more similar to the proportions found in *Felis concolor* than in *Canis latrans*, both of which have a condyle-symphysis length about equal to that of *U. scotti*. Unlike the cats, *U. scotti* has not lost the posterior molars, but instead reduced the relative tooth row length, although retaining all the teeth, by reducing the relative size of the premolars.

In dorsal view the skull is more catlike than doglike, with a short snout and broad frontals. Small postorbital

processes are present on the frontals. The postorbital cranial constriction is relatively more posterior than in living carnivores, mainly because of the small size of the anterior cerebrum. A strong sagittal crest was present. From the side the dorsal outline of the skull is arched like that of *Felis concolor*. The orbit is relatively smaller than in *Felis concolor*.

The internal nares opened between the last molars. The anteroventral rim of the narial opening is edged by a strong ridge, and a deep groove separates this ridge from the M^3 .

The cranial foramina are largely obscured by breakage or missing bone. It is clear that there is a postglenoid foramen, situated on the posteromedial side of the postglenoid process. The foramen ovale is present and is large. I cannot be sure whether an alisphenoid canal is present.

Major portions of the postcranial skeleton are present. These bones will have to await a more thorough description than I can present here. It is worthy of note that where comparable the bones are similar (except for larger size) to those of *U. bathygnathus*.

The P_4 and M^1 from Whistler Squat are not particularly diagnostic. They unquestionably are *Uintacyon*, and are assigned to *U. scotti* on the basis of general similarity to the Chisos Formation specimen. However, they could also belong to *U. bathygnathus*. The partial M^1 from Purple Bench, although resembling the equivalent anterior portion of the *Uintacyon* molar in size and form, lacks the diagnostic talonid and may belong to another genus.

Relationships.—The most probable ancestor for *Uintacyon scotti* is *U. bathygnathus* (Scott, 1888), from the Bridger Formation of Wyoming. *Uintacyon major* Matthew (1909) is so similar in size and morphology to the type of *U. bathygnathus* (PU 10607) that there can be little doubt that it is a junior synonym. All known specimens of *U. bathygnathus* (including *U. major*) are probably from the upper Bridger (C level), though the exact locality of the type is not known (Gazin, 1976). *Uintacyon scotti* is at the end of a branch of the *Uintacyon* lineage in which increase in size and increase in the crushing function of the molars were dominant features.

Family Amphicyonidae

Subfamily Daphoeninae

Genus *Daphoenus* Leidy, 1853

Daphoenus cf. *D. lambei* Russell, 1934

Porvenir local fauna

Figure 32c, d, Tables 12-13

Type.—NMC 6513, left P^4 , Cypress Hills, Saskatchewan.

Referred material.—OU 32-2-S2, maxillary fragment with part of P^3 and P^4 - M^2 ; FMNH:PM 31, mandible fragment with M^2 .

Stratigraphic position.—Lower part of Chambers Formation, Presidio Co., Texas.

Age.—Early Chadronian.

Description.—A portion of a maxilla (Fig. 32c) retains a small part of P^3 , a damaged P^4 , and M^{1-2} . Nothing can be said of the characters of P^3 because of the damage. P^4 is similar in shape to that of *Daphoenus vetus* (Brule Formation, Orellan) but is much smaller (Table 12), less robust, and higher crowned. The protocone is large and conical. Strong lingual and anterior cingula are present, and the small part of the central labial side preserved carries a distinct cingulum. I can find no characters in which this tooth differs from the type of *Daphoenus lambei* Russell (1934). M^1 is also similar to that of *D. vetus*, though smaller. The styler shelf is broad and the styler cingulum is low. The parastyle is less obvious than in *Hesperocyon* or *Miacis parvivorus*, but is still distinct. The paracone and metacone are of equal size. The paraconule and metaconule are distinct. The protocone is anteriorly placed. As is common in *Daphoenus*, the hypocone is larger than the protocone, rounded and even bulbous, and set at the lingual end of the tooth, giving it a laterally elongated appearance. M^2 is smaller than M^1 , with a narrower styler shelf which is broadest opposite the paracone. The parastyle is small and rounded. The paracone is low and also rounded. There is a very small paraconule, but the posterior part of the tooth including metacone and metaconule is damaged. The protocone is an indistinct point on a low, rounded ridge. The hypocone and attached cingulum are even more bulbous than in the M^1 , and the hypocone is much larger than the protocone.

M^2 (Fig. 32d) is much like that of other species of *Daphoenus*, though smaller (Table 13). The trigonid is short, with the protoconid slightly larger than the metaconid, and the paraconid smaller, but still distinct. The talonid is basined, with the central depression surrounded by the lingual and posterior talonid crests. The hypoconid and *crista obliqua* are relatively low. There is a small anterior labial cingulum.

Relationships.—The maxillary (OU 32-2-S2) was described and figured by Stovall (1948, Fig. 3), who considered it to be a new genus and species of canid, although he did not name it. However, its very *Daphoenus*-like molars and the virtual identity in shape and size of P^4 to the type of *D. lambei* Russell (1934; 1972, Fig. 12d and e) leave little doubt of its close relationship to *D. lambei*. Russell (1972) illustrated a referred M^1 of *D. lambei*, which looks more like the M^2 of a larger species of *Daphoenus*. This isolated tooth (NMC 9207) is practically an enlarged duplicate of the M^2 of the Vieja specimen, especially in its narrow posterior styler shelf, indented posterior margin, and very large bulbous hypocone. Both this and another referred M^1 from Cypress Hills (ROM 6331) are close in size to

the M^1 of OU 32-2-S2. The M_2 (FMNH:PM 31) is similar to *D. vetus* in form, but smaller than in *D. hartshornianus* and may reasonably be placed in *Daphoenus* cf. *D. lambei*. *D. hartshornianus* (Cope), from Orellan deposits, which is closest in size to *D. lambei*, is larger except for one questionably referred P^4 from Cypress Hills. *Daphoenus minimus* Hough (1948) was even smaller than *D. lambei*. Hough's photographs (1948, Plate 86, Figs. 3 and 4) show too little detail to be sure of either tooth or auditory structure, and the measurements, given apparently under the name "*D. gracilis*" (a nomen nudum), are very close to those of *Hesperocyon*.

Comments.—R.M. Hunt believes (from unpublished data) that only two Oligocene species of *Daphoenus* should be recognized, namely *D. vetus* and *D. hartshornianus*. If this is true these specimens would either have to be placed into one of these species (presumably *D. hartshornianus* as it is more similar in size) or set up as a new species. I cannot demonstrate this conclusion by published data. The Texas specimens are not greatly different in size from specimens referred to *Daphoenus demilo* Dawson, 1980, (M^1 AP=7.5, T=12.5, vs. OU 32-2-S2 AP=7.9, T=12.1). However, *Daphoenus demilo* is more primitive in having a wider styler shelf and smaller hypocone.

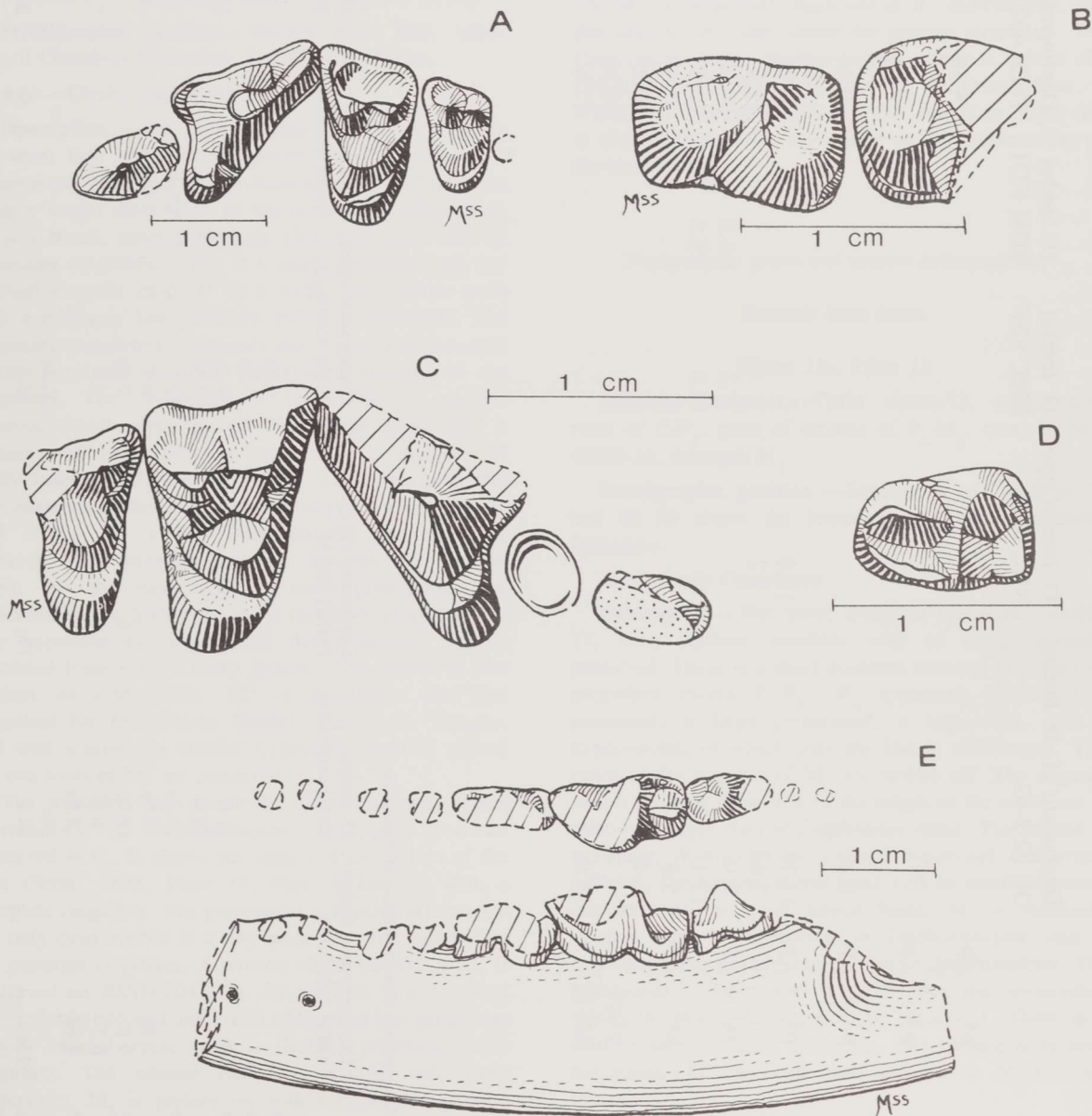


Figure 32.—A-B. *Daphoenocyon dodgei* (Scott), little Egypt Local fauna. A. TMM 40209-205, P^3 - M^2 , occlusal view. B. TMM 40209-204, talonid of M_1 and complete M_2 , occlusal view. C-D. *Daphoenus* cf. *D. lambei*, Porvenir local fauna. C. OU 32-2-S2, maxillary fragment with P^4 - M^2 , occlusal view. D. FMNH PM 31, M_2 , occlusal view. E. Daphoenine, genus and species indeterminate, TMM 40688-72, Porvenir local fauna. Partial ramus of mandible with P_4 - M_2 , occlusal and outer views.

