# THE CLARKFORKIAN LAND-MAMMAL AGE AND MAMMALIAN FAUNAL COMPOSITION ACROSS THE PALEOCENE-EOCENE BOUNDARY

KENNETH D. ROSE

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Frontispiece: Badlands at the head of Big Sand Coulee in the Clark's Fork Basin, Wyoming. Photograph taken from the west edge of Polecat Bench looking toward the southwest, with Heart Mountain and the snow covered Absaroka Range in the background. Sedimentary rocks exposed in the foreground are middle and late Clarkforkian in age.

# THE CLARKFORKIAN LAND-MAMMAL AGE AND MAMMALIAN FAUNAL COMPOSITION ACROSS THE PALEOCENE-EOCENE BOUNDARY

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Dedicated to the Memory of
PROFESSOR BRYAN PATTERSON
1909 - 1979

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# TABLE OF CONTENTS

# LIST OF FIGURES

# LIST OF PLATES

# LIST OF TABLES

# ABSTRACT

THE CLARKFORKIAN IS an early Cenozoic North American Land-Mammal Age following the late Paleocene Tiffanian and preceding the early Eocene Wasatchian. Controversy has surrounded recognition of the Clarkforkian as a valid land-mammal age, but new investigations in the type area, the Clark's Fork Basin (northern Bighorn Basin) of northern Wyoming, enable the Clarkforkian to be precisely defined and its stratigraphic limits accurately determined. As a result of a University of Michigan project in this area, more than 250 vertebrate localities (134 of Clarkforkian age) have been discovered in the upper Polecat Bench Formation and the lower Willwood Formation, and most of these have been tied to measured stratigraphic sections. Thus the precise stratigraphic occurrence and range of all Clarkforkian mammals in the type area have been established. Seventy species of mammals are recorded, of which eight are new. The beginning of the Clarkforkian is defined by the initial appearance of Rodentia, together with the genera *Esthonyx*, *Coryphodon*, and *Haplomylus*, all of which first occur at about the same time. The beginning of the Wasatchian (upper boundary of the Clarkforkian) is defined by the first appearance of Artiodactyla (*Diacodexis*), Perissodactyla (*Hyracotherium*), adapid primates (*Pelycodus*), omomyid primates (*Tetonoides*, *Teilhardina*), and hyaenodontid creodonts in the northern Western Interior. The taxa defining both the upper and lower boundaries of the Clarkforkian appear to have been immigrants. The Clarkforkian itself can be subdivided into three zones, two of them based on evolutionary stages of *Plesiadapis*. They are, successively, the *Plesiadapis gingerichi* Zone, the *Plesiadapis cookei* Zone, and the *Phenacodus-Ectocion* Zone.

Clarkforkian faunas occur also in other areas of Wyoming, southern Montana, and Colorado (and possibly elsewhere), affirming the utility of the Clarkforkian as a North American Land-Mammal Age. Faunas that may be correlative with the North American Clarkforkian include the Gashato-Naran Bulak assemblage of Mongolia and the earliest Sparnacian Meudon local fauna of the Paris Basin. Similarities between these faunas and the Clarkforkian suggest that faunal interchange between North America and both Asia and Europe occurred during or near the beginning of the Clarkforkian. Tentative correlations between the mammalian faunas of the Paris Basin and those of the North American Clarkforkian suggest that the latter spans the Paleocene-Eocene boundary and is partly latest Paleocene and partly earliest Eocene in age.

A remarkably continuous and richly fossiliferous early Cenozoic sequence of continental sediments is preserved in the northern Bighorn Basin, offering an exceptional opportunity to examine faunal diversity through time. Collections of Torrejonian, Tiffanian, Clarkforkian, and Wasatchian age were studied in order to investigate changes in faunal composition as archaic Paleocene mammalian faunas were supplanted by Eocene ones of more modern aspect. Diversity (both species richness and evenness) was very high in the Torrejonian, decreased dramatically in the Tiffanian, remained relatively low during the Clarkforkian, and rose again in the Wasatchian (mainly reflecting higher evenness). This pattern is generally similar to the patterns of change in species richness and in the proportion of entire-margined leaves in fossil megafloras, both of which indicate a decline in mean annual

temperature from late Cretaceous to late Paleocene, followed by an increase in mean annual temperature and equability from late Paleocene to early Eocene. Thus the Torrejonian and Wasatchian were probably characterized by warm climates and "predictable" environments, whereas the Tiffanian was probably much cooler and less equable, and its environment was relatively unpredictable. Conditions during the Clarkforkian were warmer and more equable than in the Tiffanian, but cooler than in the Wasatchian.

A major faunal break occurs at the Clarkforkian-Wasatchian boundary. In terms of faunal composition, the Clarkforkian was dominated by Paleocene forms, most of which became extinct or severely reduced in abundance rather abruptly at the beginning of the Wasatchian. Less than 10% of the individuals in the early Clarkforkian sample belonged to immigrant taxa, whereas nearly 50% of the individuals in the early Wasatchian fauna were immigrants. The immigrants of both ages include progenitors of modern orders of mammals.

# I
# INTRODUCTION

THE EARLY CENOZOIC was a very important period in the history of mammals. Eutherian mammals, in particular, underwent an extensive adaptive radiation and became one of the dominant elements of terrestrial communities. Paleocene mammalian faunas consisted mainly of relatively primitive forms, unlike most mammals of the present day. By the end of the early Eocene, many of these archaic Paleocene mammals had become extinct or severely reduced in abundance and diversity, and their roles had been assumed by early members of mammalian orders that are still prevalent today. Much of this transition in faunas occurred near the end of the Paleocene and the beginning of the Eocene. This was an episode of considerable significance, for it influenced the composition of all subsequent mammalian communities.

Of paramount importance to elucidating the evolution from archaic Paleocene faunas to Eocene faunas of more modern aspect is an understanding of the Clarkforkian Land-Mammal Age, which occupies the interval between the late Paleocene Tiffanian Age and the early Eocene Wasatchian Age. Considerable confusion has surrounded the Clarkforkian since the first use of the term more than 60 years ago, in reference to early Tertiary strata of northwestern Wyoming. For decades, the Clarkforkian fauna was known only from the Clark's Fork Basin in the northwestern Bighorn Basin, and even there it was poorly known. In spite of increasing paleontological exploration of early Tertiary sediments in the Western Interior, only one additional Clarkforkian assemblage had been recognized by 1960. Discrepancies in the definition of the Clarkforkian, together with inadequate understanding of its fauna, led to doubt that a stratigraphic interval with a distinctive Clarkforkian fauna could really be recognized. This culminated in a review by R. C. Wood (1967), who concluded that then-available evidence was inadequate to document the Clarkforkian as an age, faunal zone, or lithologic member of the Polecat Bench Formation.

That such a pivotal phase in mammalian history should be so poorly known was largely because no intensive systematic effort was ever made to collect fossils and carefully record their localities and stratigraphic occurrences in sediments of this interval. Subsequent to Wood's study, other authors studying fossil mammals continued to suggest the existence of a faunal interval between the Tiffanian and the Wasatchian, but satisfactory evidence was still lacking. In 1975, the University of Michigan Museum of Paleontology initiated a project, under the direction of Dr. Philip D. Gingerich, to collect fossil vertebrates intensively from throughout the upper part of the Polecat Bench Formation and the lower part of the Willwood Formation in the Clark's Fork Basin area (the type area of the Clarkforkian). A remarkably continuous sequence from Torrejonian through Wasatchian is preserved there, and it is richly fossiliferous. Stratigraphic sections were measured throughout this area, providing a framework for determining the levels of fossil-bearing sites. As a result of four seasons of field work, it is now possible to redefine the Clarkforkian, establish its boundaries, and describe its distinguishing fauna in the basin where the Age was first proposed.

Recognition of the Clarkforkian fauna in the northern Bighorn Basin substantially illuminates our understanding of the evolution of mammals and mammalian faunas in this region, but its importance would be seriously diminished if such a fauna could not be identified elsewhere. Clarification of what distinguishes this age in mammalian history has permitted several other Clarkforkian faunas to be recognized. Thus the validity of the Clarkforkian as a North American Land-Mammal Age now seems undeniable.

This report summarizes what is now known about the Clarkforkian. It is best known from the richly fossiliferous sequence in the Clark's Fork Basin, consequently most of this study focuses on the extensive collections from this area. An introduction to the geology of the area is presented in Chapter II, where I discuss some of the misunderstanding that clouded recognition of the Clarkforkian as a result of confusion of lithologic, temporal, and faunal boundaries. The stratigraphic framework for the remainder of the study is also provided in Chapter II, together with an outline of Clarkforkian localities in the type area. In Chapter III, the history of study of the Clarkforkian is briefly reviewed, and a revised definition is proposed. Diagnostic and characteristic taxa of the Clarkforkian are enumerated and the stratigraphic occurrences and ranges of all Clarkforkian taxa from the type area are provided. The chapter concludes with a discussion of the controversial subject of the age of the Clarkforkian with respect to the Paleocene-Eocene boundary, and presentation of a tentative correlation with faunas of the Paris Basin. Chapter IV is a systematic revision of the Clarkforkian fauna from the study area, and it includes a complete faunal list of all known Clarkforkian mammals. Clarkforkian faunas from outside of the Clark's Fork Basin are summarized in Chapter V, and a brief survey of non-mammalian fossils from the Clarkforkian is presented in Chapter VI. The remarkably complete and very fossiliferous sequence in the northern Bighorn Basin offers an exceptional opportunity to examine changes in faunal composition from the Paleocene into the Eocene. Chapter VII is devoted to this subject, and I have investigated the composition and diversity of mammalian assemblages from Torrejonian through early Wasatchian in the Polecat Bench-Clark's Fork Basin area. A few assemblages from outside this area have also been analyzed, to test the broader applicability of the results. Aside from establishing patterns of faunal diversity through this period, an objective of this part of the study was to determine if characteristics of faunal composition, beyond mere presence or absence of taxa, could be of use in recognizing the Clarkforkian. This aspect of the project also provides considerable insight into the time and nature of the transition from archaic to more modern mammalian faunas.

This study was presented as a doctoral dissertation in the Department of Geological Sciences at the University of Michigan. Preliminary summaries have been published by Rose (1980) and Gingerich et al. (1980).

## MENSURATION

All measurements of specimens are given in millimeters, to the nearest twentieth of a millimeter (.05 mm). Measurements of very small teeth were made using an ocular micrometer calibrated to twentieths of a millimeter, fitted to the lens of a Leitz microscope. Other measurements were taken with calipers bearing a dial micrometer calibrated also to twentieths of a millimeter.

In the course of this study, I have dealt with a variety of mammals and, hence, a diversity of dental morphologies. It is clear that consistency of tooth measurements is difficult to obtain, not only by different students, but even when measured by the same person. This is particularly true for certain highly modified teeth, such as molars of plagiomenid dermopterans and carnassials of carnivores. Where a specific orientation of teeth and mode of measurement has been prescribed by a previous author, I took measurements in the same way and have indicated this in the text. Even so, minor shifts in orientation of a specimen can lead to differences between my measurements and those of an earlier worker. I emphasize this as a caveat to students who would base conclusions heavily on measurements published by others; it is important to see and compare samples firsthand before making conclusions. Unfortunately, many authors have not clearly indicated how they took tooth measurements, and this may result in discrepancies if the orientation for measurement is not obvious. Except where otherwise specified, I have taken measurements as shown by Rose (1975a: figure 1) and Gingerich (1976b: figure 6): length is the maximum longitudinal dimension of the tooth crown, measured (as near as possible) parallel to the long axis of the tooth row; breadth is the maximum transverse dimension perpendicular to the length.

## TERMINOLOGY AND ABBREVIATIONS

In discussions of dental morphology I have employed the generally accepted terminology summarized by Van Valen (1966) and Szalay (1969a). Standard designations for teeth have been used (e.g. $P_4$, fourth [and last] lower premolar, $M^1$, first upper molar). I have applied the traditional interpretation of mammalian dental homologies (but see, for example, McKenna, 1975, and Krishtalka, 1978, for alternative views).

Acronyms for institutions housing specimens discussed herein are:

ACM—Pratt Museum of Geology, Amherst College, Amherst
AMNH—Department of Vertebrate Paleontology, American Museum of Natural History, New York
CM—Section of Vertebrate Fossils, Carnegie Museum of Natural History, Pittsburgh
FMNH—Department of Geology, Field Museum of Natural History, Chicago
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge
PU—Museum of Natural History, Princeton University, Princeton
ROM—Department of Vertebrate Paleontology, Royal Ontario Museum, Toronto
UCMP—Museum of Paleontology, University of California, Berkeley

UM—Museum of Paleontology, University of Michigan, Ann Arbor
USNM—Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington
UW—Geological Museum, University of Wyoming, Laramie
YPM—Division of Vertebrate Paleontology, Peabody Museum of Natural History, Yale University, New Haven

Other abbreviations used in the text and tables are:
L—length
B—breadth
tri—trigonid
tal—talonid
N—sample size
OR—observed range
$\bar{X}$—mean
SE—standard error
s—standard deviation
V—coefficient of variation
MNI—minimum number of individuals
a (following measurement)—approximate

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# II

# PHYSIOGRAPHIC AND GEOLOGIC SKETCH OF THE CLARK'S FORK BASIN

THE BIGHORN BASIN, of which the Clark's Fork Basin is a part, is a large structural and topographic basin in northwestern Wyoming, surrounded by the Beartooth, Absaroka, Owl Creek, Bighorn, and Pryor Mountains. From late Cretaceous into Eocene time, Laramide orogeny resulted in the uplift of these mountains and the shedding of vast amounts of sediment into the Bighorn Basin, but the elevation of the basin floor probably remained low due to rapid subsidence (Van Houten, 1944; Love, 1960). (Mackin, 1947, estimated that, during the early Eocene, the basin floor was no more than 300–450 m above sea level, and the surrounding mountains not higher than 900–1500 m above the basin floor.) Much of the terrane now stands between 1000 and 2000 m above sea level, and the highest bordering mountains rise to about 4000 m above sea level. About 5000 m of Phanerozoic sediments now cover the Precambrian floor of the basin (Van Houten, 1944; Love, 1960). Early Tertiary sediments of the Bighorn Basin have been derived from these sediments as well as from Precambrian crystalline and metamorphic rocks exposed in the Bighorn, Owl Creek, and Beartooth Mountains. Several thousand square miles of early Tertiary badlands now covering much of the basin have been dissected by the Bighorn and Clark's Fork drainage systems (Van Houten, 1944).

The Clark's Fork Basin occupies several hundred square miles in the northwestern corner of the Bighorn Basin. Most of the region is covered by Paleocene and Eocene badlands carved out by the Clark's Fork and Shoshone Rivers (Mackin, 1937; Van Houten, 1944). Several Quaternary erosion surfaces and river terraces stand a few hundred feet above the basin floor, truncating gently-dipping rocks of Cretaceous through Eocene age. The most prominent of these, Polecat Bench, is a northeast-trending terrace 3 to 5 miles wide and about 20 miles long, situated on the divide between the Shoshone and Clark's Fork Rivers. Its surface of coarse river gravels, about 5 m thick, slopes northeastward and represents a Quaternary bed of the Shoshone River. Much of the Clark's Fork Basin is littered with fragments of Mississippian Madison Limestone, remnants from the upper plate of the Heart Mountain detachment fault (Mackin, 1937; Pierce, 1965).

Two Tertiary formations are exposed in the Clark's Fork Basin: The Polecat Bench Formation, almost entirely of Paleocene age, and the Willwood Formation, predominantly of early Eocene age. Clarkforkian fossils are found in the uppermost part of the Polecat Bench Formation and the lower part of the Willwood Formation.

Consideration of the age of the Clarkforkian is deferred until the next chapter, following the definition of the Clarkforkian.

## POLECAT BENCH FORMATION

Jepsen (1940: 232) defined the Polecat Bench Formation, replacing previous use of the Fort Union Formation, "for sediments in the vicinity of Polecat Bench, about 3500 feet thick, bounded below by the *Triceratops*-bearing beds and above by *Homogalax*-bearing beds." The formation attains a maximum thickness of about 9000 feet in a structural deep in front of the Beartooth thrust southwest of Red Lodge, Montana (Moore, 1961). The Polecat Bench is lithologically heterogeneous, consisting primarily of fluviatile sandstones, silts, clays, lignites, and limestones, arranged in small-scale cyclothems (Gingerich, 1969). Jepsen recognized four stratigraphically successive units in the formation: the Mantua (sandstone) lentil, the Rock Bench Quarry beds (mainly sandstone), the Silver Coulee beds (sands and silts, including Princeton Quarry), and the Clark Fork beds (sands and silts, i.e. mudstones). The distinction between the Silver Coulee beds and the Clark Fork beds was believed by Jepsen to be chiefly a faunal one. In his view, "the Polecat Bench Formation represents the duration of the Paleocene Epoch, as now defined, from Mantua (Puerco) to Clark Fork times, inclusive" (Jepsen, 1940: 233).

The name Fort Union Formation is still employed for the sediments Jepsen called Polecat Bench Formation by the U.S. Geological Survey (e.g. Pierce, 1965) and some others. As Jepsen discussed in detail, however, the blanket application of the term Fort Union Formation for Paleocene sediments found over a wide expanse of the Western Interior renders the term almost meaningless, and it is comparable to the former unrestricted usage of the term Wasatch for early Eocene sediments. For this reason, I believe the name Polecat Bench Formation is preferable, and I shall follow much current usage and employ it here.

Sinclair and Granger (1912) suggested the names "Ralston beds" or "Ralston formation" for the uppermost strata of the "Fort Union" near McCulloch Peak and in the southern part of Polecat Bench ("the bluffs opposite Ralston station"). Due to preoccupation of this name, Granger (1914) replaced it with the term Clark Fork beds. Jepsen (1940) applied the latter name to the uppermost 500 feet (about 150 m) of the Polecat Bench Formation and believed that this interval encompassed the entire duration of a biochronological Clarkforkian unit. The Wood committee of the Geological Society of America (Wood et al., 1941: 9) adopted Jepsen's view in their formal definition of the Clarkforkian provincial age, basing it "on the Clark Fork member (and faunal zone) of the Polecat Bench Formation." (The Wood committee also raised the Clark Fork beds to member status in the Polecat Bench Formation.)

In the years since Jepsen's proposal of the Polecat Bench Formation, there has been considerable confusion about the extent of the "Clark Fork beds" and of the Clarkforkian Age. Much of this has resulted from disagreement over the location of the contact of the Polecat Bench Formation with the overlying Willwood Formation, and confusion of faunal, temporal, and formational boundaries (further discussed below). For example, Jepsen (1940: 237) remarked:

> Sinclair and Granger described locally angular unconformities between the Clark Fork and the overlying Eocene strata but in most areas the "contact" is transitional with no evidence of interruption of sedimentation. Even the widely used criterion of red color banding for distinguishing the Eocene from the underlying beds is invalid because red strata occur well down in the Clark Fork beds.

Later, when defining the Clarkforkian Willwood Formation, Van Houten (1944: 178) stated:

> Wherever the Willwood and Polecat Bench are conformable no conspicuous lithologic change marks the beginning of Willwood deposition, except red banding . . .

This was echoed by Neasham and Vondra (1972: 2169–2170):

> In areas of Fort Union-Willwood conformity the establishment of a suitable formational boundary is difficult. As proposed by Van Houten (1944), the first occurrence of red banding appears to be the best criterion for distinguishing between the two formations.

By acknowledging the presence of red banded sediments in the "Clark Fork beds," Jepsen in fact supported the placement of a substantial part of the "Clark Fork beds" in what was later named the Willwood Formation (see also Van Houten, 1944; Jepsen and Van Houten, 1947). The term "Clark Fork beds" cannot be supported as a lithologic unit, therefore, for it is defined solely by its fossil content.

Intensive studies in the Clark's Fork Basin by UM field parties demonstrate clearly that the uppermost strata of the Polecat Bench Formation are of early Clarkforkian age, an assessment based on mammalian fossils. No obvious stratigraphic break or lithologic change heralds the beginning of Clarkforkian time. Because of minor faults and covered intervals within these early Clarkforkian strata, the exact thickness of the Polecat Bench sediments that are of Clarkforkian age has not yet been precisely determined; but it appears to be slightly less than Jepsen estimated. The lowest localities now known to yield Clarkforkian mammals are SC–83, on the southeastern side of Polecat Bench, SC–179, on the western side of Polecat Bench, and a few sites approximately on strike and northwest of SC–179, in Badger Basin (Figures 2 and 3). These localities appear to lie within the upper 100 m of the Polecat Bench Formation, about 350–400 m above Princeton Quarry (more detailed discussion of Clarkforkian localities is presented later in this chapter).

## WILLWOOD FORMATION

The Willwood Formation was proposed by Van Houten (1944) for the sequence of variegated shales, mudstones, and hornblende-bearing sandstones overlying the Polecat Bench Formation. These beds had been variously called the Wasatch Formation, Bighorn Wasatch, or Knight Formation by earlier authors. The Willwood is locally unconformable on Polecat Bench and Lance sediments, particularly on the margin of the

Bighorn Basin, where sharp angular unconformities may be observed. In much of the basin, including the Sand Coulee area, however, the Willwood lies conformably on the Polecat Bench Formation and is distinguished from it mainly by the occurrence of red banding, as discussed above. (Bown, 1979, has listed additional criteria, including geometry of sandstone bodies and composition of nodules, that are of use in distinguishing the two formations.) Stow (1938) observed that the basal Willwood is characterized by an influx of hornblende, which he believed came from a new source, the "Early Acid Breccia" volcanics of the Absaroka Range. We now know that the "Early Acid Breccia" postdates the Willwood Formation; but pre-Eocene volcanic sources are known from Idaho.

The Willwood Formation is about 2500 feet (760 m) thick in the central Bighorn Basin and is slightly thicker (about 800–850 m) in the Clark's Fork Basin. Like the Polecat Bench Formation, the Willwood is fluviatile in origin. On the western margin of the Clark's Fork Basin are lower Willwood fanglomerates derived from the rising Beartooth Mountains (Flueckinger, 1971). The dominant basin deposits are channel sands and variegated overbank mudstones, laid down by low gradient meandering streams (Neasham and Vondra, 1972).

In the central and southern parts of the Bighorn Basin, sandstones comprise about 20–25% of the thickness of the Willwood Formation (Neasham and Vondra, 1972; Bown, 1979), a figure comparable with estimates from UM sections in the Clark's Fork Basin. Bown (1979) has distinguished three types of sandstones in the Willwood Formation based on areal extent and geometry. Sheet sands, of broad lateral extent (hundreds of meters to kilometers) and relatively uniform thickness, are relatively rare in the Willwood; but several have been identified in the Clark's Fork Basin and one of them, as will be shown below, is of particular interest. Apron-channel sands (scour channels 30–50 m wide with tabular lateral extensions up to hundreds of meters) are the most common type in both the Willwood and upper Polecat Bench Formations. Much smaller bodies are the shoestring sands (a few meters wide), characterized by their high thickness to breadth ratios. Bown observed mud gall conglomerates at the base of some channel sands in the southern Bighorn Basin. Channel lag deposits of this sort are common in the Polecat Bench and the Willwood of the Clark's Fork Basin, where they sometimes contain concentrations of vertebrate and plant remains.

Overbank mudstones account for the greatest volume of sediments in the Willwood Formation. The term "mudstone" has been used to refer to non-fissile fine sediments, dominated by silt but comprising clays and fine sand as well (Neasham and Vondra, 1972; Bown, 1979). Color bands of red, yellow, orange, purple, mottled orange and purple, green, gray-green, and gray have been observed by various authors, and they appear to be cyclothemic. The genesis of these color-banded beds is controversial, but there now seems to be general agreement that they are associated with incipient soil formation on alluvial plains, and that they reflect a fluctuating ground-water table or alternating (seasonal?) wet and dry conditions (Neasham and Vondra, 1972; Van Houten, 1973; McBride, 1974; Bown, 1979). Red mudstones are low in organic carbon and high in free iron and manganese. They form under oxidizing conditions resulting from drier climate or a relatively low water table. Gray and drab mudstones have little free iron and manganese and are rich in organic carbon; they indicate poor drainage (reducing conditions). There are no significant mineralogical differences between different colored mudstones (Sinclair and Granger, 1911; Neasham and Vondra, 1972; Bown, 1979). Roehler (1965) found that red-banded lower Tertiary strata (Wasatch Formation) in the Rock Springs Uplift area occur in well-drained uplands along the mountain fronts, whereas drab sediments are prevalent in the basin. Thus it appears that the formation of variegated beds may be controlled by climate, fluctuating water table, and local tectonic events, mechanisms which are not necessarily mutually exclusive.

Most of the color-banded mudstones in the Willwood Formation of the Clark's Fork Basin are red or pink, although yellow, orange, and mottled orange and drab beds have also been observed. In general, these beds are only a meter or two thick and are not laterally persistent beyond a few hundred meters. In the northern badland hills two red-banded beds can be traced for about a mile between localities SC–62 and SC–127 and locality SC–234 (Figure 2). The lower of them, occurring in the middle of SC–62, appears to correspond closely with the faunal boundary between the middle Clarkforkian *Plesiadapis cookei* Zone and the late Clarkforkian *Phenacodus-Ectocion* Zone (see Chapter III).

In summary, the majority of recent studies conclude that color bands of floodbasin mudstones, as seen in the Willwood Formation, result from oxidation, reduction, hydration, or dehydration of iron minerals, related to pedogenesis. In the Clark's Fork Basin, the iron minerals were probably derived from the Beartooth Mountains (Van Houten, 1944, 1948).

Bown (1979) presented a detailed discussion of nodules and concretions characteristic of the Sand Creek facies of the Willwood Formation (southeastern Bighorn

Basin) and provided interpretations of their geochemistry and environments of deposition. Among the most prevalent types he distinguished are calcium carbonate nodules and ferric iron concretions, both of which are frequently associated with vertebrate fossils. Calcareous nodules have been observed *in situ* in red and orange mudstones and appear to be related to pedogenesis under alternating wet and dry conditions (Van Houten, 1948; McBride, 1974; Neasham and Vondra, 1972). Bown suggested that ferric iron concretions may also be related to soil formation, for similar nodules develop in modern tropical soils. The hematite concretions often found enclosing fossil bones may have formed by precipitation of ferrous carbonate on bones, later oxidized to ferric hydroxide and dehydrated to hematite (Van Houten, 1944; Bown, 1979). Both types of nodules occur in the Willwood Formation of the Clark's Fork Basin, but calcareous nodules seem to be less abundant in Clarkforkian than in Wasatchian beds. Many mammalian fossils from localities SC–62 and SC–127 are encased in hematitic concretions. Bown (personal communication, March 1979) has observed different types of concretions in the upper Polecat Bench Formation. Calcareous concretions are not common there; rather, the prevalent kinds are black manganiferous ($MnO_2$) concretions and yellowish-brown sideritic concretions, sometimes stained by $MnO_2$. The first type is associated with a strongly oxidizing environment and the second with a reducing environment.

Minor fractions of the Willwood Formation are composed of carbonaceous shales and limestones. Bown (1979) found that carbonaceous shales in the Sand Creek facies of the Willwood Formation often occur beneath apron-channel sands, and he postulated that they formed by slow deposition in small swales. In the Clark's Fork Basin, carbonaceous shales are not restricted to this occurrence and are often found within mudstone sequences. Selenite and granular gypsum are often associated with the shales, and plant fossils are locally abundant in the shales of both the Sand Creek facies and the Clarkforkian part of the Willwood. Vertebrate fossils are almost never associated with carbonaceous shales in the Bighorn Basin, although carbonaceous mudstones have yielded vertebrates (e.g. the Clarkforkian Bear Creek local fauna). Small limestone lenses occur in the Willwood Formation of the Clark's Fork Basin, and they often contain vertebrate and molluscan fossils. Their genesis is not clear, however. They may represent minor ponds or could be concretionary. Preliminary examination of a sample from one of these limestones revealed that it consists of argillaceous micrite (B. H. Wilkinson, personal communication, 1979).

## FORMATIONAL AND FAUNAL BOUNDARIES

As outlined in the foregoing section, the best method for establishing the boundary between the Polecat Bench Formation and the Willwood Formation is to determine the lowest occurrence of red-banded sediments. This is more difficult than it may seem, for isolated red-banded zones (not clinker) have been observed well within sediments widely regarded as part of the Polecat Bench Formation (e.g. at locality SC–165, late Tiffanian, section 1 in Figure 3).

The procedure followed here was to mark the boundary at the lowest frequent occurrence of red-banded mudstones (Figure 1). In the southeastern exposures along Polecat Bench, the formations are conformable and the contact occurs in the upper part of the interval of locality SC–74. This coincides closely with previous views (Fisher, 1906; Jepsen, 1930b). Because of covered section on the western side of Polecat Bench and in the eastern part of the Clark's Fork Basin (Badger Basin), the position of the boundary there is less precisely determinable. It probably lies within the covered interval between localities SC–179 and SC–194 on the west side of Polecat Bench. In Badger Basin, bright red and pale orange mudstones occur at SC–217 and several other localities, indicating that most of these sites are in the lower Willwood Formation (see Figures 1 and 2). This contrasts with previous maps of this area (e.g. Pierce, 1965). The structure in Badger Basin, however, is more complex than in most of the Clark's Fork Basin, with frequent changes in strike and dip (Pierce, 1965). Consequently, caution must be exercised in attempting to fix the Polecat Bench-Willwood contact there. The boundary line west of Polecat Bench shown in Figure 1 is the best approximation based on data now available.

Clarkforkian fossils have not been found in Willwood sediments of the central or southern parts of the Bighorn Basin; lowest Willwood beds in these areas contain Wasatchian mammals (Bown, 1979). For this reason, Van Houten (1944) and Jepsen and Van Houten (1947) concluded that the onset of Willwood deposition was time-transgressive, a view that remains consistent with known evidence.

In the northern Bighorn Basin, early Clarkforkian fossils occur in the upper Polecat Bench Formation, where they are present in about the uppermost 100 m of the formation. Approximately 70–80% of the stratigraphic interval containing Clarkforkian fossils is within the lower Willwood Formation. It appears that Willwood deposition began somewhat earlier in the Badger Basin area than further to the southeast. This is inferred from the occurrence of early Clarkforkian mammals in

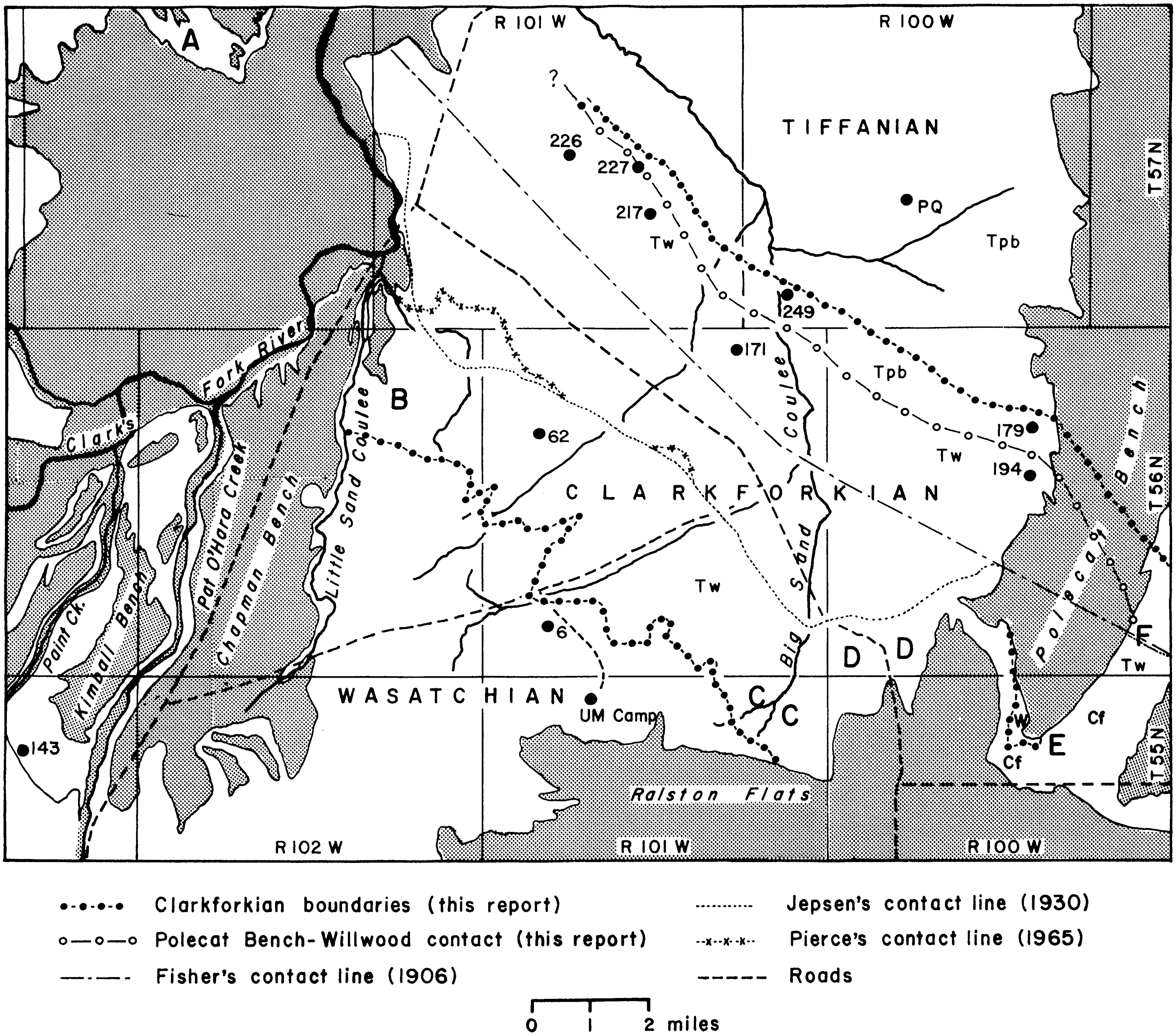


Figure 1. Map of the Clark's Fork Basin, Wyoming, showing faunal and formational boundaries as drawn in this report. The Polecat Bench-Willwood formational contact and the Paleocene-Eocene boundary lie within the Clarkforkian (some early Clarkforkian sites are located in the upper Polecat Bench Formation). Fisher's contact line was a formational boundary, also corresponding to the Cretaceous-Tertiary boundary. Jepsen's line delineated the Paleocene-Eocene boundary. Pierce mapped the Polecat Bench ("Fort Union")-Willwood formational contact, and his line coincides for the most part with Jepsen's epoch boundary. All these earlier concepts can now be modified by clearly separating the formational, epochal, and faunal boundaries. In general, strata dip gently to the southwest, with the oldest (late Tiffanian) beds in the northeastern part of the study area (see text for further details). Letters A–F designate original Clarkforkian localities of Granger and Sinclair. Selected UM sites are shown to facilitate comparison with Figure 2.

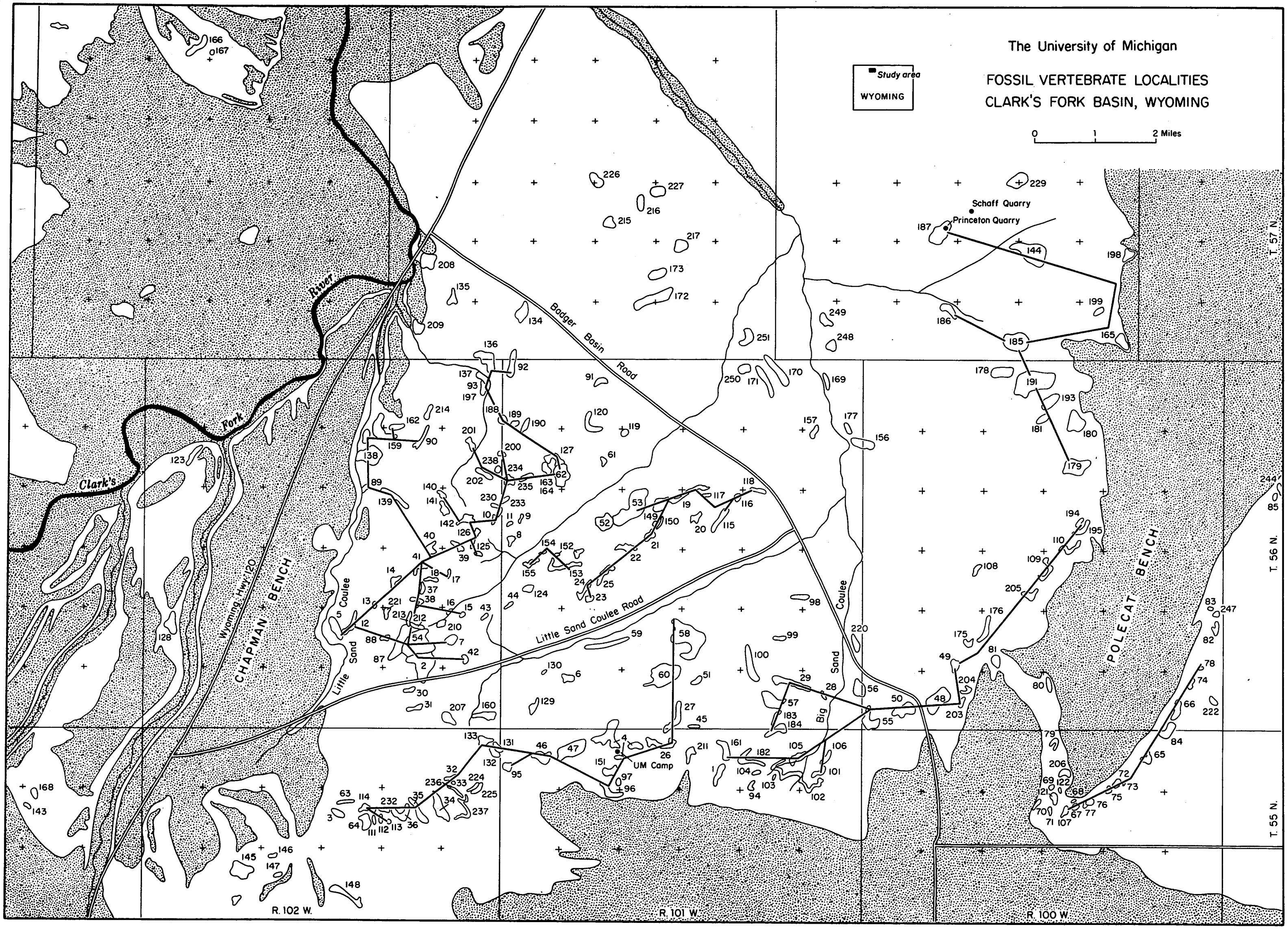


Figure 2. University of Michigan fossil vertebrate localities in the Clark's Fork Basin. All localities of late Tiffanian, Clarkforkian, and early Wasatchian age in the main part of the study area are shown (see Table 1 for index to Clarkforkian age localities). Approximate locations of the measured stratigraphic sections are shown by heavy lines (see Figure 3). The limits of the Clarkforkian in this basin and the contact of the Polecat Bench and Willwood Formations are shown in Figure 1.

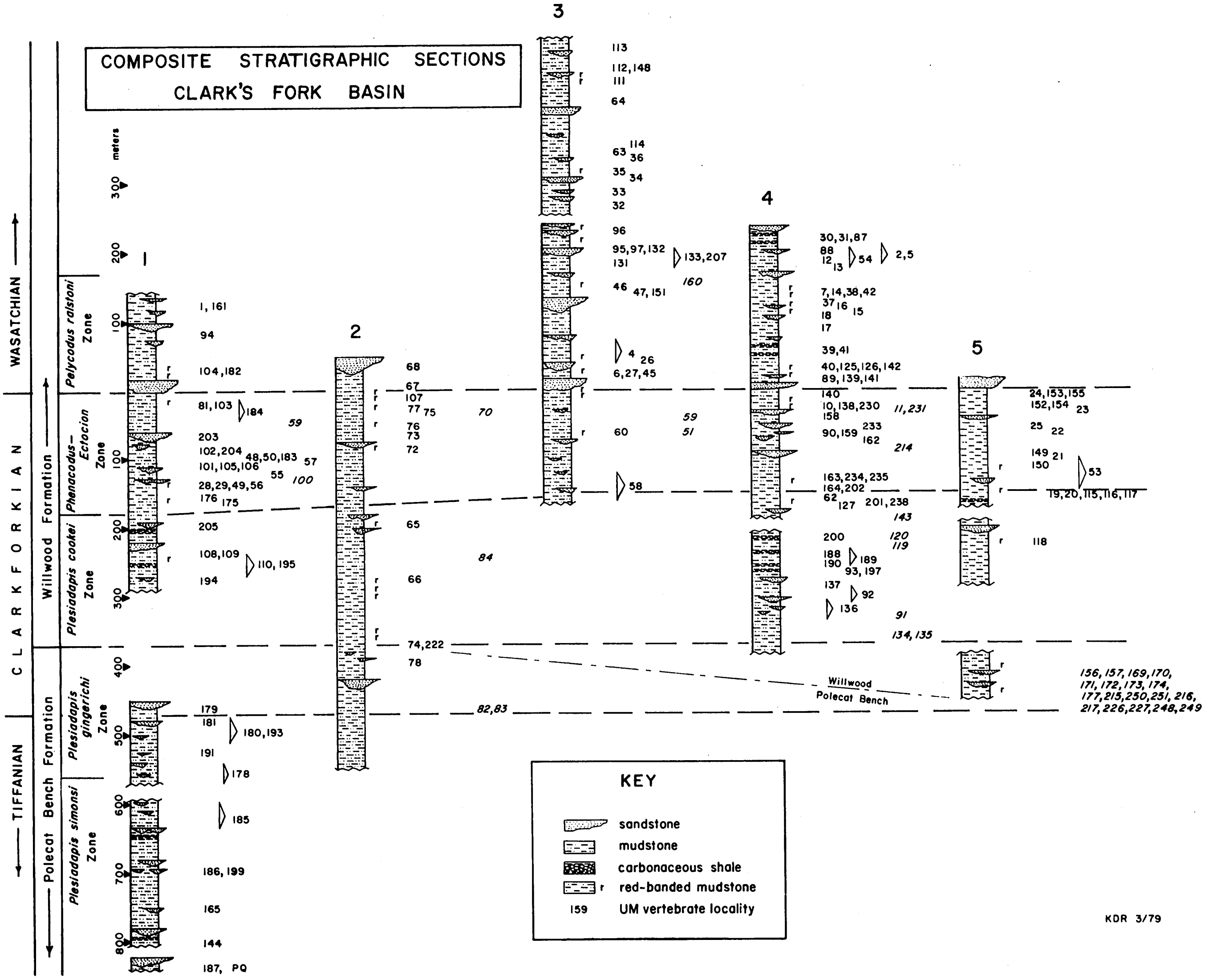


Figure 3. Composite stratigraphic sections in the Clark's Fork Basin. Positions of dominant sandstones, red-banded mudstones, and carbonaceous shales are indicated. UM fossil vertebrate localities, from Figure 2, are shown to the right of each section; italicized numbers are sites for which stratigraphic levels have been estimated from geological and/or faunal evidence. All localities are in mudstones. The extensive sheet sandstone at the Clarkforkian-Wasatchian boundary can be correlated in sections 1, 3, 4, and 5, and it is used as datum: stratigraphic levels are indicated in meters above and below the sandstone. The sandstone thins to the southeast in the Clark's Fork Basin and is not present in section 2. Beds at about this level can be roughly traced between sections 1 and 2, however, and this stratigraphic basis is used together with faunal evidence to correlate section 2 with others. Clarkforkian faunal zone boundaries are indicated by broad dashed lines. The boundary between the *Plesiadapis cookei* Zone and the *Phenacodus-Ectocion* Zone is relatively precise in sections 3, 4, and 5 and is approximate in sections 1 and 2. The *Plesiadapis gingerichi* Zone-*P. cookei* Zone boundary is located in section 2 by the lowest occurrence of *P. cookei* but in other sections is necessarily more approximate. The *P. gingerichi* Zone extends down into the late Tiffanian, and the Tiffanian-Clarkforkian boundary is recognized by the first occurrence of rodents, *Haplomylus*, *Esthonyx*, or *Coryphodon*, often together with *P. gingerichi*. The Polecat Bench-Willwood formational contact occurs within the early Clarkforkian in most of the area and appears to be time-transgressive. Locations of sections are shown in Figure 2. Each of the sections shown here is a composite of two or more smaller sections. General locations of the sections are: 1—West side of Polecat Bench to head of Big Sand Coulee; 2—Southeast side of Polecat Bench; 3—Southern badland hills south of Little Sand Coulee Road; 4 and 5—Northern badland hills north of Little Sand Coulee Road.

Willwood sediments in Badger Basin (localities SC–215, 216, 217, 226, 227, and others; Figures 2 and 3), whereas the lowest Willwood beds on the southeast side of Polecat Bench contain early middle Clarkforkian mammals (SC–74; Figure 3).

The faunal boundary between the Tiffanian and the Clarkforkian is recognized by the first appearance of rodents, *Coryphodon*, *Haplomylus*, and *Esthonyx*, all believed to be immigrants. Thus the initiation of the Clarkforkian is not here (or elsewhere, so far as known) clearly associated with any stratigraphic break or formational boundary; it is recognized solely by its fauna.

The boundary between the Clarkforkian and the Wasatchian is also recognized faunally, by the first appearance of *Hyracotherium*, *Diacodexis*, *Pelycodus*, and hyaenodontid creodonts, all immigrants. (*Hyracotherium* is a Wasatchian index fossil in the northern Western Interior, but possible Clarkforkian records of the genus are known from southern North America; see Chapters III and V.) In the Clark's Fork Basin, the Clarkforkian-Wasatchian boundary coincides with a widespread, thick sheet sandstone (Plate 1, figure 2), which can be traced across most of the region. Although other sheet sandstones have been observed below this sandstone, none approaches its areal extent.

Kraus (1979) studied this "boundary" sandstone and established that it is not a single sand, but rather a complex of channel deposits, up to 30 m thick in the vicinity of SC–9 and SC–11, that pinch out to the southeast. Thus at the southern tip of Polecat Bench (section 2 in Figure 3) the sand does not exist, and early Wasatchian faunas occur at SC–67 within 10 m above Clarkforkian ones at SC–107. (The Wasatchian fauna at SC–67 includes at least two diagnostic immigrant taxa and is similar to faunas that occur in basal Wasatchian sediments immediately above the sheet sandstone in other sections.) Near SC–67 there is no evident stratigraphic or sedimentological break of any kind. From analysis of sedimentary structures, grain size, and bedding features, the boundary sheet sand appears to have been deposited by relatively wide meandering rivers (Kraus, 1979).

Whether the sheet sand represents a major temporal hiatus is a moot question. Kraus (personal communication) suggests that a decline in rate of basin subsidence may have caused local reworking of basin sediments, resulting in the widespread deposition of this sheet sand, while finer sediments were transported out of this part of the basin. If this explanation is correct, the sand may represent a longer period of time than a comparable thickness of mudstone; but the duration of time is difficult to estimate. Although the sheet sand may be time-transgressive, it does not appear to be significantly so at our present level of resolution.

The profound faunal turnover that occurs at the Clarkforkian-Wasatchian boundary (see Chapters III and VII) may seem, at first glance, to indicate a temporal gap; but if such a hiatus were to explain the faunal differences observed, it would have to be an unconformity of major magnitude. Several factors argue against this. For example, Willwood sediments below and above the sand are essentially identical, the only sedimentological distinction being the apparent scarcity of thin lignite beds above the sheet sandstone (L. J. Hickey, personal communication). The continuous section at the southern tip of Polecat Bench crosses the Clarkforkian-Wasatchian boundary and the sheet sand is not present in this section, although the same faunal change occurs here as in areas where the sand marks the boundary. This faunal change at the Clarkforkian-Wasatchian boundary is manifest, but it is primarily characterized by influx of immigrant taxa, not by disjunct patterns of evolution within lineages. Some "punctuations" do occur, for example in the genera *Haplomylus* and *Apheliscus* (Figures 38 and 39), but they are not the sort of breaks that would be expected if a temporal hiatus were present at this boundary. (In *Haplomylus*, both Clarkforkian and Wasatchian populations increased in size through time, but a sharp shift to smaller size occurs at the Wasatchian boundary, suggesting that the Wasatchian species was an immigrant not directly derived from late Clarkforkian *Haplomylus*; see Chapter IV.) The gradually changing mammalian lineages that cross the Clarkforkian-Wasatchian boundary do so with no evident disruption in their evolutionary patterns (e.g. *Phenacolemur*, Figure 30; *Esthonyx*, Gingerich and Gunnell, 1979). Thus it is probable that the boundary sheet sandstone does not represent a significant interval of time with respect to the entire Clark's Fork Basin section.

Within the Clarkforkian of the Clark's Fork Basin, three faunal zones can be recognized (defined in Chapter III). They are, in succession, the *Plesiadapis gingerichi* Zone, the *Plesiadapis cookei*, Zone, and the *Phenacodus-Ectocion* Zone. There appears to be no stratigraphic or sedimentological unit coincident with the transition from the *P. gingerichi* Zone to the *P. cookei* Zone. In fact, the boundary between the zones lies within lower Willwood beds in much of the Clark's Fork Basin, but appears to be very close to the Polecat Bench-Willwood contact on the southeast side of Polecat Bench. The boundary between the *P. cookei* Zone and the *Phenacodus-Ectocion* Zone corresponds closely to the lower of two bright red-banded mudstones at locality

SC–62, that can be traced to SC–127 and possibly to SC–201 and SC–19. In most of the basin, however, there is no lithologic means for identifying this zonal boundary; it is purely a faunal boundary.

## OCCURRENCE OF FOSSILS

In the Polecat Bench Formation, vertebrate remains frequently occur as concentrations in clay gall conglomerates at the base of channel sandstones (see Chapter VII). In the uppermost Polecat Bench Formation, of Clarkforkian age, most vertebrate fossils occur as surface lag, eroding out of drab mudstones and, rarely, from sandstones.

Vertebrates are more widely distributed in the Willwood Formation. Nearly all occur in overbank mudstones, but scattered vertebrate remains are rarely present in channel sands (e.g. at localities SC–51 and SC–250) and limestones (e.g. at SC–29 and SC–189). There has been considerable disagreement concerning the distribution of fossil bones and teeth in Willwood mudstones. Sinclair and Granger (1911: 115) reported:

> In the Wasatch [Willwood], where fossils were obtained at many horizons in the red, blue and mottled clays, it is noticeable that those from the red clays, while at times abundant, are always fragmentary, the more resistant parts such as jaws and teeth predominating. In the blue and mottled clays associated skeletons may be expected and many of *Coryphodon* were found.

Bown (1979) observed that vertebrate fossils are rarely found in place in red mudstones, but are much more frequent in orange, purple, and especially gray mudstones. This is generally true in the Clark's Fork Basin Willwood deposits as well. In some localities (e.g. SC–62) bones and jaws have been excavated from red mudstones, but the overwhelming majority of specimens seem to be derived from gray mudstones. At many sites (e.g. SC–19, SC–117, SC–136) vertebrate fossils have been encountered weathering out of gray and drab horizons, and two sites (SC–188 and SC–195) contain local concentrations of bones *in situ* in gray mudstones.

Like Sinclair and Granger, we have found occasional specimens in varying degrees of articulation in gray mudstones (as at SC–195), but the preponderance of fossils consists of isolated elements. Few specimens show any evidence of appreciable transport, however. This suggests that most of the vertebrate fossils of the Willwood Formation resulted from subaerial accumulations of vertebrate remains, disarticulated by decomposition and scavenging (Bown, 1979). Some bones show evidence of subaerial weathering, and others were clearly gnawed by rodents, supporting this interpretation. In most surface lag accumulations of bones, as well as in some *in situ* occurrences, there is little or no size sorting of elements. Bown (1979) made similar observations with regard to early Wasatchian vertebrates from the Willwood of the southeastern Bighorn Basin. He concluded that fossil concentrations in the Willwood are the result of accumulations of bones during short periods of non-deposition (as would be expected on a floodplain), an inference supported by the consistent association of fossil bones with mudstones that Bown interpreted as ancient soil horizons.

Van Houten (1948) believed that concentrations of bones in gray and drab mudstones represented chiefly small forest and arboreal forms, whereas more scattered remains from red-banded horizons belong to "larger terrestrial ungulates and carnivores." In the Clarkforkian of the Clark's Fork Basin, gray beds often contain small mammals, but they may contain remains of large species as well; hence evidence now available does not support Van Houten's dichotomy.

Vertebrate fossils are, in general, much more common in the Willwood strata of Wasatchian age than those of Clarkforkian age. The density of specimens in Wasatchian surface lag accumulations tends to exceed that from Clarkforkian surface lags by nearly an order of magnitude. (Several early Wasatchian sites have yielded almost 500 specimens, or more [e.g. SC–4, SC–54, SC–133], whereas the most productive Clarkforkian surface localities [SC–19 and SC–136] have yielded about 100 specimens per locality.) The explanation for this contrast is not clear, but it may be related to a faster depositional rate during the Clarkforkian or to other differences in the sedimentary or pedogenetic environment.

## PALEOENVIRONMENT

One may envision the northern Bighorn Basin during the Clarkforkian as a warm, humid, forested floodplain at low elevation. Numerous meandering streams crossed the landscape, and channel relocation left many small oxbow lakes of standing water, although conditions were probably drier than in the Tiffanian. Fossil floras of the Clarkforkian indicate a warm temperate to subtropical climate (see Chapter VI), and the sediments reflect soil formation in a climate with alternating wet and dry conditions. The vertebrate fauna was relatively rich, and included terrestrial and aquatic forms. The Clarkforkian ecosystem may have resembled those of warm temperate or subtropical wooded floodbasins, such as exist in southeast Asia today.

## UNIVERSITY OF MICHIGAN CLARKFORKIAN LOCALITIES

As a result of four seasons (1975–1978) of intensive field work in the northern Bighorn Basin, the University of Michigan Museum of Paleontology has established 252 localities in the upper Polecat Bench Formation and the Willwood Formation, ranging in age from Tiffanian (late Paleocene) through early Wasatchian ("Graybullian," early Eocene). Nearly all of these sites are in the Clark's Fork Basin and on the periphery of Polecat Bench; 27 are Tiffanian in age, 134 are Clarkforkian, and 91 are Wasatchian.

Fossils in the Clarkforkian part of the section are abundant as surface lag accumulations, but concentrations that can be profitably quarried are rare. Consequently, localities were collected mainly by careful surface prospecting within a controlled stratigraphic interval, usually about 10 m thick. We may be reasonably confident that this has not resulted in significant sample biases, for even minute isolated teeth were found by this method at several sites. (It is clear, however, that very small mammals are under-represented at most localities.) At some outcrops where especially important specimens were found, matrix was screen-washed, but this rarely resulted in recovery of additional specimens. Where we found surface concentrations of small vertebrates, screenwashing was performed and was sometimes highly successful (e.g. SC–188). Vertebrate remains were excavated from positions *in situ* in mudstones at several sites (e.g. SC–62, SC–166, SC–234), but only two (SC–188 and SC–195) proved fruitful to quarry extensively.

Several stratigraphic sections were measured through the sequence of late Tiffanian, Clarkforkian, and early Wasatchian sediments, using tape and brunton. The primary objective was to determine the stratigraphic positions of as many fossil-bearing localities as possible. About two-thirds of the localities (including about two-thirds of the Clarkforkian sites) have been located in the measured sections prepared so far, and the levels of nearly all other localities can be approximated by geological evidence alone, although faunal evidence is often available as well.

The Polecat Bench and Willwood sequence of the Clark's Fork Basin is geologically simple, consisting of a monocline that dips gently to the southwest (average dips are 3–8°). A few minor faults have been observed along Polecat Bench. The beds on the western side of the southern end of Polecat Bench form a very gentle syncline. As mentioned previously, minor deformation occurs in the Badger Basin (eastern Clark's Fork Basin), hence the relative stratigraphic position of several early Clarkforkian sites there has not yet been established (Figure 3: section 5). The only region of relatively complex structure is along the Beartooth front, particularly west of Pat O'Hara Creek, where Willwood strata, including some of Clarkforkian age, have been tilted more than 30° (e.g. locality SC–143, "Paint Creek locality," Figure 2).