Table 12.—Measurements of upper dentitions of Daphnoinae.

	<i>Daphoenus</i> cf. <i>D. lambei</i> OU 32-2-S2	<i>D. lambei</i> NMC 6513	<i>D. lambei</i> NMC 9207	<i>D. lambei</i> ROM 6331	<i>Daphoenocyon dodgei</i> TMM 40209-205	<i>D. dodgei</i> CM 9256
P ¹	AP				4.7a	4.7
	T					3.2
P ²	AP				9.0a	7.4
	T					5.1
P ³	AP	8.4e			9.5	9.5
	T				5.3	6.4
P ⁴	AP	11.2e			14.0	14.4
	T	7.6e			11.5	11.0
M ¹	AP	7.9	7.2	8.0	9.7	10.7e
	T	12.1	10.6	12.3	16.5	16.0e
M ²	AP	5.8			7.3	
	T	9.4			10.8	
P ¹ -P ⁴					38.4	34.2
M ¹ -M ²	13.6				17.6	

Table 13.—Measurements of lower dentitions of Daphnoinae.

	<i>Daphoenocyon dodgei</i> TMM 40209-204	<i>D. dodgei</i> TMM 40209-784	<i>Daphoenus</i> cf. <i>D. lambei</i> FMNH PM 31	<i>Daphoeninae</i> indet. TMM 40688-72	<i>Daphoeninae</i> indet. TMM 40203-16	<i>Daphoenocyon dodgei</i> PU 11422 (type)	<i>Daphoenus lambei</i> NMC 9114
P ₂	AP			6.5a		6.0	
P ₂	AP			7.9a		8.0	
P ₃	AP	11.6		9.1e		11.0	
P ₄	T	5.9		3.5e		5.0	
M ₁	AP	13.7e		12.5	12.4e	14.0	11.9
	T	6.7e		6.7	7.0e	8.0	6.2
M ₂	AP	10.0		7.0e			
	T	6.8	7.8	4.0			
M ₃	AP	4.5a	5.4				
M ₁ -M ₃		28a		25.5e			
Jaw depth,		24.2	17e	15.8			
anterior M ₁	23e					23.0	

Genus *Daphoenocyon* Hough, 1948

Daphoenocyon dodgei Scott, 1898

Little Egypt local fauna

Figures 32a, b, Table 12-13

Type.—PU11422, Chadron Formation ("Titanotherium beds"), Hat Creek Basin, Nebraska.

Referred materials.—TMM 40209-204, ramus fragment with talonid of M_1 , M_2 and alveolus of M_3 ; 40209-205, maxilla with alveoli of C, P^{1-2} , crowns of P^3 - M^2 , and alveolus of M^3 ; 40209-784, ramus fragment with partial P_4 , roots of M_1 , entire M_2 and root of M_3 .

Stratigraphic position.—Reeves Bone Bed, upper part of Chambers Formation, Presidio Co., Texas.

Age.—Chadronian (early Oligocene).

Description.—The skull fragment shows very clearly the short face and crowded premolars characteristic of *Daphoenocyon*. There are no diastemata. P^1 had one root slightly longer than either of the roots of P^2 (Fig. 32a). P^3 is a broad, anteroposteriorly elongated cone with an encircling cingulum. There is a small posterior cusp and a small cingular cusp. P^4 is a wide, very robust tooth with a relatively low paracone and short metastyle. The cingulum completely surrounds the tooth. The parastyle forms a raised, enlarged anterolabial portion of the cingulum. The protocone is large. M^1 is shorter anteroposteriorly than that of *Daphoenus vetus*, and is similar to M^1 of the paratype specimen of *D. dodgei* (CM 9256) listed by Clark et al. (1967). There is a large but low parastyle, a broad styler shelf slightly wider than in CM 9256, and a low and rounded paracone and metacone. The paraconule is less obvious than in CM 9256, but the metaconule is more prominent. The protocone is the high point on a curved V-shaped ridge. The hypocone is larger than the protocone and is separated from it by a sharp groove. This groove is less distinct on CM 9256. M^2 is essentially like that described for *Daphoenus lambei*, but larger, broader, and with a relatively smaller hypocone. Parts of alveoli for two roots of M^3 are preserved.

The mandible has the thick, deep horizontal ramus characteristic of *Daphoenocyon*. The only premolar preserved is P_4 . It shows the same outline as that of the type (Scott, 1898, Plate 19, Figs. 6 and 7), with a complete cingulum. The protoconid is broken off, so that the only cusp visible is a tiny posthypoconid just within the posterior cingulum. A portion of the talonid of M_1 is preserved on 40209-204 (Fig. 32b). There is a short but prominent hypoconid and *crista obliqua*, a less prominent lingual talonid crest, and a distinct posterior labial cingulum. The talonid basin is shallow and opens posteriorly. M_2 is present on both mandible fragments. The crown is broad and low, with rounded crests and cusps and shallow basins. The protoconid and paraconid are strongly convex anteriorly, without a distinct carnassial notch. The hypoconid and *crista obliqua* are

low but distinct. The entoconid is only a wide spot on the lingual talonid crest. A small but prominent anterior labial cingulum is present. M_3 was small, with a single root which was indented on both sides.

Relationships.—These specimens show the generic features of *Daphoenocyon* Hough (1948) and are within the size range of *D. dodgei*. This taxon has had a fairly simple history. It was proposed by Hough to include *?Daphoenus dodgei* Scott (1898), then later redefined by Clark et al. (1967) to include a slightly different hypodigm. The genus *Daphoenocyon* is, however, questionably distinct from *Brachyrhynchocyon* Loomis (in Scott and Jepsen, 1936), as both are daphoenine carnivores with short faces and trenchant talonids on M_1 . The M^3 has apparently been lost in *B. intermedius*, and this may be adequate reason for generic separation. The Chadronian species *Daphoenocyon minor* (Clark et al., 1967) is about the same size as *B. intermedius*, a Whitneyan species. *Daphoenocyon dodgei* is larger and is distinct from either *D. minor* or *B. intermedius* on the basis of size.

Daphoeninae genus and species indeterminate

Porvenir local fauna

Figure 32e, Table 13

Referred Material.—TMM 40688-72, ramus with roots of C- P_3 , parts of crowns of P_4 - M_2 , roots of M_3 ; 40203-16, damaged M_1 .

Stratigraphic position.—Between 0 and 26.8 m (0 and 88 ft) above the lower marker bed, Chambers Formation.

Age.—Early Chadronian.

Description.—The more complete specimen, 40688-72, is a shallow mandible with no complete teeth preserved. There is a short diastema between each pair of premolars except P_3 - P_4 . P_4 apparently possessed a paraconid, a large protoconid, a hypoconid, and a hypoconulid, of which only the last is undamaged. The cusps of the trigonid of M_1 are broken off. The trigonid makes up more than 70% of the length of the tooth and is relatively larger than in *Daphoenus vetus*. The talonid is trenchant, dominated by a large hypoconid and *crista obliqua*. The lingual talonid crest with its small entoconid encloses only a small lateral basin. M_2 is relatively smaller than in *Daphoenus* or *Daphoenocyon*, and is relatively only slightly larger than in *Daphoenictis*. The protoconid is large and is taller than the metaconid, which in turn is larger than the paraconid. There is a distinct anterior labial cingulum. The talonid is broken, but appears to have been small and narrow. M_3 had two roots.

Another M_1 , TMM 40203-16, is a little larger than that of 40688-72, and probably represents a daphoenine. The talonid is broken off and its characters cannot be ascertained.

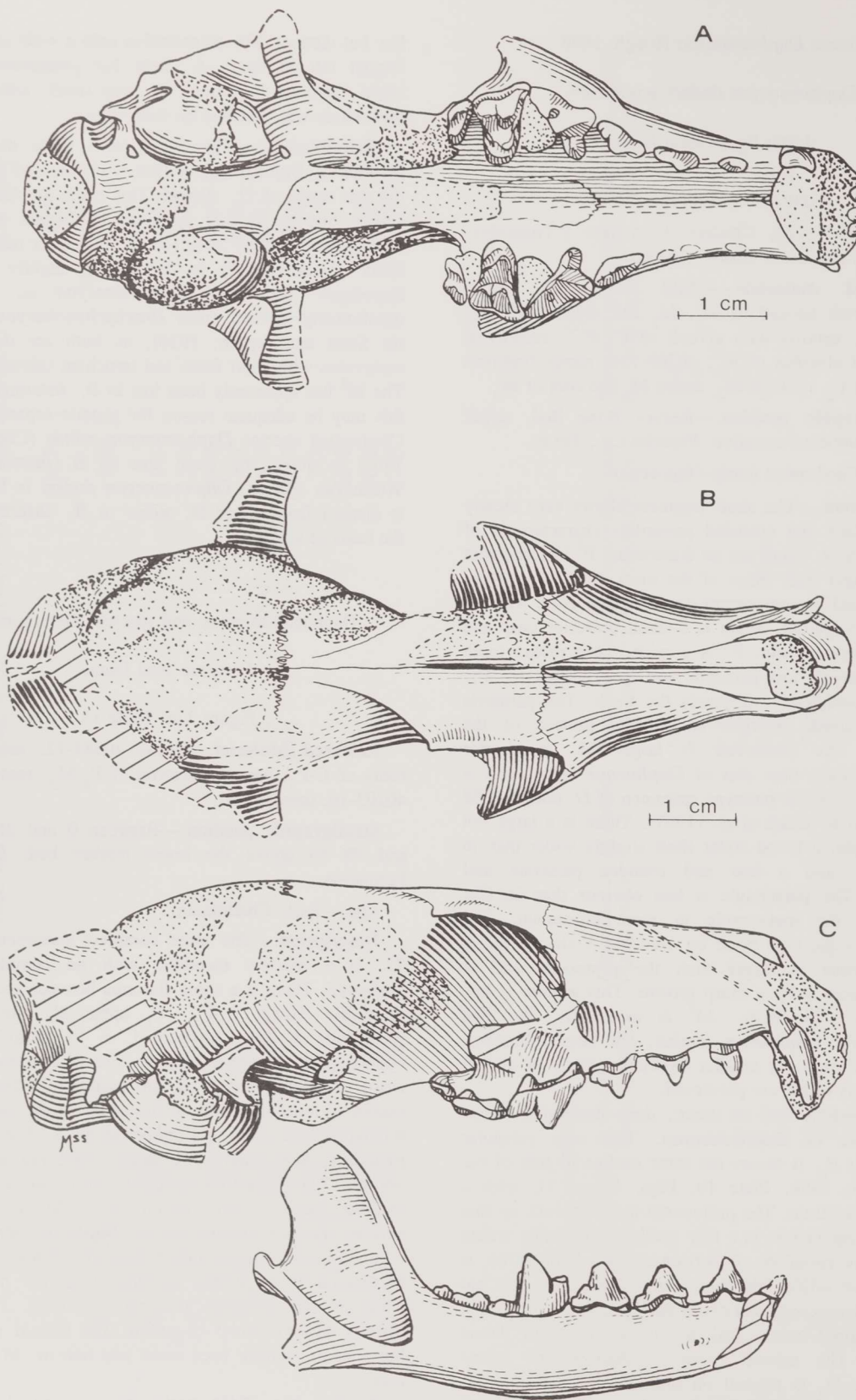


Figure 33.—*Hesperocyon wilsoni* n. sp., type, TMM 40504-126, Airstrip local fauna. A. Skull, ventral view. B. Skull, dorsal view. C. Skull and right ramus of mandible, lateral view.