All UM localities in the Clark's Fork Basin are shown in Figure 2 and their positions in the measured sections are indicated in Figure 3. Thickness of covered intervals has been estimated from the horizontal distance and the dips of adjacent beds. An index of the precise locations of all Clarkforkian sites is provided in Table 1, and comments on some of the most important of them are presented below.

All Clarkforkian sites have been placed in one of three faunal zones, here considered to be approximately equivalent to early, middle, and late Clarkforkian (see Chapter III). They are here designated, successively, the *Plesiadapis gingerichi* Zone, the *Plesiadapis cookei* Zone, and the *Phenacodus-Ectocion* Zone. Allocation of localities to faunal zones is based on diagnostic faunal elements and/or stratigraphic position. The prefix SC designates a University of Michigan (UM) locality in the Clark's Fork Basin area.

### Principal Localities in the *Plesiadapis gingerichi* Zone

*SC–83*. Stratigraphically lowest Clarkforkian site on southeastern face of Polecat Bench, located in drab sediments of the Polecat Bench Formation. Fragmentary teeth of *Esthonyx* and *Coryphodon* have been found there, indicating Clarkforkian age.

*SC–179*. Lowest Clarkforkian locality on the west side of Polecat Bench, in drab sediments of the Polecat Bench Formation. Fauna includes rodents and *Plesiadapis gingerichi.*

*Eastern Clark's Fork Basin and Badger Basin*. Eighteen sites are found in exposures in this area (SC–156, 157, 169, 170, 171, 172, 173, 174, 177, 215, 216, 217, 226, 227, 248, 249, 250, 251; see Figures 2 and 3). As noted above, their precise stratigraphic relationships are uncertain, but all appear to lie below sites yielding the *Plesiadapis cookei* Zone fauna. Rodents, *Coryphodon*, *Haplomylus*, and *Esthonyx* have been found at these sites. Some of these localities have not yet yielded age-diagnostic taxa, and they are assessed as early Clarkforkian because of their close proximity to sites of established age. Red-banded sediments occur at most of the sites, indicating that they are in the lower Willwood

Table 1. Index of UM Clarkforkian localities in the Clark's Fork Basin area.

| UM Loc. No. | Location (and section in Figure 3) | Zone |
|---|---|---|
| SC-8 | SW ¼, S 18, T 56 N, R 101 W | *Phenacodus-Ectocion* |
| SC-9 | W ½, S 18, T 56 N, R 101 W | *Phenacodus-Ectocion* |
| SC-10 | E ½, S 13, T 56 N, R 102 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-11 | SW ¼, S 18, T 56 N, R 101 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-19 | NW ¼, S 15, and NE ¼, S 16, T 56 N, R 101 W (Sec. 5) | *Plesiadapis cookei* |
| SC-20 | W ½, S 15, T 56 N, R 101 W (Sec. 5) | *Plesiadapis cookei* |
| SC-21, SC-22 | SW ¼, S 16, T 56 N, R 101 W (Sec. 5) | *Phenacodus-Ectocion* |
| SC-23, SC-24 | SW ¼, S 20, T 56 N, R 101 W (Sec. 5) | *Phenacodus-Ectocion* |
| SC-25 | NE ¼, S 20, T 56 N, R 101 W (Sec. 5) | *Phenacodus-Ectocion* |
| SC-28 | NW ¼, S 36, T 56 N, R 101 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-29 | NE ¼, S 35, and NW ¼, S 36, T 56 N, R 101 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-48 | W ½, S 32, T 56 N, R 100 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-49 | S ½, S 29, T 56 N, R 100 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-50 | SE ¼, S 31, T 56 N, R 100 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-51 | NW ¼, S 34, T 56 N, R 101 W (Sec. 3) | *Phenacodus-Ectocion* |
| SC-52 | E ½, S 17, T 56 N, R 101 W | *Phenacodus-Ectocion* |
| SC-53 | NW ¼, S 16, T 56 N, R 101 W (Sec. 5) | *Ples. cookei* and *Phenacodus-Ectocion* |
| SC-55 | SW ¼, S 31, T 56 N, R 100 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-56 | E ½, S 36, T 56 N, R 101 W, and W ½, S 31, T 56 N, R 100 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-57 | E ½, S 35, T 56 N, R 101 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-58 | W ½, S 27, T 56 N, R 101 W (Sec. 3) | *Ples. cookei* and *Phenacodus-Ectocion* |
| SC-59 | E ½, S 29, T 56 N, R 101 W (Sec. 3) | *Phenacodus-Ectocion* |
| SC-60 | NE ¼, S 33, and SE ¼, S 28, T 56 N, R 101 W (Sec. 3) | *Phenacodus-Ectocion* |
| SC-61 | SE ¼, S 8, T 56 N, R 101 W | *Plesiadapis cookei* |
| SC-62 | SE ¼, S 7, and SW ¼, S 8, T 56 N, R 101 W (Sec. 4) | *Plesiadapis cookei* |
| SC-65 | E ½, S 2, T 55 N, R 100 W (Sec. 2) | *Plesiadapis cookei* |
| SC-66 | SW ¼, S 36, T 56 N, R 100 W (Sec. 2) | *Plesiadapis cookei* |
| SC-70 | NE ¼, S 9, T 55 N, R 100 W (Sec. 2) | *Phenacodus-Ectocion* |
| SC-71 | NW ¼, S 10, T 55 N, R 100 W | *Phenacodus-Ectocion* |
| SC-72, SC-73, SC-75 | SW ¼, S 2, T 55 N, R 100 W (Sec. 2) | *Phenacodus-Ectocion* |
| SC-74 | NW ¼, S 36, T 56 N, R 100 W (Sec. 2) | *Plesiadapis cookei* |
| SC-76 | NW ¼, S 11, T 55 N, R 100 W (Sec. 2) | *Phenacodus-Ectocion* |
| SC-77 | NE ¼, S 10, T 55 N, R 100 W (Sec. 2) | *Phenacodus-Ectocion* |
| SC-78 | NE ¼, S 36, T 56 N, R 100 W (Sec. 2) | *Ples. gingerichi* |
| SC-80 | NW ¼, S 34, T 56 N, R 100 W | *Phenacodus-Ectocion* |
| SC-81 | SW ¼, S 28, T 56 N, R 100 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-82 | NE ¼, S 25, T 56 N, R 100 W (Sec. 2) | *Ples. gingerichi* |
| SC-83 | SE ¼, S 24, T 56 N, R 100 W (Sec. 2) | *Ples. gingerichi* |
| SC-84 | SW ¼, S 36, T 56 N, R 100 W (Sec. 2) | *Plesiadapis cookei* |
| SC-90 | NE ¼, S 11, T 56 N, R 102 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-91 | NE ¼, S 5, T 56 N, R 101 W (Sec. 4) | *Plesiadapis cookei* |
| SC-92 | NW ¼, S 6, T 56 N, R 101 W, and SE ¼, S 32, T 57 N, R 101 W (Sec. 4) | *Plesiadapis cookei* |
| SC-93 | NE ¼, S 1, T 56 N, R 102 W (Sec. 4) | *Plesiadapis cookei* |
| SC-98 | SE ¼, S 23, and SW ¼, S 24, T 56 N, R 101 W | *Plesiadapis cookei* |
| SC-99 | E ½, S 26, T 56 N, R 101 W | *Plesiadapis cookei(?)* |
| SC-100 | SW ¼, S 26, and NW ¼, S 35, T 56 N, R 101 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-101 | W ½, S 1, T 55 N, R 101 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-102 | SW ¼, S 1, and E ½, S 2, T 55 N, R 101 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-103 | SE ¼, S 2, T 55 N, R 101 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-105 | NW ¼, S 1, and NE ¼, S 2, T 55 N, R 101 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-106 | NW ¼, S 1, T 55 N, R 101 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-107 | NW ¼, S 10, T 55 N, R 100 W (Sec. 2) | *Phenacodus-Ectocion* |
| SC-108 | NE ¼, S 20, T 56 N, R 100 W (Sec. 1) | *Plesiadapis cookei* |
| SC-109 | NE ¼, S 21, and NW ¼, S 22, T 56 N, R 100 W (Sec. 1) | *Plesiadapis cookei* |
| SC-110 | SW ¼, S 15, T 56 N, R 100 W (Sec. 1) | *Plesiadapis cookei* |
| SC-115 | E ½, S 15, T 56 N, R 101 W (Sec. 5) | *Plesiadapis cookei* |
| SC-116 | NE ¼, S 15, T 56 N, R 101 W (Sec. 5) | *Plesiadapis cookei* |
| SC-117 | NW ¼, S 15, T 56 N, R 101 W (Sec. 5) | *Plesiadapis cookei* |
| SC-118 | SW ¼, S 11, T 56 N, R 101 W (Sec. 5) | *Plesiadapis cookei* |
| SC-119 | NW ¼, S 9, T 56 N, R 101 W (Sec. 4) | *Plesiadapis cookei* |

*(continued on following page)*

| | | |
|---|---|---|
| SC-120 | S ½, S 5, T 56 N, R 101 W (Sec. 4) | *Plesiadapis cookei* |
| SC-127 | E ½, S 7, T 56 N, R 101 W (Sec. 4) | *Plesiadapis cookei* |
| SC-134 | NE ¼, S 32, T 57 N, R 101 W (Sec. 4) | *Ples. cookei(?)* |
| SC-135 | NE ¼, S 31, and SE ¼, S 30, T 57 N, R 101 W (Sec. 4) | *Ples. cookei(?)* |
| SC-136 | NE ¼, S 1, T 56 N, R 102 W, and SW ¼, S 32, T 57 N, R 101 W (Sec. 4) | *Plesiadapis cookei* |
| SC-137 | NE ¼, S 1, T 56 N, R 101 W (Sec. 4) | *Plesiadapis cookei* |
| SC-138 | E ½, S 10, T 56 N, R 102 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-140 | NW ¼, S 13, T 56 N, R 102 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-143 | NW ¼, S 11, T 55 N, R 103 W (Sec. 4) | *Plesiadapis cookei* |
| SC-149 | center, S 16, T 56 N, R 101 W (Sec. 5) | *Phenacodus-Ectocion* |
| SC-150 | E ½, S 16, T 56 N, R 101 W (Sec. 5) | *Phenacodus-Ectocion* |
| SC-152 | NW ¼, S 20, T 56 N, R 101 W (Sec. 5) | *Phenacodus-Ectocion* |
| SC-153 | NE ¼, S 19, and NW ¼, S 20, T 56 N, R 101 W (Sec. 5) | *Phenacodus-Ectocion* |
| SC-154, SC-155 | N ½, S 19, T 56 N, R 101 W (Sec. 5) | *Phenacodus-Ectocion* |
| SC-156 | NE ¼, S 12, T 56 N, R 101 W, and NW ¼, S 7, T 56 N, R 100 W (Sec. 5) | *Ples. gingerichi* |
| SC-157 | NW ¼, S 12, T 56 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-158 | NE ¼, S 10, T 56 N, R 102 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-159 | SE ¼, S 3, and NE ¼, S 10, T 56 N, R 102 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-162 | SW ¼, S 2, T 56 N, R 102 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-163, SC-164 | S ½, S 7, T 56 N, R 101 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-166 | SE ¼, S 4, T 57 N, R 102 W | *Plesiadapis cookei* |
| SC-167 | SW ¼, S 3, T 57 N, R 102 W | *Ples. cookei(?)* |
| SC-168 | NW ¼, S 11, T 55 N, R 103 W | *Ples. cookei(?)* |
| SC-169 | NE ¼, S 1, T 56 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-170, SC-171 | N ½, S 2, T 56 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-172 | SW ¼, S 26, and SE ¼, S 27, T 57 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-173 | W ½, S 26, and E ½, S 27, T 57 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-174 | ?S 26, T 57 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-175 | SE ¼, S 29, T 56 N, R 100 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-176 | NW ¼, S 28, T 56 N, R 100 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-177 | SE ¼, S 1, T 56 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-179 | S ½, S 10, T 56 N, R 100 W (Sec. 1) | *Ples. gingerichi* |
| SC-183 | S ½, S 35, T 56 N, R 101 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-184 | S ½, S 35, T 56 N, R 101 W, and NW ¼, S 2, T 55 N, R 101 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-188 | SE ¼, S 1, T 56 N, R 102 W, and SW ¼, S 6, T 56 N, R 101 W (Sec. 4) | *Plesiadapis cookei* |
| SC-189, SC-190 | SW ¼, S 6, T 56 N, R 101 W (Sec. 4) | *Plesiadapis cookei* |
| SC-194 | S ½, S 15, T 56 N, R 100 W (Sec. 1) | *Plesiadapis cookei* |
| SC-195 | S ½, S 15, T 56 N, R 100 W (Sec. 1) [=SC-110] | *Plesiadapis cookei* |
| SC-196 | S 17 and S 18, T 53 N, R 100 W (McCulloch Peaks, not on map) | uncertain |
| SC-197 | NE ¼, S 1, T 56 N, R 102 W (Sec. 4) (?=SC-93) | *Plesiadapis cookei* |
| SC-200 | W ½, S 7, T 56 N, R 101 W (Sec. 4) | *Plesiadapis cookei* |
| SC-201 | N ½, S 12, T 56 N, R 102 W (Sec. 4) | *Plesiadapis cookei* |
| SC-202 | SE ¼, S 12, T 56 N, R 102 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-203, SC-204 | E ½, S 32, T 56 N, R 100 W (Sec. 1) | *Phenacodus-Ectocion* |
| SC-205 | SE ¼, S 21, T 56 N, R 100 W (Sec. 1) | *Ples. cookei(?)* |
| SC-208 | NW ¼, S 30, T 57 N, R 101 W | *Ples. cookei(?)* |
| SC-209 | NW ¼, S 31, T 57 N, R 101 W | *Ples. cookei(?)* |
| SC-214 | SE ¼, S 2, T 56 N, R 102 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-215 | SW ¼, S 22, T 57 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-216 | NE ¼, S 22, T 57 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-217 | NW ¼, S 26, T 57 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-220 | E ½, S 25, T 56 N, R 101 W | *Plesiadapis cookei* |
| SC-222 | SE ¼, S 36, T 56 N, R 100 W (Sec. 2) | *Plesiadapis cookei* |
| SC-226 | SW ¼, S 15, T 57 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-227 | NW ¼, S 23, T 57 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-230 | NE ¼, S 13, T 56 N, R 102 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-231 | SW ¼, S 18, T 56 N, R 101 W (Sec. 4) (=SC-11) | *Phenacodus-Ectocion* |
| SC-233 | NE ¼, S 13, T 56 N, R 102 W, and NW ¼, S 18, T 56 N, R 101 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-234, SC-235 | SW ¼, S 7, T 56 N, R 101 W (Sec. 4) | *Phenacodus-Ectocion* |
| SC-238 | SE ¼, S 12, T 56 N, R 102 W (Sec. 4) | *Plesiadapis cookei* |
| SC-248 | E ½, S 31, T 57 N, R 100 W (Sec. 5) | *Ples. gingerichi* |
| SC-250 | NE ¼, S 3, T 56 N, R 101 W (Sec. 5) | *Ples. gingerichi* |
| SC-251 | SE ¼, S 36, T 57 N, R 101 W (Sec. 5) | *Ples. gingerichi* |

Formation. Some sites are in drab mudstones and may be in the top of the Polecat Bench Formation (SC–226, 248, 249). SC–248 and SC–249 are northeast of the others and are possibly latest Tiffanian in age.

### Principal Localities in the *Plesiadapis cookei* Zone

*SC–19*. Vertebrates have been found here weathering out of gray beds; some horizons have yielded concentrations of micromammal teeth and bone fragments. A prominent red bed near the top of the interval of SC–19 can be traced to SC–20 and is probably the same as the bright red-banded mudstone in the middle of SC–62 and near the top of SC–127. The interval represented by these localities is one of the most richly fossiliferous in the Clarkforkian.

*SC–53*. Interval of this locality is relatively large, probably 30 m or more. The site was initially collected during the first field season, before faunal zones were apparent and, unfortunately, exact horizons of specimens of *Plesiadapis cookei* from SC–53 are unknown. The site appears to include the uppermost *Plesiadapis cookei* Zone but is mostly in the *Phenacodus-Ectocion* Zone. To the south of SC–53, *P. cookei* was found at the bottom of the interval at SC–58, and this site, too, appears to span parts of both zones. Because it is, in most cases, impossible to segregate those specimens pertaining to the lower *Phenacodus-Ectocion* Zone at these sites, they are considered to be in the *P. cookei* Zone in occurrences listed in Chapter IV.

*SC–62* (Plate 1, figure 1). Relatively rich locality apparently spanning the boundary between the *Plesiadapis cookei* Zone and the *Phenacodus-Ectocion* Zone but, for simplicity, herein allocated to the former. This site was worked by Princeton in the early 1960s. *P. cookei* appears to be restricted to the lower beds at the site, below a prominent red band in the middle of the locality, about 10 m above its base. This band fades to orange-red at SC–127 to the north, and becomes paler still (but still conspicuous) in a north-south trending ridge in the center of N½, sec. 7, T.56 N., R.101 W. At the top of the bluff at SC–62 is a red-banded layer (in the *Phenacodus-Ectocion* Zone) that can be traced westward through SC–163 and SC–234.

*SC–74*. Stratigraphically lowest site in this zone. Several red-banded beds occur at the top and just above SC–74, reflecting the beginning of Willwood deposition. This was apparently one of Granger's localities: "bluff NE of Ralston, on Fisher's contact line" (1912 field catalogue, reference to AMNH 16065, *Esthonyx*, referred to *E. xenicus* by Gingerich and Gunnell, 1979).

*SC–119*. "*Franimys* Hill," type locality of the rodent *Franimys amherstensis* Wood (1962). Exact stratigraphic level unknown, due to covered section; but relatively low in *P. cookei* Zone, roughly on strike and probably near level of SC–136.

*SC–136*. Well developed, predominantly drab badlands, west and south of prominent bluff in NE¼, sec. 1, T.56 N., R.102 W. One of the richest single Clarkforkian sites, yielding more than 100 specimens in the UM collection. SC–136 was previously worked by Princeton University.

*SC–143*. "Paint Creek locality," discovered and collected extensively by Princeton parties under G. L. Jepsen. The site covers a relatively small exposure and narrow stratigraphic interval in brilliantly colored mudstones, and was once believed to be of early Wasatchian age (Jepsen, 1930a). This is one of the richest Clarkforkian sites; only one other site in the study area, SC–188, has yielded more micromammals. Complex structure and isolated position of SC–143 prohibit determination of its precise stratigraphic level, but the fauna clearly indicates that it is in this zone. SC–168, just northeast of SC–143, is stratigraphically slightly higher and is here placed tentatively in the *P. cookei* Zone.

*SC–166*. Located at the base of Sugarloaf Butte, this appears to correspond to Granger's (1914) Clarkforkian site "between the mouths of Line and Little Rocky Creeks" (Figure 1, locality A).

*SC–188*. "Holly's Microsite," discovered in 1977 by B. Holly Smith. Gray mudstone at the base of this locality contains a pocket that, through quarrying and screen-washing, has yielded the richest Clarkforkian collection from a single site in the Clark's Fork Basin (Table 52). About 30 sacks (approximately one ton) of matrix have been washed and have yielded over 200 mammalian specimens. The quarry is dominated by diminutive forms otherwise rare in the Clarkforkian of the Clark's Fork Basin, but some larger specimens occur as well, and several have been excavated from drab mudstones slightly above the level of the quarry. A distinct carbonaceous shale overlies a yellow-brown mudstone at the top of the interval (10 m above the quarry) and both can be traced westward to SC–93.

*SC–195*. "Krause Quarry." The interval of this site is about 30 m thick and is dominantly drab mudstones; a red-banded bed exists at the top of the interval. The fortuitous discovery by David Krause of a partial skull of *Dissacus*, while measuring sections, prompted excavation that led to opening a quarry near the top of the interval. Krause Quarry, in gray mudstones, has yielded numerous jaws and partial skulls, mostly of relatively large mammals (e.g. *Dissacus*, *Oxyaena*, *Ectocion*). Only a small amount of this material has been prepared so far. SC–195 was worked in 1977–1978 and was later determined to be equivalent to SC–110; however, all specimens from Krause Quarry are listed as from SC–195.

*SC–196.* "Rough Gulch." This is Sinclair and Granger's (1912) and Granger's (1914) Clarkforkian locality on the southwest slopes of McCulloch Peak, secs. 17 and 18, T.53 N., R.100 W. (not shown in Figure 2; see Van Houten, 1944: plate 2, figure 3).

*SC–197.* This locality was not mapped precisely, but it is geographically and stratigraphically very close to SC–93 and in fact may be the same.

*SC–209.* "Phil's Hill," discovered in 1967 by Philip D. Gingerich. Initially worked by Princeton parties under G. L. Jepsen, this site has yielded the holotype of *Paramys annectens*, sp. nov.

### Principal Localities in the *Phenacodus-Ectocion* Zone

*SC–48, 50, 55, 56.* These are Granger's (1914: 204) localities "on both sides of the wagon road where it drops down to Big Sand Coulee from the Bighorn basin divide" (Figure 1, locality D).

*SC–76, 77.* These localities and those just to the northeast correspond closely to Sinclair and Granger's (1912: 59) Clarkforkian horizon "in the bluffs opposite Ralston station on the Burlington railroad where the beds seem to dip below the *Systemodon* horizon on the south side of the [Shoshone] river" (Figure 1, locality E).

*SC–90.* "Granger Mountain." Drab exposures in the Willwood Formation to the southeast of a prominence we have named Granger Mountain. This site, and/or localities SC–159 and SC–162 just to the west, must be Granger's locality "3 miles east of the mouth of Pat O'Hara Creek" (1912 field catalogue), which he regarded as Clarkforkian in age. The interval is relatively productive, having yielded more than 100 specimens in the UM collection (Figure 1, locality B).

*SC–101, 102, 103, 105, 106.* Mainly at the base of exposures in the head of Big Sand Coulee. These sites are probably the same as Granger's locality in the head of Big Sand Coulee (1911 and 1912 field catalogues; Figure 1, locality C). To the west and 100 m higher stratigraphically and up a steep scarp, are UM localities SC–182 and SC–104, earliest Wasatchian. They may be Granger's "Sand Coulee beds" or Stein's "upper beds, head of Big Sand Coulee" (1913 field catalogue).

*SC–107.* In gray mudstones only 10 m below early Wasatchian SC–67. The boundary sheet sandstone is not present at this locality. This may have been one of Granger's localities in the bluff north of Ralston.

*SC–234.* "Rainbow Valley." Well exposed, brightly banded outcrops that yielded a rich collection of vertebrates. Red bands here are easily traceable for up to a mile to both the east and the west.

# III
# THE CLARKFORKIAN LAND-MAMMAL AGE

## HISTORICAL SKETCH

GRANGER (1914) PROPOSED the term "Clark Fork beds" for a sequence of strata "perhaps representing the top of the Paleocene series." He observed (Granger, 1914: 204; see also Sinclair and Granger, 1912) that "the fossils obtained demonstrated clearly that this horizon is a very distinct one, older than the Gray Bull [early Wasatchian]," hence his term was biostratigraphic. Matthew (1915a,b,c), Granger (1915), and Simpson (1929c, 1937c) described most of the mammals collected by Granger and his assistants in 1911–1913 from the "Clark Fork horizon." Jepsen (1930b) described additional Clarkforkian fossils collected under his direction for Princeton University. He realized that the Clark Fork beds were recognizable chiefly by their faunal content and not on lithological criteria alone (Jepsen, 1930b, 1940). As noted earlier, Jepsen believed that the entire Clarkforkian was included in the upper part of the Polecat Bench Formation, although he observed that "red strata occur well down in the Clark Fork beds" (Jepsen, 1940: 237). Hence when Van Houten (1944) named the Willwood Formation for variegated shales and sands overlying the Polecat Bench Formation, it became clear that the Clark Fork fauna occurred in lowest Willwood sediments as well as in uppermost Polecat Bench strata. Prior to this, however, the Wood committee (1941: 9) had defined the Clarkforkian age as

> a new provincial *time* term [my emphasis], based on the Clark Fork member (and faunal zone) of the Polecat Bench formation, type locality, scarp forming divide between Bighorn and Clark Fork basins and exposures near its base, Park County, Wyoming.

The implied equivalence of the faunal age (a biochron) with a lithologic unit (that was later demonstrated to be nonequivalent) led to considerable confusion in use of the term Clarkforkian. Many authors assumed that the Clarkforkian had to fit within epoch boundaries and that it was entirely late Paleocene in age. This culminated in R. Wood's (1967) review of the Clark Fork fauna, in which he concluded that the evidence then at hand "scarcely warrants recognition of the Clark Fork as a provincial age, faunal zone, or member of the Polecat Bench Formation" (Wood, 1967: 28).

The perennial misconception that the limits of the Clarkforkian do or should conform to formational or epoch boundaries is largely responsible for skepticism about its validity as a land-mammal age, and this is particularly evident in R. Wood's analysis. The relationships of the various boundaries were discussed in Chapter II. To summarize, biostratigraphic studies in the Clark's Fork Basin demonstrate that the Polecat Bench-Willwood formational contact as well as the Paleocene-Eocene boundary both occur *within* strata of Clarkforkian age in this area.

Based on the studies of Matthew, Granger, Simpson, and Jepsen, Wood et al. (1941: 9) provided the following faunal definition and characterization of the Clarkforkian Provincial Age:

> Index fossil: *Plesiadapis cookei*
> First appearance: cf. *Coryphodon*, *Ectocion*, *Esthonyx*, *Oxyaena*
> Last appearance: *Carpolestes*, *Plesiadapis*
> Characteristic fossils: *Didymictis*, *Ectypodus*, *Phenacodus*, *Probathyopsis*, *Thryptacodon*

Because Granger (1914) had stressed the absence of perissodactyls, artiodactyls, and rodents in the Clark Fork fauna (rodents are now known to be present in the Clarkforkian), R. Wood (1967: 9, 13) assumed that

> the Clark Fork beds were defined on the basis of negative evidence, i.e., what had not been found in them, rather than on fossils actually contained in them which could be characterized as having a *distinctive Paleocene aspect* [my emphasis]. Since the type fauna was principally found in strata whose position in the section was by no means certain, and since the fauna from the only site regarded by Granger as being definitely of Paleocene age had no obvious Paleocene affinities, it is not at all certain whether or not a Clark Fork fauna can in fact be distinguished.

R. Wood then set out to determine if evidence of a distinct Clarkforkian fauna existed. He reviewed the American Museum and Princeton Clark Fork collections from which H. Wood et al. (1941) had compiled their faunal data, and he found only 107 specimens of putative Clarkforkian age, most of them in Granger's American Museum collection. Unfortunately, he excluded from consideration a large number of Clarkforkian specimens in the Princeton Museum, collected after 1930, because they are not from the original collection used to characterize the Clarkforkian (R. Wood, 1967: 19). Wood examined the three main localities of Granger's collection: the head of Big Sand Coulee (sections 1 and 2, T.55 N., R.101 W.; Figure 1, locality C), 3 miles east of the mouth of Pat O'Hara Creek (about sections 10 and 11, T.56 N., R.102 W.; Figure 1, locality B), and the bluff north of Ralston (Figure 1, locality E). The first two, which yielded the majority of the specimens, Wood considered to be probably of "Graybullian" (early Wasatchian) age, a conclusion drawn from geologic maps and a prevailing view at the time that these sites are in Eocene beds. Clarkforkian age, then thought to be late Paleocene, was precluded since these areas were mapped as Willwood Formation, considered to be Eocene. Wood (1967: 17) regarded specimens from the third site, the bluff north of Ralston (i.e., southeast side of Polecat Bench), to be "too vaguely labelled to be of any value in this study." Of the specimens not from these three sites, 13 have no more specific data than "Clark Fork beds" or "Clark Fork formation," hence Wood excluded them, too, for lack of sufficient locality or stratigraphic information. Having eliminated all these specimens from a possible Clark Fork fauna, Wood was left with only five American Museum specimens, three of which he dismissed from further consideration on similar grounds.

Turning to the Princeton collection, Wood believed he could eliminate all but two of the 18 supposed Clarkforkian specimens "on the basis of insufficiently precise locality data," or because of controversy "concerning the location of the contact between Paleocene and Eocene sediments" in the area where the specimens were found. By this procedure Wood (1967: 21) concluded that nearly all specimens attributed to the Clarkforkian are "of no value in helping to define a characteristic Clark Fork fauna." Left with only four specimens he could not eliminate from probable Clarkforkian age, he concluded that the evidence was insufficient to support recognition of the Clarkforkian.

Renewed studies of the Clarkforkian fauna by Sloan, Parris, Gingerich, and Rose, during the last decade, have demonstrated that there does exist a distinctive fauna of this age (Sloan, 1969; Gingerich, 1975, 1976b; Rose, 1975a, 1977; Parris, unpublished data). The University of Michigan project initiated in 1975 under Gingerich's direction has produced thousands of additional specimens from the type area of this land-mammal age, and it has provided stratigraphic documentation of the limits of the Clarkforkian in this region. Preliminary reports on this work were presented by Gingerich and Rose (1977) and Rose (1978a).

Mammalian faunas believed to be Clarkforkian in age have been reported from outside the Bighorn Basin by Gazin (1942, 1956b), Morris (1966, 1968), McKenna (1972a), and Schiebout (1974). These and other Clarkforkian assemblages from outside the study area will be considered in Chapter V.

## NORTH AMERICAN LAND-MAMMAL AGES

Cenozoic mammalian chronology or chronostratigraphy in North America has for several decades been based on the scheme of North American Provincial Ages introduced by H. Wood et al. (1941). The development of concepts leading to this system of Ages was summarized by Tedford (1970). Savage (1962) reviewed the geochronology of mammals in the Americas, pointing out that the Wood committee's Provincial Ages, while approximately of age magnitude, are "of purely temporal significance" (Wood et al., 1941: 1) and are not, therefore, ages in the geological sense. Formal ages, as defined by the American Commission on Stratigraphic Nomenclature (1961), are geochronologic units based on stages, which are chronostratigraphic units. Savage proposed that the temporal units of mammalian chronology therefore be designated North American Land-Mammal "Ages," the term I shall adopt here but with omission of the quotation marks. Land-mammal ages have been based on characteristic suites of genera, although none of the genera must be restricted to the age in question. First and last appearances, as well as index taxa, are important. As Savage (1975: 22) has noted, "each age is further characterized by particular species within genera that may be long-ranging. Thus, species phylogenies and stage-of-evolution continue to play a strong role in mammal-age determinations" (see also Evernden et al., 1964). The validity and utility of chronology and correlations based on land-mammal ages is predicated on the tenets that many mammalian taxa are widespread and of relatively short duration (geochronologically) and that they disperse rapidly (Savage, 1977).

Most land-mammal ages are defined, in practice, by the appearance of new taxa (immigrants). Repenning (1967: 288) has aptly addressed this subject:

> "Mammalian ages" of continental scope tend to begin with an episode of intercontinental faunal dispersal. Initially conceived by vertebrate paleontologists as periods in the evolutionary history of the continental mammalian fauna, and bounded by hiatuses in the fossil record, mammalian ages become subject to redefinition as their limiting inter-age hiatuses are reduced or eliminated and as additional discoveries refine the record of evolutionary history into a more gradational series. Then age-delimiting concepts are focused on immigrants, and age boundaries are adjusted to conform to times of immigration—often without realization that the initial standards have been changed.

There is evidence "that intercontinental dispersal of mammals actually has been intermittent," and this "is supported by the contemporaneous arrival of several exotics from the same source area" (Repenning, 1967: 289). As Repenning points out, however, minor exchanges and continuous exchange are to some degree also likely. The importance of these remarks here is that the substantial new collections described herein permit redefinition of the Clarkforkian, but its basic faunal concept has not been changed. The beginning of the Clarkforkian is defined, in the next section, by the first appearance of several forms, that is, a wave of apparent immigrants that seem to appear simultaneously in the fossil record. This is true also of the beginning of the Wasatchian.

Woodburne (1977) has suggested that land-mammal age boundaries be defined by the first appearance of a single taxon, and I have followed his proposal by selecting one of the immigrant taxa as the "standard-bearer" of the Clarkforkian. The choice, however, is essentially an arbitrary one in our present state of knowledge. The danger in setting limits of land-mammal ages by the appearance of one taxon becomes apparent if later discoveries extend the range of the "standard-bearer" but do not extend ranges of other characterizing taxa. One or two problematical specimens of the defining taxon would create a similar problem. In such cases, the concept of the age would probably still be obvious and unaltered, although a different defining taxon would be required. In practice, therefore, it may be preferable in some instances to recognize the limits of an age by the influx of more than one taxon.

Several recent papers have dealt with problems that have arisen as a result of misuse of the Wood committee's ages as geochronologic or chronostratigraphic units, rather than as the biochrons that they are and were intended to be (e.g. Savage, 1962, 1975; Tedford, 1970; Emry, 1973; Wilson, 1975; Woodburne, 1977). The most important emphasis by most authors has been placed on careful stratigraphic documentation of fossils in an effort to define land-mammal ages and their subdivisions more precisely. These data, when properly set forth, should enable the establishment of true geochronologic and chronostratigraphic units based on mammalian fossils. Guidelines for the proposal of formal stages (chronostratigraphic units), which would serve as the basis for formal ages (geochronologic units), were detailed by Savage (1962), Evernden et al. (1964), and Tedford (1970). Savage (1955) exemplified this practice in his definition of the Pliocene Cerrotejonian and Montediablan Mammal Stages of California. The same guidelines have been followed, as far as possible at present, in defining the Clarkforkian later in this chapter.

## PROBLEMATICAL SPECIMENS

It should always be borne in mind that occasional contamination or human error may be responsible for anomalous records. A single, minute tooth caught in a washing screen may be undetected and might reappear in a collection to which it does not belong. Inexperienced collectors, particularly in an unrecognized boundary area, could unknowingly mix fossils from two zones. Natural contamination might occur on slopes in a boundary area. Delay in cataloguing in the laboratory could lead to inadvertent mixing of specimens from different localities, and simple human error may result in labelling mistakes. In most cases, such problematical specimens can be readily identified by thorough study. An example of labelling error of several Clarkforkian specimens was cited by Gingerich (1977).

My objective here is not to promote skepticism of locality and stratigraphic records, for our study of earlier collections by the American Museum and Princeton has shown that this is almost always unwarranted. Anomalous records, however, particularly of taxa that bear on the definition or characterization of a land-mammal age or faunal zone, should be scrutinized carefully to assess their validity. For this reason, caution must be exercised when basing chronostratigraphic or biochronologic boundaries on the first appearance of a single taxon, as proposed by Woodburne (1977), particularly if the taxon in question is known from only one or two specimens at the level of its first appearance.

Several problematical specimens are pertinent to the characterization of the Clarkforkian. Jepsen and Wood-

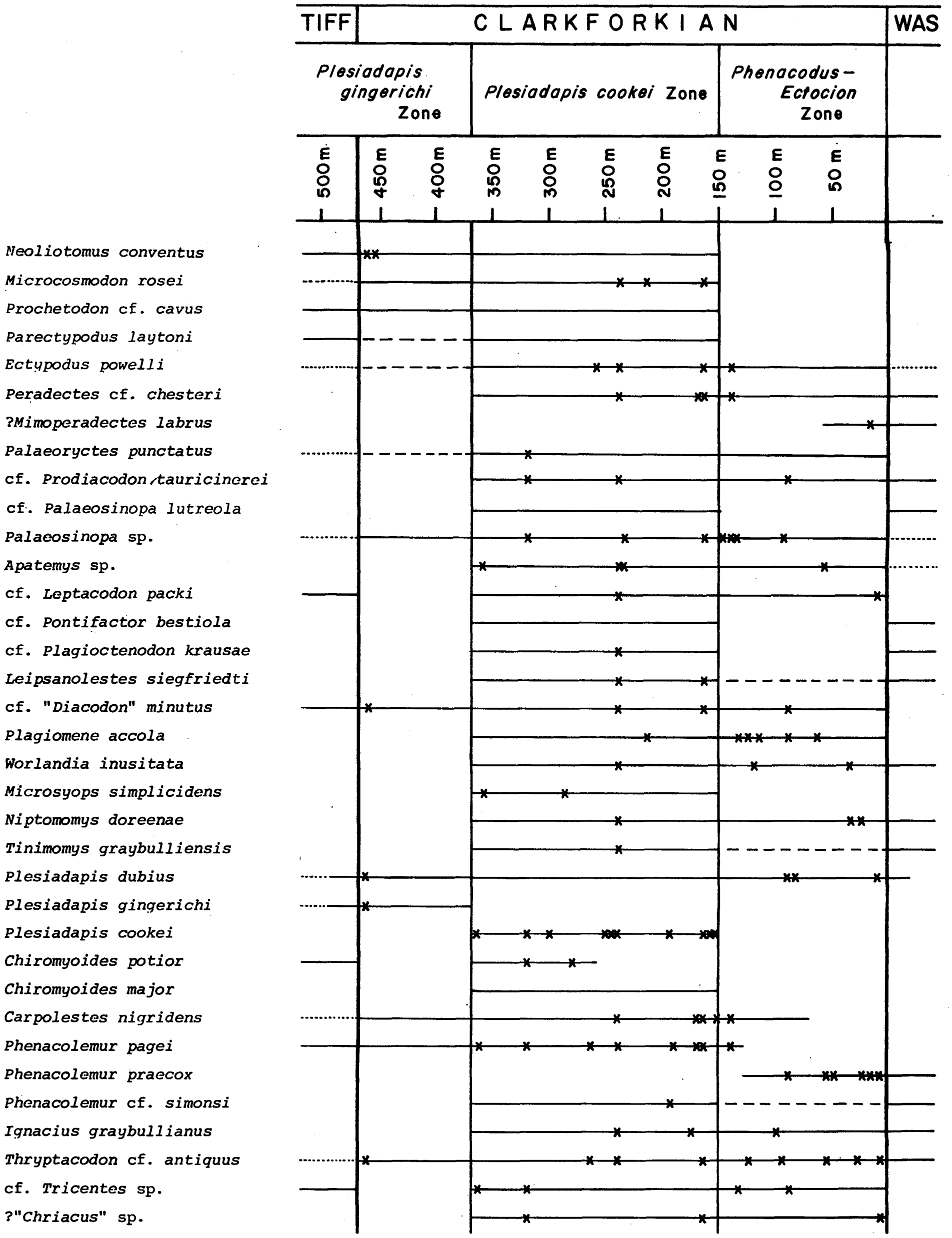
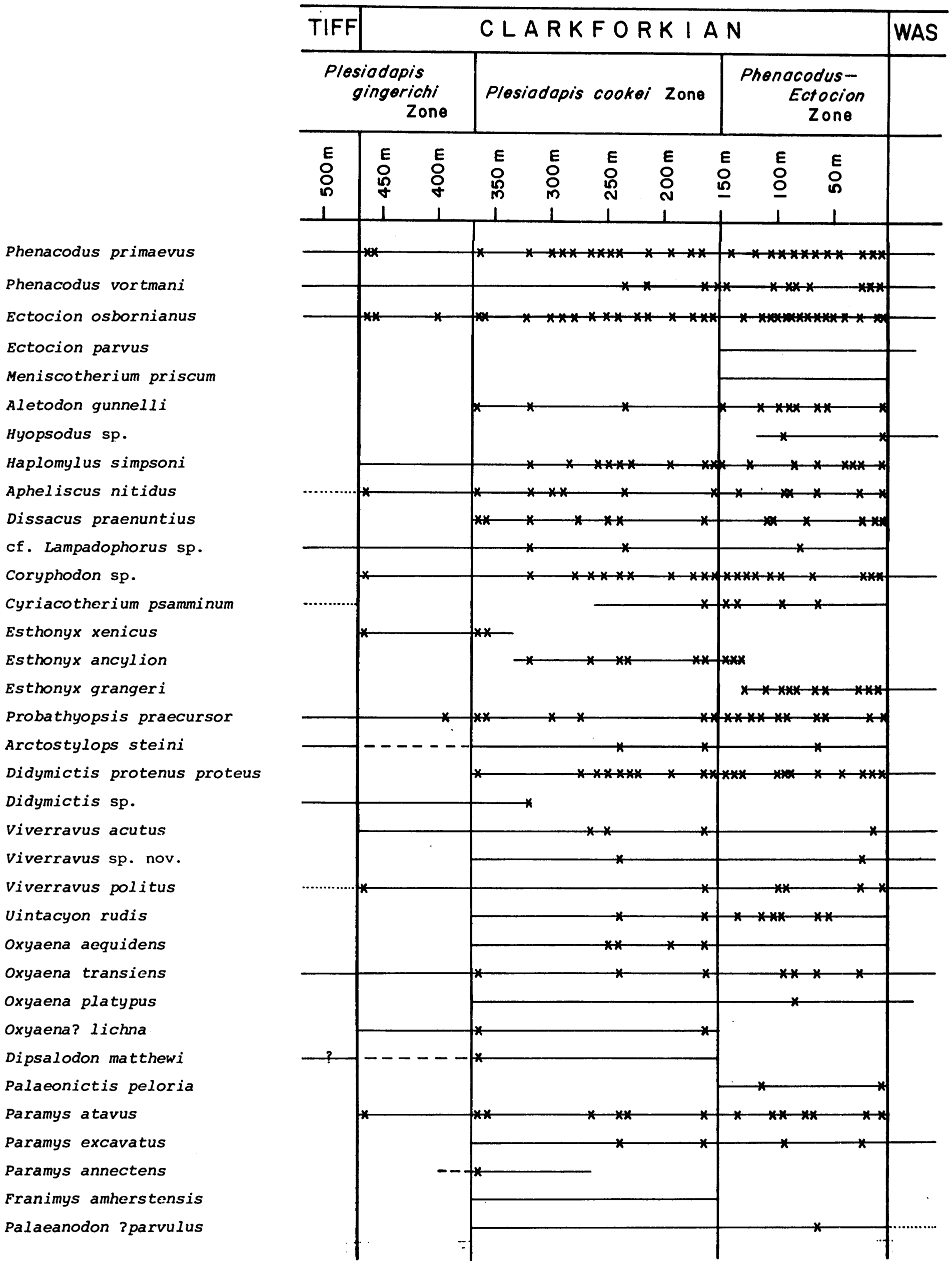


Figure 4. Ranges of Clarkforkian mammals in the Clark's Fork Basin. The occurrence of species in the Clarkforkian fauna is indicated by a solid line in each zone from which the taxon is recorded. Presence in late Tiffanian (Princeton Quarry level and later) and early Wasatchian of the Bighorn Basin is also indicated. Precise stratigraphic records in the Clarkforkian of the Clark's Fork Basin are indicated by an X. In some cases, although a species is present in a zone, precise stratigraphic data are not yet available, hence no Xs are entered. Broad dashed lines in a zone indicate the inferred presence of the species,



although no specimens have yet been found to document this. Dotted lines in late Tiffanian or early Wasatchian indicate the presence of a closely allied species believed to be directly ancestral to, or directly descended from, the taxon known in the Clarkforkian; they serve to distinguish continuing lineages from immigrants (or lines that became extinct) and from taxa whose origins are unclear.

burne (1969) described a dentary of *Hyracotherium* from late Tiffanian beds near Princeton Quarry. Intensive collecting efforts in this area by Jepsen failed to turn up any other specimens of *Hyracotherium*. Similarly, the extensive University of Michigan project in the Clark's Fork Basin (including the Princeton Quarry area) has not resulted in discovery of even a single pre-Wasatchian specimen of *Hyracotherium*, although it is abundant even in earliest Wasatchian levels. As Jepsen and Woodburne remarked, the jaw in question was not recognized as *Hyracotherium* until some time after the summer's collections were brought back to the laboratory, and their discussion implies some doubt as to the validity of the locality data. The specimen is, in fact, just as similar in preservation to Wasatchian specimens as to Tiffanian ones. While such a record can almost never be absolutely nullified, the substantial collections now known from the Clark's Fork Basin suggest very strongly that the specimen is of Wasatchian age and that it somehow became confused with Tiffanian specimens. Thus the first appearance of *Hyracotherium* in the northern Western Interior was almost certainly at the beginning of the Wasatchian.

The Princeton collection also includes two specimens of typical Wasatchian taxa in a small sample labelled "7/13/66, T.56 N., R.101 W., SW¼ S. 8" (approximately our locality SC–62, *Plesiadapis cookei* Zone). The two jaws, both uncatalogued, represent *Pelycodus* and *Homogalax*, taxa unknown before the Wasatchian anywhere in North America. All other specimens in this small collection are clearly Clarkforkian, and some are encrusted with hematite, a common mode of preservation at SC–62. Other open trays of uncatalogued specimens found in the same drawer (during my survey of the Princeton collection in September 1977) included samples from Wasatchian sites. Hence there seems little question that the jaws of *Pelycodus* and *Homogalax* are from these Wasatchian samples and that they were inadvertently put in the wrong tray.

There is a slight possibility that the two isolated teeth of *Hyopsodus* (a typical Wasatchian taxon) from the Clarkforkian (the only record of the genus of this age, see Chapter IV) represent Wasatchian contaminants. Both are from UM localities not far from Wasatchian exposures near the Clarkforkian-Wasatchian boundary, and it is conceivable that they washed down from these younger beds. This possibility is diminished, however, by the fact that there are two separate records. It appears, then, that *Hyopsodus* was present in the late Clarkforkian, although it was clearly very rare before the Wasatchian.

## DEFINITION AND CHARACTERIZATION OF THE CLARKFORKIAN

R. Wood's (1967) criticisms that the original Clarkforkian collections were small and were accompanied by relatively imprecise locality and stratigraphic data were valid. These problems complicated the task of definition and characterization of the Clarkforkian, but they did not obviate it. Indeed, the description of the Clarkforkian provided by H. Wood et al. (1941), based on the studies of Matthew, Granger, Simpson, and Jepsen, was essentially correct and is still applicable, with minor modifications. Granger (1914, and Sinclair and Granger, 1912) had stratigraphic as well as faunal evidence, even if less precise than would have been desirable, to support recognition of a Clark Fork faunal zone. As I have previously mentioned, the geology of the Clark's Fork Basin is relatively simple. Granger evidently recognized this, and he astutely assigned specimens to faunal zones based on his considerable field experience there. His assessments were borne out by Jepsen's work in the area, and in virtually all cases we can now confirm Granger's age assignments of American Museum specimens. In addition to a characterizing fauna of the Clarkforkian, it is also apparent that the absence of certain taxa is important in recognition of Clarkforkian faunas.

Basic to the recognition that "the fauna of this stage [age] exists and is distinct" (Sloan, 1969: 447) is the necessity of its clear definition and characterization. The new biostratigraphic and paleontological evidence presented in this study now provide the foundation for a precise, revised concept of the Clarkforkian.

The Clarkforkian is the North American Land-Mammal Age between the late Paleocene Tiffanian and the early Eocene Wasatchian Ages. As would be expected, its mammalian fauna is intermediate in many respects between those of the Paleocene and the Eocene. Forms that originated in the Paleocene predominate, but others typical of the Eocene first appear and become common in the Clarkforkian, thus setting this age apart from the Paleocene Puercan, Torrejonian, and Tiffanian Ages. Certain other taxa typical of the Wasatchian are conspicuously absent in the Clarkforkian, however, setting it apart from the Eocene ages. The ranges and occurrences of Clarkforkian mammals in the Clark's Fork Basin are summarized in Figures 4 and 5.

Following the proposals of Murphy (1977) and Woodburne (1977) that land-mammal age boundaries should be "based on the first appearance of a single taxon," the beginning of the Clarkforkian may be defined by the initial occurrence of the rodent *Paramys*,

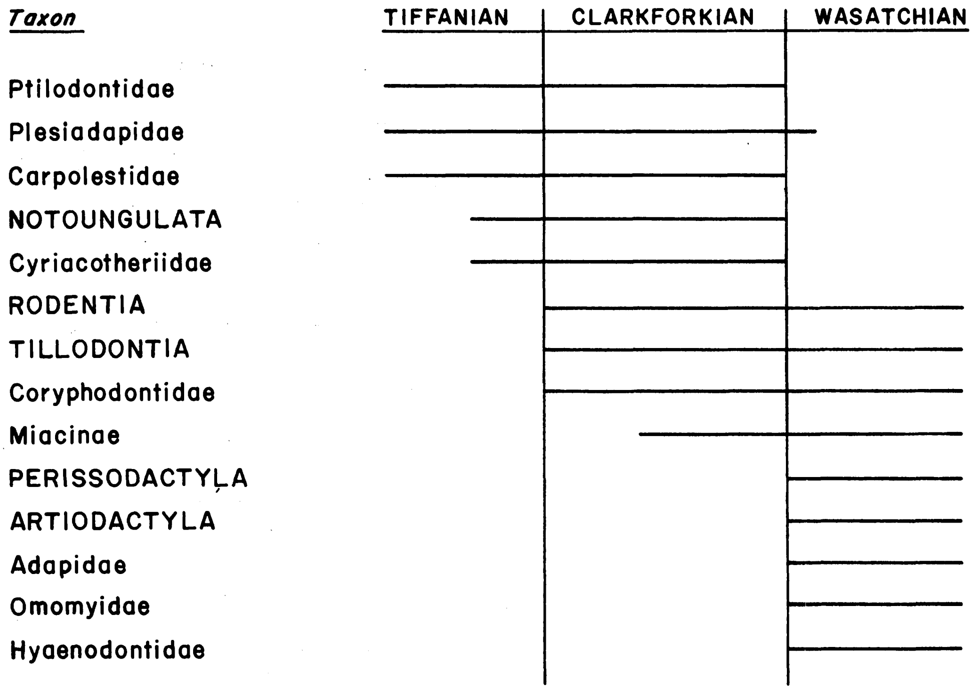


Figure 5. Ranges of some important higher taxa that are useful for defining the limits of the Clarkforkian. Families and subfamilies are in lower case; orders are in upper case.

which is at the same time the first appearance of the Rodentia. (The Wood committee, 1941, listed the first appearance of the Rodentia in the Tiffanian. This was based on the presence of rodents at Bear Creek, Montana, then believed to be of Tiffanian age, but now known to be Clarkforkian; see Chapter V.) This lower limit is recognized in practice by the mutual first appearance (apparently simultaneous with that of rodents) of the Tillodontia (*Esthonyx*), the pantodont *Coryphodon*, and the hyopsodontid *Haplomylus*. Paleontological evidence known at present suggests that all of them are immigrants. Although one or more of these taxa are present at most of the early Clarkforkian sites, no one of them is yet known at all earliest Clarkforkian localities. The upper limit of the Clarkforkian (=lower limit of the Wasatchian ) is recognized by the apparently simultaneous first appearance in the northern Western Interior of Perissodactyla (*Hyracotherium*), Artiodactyla (*Diacodexis*), Adapidae (*Pelycodus*), and Hyaenodontidae. (As noted in Chapter V, *Hyracotherium* has been found at two possible Clarkforkian sites in the southern part of the continent.) If one wishes to specify a single taxon to define the lower limit of the Wasatchian the first appearance of either *Diacodexis* or *Pelycodus* would be appropriate, as both are common and relatively widespread, and no specimens of possible pre-Wasatchian age are known. Present methods of resolution do not favor a choice between them and, in practice, presence of any of the four Wasatchian taxa listed above indicates that the upper limit of the Clarkforkian has been crossed. The first appearance of *Hyopsodus* is also, in general, a good indicator of Wasatchian age, despite discovery of two specimens in Clarkforkian beds (see Chapter IV).

In addition to the taxa that first appear at the inception of the Clarkforkian, there are several forms whose initial occurrence in the fossil record is during the Clarkforkian. The most important of these are *Plagiomene*, *Worlandia*, *Microsyops*, *Niptomomys*, *Tinimomys*, *Palaeonictis*, *Palaeanodon*, the Miacinae, and probably *Hyopsodus*. *Apheliscus* and *Viverravus* first appear early in the Clarkforkian, but both represent evolutionary first occurrences (see Woodburne, 1977), i.e., both genera appear to have evolved from Tiffanian ancestors present in the Clark's Fork Basin. Their first appearance in the Clarkforkian is to some extent a matter of taxonomic judgment. *Plesiadapis gingerichi*, a species typical of the early Clarkforkian, occurs also in latest Tiffanian sediments of the Clark's Fork Basin.

Taxa that make their last appearance in the Clarkforkian are *Plesiadapis cookei*, *Chiromyoides*, *Phenacolemur pagei*, *Carpolestes*, *Microcosmodon*, Ptilodontidae, *Lampadophorus*, *Arctostylops*, *Cyriacotherium*, and *Probathyopsis* (the latter genus possibly persists into the Wasatchian in the Wind River Basin; see Chapter IV, and Kelley and Wood, 1954).

Index fossils of the Clarkforkian (taxa known only from the Clarkforkian) include *Plesiadapis cookei*, *Carpolestes nigridens*, *Aletodon gunnelli*, *Apheliscus nitidus*, *Haplomylus simpsoni*, *Dissacus praenuntius*, *Esthonyx xenicus*, *Esthonyx ancylion*, *Cyriacotherium psamminum*, and *Paramys atavus*. Most of these taxa are known from only part of the Clarkforkian but are relatively common. Several species in addition to these are currently known only from Clarkforkian strata, but they are too scarce or limited in occurrence to be of value as index fossils at present. Most of the species listed above are known from Clarkforkian sites outside the Bighorn Basin as well as from the type area.

Other characteristic Clarkforkian mammals, besides the index fossils, are *Phenacodus primaevus*, *Phenacodus vortmani*, *Ectocion osbornianus*, *Probathyopsis praecursor*, *Coryphodon* sp., *Didymictis protenus proteus*, *Uintacyon rudis*, *Oxyaena aequidens*, *Oxyaena transiens*, *Plesiadapis dubius*, *Phenacolemur pagei*, and *Thryptacodon* cf. *antiquus*.

To summarize, the Clarkforkian is characterized by first and last appearances of some mammalian taxa, by taxa that are restricted to this land-mammal age, and by taxa that are common during the Clarkforkian but are also known before or after (Figures 4 and 5). A considerable number of these taxa have been found in deposits outside the Clark's Fork Basin, and they provide the basis for identifying other Clarkforkian faunas.

Olson (1952: 181) introduced the term "chronofauna" for a "geographically restricted, natural assemblage of interacting animal populations that has maintained its basic structure over a geologically significant period of time." Webb (1969) applied the term to certain Clarendonian mammalian faunas of Nebraska. It also seems reasonable to view the Clarkforkian assemblage of the Clark's Fork Basin as a chronofauna, although it is not yet possible to detail the precise interrelationships of the taxa involved. This localized Clarkforkian fauna involves a recurring assemblage of mammals, undoubtedly interacting (even if we cannot yet specify the interactions), that maintained stability in its basic structure for probably one to two million years. Similarly, the subsequent early Wasatchian mammalian assemblage in the Clark's Fork Basin may be considered as a separate chronofauna succeeding that of the Clarkforkian.

The faunal characterization presented here provides documentation of the Clarkforkian as a North American Land-Mammal Age. The biostratigraphic, geologic, and paleontological data comprising much of the remainder of the present study is, I believe, sufficient to support recognition of the Clarkforkian as a local stage/age as well. Savage (1962) outlined the data requisite for naming a stage (see also Evernden et al., 1964; Tedford, 1970). They may be summarized as follows:

1. A type columnar section showing subjacent and superjacent stages and the stratigraphic range of the characterizing fossil assemblage. Lithostratigraphic and biostratigraphic units must be distinguished.
2. Identification and description of characteristic taxa, including vertical stratigraphic range in the type area and throughout the geographic range.
3. Description of other columnar sections assigned to the stage, including information specified by guidelines 1 and 2.
4. Ecological interpretation, assessment of faunal provinces represented, and possible stratigraphic and geographic limits of the stage.
5. Correlations.