Relationships.—The mandible 40688-72 differs from *Daphoenus* and *Daphoenocyon* in its reduced talonid on M_1 and reduced M_2 . It resembles *Daphoenictis tedfordi* Hunt (1974b) in the enlarged trigonid and trenchant talonid of M_1 and the reduced M_2 with a large protoconid. This specimen does not show the extreme specializations of *Daphoenictis*, such as reduction of the paraconid and loss of the metaconid of M_2 . The characters of the premolars, which are tall and narrow with enlarged hypoconids in *Daphoenictis*, are not known in 40203-16, though certainly a large hypoconid was present on P_4 . This specimen may represent a new species related to *Daphoenictis*, but it is not well enough preserved to serve as a type.

Family Canidae

Genus *Hesperocyon* Scott, 1890

Hesperocyon wilsoni n. sp.

Airstrip local fauna

Figures 33-34, Tables 14-17

Type.—TMM 40504-126, skull and mandible.

Referred material.—TMM 40504-99, mandible with right and left P_{2-4} .

Stratigraphic position.—Capote Mountain Tuff, approximately 174 m (570 feet) above Bracks Rhyolite, Presidio Co., Texas.

Age.—Chadronian (early Oligocene).

Etymology.—Named for Dr. J. A. Wilson.

Diagnosis.—Skull length within the range of *H. gregarius*. Measurements of P^3 (AP), P^1 - M^2 , P^1 - P^4 , P_3 , P_4 (AP), P_1 - M_3 , and P_1 - P_4 all larger than observed range of *H. gregarius*. Molar measurements and morphology within the range of *H. gregarius*, except metacone on M^2 greatly reduced. M^3 absent.

Description.—The skull (Fig. 33) is crushed laterally and much of the bone has been weathered, but the teeth are not badly damaged. The preorbital portion of the skull is longer and was probably relatively narrower than in *Hesperocyon gregarius* (compared to several specimens from the Brule Formation, Orellan, South Dakota), although the narrowness of the snout has certainly been exaggerated by the crushing. The nasals are slightly longer than in *H. gregarius*, and the dorsal process of the premaxillary is distinctly broader and longer. The postorbital constriction is not as pronounced in the Vieja skull as in *H. gregarius*, though distortion of the bones and the endocast may be partly responsible for this difference. The sagittal crest was lyrate, with the two anterior branches of the crest remaining 7 mm apart as far posterior as the frontal-parietal suture. A distorted partial endocast shows two well developed sulci, the coronolateral and suprasylvian. Between the posterior ends of these sulci there is a dimple or incipient sulcus, possibly representing the ectolateral sulcus. There is a depression medial to the posterior end of the coronolateral for which I cannot find an equivalent in *H.*

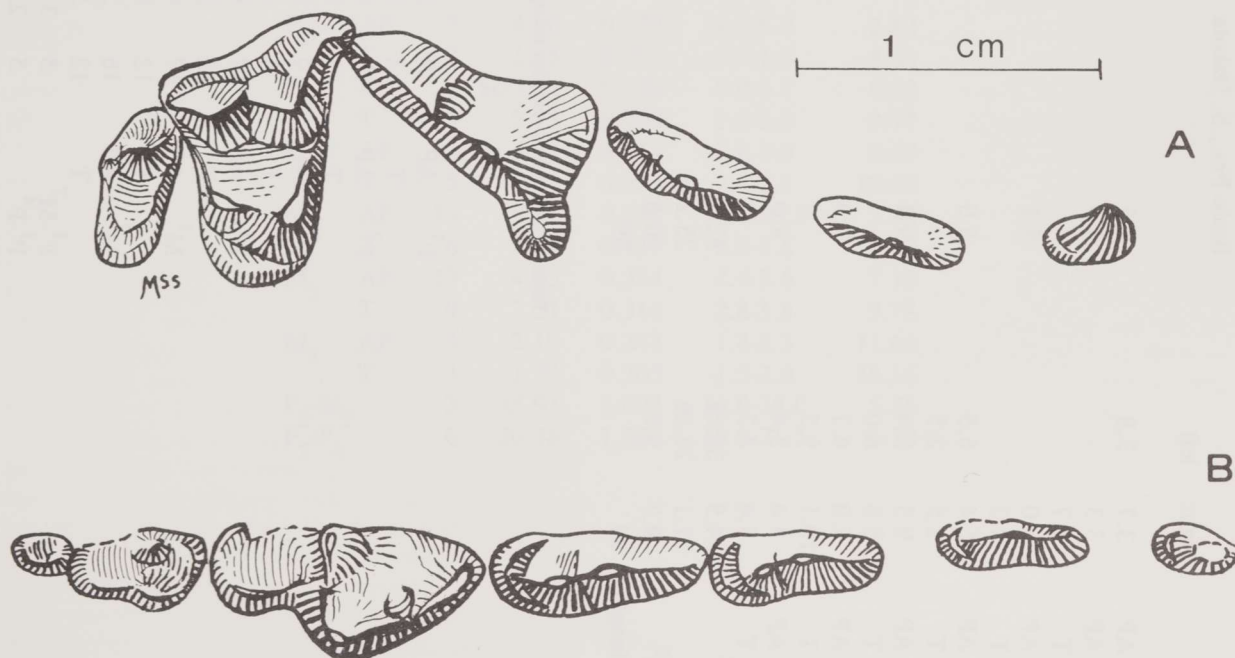


Figure 34.—*Hesperocyon wilsoni* n. sp., type, TMM 40504-126, Airstrip local fauna. A. Upper dentition, occlusal view. B. Lower dentition, occlusal view.

Table 14.—Measurements of upper denitions and skulls of *Hesperocyon*.

		<i>H. wilsoni</i> TMM 40504-126 (type)	<i>H. gregarius</i> AMNH 63850 Brule Fm., S. Dakota	<i>H. gregarius</i> AMNH 50351 Brule Fm., S. Dakota	<i>H. paterculus</i> AMNH 63943 Flagstaff Rim, Wyoming	<i>Miacis gracilis</i> CM 11900, type Myton Member, Uinta Fm.
		right	left			
C	AP	3.7	3.8			
P ¹	AP	3.3		4.2		3.4
	T	1.7		3.1		2.2
P ²	AP	5.0		1.7		5.4
	T	2.2		5.0	5.0	2.5
P ³	AP	6.4	6.5	1.9	2.2	6.3
	T	2.5		5.7	5.8	3.3
P ⁴	AP	9.3	9.4	2.5	3.2	
	T	5.8	6.0	8.5	9.1	9.1
M ¹	AP	7.0	6.7	5.2	6.0	6.4
	T	10.1	9.5	6.3	6.5	6.8
M ²	AP	3.4	3.4	8.6	9.5	9.6
	T	5.4	5.3	3.4	4.1	3.3
P ¹ -M ²		34.5	34.6e	5.1	6.9	5.6
P ¹ -P ⁴		27.1	28.0e	33.2	33e	36.5
M ¹ -M ²		9.7	9.8	25.3	25e	28.5
Skull length		94		9.6	10.1	9.7
				91		97e

Table 15.—Standard statistics for upper teeth and skull length of *Hesperocyon gregarius*.

	N	\bar{X}	S	OR	V
P ¹	AP	9	3.08	0.321	2.7-3.5
	T	2	1.6	0.144	1.5-1.7
P ²	AP	10	4.57	0.6799	3.0-5.4
	T	3	1.8	0.1	1.7-1.9
P ³	AP	9	5.57	0.369	5.0-6.0
	T	3	2.53	0.252	2.3-2.8
P ⁴	AP	17	8.98	0.578	8.0-10.0
	T	12	5.43	0.405	4.9-6.0
M ¹	AP	17	6.42	0.517	5.7-7.5
	T	12	8.85	0.667	8.0-9.8
M ²	AP	16	3.77	0.508	2.8-4.0
	T	12	5.46	0.850	4.0-6.7
P ¹ -M ²		5	31.14	2.87	26.7-33.3
P ¹ -P ⁴		5	23.88	2.26	20.2-25.5
Skull length		11	88.36	5.46	76-96
					6.18

Table 16.—Measurements of lower dentitions of *Hesperocyon*.

<i>H. wilsoni</i> TMM 40504-126 (type)			<i>H. wilsoni</i> <i>H. gregarius</i> TMM 40504-99		<i>H. gregarius</i> AMNH 5297 Logan Co., Colorado		<i>H. gregarius</i> AMNH 63850 Brule Fm., S. Dakota
		right left	right	left	right	left	
P ₂	AP	4.9	5.2	5.3e		4.8	4.9
	T	1.9	2.4			1.7	
P ₃	AP	6.5	6.9	6.7		5.5	5.5
	T	2.4	2.9			2.3	
P ₄	AP	7.2	7.8	7.6	5.8	6.1	6.2
	T	2.8	2.9		2.6	2.8	
M ₁	AP	9.1			8.8e	9.7	8.8
	T	4.7			3.8e	4.3	
M ₂	AP	4.7					4.7
	T	2.9					
M ₃	AP	2.2					2.3
	T	1.9					
P ₁ -M ₃		40.0					35.8
P ₁ -P ₄		24.4	27.0e	26.6e		18.8e	20.2

Table 17.—Standard statistics for lower teeth of *Hesperocyon gregarius*.

		N	\bar{X}	S	OR	V
P ₂	AP	7	4.96	0.140	4.8-5.2	2.82
	T	2	1.75	0.071	1.7-1.8	4.04
P ₃	AP	9	5.51	0.376	5.0-6.1	6.82
	T	3	2.13	0.208	1.9-2.3	9.77
P ₄	AP	12	6.28	0.414	5.8-7.0	6.59
	T	5	2.68	0.277	2.4-3.1	10.35
M ₁	AP	13	9.51	0.557	8.6-10.3	5.86
	T	6	4.27	0.427	3.8-4.8	10.02
M ₂	AP	13	4.93	0.354	4.4-5.6	7.19
	T	9	3.21	0.314	2.8-3.8	9.78
M ₃	AP	4	2.10	0.245	1.8-2.3	11.66
	T	3	1.70	0.265	1.5-2.0	15.56
P ₂ -M ₃		3	35.93	2.003	34.0-38.0	5.58
P ₂ -P ₄		6	20.38	1.288	18.8-21.3	6.32

gregarius. Allowing for distortion, there is little difference between the endocasts of *H. wilsoni* and *H. gregarius* (Radinsky, 1973).

The various cranial foramina are of similar sizes and in the same positions as in *H. gregarius*, as well as can be seen in this specimen. The bullae are apparently a little larger than in *H. gregarius*, but are similar in form and are firmly attached to the skull.

Only right I^1 and left I^{1-2} are preserved. These are smaller than in *H. gregarius*, simple, and equal in size. I^3 was larger, as is shown by its root. The canine is slender like that of *H. gregarius*. There is a diastema of about 4 mm between the canine and P^1 , unlike *H. gregarius* in which this diastema is less than 2 mm. P^1 is identical to that of *H. gregarius*. P^2 is likewise very similar to that of *H. gregarius*, a simple premolar without accessory cusps. P^3 is longer than in any specimen of *H. gregarius* available to me but is otherwise similar. In addition to the paracone, there is a metacone and a small metastyle. The protocone of P^4 is larger than is usual on this tooth in *H. gregarius* and the metastyle appears to be relatively slightly smaller. P^4 is about as close in appearance to that of *Miacis gracilis* (Uinta Formation, Utah, late Eocene) as it is to *Hesperocyon gregarius*, except that like *H. gregarius* it lacks a parastyle and labial cingulum. M^1 is very similar in *H. wilsoni*, *H. gregarius*, and *M. gracilis* in having a large parastyle and stylar cingulum, paracone and metacone about equal in size, small but distinct paraconule and metaconule, large anteriorly placed protocone, and a hypocone developed from the posterior lingual cingulum. The size of M^1 of *H. wilsoni* is close to the top of the range in *H. gregarius*, the hypocone is relatively slightly smaller, and the protocone basin is larger than in *H. gregarius*. The relative sizes of the protocone basins and hypocone are closer to those of *Miacis gracilis*. The M^2 is slightly smaller than the mean for *H. gregarius* (Tables 14-15), and is close in size to that of *M. gracilis*. The M^2 of *H. gregarius* is highly variable in size ($V=15.57$) but fairly constant in the presence and extent of cusps and cingula. *Hesperocyon wilsoni* differs from *H. gregarius* in the relative reduction of the metacone, which is always a distinct cusp in *H. gregarius*, usually only slightly smaller than the paracone. In *H. wilsoni* the metacone is so small as to be almost nonexistent, while the paracone remains large. In this feature it is similar to *M. gracilis*, though that species retains a distinct but very small metacone. *Hesperocyon paterculus* (Matthew, 1903) differs from *H. wilsoni* in the relatively larger M^2 and presence of M^3 , which is also present in *M. gracilis* but absent in *H. wilsoni* and *H. gregarius*.

None of the lower incisors or canines is preserved. In the type of *Hesperocyon gregarius* (Cope, AMNH 5297, the premolars are tightly packed together with no diastemata. Only small spaces are present between premolars of other specimens of this species. However, in *H. wilsoni* (Fig. 33-34) there are definite diastemata between the canine and P^1 , between P^1 and P^2 , and between P^2 and P^3 . As with the skull, the mandible is

more similar to *M. gracilis* than *H. gregarius*. The total length of the lower premolar series in *H. wilsoni* is considerably greater than in *H. gregarius* (Tables 16-17). A Student's "t" test (Simpson et al., 1960, p. 176) performed on the length of P_{1-4} , comparing *H. wilsoni* (2 individuals) to *H. gregarius* (6 individuals), gave a probability that the two samples come from a single population of less than 1 per cent. P^1 is poorly preserved but probably was much like that of *H. gregarius*. P^2 lacks the small paraconid of this tooth in *H. gregarius* and had a smaller hypoconulid. This tooth is the same size in both species. The P^3 of *H. wilsoni* is larger than that of *H. gregarius*, as is P^4 also. P^3 and P^4 differ from each other only in size. Both have a low, rounded paraconid, a tall protoconid, a distinct hypoconid, and a low hypoconid. M^1 differs from the type of *H. gregarius* only in having a taller, more conical protoconid, protoconid-paraconid blade aligned less directly anteroposteriorly, and a smaller entoconid. This tooth is approximately intermediate in morphology between *M. gracilis* and *H. gregarius*. M^2 is smaller than the average in *H. gregarius* and is near the lower end of the range in width (T). The protoconid is taller than the paraconid and the metaconid. The talonid consists of the talonid basin surrounded by a ridgelike hypoconid and a low lingual talonid crest. There is a small anterior labial cingulum. M^3 is a much reduced single rooted version of M^2 . The trigonid and talonid are discernible but tiny, and the only distinct cusp is the protoconid.

Relationships.—*Hesperocyon gregarius*, (Cope, 1873), *H. paterculus* (Matthew, 1903) and *H. wilsoni* n. sp. all have been reported from the Chadronian of North America. *Hesperocyon paterculus* appears to be a valid species, based on specimens from Pipestone Springs and Canyon Ferry Reservoir, Montana (White, 1954), the Toadstool Park area of Nebraska, and Flagstaff Rim, Wyoming. Among its distinguishing features are the relatively large size of M^2 and presence of a small M^3 . *Hesperocyon gregarius* is reported from the Peanut Peak member of the Chadron Formation, South Dakota (Clark et al., 1967) and from Cypress Hills, Saskatchewan (Russell, 1972). The Uinta C species *Miacis gracilis* is structurally very similar to all three Chadronian species of *Hesperocyon*, particularly to *H. wilsoni*. Wilson et al. (1968) listed *Miacis gracilis* as part of the Airstrip local fauna. This listing apparently was based on the type specimen of *H. wilsoni* as a result of its considerable similarity to *M. gracilis* in premolar proportions and in the form of M^2 . Though lacking the attached ossified bulla of *Hesperocyon*, *Miacis gracilis* would have needed little alteration to be classified with the Canidae, and may have been ancestral to *Hesperocyon*. The dental changes needed would have been minor; a reduction of premolars in *H. paterculus* and *H. gregarius*, loss of the tiny M^3 in *H. gregarius* and *H. wilsoni*, increase in size of M^2 in *H. paterculus*, and small changes in the orientation of the protoconid-paraconid shearing blade would have been involved.

For the statistical summary of *Hesperocyon gregarius*

(Tables 15, 17) I have examined and measured the type and several referred specimens from various institutions and localities, all of which are from the Brule Formation or its equivalents in South Dakota, Wyoming, Colorado, and Nebraska. *Hesperocyon lippincottianus* is here treated as a synonym of *H. gregarius*. The coefficients of variation (V) are not particularly high despite the heterogeneity of locality. The AP measurements of lower teeth all have a V well within the limits shown by Gingerich (1974, Text-Fig. 1) to be normal for living populations of a single species. Where possible, identifications were made or checked by comparison to the type. Measurements published by Scott and Jepsen (1936) were also included in the statistical summary.

Family Felidae? or Nimravidae?

genus and species indeterminate

Little Egypt local fauna

Figure 35

Material.—TMM 40840-43, skull fragments including partial premaxillaries and maxillaries with left I^3 , right I^{1-3} , and roots of both canines.

Stratigraphic position.—Upper part of Chambers Formation at Chalk Gap Draw, Vieja Group, Presidio County, Texas.

Age.—Chadronian (early Oligocene).

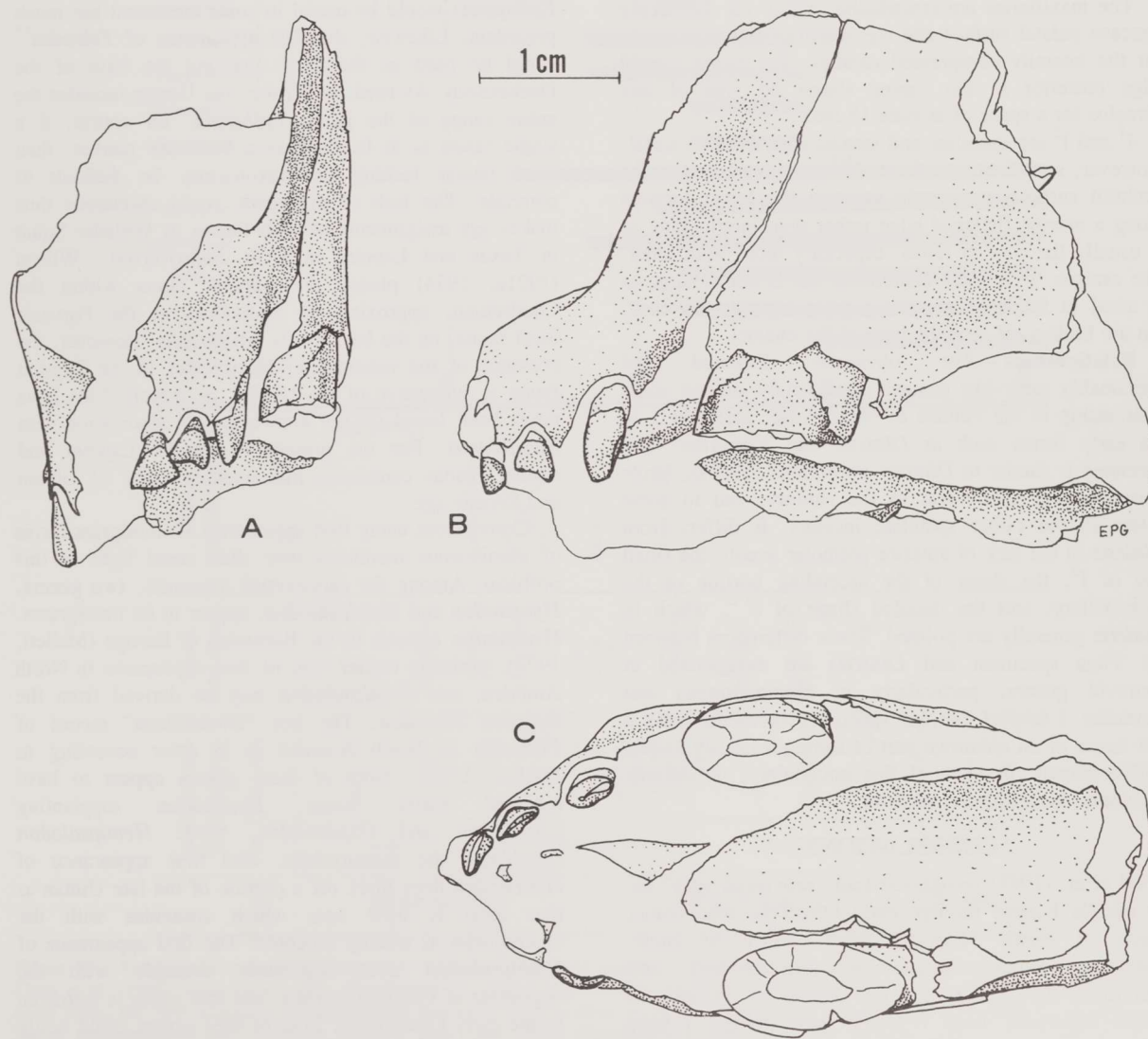


Figure 35.—?Felid, genus and species indeterminate, TMM 40840-43, Little Egypt local fauna. Crushed partial rostrum with incisors and broken canines. A. Anterior view. B. Left lateral view. C. Ventral view. Matrix and broken bone surfaces unshaded.

Description.—The bones are not individually crushed, but have become separated, offset, and forced together.

The premaxillaries are peculiarly shaped. In lateral view, the narrowest preserved part is just posterior to I^3 . The ascending portion is tall and thin, becoming broader dorsoventrally as it ascends. The portion forming the incisor aveoli projects strongly forward, but is narrow laterally. The form of the premaxillary symphysis is not obvious from the exposed bone surfaces. If the bones are separated and restored to a position in which the anteroposterior axes of the canines diverge slightly posteriorly, the anterior surfaces of the premaxillaries seem to have formed an angle or pointed arch at the symphysis, quite unlike the flattened anterior surface seen in Recent cats. There is a deeply indented diastema between the I^3 and the canine, formed largely by the ventrolateral surface of the premaxillary. The premaxillary apparently did not form part of the canine alveolus.