Most of these data are supplied herein for the Clarkforkian. Columnar sections for Clarkforkian sites outside the type area are not yet available, but some are in preparation by other workers. Similarly, range data for all Clarkforkian taxa throughout their geographic range cannot yet be provided, but some of the available data is given in Chapter V, and more detailed information should soon be available. Thus while it might appear premature to recognize the Clarkforkian as a Stage/Age in the northern Western Interior, more evidence is now known to support this status for the Clarkforkian than exists for any other early Tertiary land-mammal age. (In fact, Savage, 1962, cited the late Cretaceous through Clarkforkian sequence in the northern Bighorn Basin as an example of particular potential for description of mammalian stages.)

Independent chronostratigraphic data for the Clarkforkian-Wasatchian sequence in the Clark's Fork Basin, based on paleomagnetic stratigraphy, is under study (Butler et al., 1980, and in prep.).

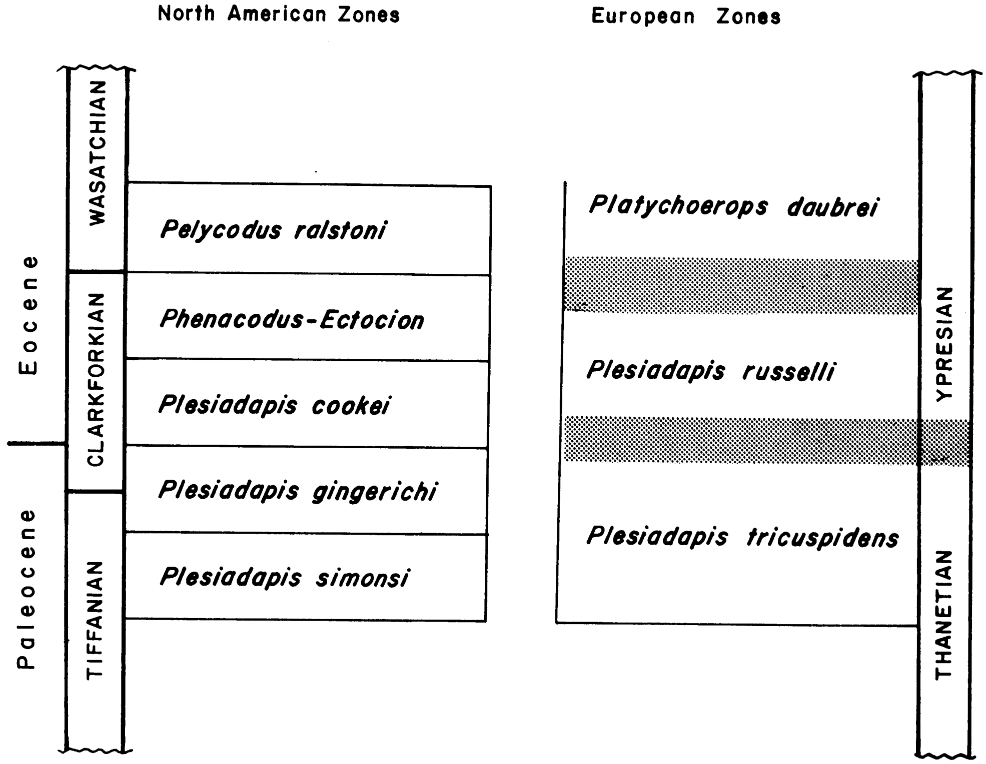


Figure 6. Late Paleocene and early Eocene faunal zones in the Western Interior of North America and the Paris Basin of Europe, showing tentative correlation of zones and position of the Paleocene-Eocene boundary.

## ZONES IN THE CLARKFORKIAN

Three faunal (biostratigraphic) zones can be distinguished in the type area of the Clarkforkian, and they are indicated in Figures 3 and 4. In biostratigraphic sequence these are the *Plesiadapis gingerichi* Zone (latest Tiffanian-early Clarkforkian), the *Plesiadapis cookei* Zone (middle Clarkforkian), and the *Phenacodus-Ectocion* Zone (late Clarkforkian). The *Plesiadapis gingerichi* Zone is contiguous at its lower limit with the late Tiffanian *Plesiadapis simonsi* Zone (Figure 6).

Faunas of the three Clarkforkian zones differ in relatively minor details, but recognition of zones from faunal evidence alone is easily achieved at most localities, based on presence or absence of characteristic taxa. The lower two zones are essentially based on the range zones of species of *Plesiadapis*. Both *Plesiadapis gingerichi* and *P. cookei* apparently evolved *in situ* in the Clark's Fork Basin, and evidence indicates that they are almost certainly segments of the same lineage. Nonetheless, a sufficient size difference exists in known collections, permitting confident identification. The Clarkforkian part of the *P. gingerichi* Zone is recognized by the mutual occurrence of *P. gingerichi* and any of the taxa characterizing the beginning of the Clarkforkian: *Paramys*, *Coryphodon*, *Esthonyx*, or *Haplomylus*. Other characteristic taxa of the Clarkforkian part of the *P. gingerichi* Zone are *Ectocion osbornianus*, *Phenacodus primaevus*, *Plesiadapis dubius*, *Esthonyx xenicus*, and *Paramys atavus*.

The upper limit of the *P. gingerichi* Zone and lower limit of the *P. cookei* Zone is defined by the evolutionary first occurrence of *P. cookei*. The duration of the *P. cookei* Zone is equivalent to the stratigraphic range of *P. cookei*. *P. cookei* disappears relatively abruptly in the type area and has not been found in strata higher than about 150 m below the Clarkforkian-Wasatchian boundary sandstone. As currently known, *Aletodon gunnelli*, a

Clarkforkian index fossil, first appears at the beginning of the *P. cookei* zone, and *Microcosmodon rosei* disappears at about the end of the zone.

The lower boundary of the *Phenacodus-Ectocion* Zone corresponds to the last appearance of *Plesiadapis cookei.* It is further recognized by the evolutionary first occurrence of *Esthonyx grangeri* and *Phenacolemur praecox* (which make their appearance during but not at the beginning of the zone). *Ectocion, Phenacodus, Probathyopsis,* and *Didymictis* are particularly common and characteristic in this zone. In faunal composition, the *Phenacodus-Ectocion* Zone differs from the preceding *Plesiadapis cookei* Zone primarily by the absence of *P. cookei.*

The stratigraphic limits of the Clarkforkian zones have been established in the study area and are depicted in Figure 3. Lithologic features in some cases appear to correspond with the zonal boundaries (see Chapter II, Formational and Faunal Boundaries). Thus some vertebrate sites that have not yielded diagnostic taxa can be confidently assigned to a faunal zone on the basis of their stratigraphic positions. (For example, localities SC–108 and 205 have produced only small collections, lacking *Plesiadapis cookei* or characteristic species of *Esthonyx, Phenacolemur,* or other genera; but their stratigraphic levels indicate that they must belong to the *P. cookei* Zone.) The important locality SC–143 ("Paint Creek locality") can be placed in the *P. cookei* Zone from substantial faunal evidence, although stratigraphic data for this site are lacking.

As we have seen, Clarkforkian faunal zones are based mainly on the stratigraphic ranges of *Plesiadapis gingerichi* and *P. cookei,* both of which appear to have short durations and, hence, are good temporal indicators. The concurrent ranges of these species and species of *Esthonyx* and *Phenacolemur* also help in identifying the zones. Lindsay (1972) and Fisher and Rensberger (1972) distinguished faunal zones in the Barstow Formation and John Day Formation, respectively, by criteria comparable to those employed here. Whether the zones distinguished in the Clarkforkian of the Clark's Fork Basin will have broad geographic applicability must await more thorough collecting elsewhere.

Biochronological correlation (Berggren and Van Couvering, 1978: 41) of faunas in the type area and outside the Bighorn Basin permits recognition of several other Clarkforkian faunas, discussed in Chapter V. Clarkforkian faunas of the Purdy Basin area (Togwotee Pass) and the Washakie Basin are in the *Plesiadapis cookei* Zone, as confirmed by the presence of *P. cookei* and characteristic species of *Phenacolemur* and *Esthonyx.* These records strengthen the probability that the temporal range of *P. cookei,* and therefore the interval of the *P. cookei* Zone, is very nearly the same through these parts of its geographic range. Faunal evidence suggests that at least the lower two zones of the Clarkforkian are present in the Plateau Valley beds in Colorado. The Bear Creek local fauna (Montana) is clearly Clarkforkian in age. Certain primitive species and the stage of evolution of other taxa suggest that the Bear Creek assemblage is early Clarkforkian (*Plesiadapis gingerichi* Zone).

## AGE OF THE CLARKFORKIAN

Questions have arisen about the validity of the Clarkforkian Land-Mammal Age because its geological age was in doubt and its boundaries were confused with formation or epoch boundaries (e.g., Wood, 1967). As discussed elsewhere, these considerations are fundamentally distinct (Gingerich, 1976b; Rose, 1977). It can be demonstrated that a distinct fauna occurs in the interval between the latest Tiffanian beds and the earliest Wasatchian beds, and the question of whether it is Paleocene or Eocene in age does not bear on its recognition and validity.

Where to place the Clarkforkian with respect to the Paleocene-Eocene boundary is, nonetheless, a pertinent and important question, and it is relevant to potential intercontinental correlations. Earliest Tertiary mammal faunas in North America were for many years considered basal Eocene in age, even well after the term Paleocene came into use in Europe. Thus Granger (1914) and others wrote of the Clark Fork as Eocene. Matthew (1920) seems to have been the first vertebrate paleontologist to apply the term Paleocene to what had been called "Basal Eocene" in North America, and since then the Clark Fork fauna has generally been considered latest Paleocene (Matthew, 1924; Jepsen 1930b, 1940; Wood et al., 1941; Van Houten, 1945; Russell, 1967; Sloan, 1969; Rose, 1975a, 1977). Recently Gingerich and I have argued that the Clarkforkian is better considered as earliest Eocene, based on comparison with mammalian faunas of the Paris Basin (Gingerich, 1976b; Gingerich and Rose, 1977), and this has begun to gain acceptance (e.g., Berggren et al., 1978). The geological age of the Clarkforkian is intimately related to the position of the Paleocene-Eocene boundary. But there is considerable disagreement about the latter, and this is largely responsible for the ambiguity of the age of the Clarkforkian. It is necessary, then, to examine what is meant by Paleocene and where its upper limit should be placed.

The term Paleocene was first used by Schimper (1874) for fossil floras from two sites in the Paris Basin. Schimper believed that these floras bear similarity to those of the Cretaceous but are even more similar to those of the Eocene. He also observed that they possess important distinctions of their own. The localities of Schimper's Paleocene clearly included both Sparnacian and Cuisian equivalents in the Paris Basin (local substages now widely regarded as Eocene), as well as Thanetian equivalents (universally considered Paleocene; see Schorn, 1971, for further discussion). Thus, according to Schimper's concept, the upper limit of the Paleocene was placed between the Ypresian (=Sparnacian and Cuisian) and Lutetian Stages, well within the Eocene, according to most current usage.

The Paleocene-Eocene boundary was one of the primary concerns of the Colloque sur l'Éocene held in Paris in 1968. The participants concluded that "Schimper's definition is inexact and contradictory and cannot, consequently, serve as a valid historical reference" (Colloque sur l'Éocene, 1969: 470; see also Pomerol, 1969). Pomerol summarized the three prevailing views of the Paleocene-Eocene boundary. Some micropaleontologists place the boundary at the base of the Cuisian, thus considering the Sparnacian to be Paleocene; others place it at the base of the Ilerdian (late Thanetian and Sparnacian equivalent). Most students of the Paris Basin—vertebrate paleontologists, palynologists, and invertebrate paleontologists concerned with continental mollusks—place the boundary at the base of the Ypresian (i.e. at the base of the Sparnacian substage). Mollusks, pollen, and especially mammals display "une coupure nette" between the Thanetian and the Sparnacian (Pomerol, 1969). The Colloque sur l'Éocene reported that "in the United States [this faunal break] corresponds to the 'Clarkforkian'-Wasatchian limit" (p. 470). This now appears to be only partly true (see below).

The controversy over placement of the Paleocene-Eocene boundary emphasizes the fact that a fixed boundary is not always appropriate for all fossil evidence. Savage (1975: 18) addressed this point:

> The search for 'more refined boundaries . . . for Lyellian series-epochs, and for the still-larger categories in our chronostratigraphic and geochronologic hierarchies has been an exercise in futility, in my opinion. I propose that we leave the erathems-eras, systems-periods, and series-epochs as the vaguely-bounded bulk units that we inherited . . .

Indeed, agreement on the Paleocene-Eocene boundary may be possible only when and if absolute dating becomes a practical means for fixing the boundary. At present there is no consensus on the absolute date of the boundary. Many students date the Thanetian-Ypresian boundary at about 53.5 my B.P. (e.g. McKenna et al., 1973; Berggren et al., 1978; Hardenbol and Berggren, 1978), but Odin (1978 and earlier papers) dates the lower limit of the Ypresian at 51 my B.P. Rubinstein and Gabunia (1978), employing two different constants to determine the date of the boundary (from Nigerian glauconites), proposed that it occurs at 53.0–56.1 my B.P. or 55.6–58.9 my B.P. (The discrepancies in these dates result partly from the use of different constants by Soviet scientists.) Absolute dates bearing on the Paleocene-Eocene boundary in North America are not yet available. Consequently, it is preferable at present to place the Paleocene-Eocene boundary for North America where it will conform most closely to that accepted in Europe, particularly in the Paris Basin, and to determine this by correlation of mammalian faunas.

The most substantial faunal break in the Clark's Fork Basin sequence occurs at the Clarkforkian-Wasatchian boundary (see Chapter VII), as previous workers have observed. It might be argued that this should be recognized as the Paleocene-Eocene boundary and that the entire Clarkforkian is therefore Paleocene in age. This has been the traditionally accepted view. But the distinctive aspect of the Clarkforkian is not its continuing Tiffanian lineages; rather it is the first appearance of several immigrant taxa typical of the Wasatchian. Among them are *Esthonyx*, *Coryphodon*, and rodents, which make their initial European appearance in the early Sparnacian of the Paris Basin (at Meudon). Consequently it has been argued that the Clarkforkian correlates more closely with early Sparnacian than with Thanetian and, therefore, that its age is early Eocene (Gingerich, 1976b; Gingerich and Rose, 1977). This assessment was made early in our study of the Clarkforkian, before existence of the early Clarkforkian *P. gingerichi* Zone was realized.

Reappraisal of the evidence, especially the closely parallel lines of *Plesiadapis* known from the northern Bighorn Basin and the Paris Basin, suggest that the early Clarkforkian (*P. gingerichi* Zone) correlates most closely with the upper *P. tricuspidens* Zone (latest Thanetian, late Paleocene), whereas the middle Clarkforkian (*P. cookei* Zone) correlates most closely with the *P. russelli* Zone (early Sparnacian=early Ypresian, early Eocene; see discussion under *Plesiadapis gingerichi* in Chapter IV for justification of these correlations). These correlations are founded on the inference that the corresponding plesiadapids in North America and Europe are very closely related and may be geographic subspecies of the same species. Figure 6 shows the tentative correlation of North American and European faunal zones. If the correlations are correct, then rodents, *Esthonyx*, and *Coryphodon* appear to have reached Europe slightly later than their first occurrence in North America (see also Wood, 1977), whereas *Hyracotherium* (also present at Meudon) may occur in Europe slightly earlier than in the northern Western Interior of North America. These discrepancies indicate that the proposed correlations may require adjustment when the stratigraphy and earliest Sparnacian faunas of the Paris Basin become better known. Evidence now at hand suggests that there is a time (sedimentological) gap between the *P. tricuspidens* Zone and the *P. russelli* Zone (Rat, 1965), hence the durations and boundaries of these zones cannot now be resolved. The mammalian fossil record is now more complete and better known in North America than in Europe. We must now accumulate additional data from the Paris Basin in order to test and improve the tentative correlation proposed here.

Some may object to this correlation between North American and European plesiadapid zones on the grounds that they are homotaxial, but not necessarily synchronous (e.g. Berggren and Van Couvering, 1978). Although this possibility cannot be excluded, there is considerable evidence that mammalian dispersal in some cases occurs so rapidly as to be unresolvable in geochronological terms (Elton, 1958; Savage, 1977: 431–435). Berggren and Van Couvering have, in fact, employed this principle to establish the *Hipparion* datum in the Old World. They state (1978: 42):

> The FAD [first appearance datum] of a highly successful immigrant mammal taxon would be geochronologically synchronous throughout its range.

Although such an event clearly required some period of time, in many cases it was probably effectively synchronous within present methods of resolution. It becomes a matter of thorough study, then, to determine which taxa offer optimum potential for attempted biochronological correlations, and Gingerich (1975, 1976b) has demonstrated that plesiadapids are among them. The very close resemblance and relationship between North American and European plesiadapids, together with close resemblance of faunas and mutual first occurrences of certain mammalian taxa, offer strong evidence that the North American and Paris Basin zones are very nearly synchronous.

The Clarkforkian is, therefore, best viewed as a land-mammal age that is in part latest Paleocene and in part earliest Eocene. In this study, the Paleocene-Eocene boundary is considered to coincide, to the best of our resolution, with the boundary between the *Plesiadapis gingerichi* and *Plesiadapis cookei* Zones. Thus it must be judged somewhat arbitrarily and does not bear the hallmark of a major faunal break. This position of the boundary, however, has the advantage of offering the greatest probability that European and North American vertebrate paleontologists will employ a Paleocene-Eocene boundary that is isochronous.

# IV
# SYSTEMATIC PALEONTOLOGY OF CLARKFORKIAN MAMMALS

R. WOOD (1967) listed 21 mammalian species in the original American Museum and Princeton University Clarkforkian collections. The UM collections that are described in this chapter include at least 70 species from the study area in the Clark's Fork Basin, although a few of them represent successive stages in a single lineage. The revision of the Clarkforkian fauna presented here is based primarily on collections from the type area (Clark's Fork Basin, excluding Bear Creek, for which see Chapter V). Eight new species are described herein (one of them from the late Tiffanian of the Clark's Fork Basin and the Clarkforkian of the Togwotee Pass area), and several other species and five genera are also new and have been described elsewhere (Bown and Rose, 1979; Gingerich, 1977, 1978; Gingerich and Gunnell, 1979; Krause, 1980; Rose and Krause, in press; Gingerich, Schankler and Winkler, in prep.) Inferred ranges and actual stratigraphic occurrences of the 70 species in the Clark's Fork Basin are summarized in Figure 4.

About 10–20 additional species have been identified from Clarkforkian beds outside the study area. With the single exception mentioned above, these taxa are not treated separately in this chapter, but the local faunas from which they come are reviewed in Chapter V. All known Clarkforkian mammalian taxa are listed in Table 2.

Some of the genera and families of Clarkforkian mammals are in serious need of detailed revision beyond the scope of the present work. Accordingly, some of the species identifications should be regarded as tentative, pending completion of more thorough systematic studies, some of which are well underway.

Referred specimens listed under each taxon in this chapter include only those in the UM collection, although pertinent specimens from other collections have been noted in the discussions. The designation "miscellaneous isolated teeth" in the referred specimen listing indicates specimens not separately catalogued but included in numbered lots of teeth and bones from various localities. This systematic review does not include specimens collected after the 1978 field season except for the multituberculates (information on multituberculates collected in 1979 is from Krause, 1980).

### Class MAMMALIA Linnaeus, 1758
### Subclass ALLOTHERIA Marsh, 1880
### Order MULTITUBERCULATA Cope, 1884

Krause (1980) presented a thorough report on the multituberculates of the Clarkforkian, including all specimens found through the 1979 field season. The specimens of Clarkforkian multituberculates in the UM collection and their occurrences are summarized below, and the reader is referred to Krause's publication for measurements, descriptions, and other details.

### Family Eucosmodontidae (Jepsen, 1940)
### Subfamily Eucosmodontinae Jepsen, 1940
### *Neoliotomus* Jepsen, 1930
### *Neoliotomus conventus* Jepsen, 1930

Figure 7A–C

*Referred Specimens.*—UM nos. 66200 and 68746.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–83, 179); *Plesiadapis cookei* Zone (SC–143: Jepsen, 1930a).

*Discussion.*—The holotype of *Neoliotomus conventus* is from the Paint Creek locality (SC–143) of middle Clarkforkian age (not "Lower Wasatch Gray Bull beds" as reported by Jepsen 1930a). The species is also known from Princeton Quarry (late Tiffanian, see Table 42). Granger and Simpson (1928) named *Eucosmodon ultimus* (subsequently transferred to *Neoliotomus*) from the "Sand Coulee beds" (earliest Wasatchian) of the Clark's Fork Basin. According to Granger's 1912 field notes, the holotype of *N. ultimus*, AMNH 16103, came from three miles southeast of the mouth of Pat O'Hara Creek, and was associated with *Hyracotherium* and *Pelycodus*. It is, therefore, unquestionably of early Wasatchian age. *N. conventus* is larger than *N. ultimus*, but there are no other significant differences between them. Krause's (1980) study indicates that *N. ultimus* evolved directly from *N. conventus*, and that the transition was gradual.

Table 2. Mammalian fauna of the Clarkforkian

- Subclass ALLOTHERIA
  - Order MULTITUBERCULATA
    - Family Eucosmodontidae
      - _Neoliotomus conventus_
      - _Microcosmodon rosei_
    - Family Ptilodontidae
      - _Prochetodon_ cf. _cavus_
    - Family Neoplagiaulacidae
      - _Ectypodus powelli_
      - _Parectypodus laytoni_
- Subclass THERIA
  - Infraclass METATHERIA
    - Order POLYPROTODONTA
      - Family Didelphidae
        - _Peradectes_ cf. _chesteri_
        - *(cf. _Peradectes_ sp.)
        - ?_Mimoperadectes labrus_
  - Infraclass EUTHERIA
    - Order PROTEUTHERIA
      - Family Paleoryctidae
        - _Palaeoryctes punctatus_
      - Family Leptictidae
        - cf. _Prodiacodon tauricinerei_
      - Family Pantolestidae
        - cf. _Palaeosinopa lutreola_
        - _Palaeosinopa_ sp.
        - *(cf. _Palaeosinopa didelphoides_)
      - Family Pentacodontidae
        - *_Protentomodon ursirivalis_
        - *?_Aphronorus_ sp.
      - Family Apatemyidae
        - (_Apatemys_ sp.)
        - *_Apatemys kayi_
    - Order LIPOTYPHLA
      - Family Nyctitheriidae
        - cf. _Leptacodon packi_
        - cf. _Pontifactor bestiola_
        - cf. _Plagioctenodon krausae_
      - Family Erinaceidae
        - _Leipsanolestes siegfriedti_
    - ?Order LIPOTYPHLA, incertae sedis
      - cf. "_Diacodon_" _minutus_
    - Order DERMOPTERA
      - Family Plagiomenidae
        - _Plagiomene accola_, sp. nov.
        - *_Planetetherium mirabile_
        - _Worlandia inusitata_
    - Order PRIMATES
      - Family Microsyopidae
        - _Microsyops simplicidens_, sp. nov.
        - _Niptomomys doreenae_
        - _Tinimomys graybulliensis_
      - Family Plesiadapidae
        - _Plesiadapis dubius_
        - _Plesiadapis gingerichi_, sp. nov.
        - _Plesiadapis cookei_
        - _Chiromyoides potior_
        - _Chiromyoides major_
      - Family Carpolestidae
        - _Carpolestes nigridens_
      - Family Paromomyidae
        - _Ignacius graybullianus_
        - _Phenacolemur pagei_
        - _Phenacolemur praecox_
        - _Phenacolemur_ cf. _simonsi_
    - Order CONDYLARTHRA
      - Family Arctocyonidae
        - _Thryptacodon_ cf. _antiquus_
        - *_Thryptacodon pseudarctos_
        - *_Anacodon? nexus_
        - *_Lambertocyon ischyrus_
        - cf. _Tricentes_ sp.
        - ?"_Chriacus_" sp.
      - Family Phenacodontidae
        - _Phenacodus primaevus_
        - _Phenacodus vortmani_ (?=_Phenacodus almiensis_)
        - (_Phenacodus_ sp.)
        - _Ectocion osbornianus_
        - _Ectocion parvus_
        - *_Prosthecion major_
      - Family Meniscotheriidae
        - _Meniscotherium priscum_
      - Family Hyopsodontidae
        - _Aletodon gunnelli_
        - _Hyopsodus_ sp.
        - _Haplomylus simpsoni_, sp. nov.
        - _Apheliscus nitidus_
        - *_Phenacodaptes sabulosus_
    - Order MESONYCHIA
      - Family Mesonychidae
        - _Dissacus praenuntius_
        - *(_Dissacus_ sp.)
    - Order TAENIODONTA
      - Family Stylinodontidae
        - *_Lampadophorus lobdelli_
        - **_Lampadophorus expectatus_
        - (cf. _Lampadophorus_ sp.)
    - Order PANTODONTA
      - Family Titanoideidae
        - **_Titanoides primaevus_
        - **_Titanoides zeuxis_
        - **_Titanoides_ sp.
      - Family Barylambdidae
        - *_Barylambda faberi_
        - **_Haplolambda quinni_
        - *_Leptolambda schmidti_
      - Family Coryphodontidae
        - _Coryphodon_ sp.
      - Family Cyriacotheriidae
        - _Cyriacotherium psamminum_
    - Order TILLODONTIA
      - Family Esthonychidae
        - _Esthonyx xenicus_
        - _Esthonyx ancylion_
        - _Esthonyx grangeri_
    - Order DINOCERATA
      - Family Uintatheriidae
        - _Probathyopsis praecursor_
        - **_Probathyopsis newbilli_
        - **_Bathyopsoides harrisorum_

Order NOTOUNGULATA
Family Arctostylopidae
*Arctostylops steini*

Order CARNIVORA
Family Miacidae
*Didymictis protenus proteus*
*Didymictis*, ?undescribed species
*Viverravus acutus*
*Viverravus*, sp. nov. (undescribed)
*Viverravus politus*
*Uintacyon rudis*

Order CREODONTA
Family Oxyaenidae
*Oxyaena aequidens*
*Oxyaena transiens*
*Oxyaena platypus*
*Oxyaena? lichna*, sp. nov.
*Dipsalodon matthewi*
**Dipsalodon churchillorum*, sp. nov.
cf. *Dipsalodon*, ?undescribed species
*Palaeonictis peloria*, sp. nov.

Order RODENTIA
Family Paramyidae
*Paramys atavus*
*Paramys* cf. *excavatus*
*Paramys annectens*, sp. nov.
*Franimys amherstensis*

Order Uncertain
Suborder PALAEANODONTA
Family Metacheiromyidae
*Palaeanodon ?parvulus*

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* Taxon known from Clarkforkian outside of the study area, but not from the study area in the Clark's Fork Basin.

**Taxon known from lower part of Plateau Valley beds, probably latest Tiffanian (see Chapter V), but possible Clarkforkian age cannot yet be excluded.

A taxon shown in parentheses may not be taxonomically distinct from another congeneric species listed here.

### Subfamily Microcosmodontinae Holtzman and Wolberg, 1977
### *Microcosmodon* Jepsen, 1930
### *Microcosmodon rosei* Krause, 1980

*Referred Specimens.*—UM nos. 71299, 71547–71550, 72039, 72049–72053, 72500–72502, 72662 (holotype), 72665, 72667, 72678, 72694, 72699, 72702, 72703.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–226) and *Plesiadapis cookei* Zone (SC–116, 117, 143, 188, 200); latest record of a microcosmodontine.

*Discussion.*—*Microcosmodon rosei* is the smallest species of *Microcosmodon*. It has three serrations on $P_4$, in contrast to the Tiffanian species *M. conus* Jepsen, which has five, and *M. woodi* Holtzman and Wolberg, which has five or six (Krause, 1980). The holotype of *M. rosei* is from SC–188. See Krause (1980) for illustrations of this species.