The maxillaries are remarkable mainly for the deeply concave palatal surface and the absence of alveoli except for the laterally compressed canines. The raised ventral edge posterior to the canine shows no sign of any alveolus for a space of at least 15 mm.

I^1 and I^2 are spatulate and smaller than I^3 , as is usual. However, seen from the front, I^{1-2} are very broad at the occlusal surface, apparently meeting the lower incisors along a narrow flattened edge rather than interlocking as is usually the case in felids, especially those with saber-like canines. I^3 is more caniniform but is not as large as is usual in felids. The canines were laterally flattened, but are broken off near the base of the enamel.

Relationships.—The obviously flattened and presumably saber-like canines immediately suggest some relationship to the Felidae or Nimravidae, particularly to the early forms such as *Dinictis* and *Nimravus*. The specimen is similar to *Dinictis squalidens* (Orellan, Brule Formation) in size, form of the canines, and to some extent in the rather spatulate incisors. It differs from *Dinictis* in the lack of anterior premolar aveoli, the small size of I^3 , the shape of the ascending portion of the premaxillary, and the detailed shape of I^{1-2} , which in *Dinictis* generally are pointed. These differences between the Vieja specimen and *Dinictis* are exaggerated in nimravid genera, particularly in *Hoplophoneus* and *Eusmilus*. I suspect that this specimen represents either a new taxon or an unknown part of some previously known catlike animal. In view of this uncertainty, no definite taxonomic assignment is possible.

CORRELATIONS

Wood et al. (1941) recognized four "provincial ages" for the middle Eocene through early Oligocene mammalian faunas of North America, from earliest to latest: Bridgerian, Uintan, Duchesnean (all Eocene), and Chadronian (Oligocene). For this discussion, in order to remain consistent with Wilson's later papers, I have arbitrarily used only three of these names (Bridgerian, Uintan and Chadronian) as advocated by Wilson et al. (1968). Wilson (1977b), p. 33-37 has given in detail

the reasons for avoiding the name "Duchesnean". For any of these names to be useful, they must be capable of definition. Biostratigraphic terminology using concurrent range zones should provide the best definitions and would allow for further subdivision of the "provincial ages"; this subject has been thoroughly discussed by Tedford (1970), Emry (1973, 1981) and Woodburne (1977). The definition of the Chadronian given by Wood et al. (1941) as "the time during which *Mesohippus* and titanotheres co-existed" describes a concurrent range in a broad sense and sets useful boundaries. Neither the Duchesnean nor the Uintan has been defined in such terms; rather, each was defined using an assemblage zone concept which cannot provide sharp boundaries. Since no single biostratigraphic event was used to mark each boundary, it has fallen upon later workers to choose suitable events as have seemed most appropriate. A definition of the base of the Uintan as the first appearance of *Epihippus* (presumably the time at which *Orohippus* evolved into *Epihippus*) would be useful in some areas and has much precedent. Likewise, the first appearance of *Teleodus*** could be used as the event marking the base of the Duchesnean. As used by Wilson, the Uintan includes the entire range of the genus *Epihippus*. Of course, if a single taxon is to be used as a boundary marker, then local faunas lacking this taxon may be difficult to correlate. The lack of diagnostic equid specimens thus makes age assignments of such faunas as Whistler Squat in Texas and Lapoint in Utah controversial. Wilson (1971a, 1974) placed the Lapoint fauna within the Chadronian, approximately equivalent to the Porvenir local fauna, on the basis of its artiodactyls. However, the presence of the mesonychid *Hessolestes* in the Lapoint fauna is suggestive of the Uintan, as mesonychids have never been found (to my knowledge) in association with *Mesohippus*. For the present I consider Lapoint and similar faunas containing mesonychids to be of Uintan and Eocene age.

Correlations using first appearance of immigrant forms of carnivorous mammals may shed some light in this problem. Among the carnivorous mammals, two genera, *Hyaenodon* and *Hemipsalodon*, appear to be immigrants. *Hyaenodon* appears in the Bartonian of Europe (Mellett, 1977), probably earlier than its first appearance in North America, and *Hemipsalodon* may be derived from the Eurasian *Pterodon*. The one "Duchesnean" record of *Pterodon* in North America is in error according to Mellett (1977). Both of these genera appear to have replaced native forms, *Hyaenodon* supplanting *Limnocyon* and *Oxyaenodon*, while *Hemipsalodon* supplanted the mesonychids. The first appearance of *Hyaenodon* does mark off a portion of the late Uintan as that term is used here which coincides with the Duchesnean as usually accepted. The first appearance of *Hemipsalodon* does apparently coincide with the beginning of Chadronian time, and this genus is restricted to the early Chadronian. Both of these genera could easily be placed into a system of concurrent range zones, and can provide secondary criteria for the definition of provincial age boundaries.

* However, see Wilson (1984) for a modification of this view.

** Now *Duchesneodus* Lucas and Schoch (1982).

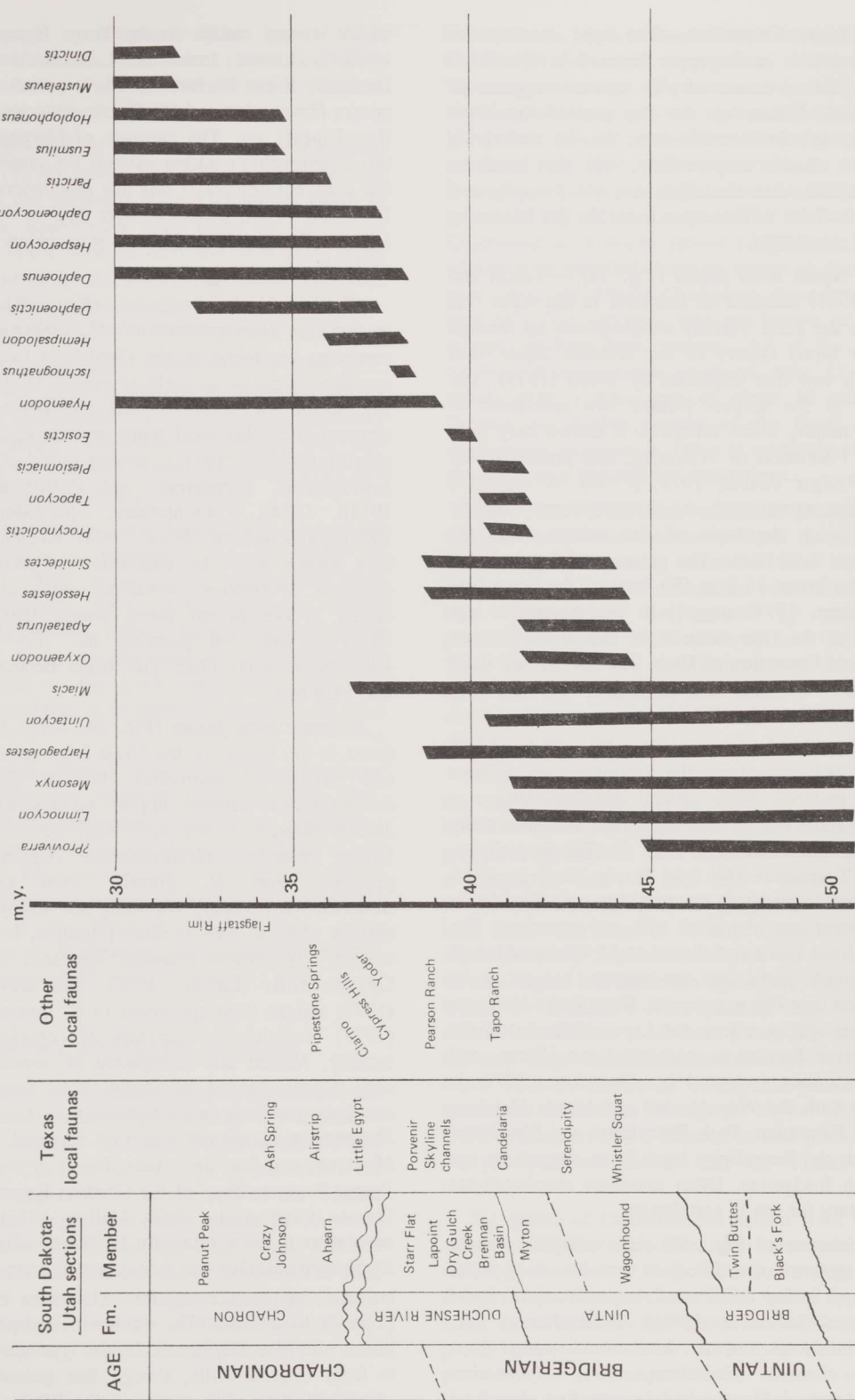


Figure 36.—Stratigraphic ranges of Uintan and Chadronian carnivore genera. Information taken largely from Black and Dawson (1966), Clark et al. (1967), and original data. Correlations of faunas as given here are based on published radiometric dates where possible. In some cases, the first appearance of an apparent immigrant form is used, as in the correlation of Lapoint, Skyline Channels, and Pearson Ranch (*Hyaenodon*), and of Clarno, Cypress Hills, and Yoder (*Hemiposalodon*). Inclined lines between units in the three left-hand columns indicate uncertainty in placement of boundaries relative to the absolute time scale. The double wavy line below the Ahearn member of the Chadron Formation indicates an abrupt geographical shift. Placements of all faunas and generic ranges with respect to each other and to absolute dates are necessarily approximate and subject to revision.

Lower Chisos Formation.—The type locality for *Uintacyon scotti* is in the upper Uinta B at Kennedy's Hole, Utah. The presence of this species suggests an early to middle Uintan age for this part of the lower Chisos Formation. Radiometric dates for the underlying Alamo Creek Basalt vary widely, but the basalt is probably not older than the oldest date (44.3 m.y.), well within the 40-47 M.Y. time span listed for the Uintan by McKenna et al. (1973).

Whistler Squat local fauna (Fig. 36).—Wilson and Schiebout (1981) included all localities in the Agua Fria section from the basal Tertiary conglomerate up through the Whistler Squat Quarry in the Whistler Squat local fauna, which was first described by Wood (1973). The lowest part of the section yielded two specimens of *?Proviverra major*, which otherwise is known only from the Bridger Formation of Wyoming, and probably only the upper Bridger (Gazin, 1976, p. 10). A suggested Bridgerian age agrees with the determination made by Wood (1973) on the basis of the rodents from the Whistler Squat local fauna. The presence of *Leptoreodon marshi* in the lower 15.2 m (50 feet) of the Agua Fria section (Wilson, 1974) suggests a post-Bridgerian age assignment, as the type material of this species comes from the Uinta Formation of Utah. The radiometric dates of 48.6 to 42.9 m.y. at Whistler Squat (Wilson, 1980) also are compatible with a Uintan age assignment.

Serendipity local fauna (Fig. 36).—Wilson and Schiebout (1981) considered the Serendipity local fauna to include material from several localities above a prominent marker bed in the Agua Fria area informally known as the Strawberry tuff (Fig. 4). The Serendipity, Unio Cliff, Titanotheres Hill, and Purple Bench localities have furnished fragmentary material, but only *Simidectes* and *Hessolestes* are identified with any certainty. The Serendipity local fauna is believed to be Uintan although the whole fauna, particularly the rodents, has yet to be studied. Other than this occurrence, *Hessolestes* is known only from one specimen from the Lapoint Member of the Duchesne River Formation, possibly latest Uintan, and *Simidectes magnus* (reported by Gustafson, 1979) is known from both the Wagonhound and Myton Members of the Uinta Formation. Both *Hessolestes* and *Simidectes magnus* from the Serendipity local fauna suggest an age younger than Bridgerian. Other carnivore specimens are too fragmentary for use in correlation.

Skyline channels (Fig. 36).—An adapid primate (*Mahgarita stevensi*) was described from this local fauna by Wilson and Szalay (1976) and *Amyndontopsis bodei* by Wilson and Schiebout (1981). *Hyaenodon* cf. *H. vetus* and *Simidectes magnus*, have been reported from the Skyline channels (Gustafson, 1979). *Hyaenodon vetus* and *Amyndontopsis bodei* were first described from the Pearson Ranch local fauna, Sespe Formation, California, considered by Stock (1948) to be of late Eocene age. *Hyaenodon* occurs there with *Simidectes merriami* Stock, in the only other known association of *Simidectes* and *Hyaenodon*. A *Hyaenodon* specimen referred to *Hyaenodon* cf. *H. vetus* by Mellett, (1977)

which is very similar to the Texas *Hyaenodon* cf. *H. vetus* is known from the Lapoint Member of the Duchesne River Formation. The association of the two genera *Hyaenodon* and *Simidectes* suggests a late Eocene (late Uintan) age. The presence of *Harpagolestes* sp. in this stratigraphic position extends the range of the genus but does not contradict this age assignment. Wilson and Schiebout (1981) report a K/Ar date of 41.7 ± 1.6 m.y. from a biotite bearing ash just below the Skyline channels.

Candelaria local fauna (Fig. 36).—The large mesonychid *Harpagolestes* cf. *H. uintensis* is the only carnivore yet found in the Candelaria local fauna. The specimen suggests an early to middle Uintan age, but is not useful for more detailed correlation. Other taxa reported from this local fauna include *Epihippus* cf. *E. gracilis* (Forsten, 1971a), several artiodactyls, including *Leptoreodon*, *Toromeryx*, and *Protoreodon* (Wilson, 1971b, 1974), a brontothere, *Sthenodectes* (Wilson, 1977a), and rodents (Wood, 1974). Evidence from these taxa agrees with the conclusion of Wood that "the Colmena [Formation containing the Candelaria local fauna] is post-Myton [local fauna, Uinta Formation, Utah] in age, but probably not very much later." Radiometric dates place this fauna between $40 \pm$ m.y. and 38.6 m.y.

Porvenir local fauna (Fig. 36).—The Porvenir local fauna is the richest of the Vieja local faunas in number and variety of carnivores. Of the Porvenir taxa, *Ischnognathus savagei* supplies no data for correlation. *Miacis australis* is not much more advanced than some Uintan miacids. *Hemipsalodon viejaensis* is more primitive than *H. grandis* from Cypress Hill, Saskatchewan, Yoder, Wyoming and Clarno, Oregon. It may be older as well as more primitive, or a geographic variant. *Hyaenodon crucians* has been reported from Cypress Hills (Lambe, 1908), and although Russell (1972) assigns these specimens to *H. mustelinus*, Mellett (1977) continues to recognize *H. crucians* from this locality. Mellett also recognized *H. crucians* from the early Chadronian of Wyoming. Most specimens of *H. crucians* are from late Chadronian or Orellan deposits. *Hyaenodon montanus* was first reported from Toston, Montana, and has since been found in the Ahearn and Peanut Peak members of the Chadron Formation in South Dakota (Clark et al., 1967). Mellett (1977) considers *H. montanus* to be a primarily middle Chadronian species. *Daphoenus lambei* was first reported from Cypress Hills but has not been recognized elsewhere except in the Porvenir local fauna. The unidentified daphoenine looks like a primitive *Daphoenictis*, the type species of which is from Cypress Hills, though this genus itself is not identifiable here. Other taxa in the Porvenir local fauna include *Poabromylus kayi*, the type of which is from the Lapoint Member and referred specimens of which have been found in early Chadronian localities in Wyoming and South Dakota, *Oromeryx*, *Hidrosotherium*, *Hendryomeryx defordi*, *Protoreodon*, *Agriochœrus*, merycoidodonts, a primitive *Mesohippus* (*M. texanus*), *Haplohip-*

pus, *Brachyhyops wyomingensis* (also known from Lapoint), *Archeotherium*, insectivores (Novacek, 1976), brontotheres including *Teleodus* and *Menodus* (Wilson, 1977), and rodents (Wood, 1974).

The data provided by the carnivores are consistent with Wood's (1974) conclusion that the Porvenir local fauna may be the earliest known Chadronian fauna in North America. Radiometric dates place the age of the Porvenir local fauna between 36.5 and 38.6 m.y., older than the dates given for the Clarno local fauna (36.4 m.y. or older) or the White River Formation at Flagstaff Rim, Wyoming (Emry, 1973; an oldest date of 35.7 m.y.).

Little Egypt Local Fauna (Fig. 36).—Of these taxa, the felid? rostrum gives no correlative data, and *Miacis cognitus* is an anachronism, a late surviving, relatively unspecialized miacid. *Daphoenocyon dodgei* was first described from the Chadron Formation in Nebraska, and is common at Pipestone Springs, Montana.

A correlation of the Little Egypt local fauna with Pipestone Springs is reasonable on the basis of *Daphoenocyon*. This agrees with information from insectivores (Novacek, 1976), rodents (Woods, 1974), and artiodactyls (Wilson, 1971a). Time constraints placed by radiometric dates are the same as for the Porvenir local fauna, but as the Little Egypt local fauna is stratigraphically higher it is probably closer to the 36.5 m.y. figure.

Airstrip Local Fauna (Fig. 36).—The specimen referred to *Hyaenodon crucians* gives no usable data. The three skulls of *Hyaenodon raineyi* n. sp. represent a species unknown elsewhere. *Hesperocyon wilsoni* n. sp. seems to have been derived from the Uintan *Miacis gracilis*, and its record here may be the earliest yet for *Hesperocyon*. It is, however, distinct from other Chadronian species. Radiometric dates limit the Airstrip local fauna to between 32.3 and 37.5 m.y.

SUMMARY AND CONCLUSIONS

The carnivore fossils of the three west Texas sections are arranged in a stratigraphic sequence (Fig. 36) similar to that recorded elsewhere in North America (Black and Dawson, 1966; Clark et al., 1967). In particular, the mesonychids disappear about at the end of the Uintan, the creodonts are reduced to three genera in the early Chadronian and to one in the late Chadronian, the true carnivores increase in numbers and diversity in the early Chadronian, the miacids (also Order Carnivora) dwindle though they last well into the early Chadronian, and finally extant families appear, though clearly not until well into the Chadronian.

The quality of the carnivore record in west Texas is still relatively poor. There are approximately 20 genera of carnivores living in North America today, some of which include several species. In any one area of the continent, especially in middle latitudes, it is common to find from ten to twenty carnivore species, usually representing almost as many genera, present within

historic times. A few fossil faunas, for instance that of the Bridger Formation (Bridgerian, middle Eocene) of Wyoming with about 15 genera and the Brule Formation (Orellan, middle Oligocene) of South Dakota with about 17 genera, appear to reflect a similar diversity of carnivore taxa. The total carnivore fauna of the Uinta Formation of Utah has slightly fewer taxa (from 9 to 12 genera, if Fig. 36 is accurate). The same is true of the Chadronian as a whole (about 12 genera). However, a minimum in recorded diversity occurs at about 39 to 40 m.y., near the Uintan-Chadronian boundary, at which time only five carnivore taxa are known or confidently inferred to have been present. All of the west Texas localities together have produced only 12 identifiable genera from a time span of about 10 million years. Despite the relative paucity of the fossil record, the stratigraphic sequence in Texas is relatively complete and can serve as a standard for comparison.

The Uintan-Chadronian transition produced marked changes in the carnivorous mammal faunas in North America. It is becoming clear that these changes were complex. Few ancestor-descendant relationships have yet been documented. Replacement by unrelated and probably immigrant forms seems to have been common. There are still so few specimens known from this time span that any new finds are likely to produce major changes in our perception of taxonomic and phylogenetic patterns.

Three genera of mesonychids, *Mesonyx*, *Harpagolestes*, and *Hessolestes*, are known from the Uintan. The latter two have been reported from Texas. *Hessolestes* is present in the Lapoint local fauna, stratigraphically above a radiometric date of 39.3 m.y. (McDowell et al., 1973), and *Harpagolestes* is present in the Candelaria local fauna with dates of 40 m.y. below and 38.6 m.y. above and in the Skyline local fauna. If, as I suspect, the 40 m.y. figure is a minimum age for the Candelaria local fauna, the Candelaria *Harpagolestes* may be somewhat older. Nevertheless, at all three places the mesonychid is the only large carnivorous mammal known in a small fauna. Thus the number of mesonychid genera remains at three from the Bridger through the Myton Member of the Uinta Formation, and is reduced to two (possibly one) in the poorly known faunas near the Uintan-Chadronian boundary.

Six genera of Creodonta are known from the Bridger (Gazin, 1976) but only three, all limnocyonids, survive well into the Uintan. Only *?Proviverra major* has been found in the Whistler Squat local fauna, apparently the latest occurrence of this genus in North America. A poorly preserved toothless skull from Unio Cliff, also part of the Serendipity local fauna, may be a limnocyonid, but comparisons sufficient to prove this have not been made. The evidence suggests that the reduction of native creodonts began early in the Uintan and was complete before the beginning of the Chadronian. Both *Hyaenodon* and *Hemipsalodon*, the common Oligocene creodonts, appear to be specialized Eurasian immigrants. *Hemipsalodon* may have taken over

the large-carnivore niches vacated by the mesonychids. In turn, *Hemipsalodon* disappears with the advent of large species of *Hyaenodon*.

Among the Miacidae, 5 genera are listed from the Uintan by Black and Dawson (1966), a reduction of 1 genus from the Bridgerian. Many of these are small animals, generally poorly known, and the existence of small miacids in the Texas Uintan is only suggested by some unassignable fragments from the Whistler Squat local fauna. *Uintacyon* evidently was common in the early Uintan, and both large (*U. scotti*) and small (*U. acutus*) species are present in the Uinta section. *Uintacyon scotti* is present in the Chisos section and a species of similar size is present in the Whistler Squat local fauna. The genus *Tapocyon* seems to have developed from *Uintacyon* and to have been widespread (occurrences in California, Wyoming, and Utah) in part of the Uintan. The genus *Miacis* was also present, but except for the type of *M. gracilis*, a possible canid ancestor, the genus is represented by only very poor specimens from the Uintan. The occurrence of *Miacis cognitus* in the Little Egypt local fauna is the latest record of a miacid from North America.

Daphoenines certainly were present in the late Eocene. *Daphoenus demilo*, from the late Eocene of Badwater Creek, Wyoming, has been described by Dawson (1980). *Eosictis affinovi*, a supposed late Eocene felid, bears a canine tooth almost identical to that of the daphoenine

Daphoenocyon as well as similarly reduced and crowded premolars. This specimen may represent the earliest occurrence of *Daphoenocyon*. Three genera are present in the Chadronian, of which *Daphoenocyon* is the most common (Hunt, 1974b). *Daphoenus* occurs earlier (at least in the Texas sections), and becomes the common genus in the Orellan, but is not well known in the Chadronian. A third genus, *Daphoenictis* (Hunt, 1974b) is distinct and specialized in the Chadronian.