### Family Ptilodontidae Gregory and Simpson, 1926
### *Prochetodon* Jepsen, 1940
### *Prochetodon* cf. *cavus* Jepsen, 1940

*Referred Specimen.*—UM 71311.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–226); *Plesiadapis cookei* Zone (SC–143: Jepsen, 1940; also see Krause, 1980).

*Discussion.*—UM 71311 is a partial skull and mandible, the most complete specimen of *Prochetodon* known. It has been described and figured by Krause (1980). The holotype and original sample of *P. cavus* are from the late Tiffanian Princeton Quarry (Jepsen, 1940), and the Clarkforkian specimens of *Prochetodon* cf. *cavus* are the latest occurrence of the genus known (see discussion by Krause). The latter specimens differ from *P. cavus* in morphology of the premolars and by their slightly larger size.

### Family Neoplagiaulacidae Ameghino, 1902
### *Parectypodus* Jepsen, 1930
### *Parectypodus laytoni* Jepsen, 1940

Figure 7D

*Referred Specimens.*—UM nos. 68290, 72695–72698, 72701, and, tentatively, UM 71551.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–143).

*Discussion.*—These specimens are essentially indistinguishable from the original sample of *Parectypodus laytoni* from Princeton Quarry. They are smaller and have fewer apical cusps on $P_4$ than early Wasatchian *P. simpsoni* Jepsen (1930a), and they have more apical cusps than early Wasatchian *Parectypodus* species A of Van Valen and Sloan (1966: figure 5; Bown, 1979) but are similar in size.

### *Ectypodus* Matthew and Granger, 1921
### *Ectypodus powelli* Jepsen, 1940

Figure 7E

*Referred Specimens.*—UM nos. 67015, 69224, 69868, 71552–71556, 71783, 71784, 72013–72037, 72040–72048, 72668–72677, 72679, 72680, 72683–72691, 72704–72707, 72709, 72710.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–115, 116, 120, 143, 188, 195); *Phenacodus-Ectocion* Zone (SC–29).

*Discussion.*—Clarkforkian specimens of *Ectypodus* are similar to late Tiffanian *E. powelli* (holotype and original sample from Princeton Quarry) and to early Wasatchian *E. tardus* Jepsen (1930a), and they are

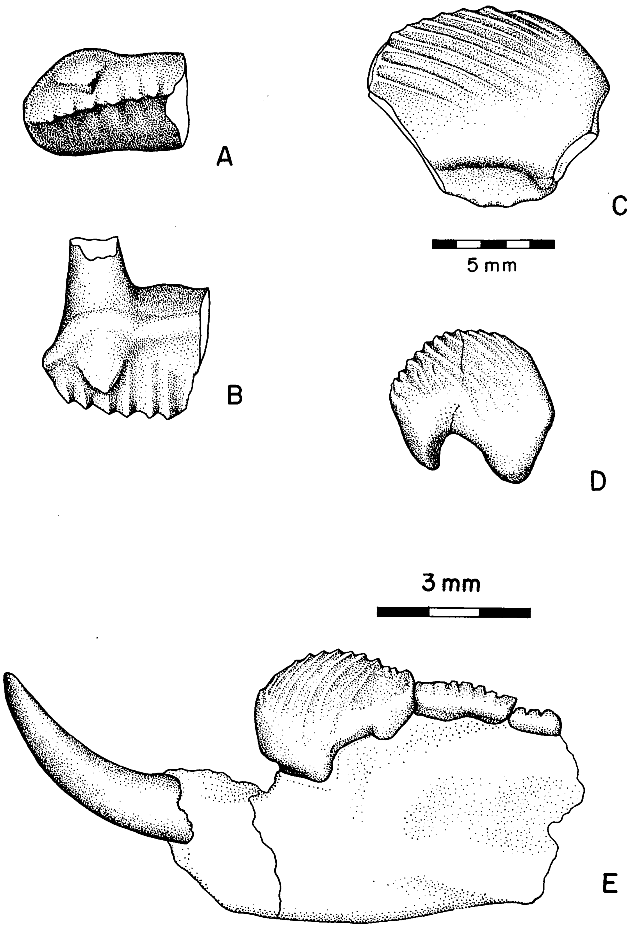

Figure 7. Multituberculates. A and B, *Neoliotomus conventus*, UM 66200, from SC–83: incomplete left $P^4$, crown and labial views. C, *Neoliotomus conventus*, UM 68746, from SC–179: right $P_4$, labial view. D, *Parectypodus laytoni*, UM 68290, from SC–143: right $P_4$, labial view. E, *Ectypodus powelli*, UM 71783, from SC–188: left dentary with I, $P_4$–$M_2$, labial view. 5 mm scale pertains to A–C, 3 mm scale to D–E.

assigned to *E. powelli* because of their similar size. The majority of specimens have been discovered by screenwashing at SC–188. The most complete specimen, UM 69868, from the quarry at SC–195, includes both dentaries and the first known upper dentition of *E. powelli* (see Krause, 1980).

### Subclass THERIA Parker and Haswell, 1897
### Infraclass METATHERIA Huxley, 1880
### Order POLYPROTODONTA Owen, 1866
### Family Didelphidae Gray, 1821

### *Peradectes* Matthew and Granger, 1921
### *Peradectes* cf. *chesteri* (Gazin, 1952)

Figure 8, Table 3

*Referred Specimens.*—UM nos. 65001, 65359, 66735, 66740, 66914, 68867, 71649, 71663.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–19, 117, 127, 188); *Phenacodus-Ectocion* Zone (SC–29).

*Discussion.*—These are the first marsupials recorded from the Clarkforkian, and among them are some of the best preserved specimens of didelphids from the early Eocene of North America. The most complete specimen, UM 66914, includes both dentaries (the right one with $M_{1-4}$) and the left maxilla with $P^{2-3}$–$M^{1-4}$. The left side is locked in occlusion and the specimen is partly encased in hard matrix, consequently delicate preparation will be necessary before it can be studied. UM 71663 is the best dentary from the Clarkforkian, preserving right $M_{1-4}$ and part of $P_3$ (Figure 8). Other specimens include a few other jaw fragments and several isolated teeth.

The Clarkforkian specimens are very similar morphologically to both Tiffanian *Peradectes elegans* Matthew and Granger (1921) and Wasatchian *P. chesteri* (Gazin, 1952). These two species differ mainly in size, the latter being somewhat smaller, and the Clarkforkian specimens conform more closely to *P. chesteri* in this regard. They are essentially identical to specimens of *P. chesteri* from the No Water fauna, early Wasatchian, of the southern Bighorn Basin (Bown, 1979). The lower molars are characterized by closely appressed hypoconulid and entoconid, the latter less acute and separated more from the metaconid than in *Peratherium*. The hypoconulid is less lingually situated and does not project posteriorly so much as in *Peratherium*. In the upper molars (UM nos. 66735, 66740, and 71649) the paracone is slightly smaller than the metacone, and both conules are present but very small. Stylar cusps B and D are prominent, cusp A is slightly smaller, cusp C smaller still, and cusp E the smallest. These features are characteristic of *Peradectes* as defined by Setoguchi (1973) and Bown (1979).

The classification and interrelationships of early Tertiary didelphids are poorly understood. Setoguchi (1973, 1975) has studied North American forms, and Crochet (1977a,b) has concentrated on European didelphids but has also considered North American taxa. Their systematic arrangements differ from previous classifications and are in disagreement with each other on several points, such as the species that are valid and the genera to which they should be assigned. Whereas many authors have considered *Peratherium* to be a valid North American genus, Crochet would restrict usage of this genus to European species, resurrecting Cope's *Herpetotherium* for the North American species allo-

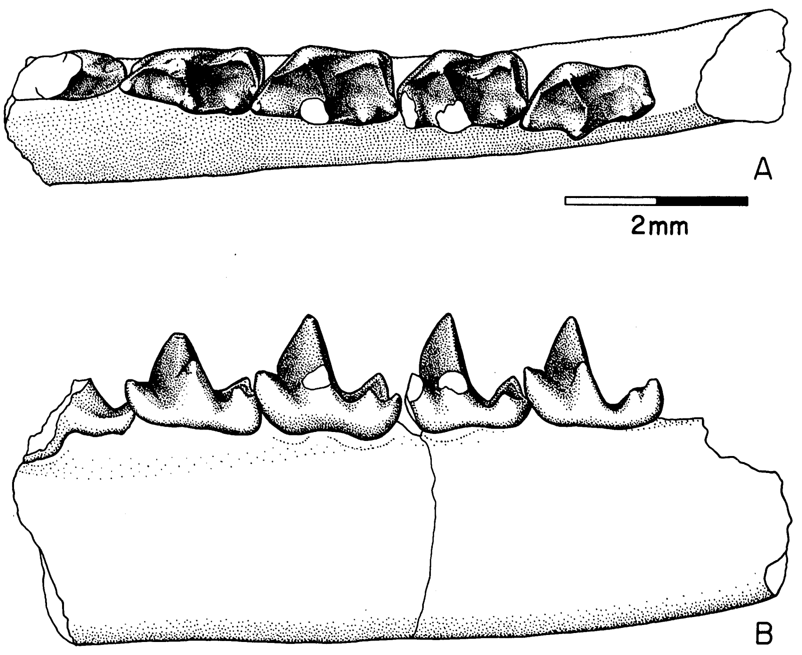

Figure 8. *Peradectes* cf. *chesteri*, UM 71663, from SC–188: right dentary with $M_{1-4}$ and the heel of $P_3$. A, crown, and B, lingual views.

Table 3. Measurements of lower teeth of Clarkforkian *Peradectes* cf. *chesteri*.

| | UM 65001 (SC–19) | UM 65359 (SC–29) | UM 66914 (SC–127) | UM 71649 (SC–188) | UM 71663 (SC–188) | USNM 19199 holotype, *P. chesteri* |
|---|---|---|---|---|---|---|
| $P_2L$ | | 0.85 | | | | |
| $P_2B$ | | | | | | |
| $P_3L$ | | 1.00 | | | | |
| $P_3B$ | | 0.50 | | | 0.60 | |
| $M_1L$ | 1.35a | 1.35a | 1.45 | | 1.50 | |
| $M_1B$ | 0.80 | 0.90a | | | 0.75 | |
| $M_2L$ | 1.55 | 1.55a | 1.50 | | 1.55 | |
| $M_2B$ | 0.90 | | 0.85 | | 0.90 | |
| $M_3L$ | | 1.55 | | | 1.50a | 1.4a |
| $M_3B$ | | 1.10a | | | 0.90 | 0.8a |
| $M_4L$ | | | | 1.45 | 1.50 | |
| $M_4B$ | | | | 0.85 | 0.80 | |

Measurement of additional teeth of UM 66914 will be possible after preparation. Dimensions of the holotype of *P. chesteri* are from Gazin (1952: 18).

cated by others to *Peratherium*. Crochet considers *Peradectes* to be present in both Europe and North America. I have followed Kirsch (1977) in recognizing several orders of marsupials and assigning the didelphids to the order Polyprotodonta.

*Peradectes chesteri* was first described from the lower Eocene "Knight" (=Wasatch) Formation of western Wyoming by Gazin (1952), who assigned it to the genus *Peratherium*. McKenna (1960) described *Peradectes protinnominatus* from the early Eocene Four Mile fauna

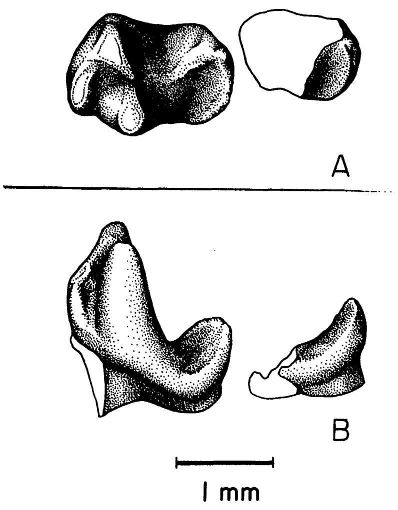

Figure 9. *Palaeoryctes punctatus*, UM 69232, from SC–136: right $M_{2-3}$(?). A, crown, and B, lingual views.

of northern Colorado. Setoguchi (1973) and Bown (1979) consider these two species to be conspecific and to belong in *Peradectes*, an assessment I follow here.

Three of the Clarkforkian specimens come from the quarry at SC–188. Another specimen from that site, UM 71645, a left dentary with seven teeth, may belong to a didelphid about 25% smaller than *Peradectes* cf. *chesteri*. The specimen requires considerable preparation before an accurate identification can be made.

### *Mimoperadectes* Bown and Rose, 1979
### ?*Mimoperadectes labrus* Bown and Rose, 1979

*Referred Specimen.*—UM 71684.

*Occurrence.*—Upper *Phenacodus-Ectocion* Zone (SC–81).

*Discussion.*—A trigonid of a right lower molar, UM 71684, is didelphid in structure and has subequal paraconid and metaconid. It is similar in morphology and size to specimens of *Mimoperadectes labrus* Bown and Rose (1979) and, if it proves to belong to that species, it extends the range of this rare marsupial into the Clarkforkian.

The holotype of *M. labrus* is from the basal Wasatchian at locality SC–69, a site in close proximity both geographically and stratigraphically to SC–81. SC–69 is about two miles south-southeast of SC–81 and is not more than 50 m above it. Hence it is not surprising to find *M. labrus* in uppermost Clarkforkian beds of the same area.

### Infraclass EUTHERIA Gill, 1872
### Order PROTEUTHERIA (Romer, 1966)
### Family Palaeoryctidae (Winge, 1917)
### *Palaeoryctes* Matthew, 1913
### *Palaeoryctes punctatus* Van Valen, 1966

Figure 9

*Referred Specimen.*—UM 69232.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–136).

*Discussion.*—UM 69232, a right dentary with ?$M_2$ and the talonid of ?$M_3$, is only the second specimen of a palaeoryctid collected from the Clarkforkian of the type area. The complete molar has a very high trigonid with a low, shelf-like paraconid, and a small, relatively narrow talonid with a high hypoconid, characteristic features of *Palaeoryctes*. The specimen closely resembles the holotype of *P. punctatus* (as far as the two can be compared) and is also very similar to, but slightly smaller than, undescribed specimens of *Palaeoryctes* sp. from the Princeton Quarry level (late Tiffanian, e.g. PU nos. 14158, 17806, 19394).

Van Valen (1966) proposed *Palaeoryctes punctatus* for a single specimen, AMNH 15850, from the "blue beds" in the head of Big Sand Coulee. It now seems probable that this specimen is from the upper Clarkforkian (*Phenacodus-Ectocion* Zone) in the vicinity of locality SC–102. Simpson (1937c) remarked that the specimen might represent a new genus, but he deferred description of a new taxon until better preserved material was available. He characterized the specimen as "suggestive of *Nyctitherium*." The holotype is, then, somewhat younger than UM 69232.

Measurements of UM 69232 are: ?$M_2$L=1.60, B trigonid=1.10, B talonid=0.90; ?$M_3$L=1.30a, B talonid=0.85a.

### Family Leptictidae Gill, 1872
### *Prodiacodon* Matthew, 1929
### cf. *Prodiacodon tauricinerei* (Jepsen, 1930)

*Referred Specimens.*—UM nos. 65471, 66520, 67004.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–136, 188); *Phenacodus-Ectocion* Zone (SC–48).

*Discussion.*—Leptictids are exceedingly rare in the Clarkforkian collection, and the specimens listed here—two isolated lower molars and a poorly preserved maxilla with several broken teeth—contribute little more than a record of the family during the Clarkforkian. The specimens have relatively high, acute cusps (especially in the upper teeth, UM 65471), a characteristic of *Prodiacodon* (Novacek, 1977).

Among leptictids, the specimens are closest in size to *Prodiacodon tauricinerei*, first described from the early Wasatchian of the Bighorn Basin (Jepsen, 1930a).

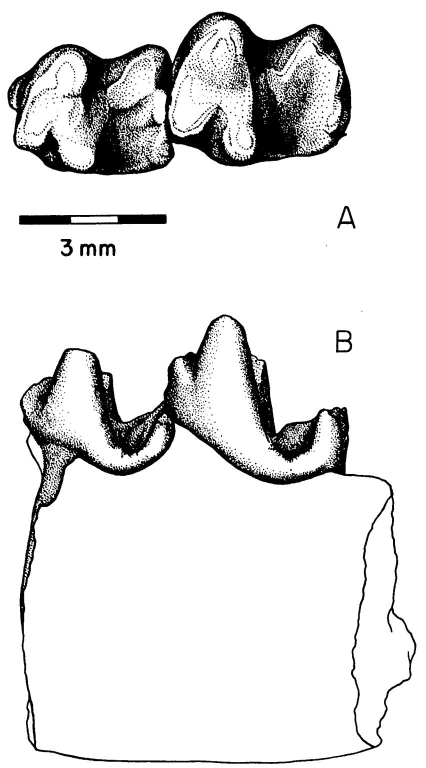

Figure 10. Cf. *Palaeosinopa lutreola*, UM 68281, from SC-167: right dentary with $M_{1-2}$. A, crown, and B, lingual views.

Jepsen placed the species in the genus *Diacodon*, which was synonymized in part with *Prodiacodon* and in part with *Palaeictops* by Novacek. Novacek placed Jepsen's species in *Prodiacodon*. I have followed Novacek's recent revision, although I do not believe that his criteria for separating the latter two genera are consistently applicable (an observation shared by Bown, 1979). If the Clarkforkian specimens prove to belong to *Prodiacodon tauricinerei*, they would be the oldest record of this species.

The upper teeth are too poorly preserved to permit accurate measurement. The dimensions of the lower teeth are: UM 66520, left ?$M_2$, L=2.30, B trigonid=2.00, B talonid=1.70; UM 67004, right $M_3$, L=2.35, B trigonid=1.70, B talonid=1.20.

### Family Pantolestidae Cope, 1884
### *Palaeosinopa* Matthew, 1901
### cf. *Paleosinopa lutreola* Matthew, 1918
Figure 10

*Referred Specimen.*—UM 68281.

*Occurrence.*—*Plesiadapis cookei* Zone (SC-167)

*Discussion.*—UM 68281 is a fragmentary right dentary with $M_{1-2}$ from near Sugarloaf Butte. Except for its slightly larger size, $M_2$ in the specimen is similar to that in the holotype of *Palaeosinopa lutreola*, AMNH 15100 (right dentary with $M_{2-3}$). The trigonids of $M_{1-2}$ in the Clarkforkian specimen are high and transversely broad, broader than the talonids. The metaconid is as high (on $M_1$) or higher (on $M_2$) than the protoconid, and the paraconid is low and shelf-like. The talonids are comparatively short and the talonid basins are open lingually due to a deep talonid notch. The specimen is unusual in having essentially no entocristid, the entoconid rising abruptly behind the talonid notch. As in specimens of *Paleosinopa* there is a posteriorly placed mental foramen beneath $M_1$.

The holotype of *P. lutreola* is from Wasatchian (upper "Graybullian") strata on Elk Creek, central Bighorn Basin. Matthew (1918) referred a specimen from the Clark's Fork Basin, AMNH 16170, to this species. It is recorded from "five miles southeast of the mouth of Pat O'Hara Creek" and is, therefore, of earliest Wasatchian age, as Matthew suggested. Other Wasatchian specimens have been allocated to *P. lutreola* by Delson (1971), Guthrie (1971), Bown (1979), and Bown and Schankler (1980). Matthew distinguished *P. lutreola* from other species of *Palaeosinopa* chiefly by its small size. Among described species of *Palaeosinopa*, UM 68281 can only beong to *P. lutreola*, and it would be the oldest record of this species. However, it may represent an undescribed species, and the relatively high trigonid and the absence of an entocristid suggest palaeoryctid affinities. Larger samples are required to investigate this possibility.

The dimensions of UM 68281 are: $M_1L$=3.40, B=2.60; $M_2L$=3.80, B=3.20. [Additional parts of this specimen not discussed or illustrated here were found by M. J. Schoeninger in 1980.]

### *Palaeosinopa* sp.

*Referred Specimens.*—UM nos. 65552, 66632, 69273, 71013, 71014, 71509, and tooth fragments in UM nos. 66925, 68029, 69235.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC-156, 171, 226); *Plesiadapis cookei* Zone (SC-108, 127, 136); *Phenacodus-Ectocion* Zone (SC-50, 163, 176, 202).

*Discussion.*—The specimens considered here are for the most part very fragmentary, consisting of a single tooth or part of a tooth. UM 69273 includes a somewhat damaged left maxilla with $P^4$-$M^3$ and poorly preserved dentaries. The sample is, however, sufficient to document the presence of one or two moderately large species of *Palaeosinopa* in the Clarkforkian. The specimens most closely resemble *P. simpsoni* (Tiffanian) and *P. didelphoides* (Wasatchian) [see also Gingerich (1980b)].

*Palaeosinopa didelphoides* was initially described from the Lostcabinian of the Wind River Basin. Matthew (1918) allocated specimens from the early Wasatchian of the Bighorn Basin to this species, but he suggested that they might be variants of the slightly larger *P. veterrima*, earlier described from the Bighorn Basin. Delson (1971) regarded *P. veterrima* as a synonym of *P. didelphoides*, but Bown and Schankler (1980) retain both species. The Clarkforkian specimens are smaller than *P. veterrima*.

Van Valen (1967) proposed *Palaeosinopa simpsoni* for two upper molars from the Tiffanian Scarritt Quarry, and Dorr (1977) allocated a partial skull from the late Tiffanian Dell Creek Quarry to this species [see also Gingerich (1980b)]. *P. simpsoni* is similar in size to *P. didelphoides*, differing from it in minor aspects of upper molar morphology. UM nos. 69273 and 71509 resemble *P. simpsoni* in having a basal, lingually displaced hypocone and low conules with central conule wings on $M^1$; however, the Clarkforkian specimens are somewhat larger, especially in transverse dimensions, than *P. simpsoni*.

*Measurements*: UM 66632, right $M_2$L=5.25, B=3.80; UM 69273, $P^4$–$M^3$, $P^4$L=4.75, B=5.20, $M^1$L=5.20, B=6.65, $M^2$L=5.85, B=8.95, $M^3$L=3.55, B=8.30; UM 71014, left $M_1$ or $M_2$, L=5.35, B=3.70; UM 71509, right $M^1$L=4.30, B=6.20.

### Family Apatemyidae Matthew, 1909
### *Apatemys* Marsh, 1872
### *Apatemys* sp.

*Referred Specimens.*—UM nos. 68592, 71012, 71481, and lower incisor fragments in UM nos. 66535, 67149, 69945.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–109, 134, 143, 188); *Phenacodus-Ectocion* Zone (SC–99, 233).

*Discussion.*—This sample includes three incomplete dentary fragments and several incisor fragments. They compare most closely with *Apatemys kayi*, initially described from the Clarkforkian Bear Creek local fauna (Simpson, 1929b), and *A. chardini*, named from the early Wasatchian of the Bighorn Basin (Jepsen, 1930a). Two of the specimens, UM nos. 68592 and 71012, preserve a two-rooted alveolus for $P_4$, a feature considered characteristic of *A. chardini* (Bown and Schankler, 1980; these authors tentatively include UM 68592 in *A. chardini*). UM 68592 also preserves $P_1$ (or $P_2$, see West, 1973a), an unusual one-rooted procumbent tooth with a long and somewhat trenchant crown. The incisors here referred to *Apatemys* exhibit the characteristic weakly serrated lateral edge that is distinctive of many apatemyids.

Simpson originally placed *Apatemys kayi* in the genus *Labidolemur*, and Jepsen assigned *A. chardini* to a new genus, *Teilhardella*. McKenna (1963) suggested that both *Labidolemur* and *Teilhardella* might prove to be synonyms of *Apatemys*. Subsequent authors have considered both species to belong to *Apatemys*, regarding *Teilhardella* as a junior synonym of *Apatemys* but retaining *Labidolemur* for the Tiffanian species *L. soricoides* (West, 1973c; Bown and Schankler, 1980). In his review of North American apatemyids, West (1973c) grouped all Clarkforkian through Bridgerian apatemyids in one species, *A. bellus*, thereby synonymizing nine species previously placed in three different genera. This now appears to be an oversimplification. Bown and Schankler (1980) have reviewed early Eocene apatemyids and have commented extensively on West's revision. They conclude that at least three lineages of *Apatemys* can be discerned in the early Eocene. Bown and Schankler recognize two species from the Clarkforkian and early Wasatchian, *A. kayi* and *A. chardini*. In their view, *A. chardini* is the smallest species of *Apatemys*. *A. kayi* is larger than *A. chardini* and further differs from it by having a reduced, one-rooted $P_4$. The specimens here referred to *Apatemys* are, in these features, closer to *A. chardini*. Larger samples will be required to determine if *A. kayi* from Bear Creek is really different from the specimens recorded here from the type area.

### Order LIPOTYPHLA Haeckel, 1866

Concepts of the composition of the Lipotyphla, or "true insectivores," have varied considerably over the years. There is still no consensus, but it is universally accepted that at least the Erinaceomorpha and the Soricomorpha are included. I follow Butler (1972) in giving the Lipotyphla ordinal rank, although most earlier authors have considered it as a suborder of the order Insectivora. Recognition of an order Lipotyphla emphasizes that the Proteutheria may not be specially related to the Lipotyphla. McKenna (1975) raised the Erinaceomorpha and the Soricomorpha to ordinal rank in his grandorder Insectivora, which is essentially equivalent to the usage followed here.

Few groups of early Tertiary mammals are so poorly understood as the lipotyphlan insectivores. Most classifications of lipotyphlans disagree and there is considerable debate concerning their interrelationships. Both problems are obvious from perusal of the recent literature on the group (e.g., Van Valen, 1967; Robinson, 1968b,c; McKenna, 1968; Russell et al., 1975; Krishtalka, 1976a,b, 1977; Bown and Schankler, 1980). Disagreements have arisen because, in some cases, only small samples were available or were considered, or because only selected taxa were examined. Few studies have attempted to assess intraspecific variation, hence we know very little of the limits of such variation in early Tertiary lipotyphlans. Consequently, there is no consensus on the composition of families, the validity of various genera and species, or the proper generic assignments of many species.

A major source of uncertainty in lipotyphlan classification derives from the nature of the fossil evidence. Most taxa are known only from fragmentary jaws and teeth, and the proper association of upper and lower teeth is uncertain for many taxa. It appears that subtle differences in morphology of $P_4$ (e.g. position, size, and height of the paraconid, size and development of the talonid) and of the molars (e.g. development of the paraconid, position and strength of the hypoconulid), and in relative proportions of $P_4$ and the molars, may be taxonomically significant. Such minor differences, however, may dictate assignment of very similar specimens to different genera or even different families. How many of these differences result from intraspecific variability is unknown. Basicranial evidence has been shown to be important in understanding insectivore relationships, and a better knowledge of the anterior dentition would help, but these are unavailable for most taxa. It may be that many early Tertiary lipotyphlans simply cannot be consistently distinguished on the basis of cheek teeth alone.

There is a possibility that some forms now classified as lipotyphlans are actually chiropterans. A close parallel exists in the dentitions of primitive bats and lipotyphlans (see Russell et al., 1973). Concerning a Wasatchian specimen of *Nyctitherium celatum* (AMNH 15103, now assigned to *Pontifactor*, see below), Matthew (1918: 603–604) wrote that "the molar teeth are much like those of *Vespertilio*," and he mentioned some associated bones "suitable in size and proportions for the shafts of chiropteran fore limb bones," but the latter do not appear to be diagnostic.

I have followed, in general, the classification adopted by Krishtalka (1976a, b), not because I endorse it fully, but rather because his studies are the most recent ones concerning the taxa known from the Clarkforkian. The Clarkforkian collection includes some twenty jaw fragments and many isolated teeth of small lipotyphlans. They are among the smallest mammalian fossils known from the Clarkforkian. Many were obtained by screen-washing matrix from SC–188, but a significant number of specimens are surface finds. By the most conservative estimate, at least five species are present, but there may be more. Some probably represent new species, but I believe it would be counterproductive to propose new taxa here, in view of the instability of lipotyphlan classification. Hence I have adopted a more conservative course of comparing each morphological group with the described species to which it is most similar. Measurements of these specimens have been taken in the manner shown for leptictids by Novacek (1977: figure 2).