The earliest canid in the Texas sections is *Hesperocyon wilsoni*, in the Airstrip local fauna. It was apparently a contemporary of *H. paterculus*. *Hesperocyon gregarius* has been reported from Cypress Hills, but is most common in the Orellan. The differentiation of the Canidae very likely began in the Chadronian, but our knowledge of the species is incomplete.

The origins of the Felidae and Nimravidae still are uncertain. The earliest good record of nimravids is in the Chadronian White River Formation at Flagstaff Rim, Wyoming (Emry, 1973), but these specimens have not been studied. The fragmentary specimen from the Little Egypt local fauna may be earlier, but I am not certain what it is. *Eosictis* from the Brennan Basin Member of the Duchesne River Formation has a canine much like that of the amphicyonid *Daphoenocyon* and is probably not a felid. Both felids and nimravids may be Eurasian immigrants, as were the Oligocene creodonts.

REFERENCES

- Black, C.C. and M.R. Dawson, 1966. A review of late Eocene mammalian faunas from North America. *Amer. J. Sci.*, 264:321-349.
- Bowdich, T.E., 1821. An analysis of the natural classifications of Mammalia for the use of students and travellers. Paris, J. Smith, 115 p.
- Clark, J., J. Beerbower and K. Kietzke, 1967. Oligocene sedimentation, stratigraphy, paleoecology and paleoclimatology in the Big Badlands of South Dakota. *Fieldiana: Geol. Mem.* 5, 158 p.
- Cope, E.D., 1872. Third account of new Vertebrata from the Bridger Eocene of Wyoming Territory. *Paleontol. Bull.* 3; reprinted in *Proc. Amer. Phil. Soc.*, 12:469-472 (1873).
- , 1873. Third notice of extinct Vertebrata from the Tertiary of the Plains. *Palaeontol. Bull.*, 16:1-8.
- , 1875. On the supposed Carnivora of the Eocene of the Rocky Mountains. *Paleontol. Bull.*, 20:1-4.
- , 1880. On the genera of the Creodonta. *Proc. Amer. Phil. Soc.*, 19:76-82.
- , 1881. A new type of Perissodactyla. *Amer. Nat.*, 15:1017-1018.
- Davis, D., 1964. The giant panda: A study of evolutionary mechanisms. *Fieldiana: Zool. Mem.* 3, 339 p.
- Dawson, M.R., 1980. Paleontology and Geology of the Badwater Creek area, central Wyoming: Part 20, The late Eocene Creodonta and Carnivora. *Ann. Carnegie Mus.*, 49(4):79-91.
- DeFord, R.K., 1958. Tertiary formations of Rim Rock Country, Presidio County, Trans-Pecos Texas. *Texas J. Sci.*, 10(1), 37 p.
- Douglass, E., 1901. Fossil mammalia of the White River Beds of Montana. *Trans. Am. Phil. Soc.*, 20:237-279.
- Emry, R.J., 1973. Stratigraphy and preliminary biostratigraphy of the Flagstaff Rim area, Natrona County, Wyoming. *Smithson. Contrib. Paleobiol.*, 18, 43 p.
- , 1981. Additions to the mammalian fauna of the type Duchesnean, with comments on the status of the Duchesnean "Age". *J. Paleontol.*, 55(3):563-570.
- Evernden, J.F., D.E. Savage, G.H. Curtis and G.T. James, 1964. Potassium-argon dates and the Cenozoic mammalian chronology of North America. *Amer. J. Sci.*, 262:145-198.
- Forsten, A., 1971a. *Epihippus* from the Vieja Group, Trans-Pecos Texas. *Pearce-Sellards Ser.*, 18:1-5.
- , 1971b. Comparisons of populations of *Mesohippus* from Trans-Pecos Texas and the Big Badlands, South Dakota. *Pearce-Sellards Ser.*, 18:12-15.
- Gazin, C.L., 1976. Mammalian faunal zones of the Bridger middle Eocene. *Smithson. Contrib. Paleobiol.*, 26, 25 p.
- Gill, T., 1872. Arrangement of the families of mammals with analytical tables. *Smithson. Misc. Coll.*, 11(1), 98 p.
- Gingerich, P.D., 1974. Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. *J. Paleontol.*, 48(5):895-903.
- Goldich, S.S. and A.A. Elms, 1949. Stratigraphy and petrography of the Buck Hill Quadrangle, Texas. *Bull. Geol. Soc. Amer.*, 60:1133-1183.
- Gray, J.E., 1821. On the natural arrangement of vertebrate animals. *London Med. Reposit.*, 15(1):296-310.
- Gregory, W.K. and M. Hellman, 1939. On the evolution and major classification of the civets (Viverridae) and allied fossil and Recent Carnivora: a phylogenetic study of the skull and dentition. *Proc. Amer. Phil. Soc.*, 81:309-392.
- Gustafson, E.P., 1977. Carnivorous mammals of the late Eocene and early Oligocene of Trans-Pecos Texas. Dissertation, Univ. Texas at Austin, 209 p.
- , 1979. Early Tertiary vertebrate faunas Big Bend area Trans-Pecos Texas: *Simidectes* (Mammalia, Insectivora). *Pearce-Sellards Ser.*, 31, 9 p.
- Harris, J.M., 1967. *Toxotherium* (Mammalia, Rhinocerotidae) from western Jeff Davis County, Texas. *Pearce-Sellards Ser.*, 9, 7 p.
- Harris, J.M. and A.E. Wood, 1969. A new genus of eomyid rodent from the Oligocene Ash Spring local fauna of Trans-Pecos Texas. *Pearce-Sellards Ser.*, 14, 7 p.
- Hough, J.R., 1948. A systematic revision of *Daphoenus* and some allied genera. *J. Paleontol.*, 22:573-600.
- Hunt, R.M., Jr., 1974a. The auditory bulla in Carnivora: an anatomical basis for reappraisal of carnivore evolution. *J. Morph.*, 143:21-76.
- , 1974b. *Daphoenictis*, a cat-like carnivore (Mammalia, Amphicyonidae) from the Oligocene of North America. *J. Paleontol.*, 48:1030-1047.
- Laizer, L. de, and de Parieu, 1838. Description et détermination d'une mâchoire fossile, *Hyaenodon leptorhynchus*. *C.R. Acad. Sci. Paris*, 7:442.
- Lambe, L.M., 1908. The Vertebrata of the Oligocene of the Cypress Hills, Saskatchewan. *Canad. Dept. Mines, Geol. Surv. Branch, Contrib. Canad. Paleontol.*, 3 (Quarto), 65 p.
- Leidy, J., 1853. Not titled. *Proc. Acad. Nat. Sci. Phila.*, 1853:392-394.
- , 1869. The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a

- synopsis of the mammalian remains of North America. J. Acad. Nat. Sci. Phila., ser. 2, 7:1-472.
- , 1872. Remarks on fossils from Wyoming. Proc. Acad. Nat. Sci. Phila., 1872:276-277.
- Lucas, S.G., and R.M. Schoch, 1982. *Duchesneodus*, a new name for some titanotheres (Perissodactyla, Brontotheriidae) from the late Eocene of Western North America. J. Paleontol., 56(4):1018-1023.
- MacIntyre, G.T., 1966. The Miacidae (Mammalia, Carnivora) part I. The systematics of *Ictidopappus* and *Protictis*. Bull. Amer. Mus. Nat. Hist., 131:115-230.
- Matthew, W.D., 1903. The fauna of the *Titanotherium* beds, at Pipestone Springs, Montana. Bull. Amer. Mus. Nat. Hist., 19:197-226.
- , 1909. The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. Mem. Amer. Mus. Nat. Hist., 9:291-567.
- Maxwell, R.A., 1968. The Big Bend of the Rio Grande. Univ. Texas Bur. Econ. Geol. Guidebook 7, 138 p.
- Maxwell, R.A., J.T. Lonsdale, R.T. Hazzard and J.A. Wilson, 1967. Geology of Big Bend National Park. Univ. Tex. Bur. Econ. Geol. Publ. 6711, 320 p.
- McDowell, F.W., 1979. Potassium-argon dating in the Trans-Pecos volcanic field, *In* Walton, A.W., and C.D. Henry, *editors*, Cenozoic geology of the Trans-Pecos volcanic field: Texas Bur. Econ. Geol. Guidebook 19, 10-18.
- McDowell, F.W., J.A. Wilson and John Clark, 1973. K-Ar dates for biotite from two paleontologically significant localities: Duchesne River Formation, Utah and Chadron Formation, South Dakota. Isochron/West 7, 11-12.
- McGrew, P.O., 1953. A new and primitive Early Oligocene horse from Trans-Pecos Texas. Fieldiana: Geol., 10:167-171.
- , 1971. *Mesohippus* from the Vieja Group, Trans-Pecos Texas. Pearce-Sellards Ser., 18:6-11.
- McKenna, M.C., D.E. Russell, R.M. West, C.C. Black, W.D. Turnbull, M.R. Dawson and J.A. Lillegraven, 1973. K/Ar recalibration of Eocene North American land-mammal "ages" and European ages. Abstr. Prog., Geol. Soc. Amer. Ann. Meeting, Dallas, Texas.
- Mellet, J.S., 1969. A skull of *Hemipsalodon* (Mammalia, Deltatheridia) from the Clarno Formation of Oregon. Amer. Mus. Novit., 2387, 19 p.
- , 1977. Paleobiology of North American *Hyaenodon* (Mammalia, Creodonta). Contributions to Vertebrate Evolution, vol. 1, S. Karger, New York, N.Y., 134 p.
- Merriam, C.H., 1918. Review of the grizzly and big brown bears of North America. North American Fauna, 41, 136 p.
- Miller, M.E., G.C. Christensen and H.E. Evans, 1964. Anatomy of the dog. W.B. Saunders Co., Philadelphia, 941 p.
- Moon, C.G., 1953. Geology of Agua Fria Quadrangle, Brewster County, Texas. Geol. Soc. Amer. Bull., 61:151-196.
- Novacek, M.J., 1976. Early Tertiary vertebrate faunas, Vieja Group, Trans-Pecos Texas: Insectivora. Pearce-Sellards Ser., 23, 17 p.
- Osborn, H.F., 1895. Fossil mammals of the Uinta Basin. Bull. Amer. Mus. Nat. Hist., 7:71-105.
- , 1910. The Age of Mammals in Europe, Asia and North America. MacMillan Co., New York, 635 p.
- Peterson, O.A., 1919. Report upon the material discovered in the upper Eocene of the Uinta Basin by Earl Douglass in the years 1908-1909, and by O.A. Peterson in 1912. Ann. Carnegie Mus., 12:40-168.
- , 1931a. New mesonychids from the Uinta. Ann. Carnegie Mus., 20:333-339.
- , 1931b. New species from the Oligocene of the Uinta. Ann. Carnegie Mus., 21:61-78.
- Piveteau, J., 1935. Etudes sur quelques crèodontes des Phosphorites de Quercy. Ann. Paleontol., 24:75-95.
- , 1962. L'encephale de *Viverrarus angustidens*, Miacidè des phosphorites du Quercy. Ann. Paleontol., 48:163-175.
- Radinsky, L.B., 1969. Outlines of canid and felid brain evolution. Ann. New York Acad. Sci., 167(1):277-288.
- , 1971. An example of parallelism in carnivore brain evolution. Evolution, 25(3):518-522.
- , 1973. Evolution of the canid brain. Brain, Behavior and Evolution, 7:169-202.
- Romer, A.S., 1966. Vertebrate Paleontology. Univ. Chicago Press, Chicago, 3rd Ed., 468 p.
- , 1970. The vertebrate body. W.B. Saunders Co., Philadelphia, 4th Ed., 601 p.
- Russell, L.S., 1934. Revision of the lower Oligocene vertebrate fauna of the Cypress Hills Saskatchewan. Trans. Roy. Canad. Inst., 20(1):49-67.
- , 1972. Tertiary mammals of Saskatchewan. Part II: The Oligocene fauna, non-ungulate orders. Life Sci. Contrib., Roy. Ont. Mus. 84, 97 p.
- Rutimeyer, L., 1862. Eocene Säugethiere aus dem Gebiet des schweizerischen Jura. Allg. Schweizerische Gesell., neue Denkschrifte, 19:1-98.
- Savage, R.J.G., 1965. Fossil mammals of Africa: 19. The Miocene Carnivora of East Africa. Bull. British Mus. (Nat. Hist.): Geol., 10(8):239-316.
- Schiebout, J.A., 1974. Vertebrate Paleontology and Paleocology of Paleocene Black Peaks Formation, Big Bend National Park, Texas. Texas Mem. Mus. Bull., 24, 88 p.