### Family Nyctitheriidae Simpson, 1928
### *Leptacodon* Matthew and Granger, 1921
### cf. *Leptacodon packi* Jepsen, 1930

Figure 11, Table 4

*Referred Specimens.*—UM nos. 66195, 68866, 71650, 71661, 71662, 71840, 71841.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–188) and *Phenacodus-Ectocion* Zone (SC–81).

*Discussion.*—These specimens, nearly all of which were collected by screen-washing matrix from SC–188, include some of the best preserved insectivore jaws known from the Clarkforkian. They bear many close resemblances to late Tiffanian *Leptacodon packi*. Subtle differences among the specimens suggest that two species may be included here. In addition to *L. packi*, these specimens are similar to *Pontifactor* sp. (AMNH 15103, referred to *Pontifactor* by Krishtalka, 1976b; the specimen includes the only associated lower and upper teeth known for the genus), *Saturninia* (middle Eocene-middle Oligocene of Europe; Sigé, 1976), and less so to *Mckennatherium ladae*. They are within the size range of both *L. packi* and *Pontifactor*, and slightly larger than *M. ladae*. The similarities to these species are not exact, however, and it is probable that the Clarkforkian specimens belong to a species of nyctitheriid as yet undescribed. They may be the lower teeth of the species identified below as cf. *Pontifactor* sp.

The best specimens are UM 71650, a left dentary with $P_2$-$M_3$ (Figure 11), and UM 71661, a right dentary with $P_4$-$M_2$. Their molar morphology is, in many traits, intermediate between those of *L. packi* and of *Pontifactor*. In unworn specimens (e.g. UM 71650) the paraconids are cuspate as in *L. packi*. The paracristids quickly become shelf-like with wear (e.g. UM 71661), however, thus resembling *Pontifactor*. The trigonids of the Clarkforkian specimens are more open than in *Pontifactor* and, in most of them, slightly less open than in *L. packi*. In a few specimens (UM nos. 68866 and 71662), the trigonids are almost exactly like those of *L.*

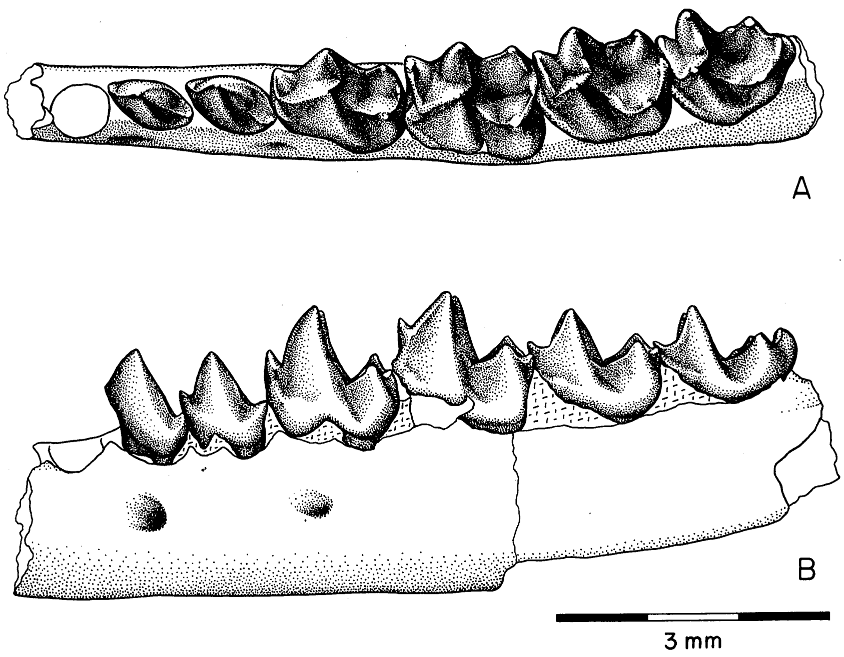

Figure 11. Cf. *Leptacodon packi*, UM 71650, from SC-188: left dentary with $P_2$–$M_3$. A, crown, and B, labial views.

*packi*, but the hypoconulids are more acute and project more posteriorly, as in *Pontifactor*. The talonids of UM 71650 and UM 71661 are slightly broader and have a more reduced hypoconulid than in *L. packi*. $M_1$, $M_2$, and $M_3$ are all about the same size in the Clarkforkian specimens.

The premolars differ in morphology from those of both *L. packi* and *Pontifactor*, but the significance of the differences is unknown. $P_2$ and $P_3$ are preserved only in one specimen, UM 71650. $P_2$ is two-rooted, as in *L. packi*, and is smaller but higher crowned than $P_3$. Its anterior basal cusp and talonid heel are minute. $P_3$ has a small but distinct anterior basal cusp and a weakly basined talonid. It is much smaller and lower crowned than $P_4$. $P_3$ in *L. packi* (PU 14140, Princeton Quarry) is relatively larger, almost as high crowned as $P_4$, and has a simple talonid. ($P_2$ and $P_3$ are unknown in *Pontifactor*.) $P_4$ in the Clarkforkian specimens is submolariform and slightly narrower than $M_1$. The paraconid and metaconid are both prominent, but the paraconid is noticeably lower than the metaconid. The talonid basin of $P_4$, although narrower than that of the molars, is well developed, with a distinct hypoconid and entoconid. A poorly defined hypoconulid is sometimes present (UM 71661). $P_4$ differs from that of *L. packi* in having a much broader talonid basin, a larger and higher paraconid (as high as the metaconid in UM 71661) that is less anteriorly-situated, and a large metaconid directly lingual, not posterolingual, to the protoconid. It differs from $P_4$ of *Pontifactor* in having a larger paraconid and in being larger relative to $M_1$; in other aspects it is structurally similar. ($P_4$ in AMNH 15103, *Pontifactor* sp., has been identified as a deciduous tooth [Matthew, 1918; Krishtalka, 1976b], apparently because of its molariform nature and the presence of an erupting $M_3$ in the specimen. However, it is similar to permanent $P_4$ in other nyctitheres and it shows almost no wear, both features suggesting that it is a permanent tooth.)

The minor differences in molar structure and the contrasts in the premolar series between the Clarkforkian specimens and *Leptacodon packi* suggest that they are not conspecific. The characteristics of the specimens indicate that a nyctithere is represented, however, and that it is probably closely related to *L. packi*, to *Pontifactor*, or to both. *L. packi* is known from the late Tiffanian Princeton and Schaff Quarries of the Clark's Fork Basin (Jepsen, 1930b) and possibly also from the Tiffanian of Alberta (Krishtalka, 1973). It is generally

Table 4. Measurements of lower teeth of cf. *Leptacodon packi.*

| | UM 66195 | UM 68866 | UM 71650 | UM 71661 | UM 71662 | UM 71840 |
|---|---|---|---|---|---|---|
| $P_2L$ | | | 0.85 | | | |
| $P_2B$ | | | 0.55 | | | |
| $P_3L$ | | | 0.95 | | | |
| $P_3B$ | | | 0.65 | | | |
| $P_4L$ | | | 1.40 | 1.30 | | 1.40 |
| $P_4B$ tri | | | 1.00 | 0.70 | | 0.80 |
| $P_4B$ tal | | | 0.90 | 0.75 | | 0.70 |
| $M_1L$ | | | 1.45 | 1.40 | 1.40 | |
| $M_1B$ tri | | | 1.15 | 0.90 | 0.90 | |
| $M_1B$ tal | | | 1.15 | 1.00 | 1.00 | |
| $M_2L$ | | 1.60 | 1.40 | 1.35 | 1.50 | |
| $M_2B$ tri | | 1.00 | 1.20 | 0.90 | 1.00a | |
| $M_2B$ tal | 1.10 | 1.00 | 1.15 | 1.00 | 1.00 | |
| $M_3L$ | 1.50 | | 1.45 | | | |
| $M_3B$ tri | 1.10 | | 1.15 | | | |
| $M_3B$ tal | 0.85 | | 0.85 | | | |

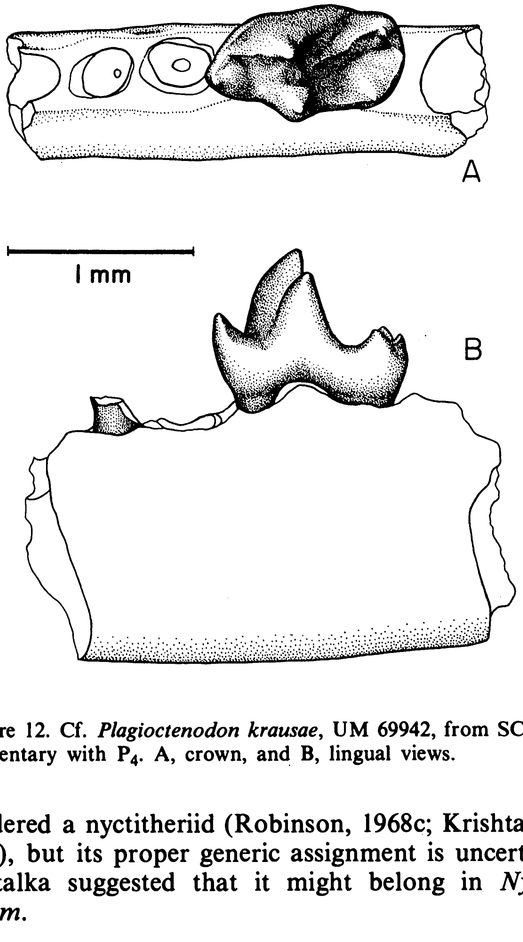

Figure 12. Cf. *Plagioctenodon krausae*, UM 69942, from SC–143: right dentary with $P_4$. A, crown, and B, lingual views.

considered a nyctitheriid (Robinson, 1968c; Krishtalka, 1976b), but its proper generic assignment is uncertain. Krishtalka suggested that it might belong in *Nyctitherium.*

### *Plagioctenodon* Bown, 1979
### cf. *Plagioctenodon krausae* Bown, 1979

Figures 12, 13

*Referred Specimens.*—UM nos. 69942, 71686, 71688, 71689.

*Occurrence.—Plesiadapis cookei* Zone (SC–143, 188).

*Discussion.*—This sample includes the smallest mammalian teeth in the Clarkforkian collection, about the same size as those of the primate *Tinimomys.* The specimens consist of only isolated teeth, three of which are complete (UM 69942, right $P_4$; UM 71689, right $M_1$; and 71686, left $M_2$). They are about the size of the teeth of the diminutive middle and late Paleocene *Leptacodon munusculum* and are similar to it morphologically. The Clarkforkian teeth appear to be closer, however, to the early Wasatchian *Plagioctenodon krausae* Bown 1979, from the southern Bighorn Basin.

$P_4$ is submolariform, with a well developed trigonid and a narrow talonid basin (Figure 12). The trigonid is slightly extended anteroposteriorly, and the paraconid is large and cuspate but lower than the metaconid. The talonid basin is flanked by a distinct hypoconid and entoconid and a minute hypoconulid. The tooth is virtually identical to $P_4$ in the holotype of *P. krausae*, UW 9682, and in UW nos. 7047 and 9592. The Clarkforkian molars are very similar to those of *P. krausae* in displaying a more compressed trigonid on $M_2$ than on $M_1$ and in having distinct hypoconulids. As in *P. krausae*, the hypoconulid of $M_1$ is situated equidistant between the entoconid and the hypoconid, whereas that of $M_2$ is somewhat closer to the entoconid. $M_1$ (UM 71689) is narrower than in most specimens of *P. krausae*, but $M_2$ (UM 71686, Figure 13) is broad. The paraconids of $M_1$ and $M_2$ are relatively low, as in *P. krausae*, but are more cuspate. The three Clarkforkian teeth are smaller than most specimens of *P. krausae* I examined, but they are similar in size to UW nos. 7047 and 9624. They may

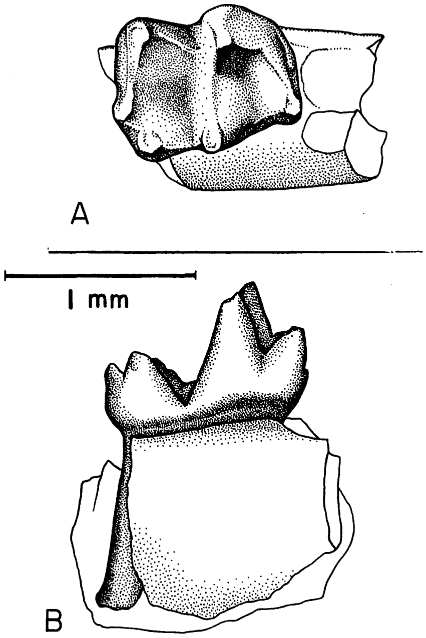

Figure 13. Cf. *Plagioctenodon krausae*, UM 71686, from SC–188: left dentary with $M_2$. A, crown, and B, lingual views.

represent a slightly smaller Clarkforkian predecessor of early Wasatchian *P. krausae*.

Measurements of these specimens are: UM 69942, $P_4L$=1.05, B trigonid=0.50, B talonid=0.50; UM 71689, $M_1L$=1.15, B trigonid=0.75, B talonid=0.70; UM 71686, $M_2L$=1.10, B trigonid=0.90, B talonid=0.90.

### *Pontifactor* West, 1974

### cf. *Pontifactor bestiola* West, 1974

Figure 14

*Referred Specimens.*—UM 71032.

*Occurrence.—Plesiadapis cookei* Zone (SC–143).

*Discussion.*—A single upper tooth from the Paint Creek locality (SC–143) appears to represent the nyctithere *Pontifactor* or a closely allied form. UM 71032 is very small, within the size range of *P. bestiola* (West, 1974; Bown, 1979), and it closely resembles that species in morphology. Like *Pontifactor*, the Clarkforkian tooth has a strongly developed W-shaped ectoloph and a prominent mesostyle, traits that distinguish *Pontifactor* from all other North American nyctitheriids. The parastylar region in UM 71032 is somewhat expanded, and a tiny, acute stylar cusp is situated between the mesostyle and the postmetacrista, as in some specimens of *Pontifactor*. This tooth resembles early Wasatchian specimens of *Pontifactor* (Bown, 1979) but differs from the holotype and other Bridgerian specimens of *P. bestiola* (West, 1974) in having a lingually-displaced hypocone that is noticeably internal to the protocone. It differs from the Bridgerian sample also in having more prominent conules and hypocone, and a distinct, acute pericone anterolingual to the protocone. (The pericone is present but smaller in some specimens of *Pontifactor*, but not in the holotype.) Lower teeth of the Clarkforkian form have not been identified, but it is possible that specimens described above as cf. *Leptacodon packi* belong to the same species as UM 71032.

Figure 14. Cf. *Pontifactor bestiola*, UM 71032, from SC–143: right ?$M^1$. Crown view.

The monotypic genus *Pontifactor* was originally based on a small sample of upper teeth, most of them isolated, from the Bridgerian of southwestern Wyoming. Krishtalka (1976b) expanded its temporal and geographic range by transferring a specimen earlier identified as *Nyctitherium celatum* (AMNH 15103 from the early Wasatchian of the Bighorn Basin, Matthew, 1918) to *Pontifactor* sp., an assignment with which I concur. As noted above, Bown (1979) has reported specimens near *P. bestiola* from the early Wasatchian No Water fauna of the southern Bighorn Basin. As Bown indicated, PU 17671, a nearly complete palate from "Hackberry Hollow" (SC–192), appears to represent a species of *Pontifactor*. This specimen is of early Wasatchian age and probably belongs to the same species as AMNH 15103. In his study of the early Wasatchian Four Mile Fauna, McKenna (1960) referred several specimens to ?"*Nyctitherium*" sp., comparing them closely with AMNH 15103. The two figured specimens, UCMP 44079 and 44961 (McKenna, 1960: figures 27 and 28), are very similar to AMNH 15103 and to specimens of *P. bestiola*. Certain minor differences between the Bridgerian sample of *P. bestiola* and the Wasatchian and Clarkforkian specimens, such as the position of the hypocone, may indicate that the older specimens belong to a different species of *Pontifactor*.

UM 71032 also resembles *Remiculus deutschi*

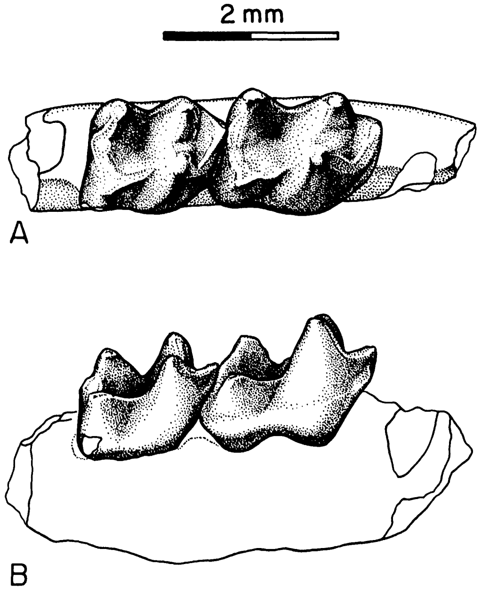

Figure 15. *Leipsanolestes siegfriedti*, UM 71660, from SC–188: right dentary with $M_{1-2}$. A, crown, and B, labial views.

(Russell, 1964), a small species from the late Paleocene of France. *Remiculus* was initially regarded as a mixodectid (Russell, 1964; Szalay, 1969a), but West (1974) and Krishtalka (1976b) believe it is a nyctitheriid. Like *Pontifactor*, *Remiculus* is characterized by a W-shaped ectoloph and a prominent mesostyle in the upper molars. However, it is much larger than *Pontifactor* or any other nyctitheriid, and it differs from *Pontifactor* in having a less anteriorly oriented protocone. In *Pontifactor* the upper molars, especially $M^1$, have an oblique appearance because the lingual part of each tooth is skewed anteriorly, a condition not present in *Remiculus*.

UM 71032 is the oldest known occurrence of a *Pontifactor*-like nyctitheriid. West (1974) postulated that *P. bestiola* could be derived from *Nyctitherium celatum* (apparently alluding to AMNH 15103, now referred to *Pontifactor*). The Clarkforkian specimen described here is older than known specimens of *Nyctitherium*, and its morphology suggests that the ancestry of *Pontifactor* may be sought among primitive nyctitheres of the *Leptacodon* group.

Dimensions of UM 71032 are: L=1.45, B anterior=1.55, B posterior=1.80.

### Family Erinaceidae Bonaparte, 1838
### *Leipsanolestes* Simpson, 1928

### *Leipsanolestes siegfriedti* Simpson, 1928
Figure 15, Table 5

*Referred Specimens.*—UM nos. 66751, 71660.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–117, 188).

*Discussion.*—UM 71660, a fragmentary right dentary with $M_{1-2}$, is indistinguishable from the type and referred specimens of *Leipsanolestes siegfriedti* from Bear Creek. It has relatively broad, low-crowned teeth, with shelf-like paracristids, broad talonid basins, and high entoconids. $M_1$ is larger than $M_2$. UM 66751, a left dentary with $M_1$, part of $M_2$, and the roots of $P_4$, is slightly larger than UM 71660 but otherwise morphologically identical to it. Its provenance, SC–117, is about 80 m stratigraphically above SC–188, the locality of UM 71660. UM 66751 is best referred to *L. siegfriedti.*

Two other specimens, both from the *Phenacodus-Ectocion* Zone, may be considered here. UM 71690, from SC–164, is an edentulous left mandibular fragment with roots of $M_{1-3}$ that decrease in size posteriorly. It is almost exactly the same size as UM 66751 and may be referable to *L. siegfriedti.* A partial left dentary with $P_4$-$M_1$, UM 68209, from SC–159, is larger than any of these specimens but closely similar in structure to *L. siegfriedti.* It also closely resembles the adapisoricid *Macrocranion nitens* (*sensu* Krishtalka, 1976a), differing mainly in having a clearly submolariform $P_4$, with both paraconid and metaconid large, and a well formed but narrow talonid basin. These features seem to ally the specimen more closely with *Leipsanolestes.*

UM nos. 71660, 66751, and 68209, from successive stratigraphic levels, form a sequence of increasing size. It seems likely that they represent segments of a single evolving lineage. When larger samples are available, UM 68209 may prove to belong to a distinct species in this lineage, but until then it may be designated *Leipsanolestes* cf. *siegfriedti.*

*L. siegfriedti* or a closely related form has been reported from the early Wasatchian of the Powder River Basin (Krishtalka, 1976a) and the southern Bighorn Basin (Bown, 1979). It is also known from the Clarkforkian of the Togwotee Pass area and Bitter Creek area, Wyoming (see Chapter V), as well as from Bear Creek.

*Leipsanolestes* has been placed by various authors in the Adapisoricidae, Amphilemuridae, and Erinaceidae, and it has been regarded as a synonym of *Leptacodon*, *Talpavus*, and *Entomolestes*. (Krishtalka considers *Leptacodon* to be a nyctitheriid, *Talpavus* to be an adapisoricid, some species of *Entomolestes* to be adapisoricids and others of this genus possibly to be erinaceids.) Surprisingly, Simpson did not include *Leipsanolestes* in his classification of 1945, either as a valid name or a synonym. *Leipsanolestes* was recently revived

Table 5. Measurements of lower teeth of *Leipsanolestes*.

| | AMNH 22157, holotype, *L. siegfriedti* | AMNH 22179, *L. siegfriedti* | UM 71660, *L. siegfriedti* | UM 66751, *L. siegfriedti* | UM 68209, cf. *L. siegfriedti* |
|---|---|---|---|---|---|
| $P_4L$ | | 1.50 | | | 1.65 |
| $P_4B$ tri | | 1.15 | | | 1.00 |
| $P_4B$ tal | | 0.90a | | | 1.15 |
| $M_1L$ | | 1.70 | 1.70 | 1.80 | 2.00 |
| $M_1B$ tri | | 1.45 | 1.25 | 1.55 | 1.55a |
| $M_1B$ tal | | 1.45 | 1.25 | 1.60 | 1.65 |
| $M_2L$ | 1.55 | 1.50 | 1.40 | | |
| $M_2B$ tri | 1.30 | 1.40 | 1.15 | | |
| $M_2B$ tal | 1.35 | 1.40 | 1.10 | | |
| $M_3L$ | 1.55 | | | | |
| $M_3B$ tri | 1.05 | | | | |
| $M_3B$ tal | 1.05 | | | | |

Dimensions of AMNH nos. 22157 and 22179 were measured from epoxy casts.

as a valid genus by Russell et al. (1975) and Krishtalka (1976a), a judgment with which I agree. I tentatively follow Krishtalka's transfer of the genus to the Erinaceidae, based principally on the progressive decrease in size from $M_1$ to $M_3$ and on the molar structure. Krishtalka (1976a: 28) also listed "a premolariform $P_4$" as a shared-derived feature of early Tertiary erinaceids, but this does not hold for *Leipsanolestes*, which has a submolariform $P_4$. (Krishtalka in fact acknowledged this by observing that "in comparison to *Macrocranion nitens* [an adapisoricid], $P_4$ of *Leipsanolestes* is semimolariform rather than premolariform" [Krishtalka, 1976a: 32]).

### Order LIPOTYPHLA, Incertae sedis

The Clarkforkian collection includes a few teeth that are recognizable as lipotyphlan but are not readily identifiable to a lower taxon. Some are upper teeth that may belong to one of the species described above from lower teeth. One specimen is a lower jaw fragment that appears to represent a species distinct from any reported above.

Three upper molars, UM nos. 71845, 71846, and 71847, from SC–188, are very similar to UM 71032 (cf. *Pontifactor bestiola*), but they do not have a W-shaped ectoloph and a strong mesostyle. In all of them, the paracone is slightly larger than the metacone, the conules are distinct and have both pre- and postconule cristae, and the protocone is shifted somewhat forward of the midline of the tooth. Each tooth has a small anterolingual cingulum and a well developed hypocone or hypocone shelf (UM 71845 has an acute hypocone oriented posterolingual to the protocone). These characters suggest affinity with the Nyctitheriidae. It is possible that these are upper teeth of cf. *Leptacodon packi* described above, but they differ in certain details from upper teeth allocated to *L. packi* from Princeton Quarry (e.g. PU 14166).

UM 68288, a right dentary fragment with $M_2$ and the talonid of $M_1$ from SC–143, appears to belong to a lipotyphlan species different from any identified so far from the Clarkforkian. $M_1$ and $M_2$ are very nearly the same size, suggesting that the form represented is either a nyctitheriid or an adapisoricid. The specimen contrasts with all other small insectivores in the collection by having a particularly long and prominent cristid obliqua that extends anterolingually to the metaconid and forms a distinct shelf on the back of the trigonid. Its paracristid is low and shelf-like.

### cf. "*Diacodon*" *minutus* Jepsen, 1930

Figure 16, Table 6

*Referred Specimens.*—UM nos. 65554, 66742, 71232, 71685, 71687, 71842, 71843, 71844.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–82); *Plesiadapis cookei* Zone (SC–117, 188, 220); *Phenacodus-Ectocion* Zone (SC–50).

*Discussion.*—Included in this sample are several fragmentary specimens of lower and upper teeth (none of them associated) that are very similar in size and structure to late Tiffanian "*Diacodon*" *minutus* Jepsen (1930b) from the Princeton Quarry level. It is possible that more than one species is represented here, or that the upper and lower teeth do not belong to the same species; nevertheless, the close resemblance of these specimens to "*Diacodon*" *minutus* indicates that it is reasonable to interpret them as representatives of one species near or identical with "*D.*" *minutus*.

The most complete specimens are UM 71232, an incomplete right dentary with $M_1$, $M_3$, and the talonid of $M_2$ (Figure 16), and UM 65554, a partial left maxilla

Table 6. Measurements of Clarkforkian teeth of cf. "*Diacodon*" *minutus*.

| | UM 65554 | UM 66742* | UM 71232 | UM 71685* | UM 71687* | UM 71842* | UM 71843* | UM 71844* |
|---|---|---|---|---|---|---|---|---|
| $M_1L$ | | | 1.85 | 1.90 | 1.75 | | | |
| $M_1B$ tri | | | 1.15 | 1.35 | 1.35 | | | |
| $M_1B$ tal | | | 1.25 | 1.45 | 1.40 | | | |
| $M_2L$ | | 1.80 | 1.85a | | | 1.80 | | |
| $M_2B$ tri | | 1.30 | | | | 1.65 | | |
| $M_2B$ tal | | 1.30 | 1.30 | | | 1.55 | | |
| $M_3L$ | | | 1.75a | | | | | |
| $M_3B$ tri | | | 1.15 | | | | | |
| $M_3B$ tal | | | | | | | | |
| $P^4L$ | 1.70 | | | | | | | |
| $P^4B$ | 2.00a | | | | | | | |
| $M^1L$ | 1.90 | | | | | | | 1.90 |
| $M^1B$ | 2.25 | | | | | | | 2.80 |
| $M^2L$ | 1.75 | | | | | | 1.75 | |
| $M^2B$ | | | | | | | 2.50 | |

*Measurements based on an isolated tooth. First and second molars in this species are very similar in size and it is possible that the tooth position of one or more of these is misidentified.