- Schlosser, M., 1886. Über das Verhältnis der Cope'schen Creodonta zu den übrigen Fleischfressern. *Morph. Jahrb.*, 18:287-294.
- Schlaikjer, E.M., 1935. Contributions to the stratigraphy and paleontology of the Goshute Hole Area, Wyoming. III. A new basal Oligocene formation. *Bull. Mus. Comp. Zool. Harvard*, 76:71-93.
- Scott, W.B., 1888. On some new and little known creodonts. *J. Acad. Nat. Sci. Phila.*, 9:155-185.
- , 1890. The dogs of the American Miocene. *Princeton Coll. Bull.*, 2:37-39.
- , 1898. Notes on the Canidae of the White River Oligocene. *Trans. Amer. Phil. Soc.*, n.h5, 19:325-415.
- , 1945. The mammalian fauna of the Duchesne River Oligocene. *Trans. Amer. Phil. Soc.*, n.h5, 34, pt. 3:209-252.
- Scott, W.B., and Jepsen, 1936. The mammalian fauna of the White River Oligocene, Part I. Insectivora and Carnivora. *Trans. Amer. Phil. Soc.*, n.h5, 28(1), 153 p.
- Scott, W.B. and H.F. Osborn, 1889. The Mammalia of the Uinta Formation. *Trans. Amer. Phil. Soc.*, 16:461-572.
- Simpson, G.G., 1931. A new classification of mammals. *Bull. Amer. Mus. Nat. Hist.*, 59:259-293.
- , 1945. The principles of classification and a classification of mammals. *Amer. Mus. Nat. Hist. Bull.*, 85, 350 p.
- Simpson, G.G., Ann Roe and R.C. Lewontin, 1960. *Quantitative Zoology*, rev. ed., Harcourt, Brace and World, N.Y., Chicago, vii + 440 p.
- Stevens, J.B., 1969. Geology of the Castolon area, Big Bend National Park, Brewster County, Texas. Dissertation, Univ. Texas, Austin, 129 p.
- Stevens, J.B., M.S. Stevens and J.A. Wilson, 1975. Stratigraphy of Pruett and Duff Formations, Agua Fria and Tascotal Mesa Quadrangles, Brewster County, Texas. *Abstr. Prog., South-Central Section, Geol. Soc. Amer.*, 237.
- Stevens, J.B., M.S. Stevens and J.A. Wilson, 1984. Devil's Graveyard Formation (new), Eocene and Oligocene age, Trans-Pecos Texas. *Tex. Mem. Mus. Bull.* 32:1-21.
- Stevens, M.S., J.B. Stevens and M.R. Dawson, 1969. New early Miocene formation and vertebrate local fauna, Big Bend National Park, Brewster County, Texas. *Pearce-Sellards Ser.*, 15, 53 p.
- Stock, C., 1933a. Hyaeodontidae of the upper Eocene of California. *Proc. Natl. Acad. Sci.*, 19:434-440.
- , 1933b. A miacid from the Sespe upper Eocene, California. *Proc. Natl. Acad. Sci.*, 19:481-486.
- , 1948. Pushing back the history of land mammals in western North America. *Bull. Geol. Soc. Amer.*, 59:327-332.
- Stovall, J.W., 1949. Chadron vertebrate fossils from below the Rim Rock of Presidio County, Texas. *Amer. J. Sci.*, 246:78-95.
- Swanson, D.A. and P.T. Robinson, 1968. Base of the John Day Formation in and near the Horse Heaven mining district, north-central Oregon. *U.S. Geol. Surv. Prof. Paper*, 600-D:D154-161.
- Szalay, F.S., 1969a. Mixodectidae, Microsyopidae, and the Insectivore-Primate transition. *Bull. Amer. Mus. Nat. Hist.*, 140(4):195-330.
- , 1969b. Origin and evolution of function of the mesonychid condylarth feeding mechanism. *Evolution*, 23:703-720.
- Szalay, F.S. and S.J. Gould, 1966. Asiatic Mesonychidae (Mammalia, Condylarthra). *Bull. Amer. Mus. Nat. Hist.*, 132(2):127-174.
- Tedford, R.H., 1970. Principles and practices of mammalian geochronology in North America. *Proc. North American Paleontological Convention*, 1969:666-703.
- Thorpe, M.R., 1923. Notes on the Bridger (Eocene) Carnivora. *Amer. J. Sci.*, ser. 5, 5:23-39.
- Trouessart, E.L., 1885. Catalogue des mammifères vivants et fossiles. *Ordre des Carnivores. Bull. Soc. Etudes Sci. Angers*, suppl. to v. 14 of year 1884:1-108.
- van der Klaauw, C.J., 1931. The auditory bulla in some fossil mammals. *Bull. Amer. Mus. Nat. Hist.*, 52:1-352.
- Van Valen, Leigh, 1965. Some European Proviverrini (Mammalia, Deltatheridia). *Paleontology*, 8:638-665.
- , 1966. Deltatheridia, a new order of mammals. *Bull. Amer. Mus. Nat. Hist.*, 132:1-143.
- , 1967. New Paleocene insectivores and insectivore classification. *Bull. Amer. Mus. Nat. Hist.*, 135(5):217-284.
- , 1974. *Deltatheridium* and marsupials. *Nature*, 248:165-166.
- Walton, A.W., 1972. Sedimentary petrology and zeolitic diagenesis of the Vieja Group (Eocene-Oligocene), Presidio County, Texas. Dissertation, Univ. Texas, Austin, 264 p.
- , 1977. Petrology of volcanic sedimentary rocks, Vieja Group, Southern Rim Rock Country, Trans-Pecos Texas. *J. Sed. Pet.*, 47(1):137-157.
- West, R.M., 1982. Fossil mammals from the lower Buck Hill Group, Eocene of Trans-Pecos Texas: Marsupicarnivora, Primates, Taeniodonta, Condylarthra, bunodont Artiodactyla and Dinocerata. *Pearce-Sellards Ser.*, 35, 20 p.
- White, T.E., 1954. Preliminary analysis of the fossil vertebrates of the Canyon Ferry Reservoir area. *Proc. U.S. Natl. Mus.*, 103(3326):395-438.
- Wilson, J.A., 1965. Cenozoic history of the Big Bend area, west Texas. In *Geology of the Big Bend area, Texas, Field trip guidebook with road log and papers on natural history of the area*. West Texas Geol. Soc., 65-51:34-36.
- , 1966. A new primate from the earliest Oligocene, West Texas, preliminary report. *Folia Primatol.*, 4:227-248.

- _____, 1967. Early Tertiary mammals. *In* Maxwell, R.A., J.T. Lonsdale, R.T. Hazzard and J.A. Wilson: Geology of Big Bend Nat. Park, Univ. Tex. Bur. Econ. Geol. Publ., 6711:157-169.
- _____, 1971a. Early Tertiary vertebrate faunas, Vieja Group, Trans-Pecos Texas: Entelodontidae. Pearce-Sellards Ser., 17, 17 p.
- _____, 1971b. Early Tertiary vertebrate faunas, Vieja Group, Trans-Pecos Texas: Agriochoeridae and Merycoidodontidae. Texas Mem. Mus. Bull., 18, 83 p.
- _____, 1972. Vertebrate biostratigraphy of Trans-Pecos Texas and northern Mexico in the geologic framework of the Chihuahua tectonic belt. West Texas Geol. Soc., R.K. DeFord Symposium, 157-166.
- _____, 1974. Early Tertiary faunas, Vieja Group and Buck Hill Group, Trans-Pecos Texas: Protoceratidae, Camelidae, Hypertragulidae. Texas Mem. Mus. Bull., 23, 34 p.
- _____, 1977a. Early Tertiary vertebrate faunas, Big Bend area Trans-Pecos Texas: Brontotheriidae. Pearce-Sellards Ser., 25, 17 p.
- _____, 1977b. Stratigraphic Occurrence and Correlation of Early Tertiary Vertebrate Faunas, Trans-Pecos Texas, Part 1: Vieja Area. Texas Mem. Mus. Bull., 25, 42 p.
- _____, 1980. Geochronology of the Trans-Pecos volcanic field. New Mexico Geol. Soc. Guidebook, 31st Field Conf., Trans-Pecos Region, 205-211.
- _____, 1984. Vertebrate faunas 49 to 36 million years ago and additions to the species of *Leptoreodon* (Mammalia, Artiodactyla) found in Texas. J. Vert. Paleontol., 4(2):199-207.
- Wilson, J.A. and J.A. Schiebout, 1981. Early Tertiary vertebrate faunas, Trans-Pecos Texas: Amynodontidae. Pearce-Sellards Ser., 33, 62 p.
- _____, 1984. Early Tertiary vertebrate faunas, Trans-Pecos Texas: Ceratomorpha less Amynodontidae. Pearce-Sellards Ser., 39, 47 p.
- Woodburne, M.O., 1977. Definition and characterization in mammalian chronostratigraphy. J. Paleontol., 51:220-234.
- Wortman, J.L., 1901-1902. Studies of Eocene Mammalia in the Marsh collection. I. Carnivora. Amer. J. Sci., ser. 4; 11:333-348, 437-450; 12:143-154, 196-206, 281-296, 377-382, 421-432; 13:39-46, 115-128, 197-206, 433-448; 14:17-23.
- Wortman, J.L. and W.D. Matthew, 1899. The ancestry of certain members of the Canidae, the Viverridae and Procyonidae. Bull. Amer. Mus. Nat. Hist., 12:109-139.

TEXAS MEMORIAL MUSEUM
The University of Texas at Austin
2400 Trinity, Austin, Texas 78705