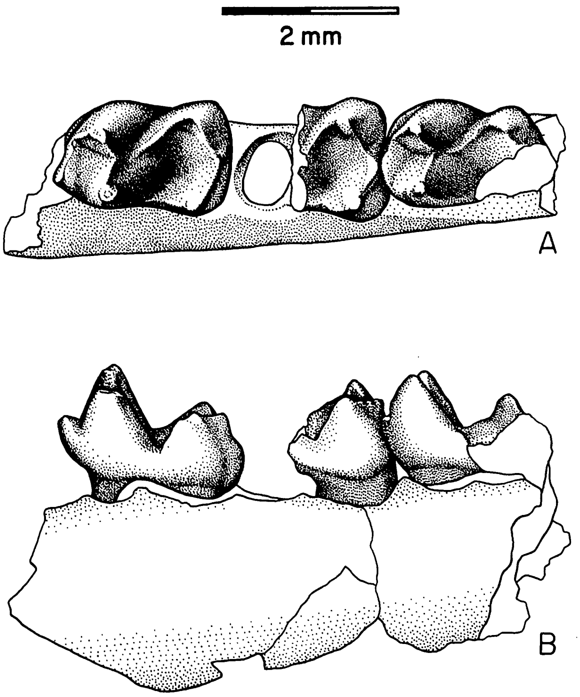

Figure 16. Cf. "*Diacodon*" *minutus*, UM 71232, from SC-220: right dentary with $M_1$ and partial $M_{2-3}$, crown and lingual views.

with $P^4$-$M^1$ and the labial part of $M^2$. Other specimens consist of isolated molars. The paraconid is lower and cuspate on $M_1$ and more reduced on $M_2$ (UM nos. 66742 and 71842) and $M_3$. When worn the paracristid appears low and shelf-like. The trigonids of $M_2$ and $M_3$ are compressed anteroposteriorly. The talonids are broad and basined with a distinct hypoconulid. $M_2$ appears to be slightly larger than $M_1$, and $M_3$ is slightly smaller than $M_1$. $P^4$ is slightly smaller than $M^1$ and has a large paracone and protocone, a small metacone closely appressed to the paracone, and a minute parastyle. The metacone of $P^4$ is slightly larger than in "*D.*" *minutus* (PU 14371). The upper molars have small but well defined conules with pre- and postconule cristae, an adaptation for well developed "en echelon" shearing, which is also found in some other early insectivores as well as in archaic primates. Anteriorly there is a short cingulum on the lingual part of each molar, and posteriorly there is a prominent, broad hypocone shelf, although the hypocone itself is variably expressed. These upper teeth (UM nos. 65554, 71843, and 71844) are essentially identical to those of "*D.*" *minutus* from Princeton Quarry, except that the Clarkforkian teeth are slightly larger.

Aside from their larger size and the reduced paraconids of $M_2$ and $M_3$, the lower teeth referred here closely resembly those of cf. *Leptacodon packi* described above. As Krishtalka (1976a: 10) stated, "'*Diacodon*' *minutus* is not a species of the leptictids *Diacodon* or *Palaeictops* or of the nyctitheriid *Leptacodon*. . . . The generic and familial status of this species is in doubt." Krishtalka noted a close resemblance between "*D.*"

*minutus* and Thanetian *Adunator lehmanni* from Walbeck, Germany, especially in the lower dentition, and he concluded that both species might be adapisoricid-like hyopsodontids. This seems unlikely, in view of various dental specializations of "*D.*" *minutus* that are typical of early insectivores but not of hyopsodontids (e.g. the emphasis on shearing in the molars). The Clarkforkian specimens described here, as well as the Princeton Quarry sample of "*D.*" *minutus*, appear to be lipotyphlans, even if their precise affinities within the order remain uncertain.

### Order DERMOPTERA Illiger, 1811
### Family Plagiomenidae Matthew, 1918
### Subfamily Plagiomeninae Matthew, 1918
### *Plagiomene* Matthew, 1918
### *Plagiomene accola*, sp. nov.

Figure 17, Tables 7, 8

*Holotype.*—UM 71443, left maxilla with $P^4$-$M^2$ and roots of $P^3$, found by William S. Bartels, at locality SC–234 (*Phenacodus-Ectocion* Zone).

*Hypodigm.*—Holotype and UM nos. 65472 (right dentary with part of $P_4$ and $M_1$), 65636 (right dentary with $P_3$-$M_3$), 69321 (right dentary with $P_{3-4}$), 71033 (lingual part of right $P^4$), 71447 (right dentary with $P_4$-$M_2$, trigonid of $M_3$, and roots of all anterior teeth, and left dentary with damaged $M_{2-3}$), 71642 (right dentary with $M_{1-2}$).

*Horizon and Locaity.*—Willwood Formation, Clarkforkian, *Plesiadapis cookei* Zone (SC–200: UM 71642), *Phenacodus-Ectocion* Zone (SC–48: UM 65472; SC–55: UM 65636; SC–90: UM 71033; SC–202: UM 69321; SC–234: holotype and UM 71447), all Clark's Fork Basin, northern Bighorn Basin, Wyoming.

*Etymology.*—Latin *accola* (masc.), neighbor, in allusion to the geographic and stratigraphic proximity of representatives of the new species to those of another recently discovered Clarkforkian plagiomenid, *Worlandia inusitata*.

*Diagnosis.*—Teeth significantly smaller than in *Plagiomene multicuspis*, about 15–25% smaller in most dimensions; larger than in *Worlandia* and *Planetetherium*. Lower dental formula 3.1.4.3, as in *Plagiomene multicuspis*, but unlike *Worlandia* (and probably *Planetetherium*). Lower cheek teeth lower crowned and with cusps less acute and ectocingulids weaker than in *P. multicuspis*. $P_4$-$M_2$ relatively slightly broader than in *P. multicuspis*. $P_4$ and $M_1$ about same length; $P^4$ longer than $M^1$. Upper and lower molars decreasing in size posteriorly to more marked degree than in *P. multicuspis*.

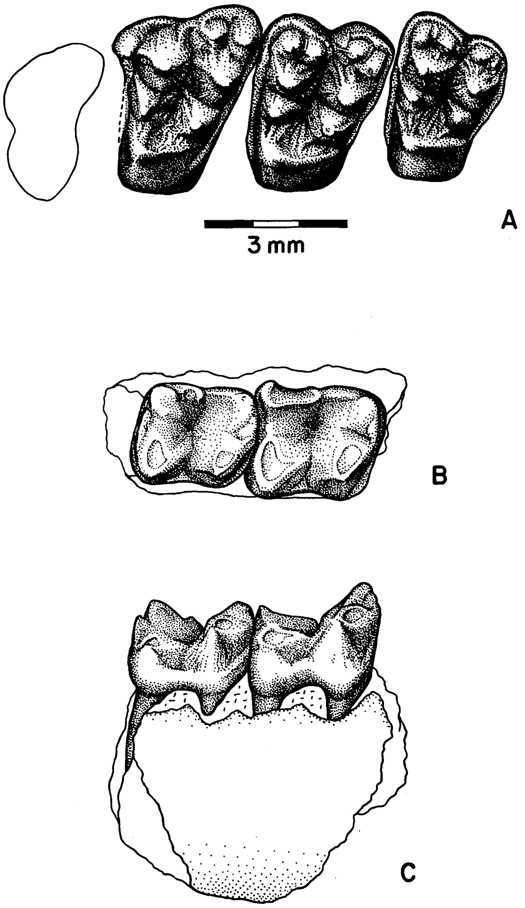

Figure 17. *Plagiomene accola*, sp. nov. A, Holotype, UM 71443, from SC–234: left maxilla with $P^4$-$M^2$, crown view. B and C, UM 71642, from SC–200: right dentary with $M_{1-2}$, crown and labial views.

*Description.*—*Plagiomene accola* is represented by jaw fragments and teeth including $P^4$-$M^2$ and $P_3$-$M_3$. UM 71447 includes parts of both dentaries and preserves the roots of all the teeth anterior to $P_4$ on the right side. It shows conclusively that *P. accola* had a lower dental formula of 3.1.4.3, as in *Plagiomene multicuspis*. $I_1$ was much larger than $I_2$ and $I_3$. The canine and $P_1$ were small one-rooted teeth. The right dentary of UM 71447 is in two parts that do not fit perfectly, hence the root configuration of $P_2$ cannot be positively determined, but it appears to have had two roots. $P_3$ clearly was two-rooted. Both species of *Plagiomene* possessed two more lower antemolar teeth than in *Worlandia inusitata*.

Table 7. Measurements of teeth of *Plagiomene accola*, sp. nov.

| | UM 65472 | UM 65636 | UM 69321 | UM 71447 | UM 71642 |
|---|---|---|---|---|---|
| $P_3L$ | | 3.00 | 2.80 | | |
| $P_3B$ (talonid) | | 2.15 | 1.70 | | |
| $P_4L$ | 3.45a | 3.35 | 3.30 | 3.10 | |
| $P_4B$ (trigonid) | | 2.60 | 2.40 | 2.40 | |
| $P_4B$ (talonid) | 2.85 | 3.10 | 2.70 | 3.05 | |
| $M_1L$ | 3.40 | 3.30a | | 3.45 | 3.00 |
| $M_1B$ (trigonid) | 2.65 | 2.80 | | 2.80 | 2.65 |
| $M_1B$ (talonid) | 2.90 | 3.10 | | 3.30 | 2.75 |
| $M_2L$ | | 2.90a | | 2.90 | 2.70 |
| $M_2B$ (trigonid) | | 2.85a | | 2.25 | 2.35 |
| $M_2B$ (talonid) | | 3.00a | | 2.30 | 2.30 |
| $M_3L$ | | | | | |
| $M_3B$ (trigonid) | | 2.25 | | 2.20 | |

| | UM 71443, holotype |
|---|---|
| $P^4L$ | 3.25 |
| $P^4B$ | 3.90 |
| $M^1L$ | 2.65 |
| $M^1B$ | 4.00 |
| $M^2L$ | 2.20 |
| $M^2B$ | 3.45 |

M2 in UM 65636 is damaged and its breadth measurements may be artificially high.

Table 8. Metrical data for teeth of *Plagiomene accola*, sp. nov.

| | N | OR | $\bar{X}$ ± SE | s | V |
|---|---|---|---|---|---|
| $P_3L$ | 2 | 2.80-3.00 | 2.90 | | |
| $P_3B$ tal | 2 | 1.70-2.15 | 1.93 | | |
| $P_4L$ | 4 | 3.10-3.45 | 3.30 ± .07 | .147 | 4.5 |
| $P_4B$ tr | 3 | 2.40-2.60 | 2.47 ± .07 | .115 | 4.7 |
| $P_4B$ tal | 4 | 2.70-3.10 | 2.93 ± .09 | .185 | 6.3 |
| $M_1L$ | 4 | 3.00-3.45 | 3.29 ± .10 | .202 | 6.1 |
| $M_1B$ tr | 4 | 2.65-2.80 | 2.73 ± .04 | .087 | 3.2 |
| $M_1B$ tal | 4 | 2.75-3.30 | 3.01 ± .12 | .239 | 7.9 |
| $M_2L$ | 2 | 2.70-2.90 | 2.80 | | |
| $M_2B$ tr | 2 | 2.25-2.35 | 2.48 | | |
| $M_2B$ tal | 2 | 2.30 | 2.30 | | |
| $M_3B$ tr | 2 | 2.20-2.25 | 2.23 | | |

Tabulation excludes $M_2$ measurements of UM 65636.

Available evidence suggests that Clarkforkian *Planetetherium mirabile* had also reduced its anterior lower dentition as in *Worlandia*.

*Plagiomene accola* differs most strikingly from early Wasatchian *P. multicuspis* by its much smaller size (Tables 8 and 9). Specimens referred to *P. multicuspis* show considerable variability in size (Rose and Simons, 1977), but only the smallest of them approach the upper end of the range in the Clarkforkian species, and none shows the marked decrease in molar size posteriorly that is characteristic of *P. accola*. A sample of *P. multicuspis* from the early Wasatchian of the central Bighorn Basin is compared here with the Clarkforkian sample of *P. accola*. Since $P^4_4$, $M^1_1$, and $M^2_2$ may be extremely difficult to distinguish between in fragmentary specimens or isolated teeth, the statistics in the tables include only specimens in which positive determination of tooth position could be made. A Student's *t*-test comparing lengths of $M_1$ and $M_2$ in the two samples showed a highly significant difference ($p<.001$). Only a small sample of upper teeth of *P. multicuspis* ($n=3$ or 4) was available for comparison with the holotype of *P. accola*. Nonetheless, the *t*-test indicated significant difference in length of $P^4$ ($p<.10$) and more significant differences in all other dimensions ($p<.05$).

In addition to size difference, *Plagiomene accola* has somewhat lower crowned cheek teeth than *P. multicuspis*. In comparably worn specimens, the cusps of *P. accola* appear to be blunter and the ectocingulids of the lower molariform teeth are less prominent. The paraconid and metaconid of $M_{1-3}$ are more closely appressed than in most specimens of *P. multicuspis*. Perhaps most important, *P. accola* shows a marked progressive decrease in size from the first molar to the last. In these features, particularly the relative size of the molars, *P. accola* more closely resembles *Worlandia inusitata* and

Table 9. Metrical data for teeth of early Wasatchian *Plagiomene multicuspis**

| | N | OR | $\bar{X} \pm SE$ | s | V |
|---|---|---|---|---|---|
| $P_3$L | 8 | 3.00-3.60 | 3.28 ± .09 | .243 | 7.4 |
| $P_3$B tal | 9 | 1.95-2.50 | 2.23 ± .07 | .203 | 9.1 |
| $P_4$L | 13 | 3.50-4.25 | 3.81 ± .07 | .263 | 6.9 |
| $P_4$B tri | 12 | 2.60-2.95 | 2.78 ± .04 | .141 | 5.1 |
| $P_4$B tal | 14 | 2.75-3.60 | 3.20 ± .06 | .238 | 7.4 |
| $M_1$L | 10 | 3.60-4.25 | 3.89 ± .07 | .208 | 5.3 |
| $M_1$B tri | 10 | 2.50-3.55 | 2.96 ± .09 | .290 | 9.8 |
| $M_1$B tal | 9 | 2.85-3.55 | 3.30 ± .09 | .266 | 8.1 |
| $M_2$L | 4 | 3.50-4.00 | 3.73 ± .11 | .222 | 6.0 |
| $M_2$B tri | 4 | 2.50-3.10 | 2.80 ± .12 | .248 | 8.9 |
| $M_2$B tal | 5 | 2.65-3.15 | 2.93 ± .08 | .182 | 6.2 |
| $M_3$L | 3 | 3.70-3.90 | 3.78 ± .06 | .104 | 2.8 |
| $M_3$B tri | 4 | 2.05-2.30 | 2.18 ± .06 | .119 | 5.5 |
| $P^4$L | 3 | 4.00-4.50 | 4.22 ± .15 | .257 | 6.1 |
| $P^4$B | 3 | 4.85-5.20 | 5.02 ± .10 | .176 | 3.5 |
| $M^1$L | 4 | 3.50-3.90 | 3.75 ± .10 | .191 | 5.1 |
| $M^1$B | 4 | 4.70-5.20 | 4.99 ± .12 | .232 | 4.6 |
| $M^2$L | 4 | 3.10-3.70 | 3.39 ± .15 | .307 | 9.1 |
| $M^2$B | 4 | 4.25-5.00 | 4.75 ± .17 | .339 | 7.1 |

*Sample includes YPM nos. 23096, 23578, 23612, 24945, 24948, 24951, 24952, 24954, 24957, 24958, 24965, 24966, 24968, 24969, 24971, 24972, 30575, 30581, 30624, 36628; AMNH 15208; UM 63824; all from early Wasatchian of the central Bighorn Basin, Wyoming.

Table 10. Metrical data for lower teeth of Clarkforkian *Planetetherium mirabile**

| | N | OR | $\bar{X} \pm SE$ | s | V |
|---|---|---|---|---|---|
| $P_4$L | 3 | 2.35-2.65 | 2.48 ± .09 | .153 | 6.2 |
| $P_4$B tri | 3 | 1.85-1.95 | 1.90 ± .03 | .050 | 2.6 |
| $P_4$B tal | 3 | 1.95-2.20 | 2.07 ± .07 | .126 | 6.1 |
| $M_1$L | 4 | 2.25-2.50 | 2.43 ± .06 | .119 | 4.9 |
| $M_1$B tri | 4 | 2.10-2.30 | 2.21 ± .04 | .085 | 3.8 |
| $M_1$B tal | 4 | 2.20-2.45 | 2.33 ± .05 | .104 | 4.5 |
| $M_2$L | 3 | 2.25-2.35 | 2.28 ± .03 | .058 | 2.5 |
| $M_2$B tri | 3 | 2.10-2.40 | 2.22 ± .09 | .161 | 7.3 |
| $M_2$B tal | 3 | 1.85-2.10 | 1.98 ± .07 | .126 | 6.4 |

*Sample includes AMNH nos. 22161, 22162, 22206, and PU 17711, all from Clarkforkian Eagle Coal Mine at Bear Creek, Montana.

*Planetetherium mirabile* (Table 10), two other Clarkforkian plagiomenids. *P. accola* clearly contrasts with *Worlandia* in lower dental formula and in morphology of $P_{3-4}$, as well as in size. It differs from *Planetetherium* in having weaker cingulids and higher cusps, as well as by being significantly larger ($p<.001$ for lengths of $P_4$, $M_1$, and $M_2$). *Planetetherium* is distinctive also because the talonid of its $M_2$ is markedly narrower than the trigonid, a contrast to both *Plagiomene* and *Worlandia*.

The morphology of the lower teeth is most clearly seen in UM nos. 65472, 69321, and 71642. When unworn (UM 65472) the enamel is highly crenulated, more so than in most specimens of *P. multicuspis*. UM nos. 65636 and 71447 are more complete than other specimens but are, unfortunately, less well preserved, both showing some degree of postmortem crushing (which has damaged the crowns of UM 65636).

Another specimen, UM 68221 (locality SC-162, *Phenacodus-Ectocion* Zone), is a nearly complete left horizontal ramus lacking the crowns of the teeth. The shape of the jaw and the configuration of the roots indicate that it represents a plagiomenid, and it appears to have the same dental formula as *Plagiomene*. UM 68221 is smaller than *P. accola*, however, and its taxonomic assignment is uncertain.

$P^4$-$M^2$ are well preserved in the holotype of *P. accola* (Figure 17A). They are very similar to their counterparts in *P. multicuspis* but are smaller and have more crenulated enamel and blunter cusps. $M^2$ is smaller relative to $M^1$ than in *P. multicuspis*. $P^4$ differs from that in all other plagiomenids in stylar cusp development. There is a prominent parastyle and a pair of stylar cusps labial to the metacone, but no cusp posterolabial to the paracone as occurs in *P. multicuspis*. *Worlandia* has a very weak parastyle or no parastyle, and only one well defined stylar cusp posterolabial to the metacone (Bown and Rose, 1979). *Planetetherium* appears to be like *Worlandia* in this regard (Szalay, 1969a: figure 7). A larger sample of *P. accola* will be required to determine if this arrangement of stylar cusps is diagnostic of the species or is an individual variation.

*Discussion.*—This is the older of the two described species of *Plagiomene*. It is less progressive than *P. multicuspis* in having lower and flatter crowned teeth, weaker cingulids, and fewer stylar cusps on $P^4$. It appears to be more specialized than the Wasatchian species in the greater reduction in size from the first molar to the third, but this would not necessarily bar *P. accola* from the ancestry of *P. multicuspis*. In most features, then, *P. accola* is a good morphological ancestor for *P. multicuspis*, and its stratigraphic and geographic occurrences strengthen the probability that it was the phylogenetic antecedent. Rose (1973) described excellently-preserved dentaries of *Plagiomene multicuspis* (PU nos. 14551 and 14552) from the early Wasatchian at "Hackberry Hollow" (SC-192) in the northern Bighorn Basin. These specimens belonged to an exceptionally small individual, overlapping the size range of *P. accola* in dimensions of $P_3$ and $P_4$, but with longer molars. Morphologically it belongs to *P. multicuspis*. However, this specimen and several small individuals in the UM early Wasatchian collection from the

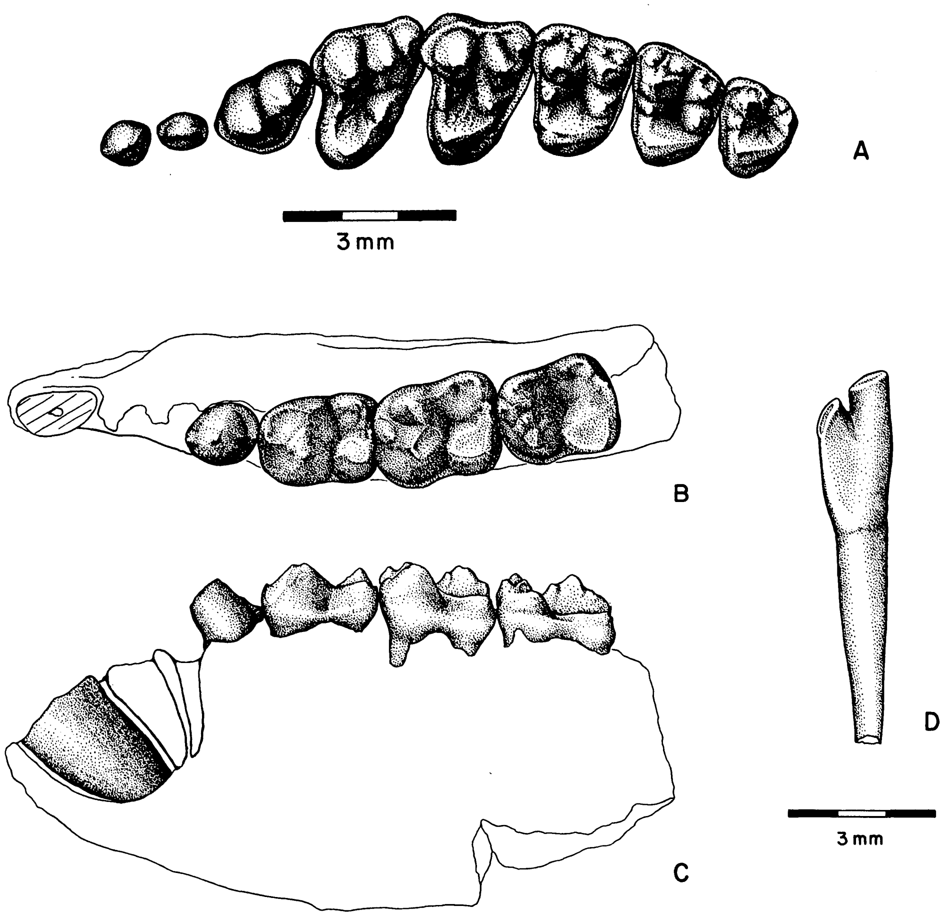

Figure 18. *Worlandia inusitata*. A, UM 69600, from SC-188: palate with nearly complete dentition; shown are left C-$P^{1-4}$-$M^{1-3}$, $P^1$ reconstructed from right side. B and C, Holotype, UM 68381, from SC-188: left dentary with $P_{2-4}$-$M_1$ and root of incisor, crown and labial views. D, UM 71044, from SC-188: ?lower left incisor of *?Worlandia inusitata*. (A-C from Bown and Rose, 1979).

Clark's Fork Basin (e.g. UM 65319) tend to bridge the gap in size between *P. accola* and typical *P: multicuspis* and are further evidence of an ancestor-descendant relationship between these two species.

*Planetetherium mirabile* from the Clarkforkian at Bear Breek closely approaches *Plagiomene accola* in size and in certain morphological features. *Planetetherium mirabile* is clearly distinct from *Plagiomene accola*, but the resemblance between them and the still nebulous nature of the lower anterior dentition in the Bear Creek form raise genuine problems for its classification. Bown and Rose (1979) proposed a new subfamily, Worlandiinae, to accommodate *Planetetherium* and *Worlandia*. While this remains the best interpretation, better preserved specimens that unequivocally show the configuration of the anterior teeth will be needed to clarify the precise affinities of *Planetetherium*.

### Subfamily Worlandiinae Bown and Rose, 1979

### *Worlandia* Bown and Rose, 1979

### *Worlandia inusitata* Bown and Rose, 1979

Figures 18, 19, Table 11

*Referred Specimens.*—UM nos. 65122, 68381 (holotype), 68387-68392, 69220, 69600-69603, 71038-71043, 71608, 71609, 71610.

*Occurrence.*—*Plesiadapis cookei* Zone (SC-188). Reported previously also from the *Phenacodus-Ectocion* Zone (SC-23, 100).

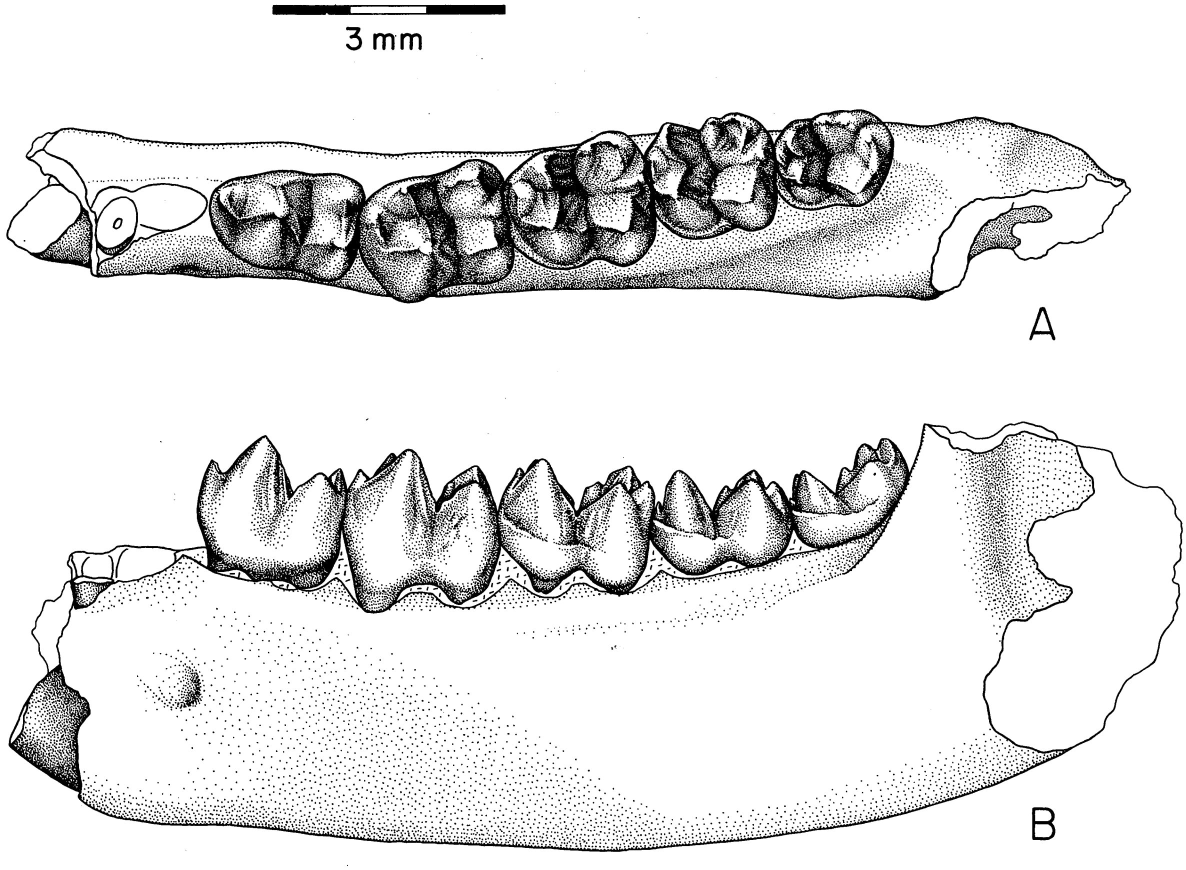

Figure 19. *Worlandia inusitata*, composite left lower dentition based on UM nos. 69601 (left dentary with $P_4$-$M_3$) and 69602 (left dentary with $P_3$-$M_2$ and roots of incisor and ?canine), from SC–188: A, crown, and B, labial views.

*Discussion.*—Bown and Rose (1979) recently described this distinctive small plagiomenid on the basis of mandibular fragments, a nearly complete palate, and several isolated teeth from Clarkforkian and early Wasatchian beds of the Bighorn Basin. Additional specimens listed here more than double the size of the original sample. All of the new material is from the same locality, SC–188, as most of the original sample, including the holotype (UM 68381) and the palate (UM 69600). They were collected mainly by quarrying and screen-washing. A considerable collection of fossil mammals is now known from SC–188, largely as a result of these two collecting techniques, and *Worlandia inusitata* ranks second in abundance among 30 species (Table 52). [Additional collecting at SC–188 in 1979 has demonstrated that *Worlandia* ranks third in abundance, after *Paramys atavus* and *Ectypodus powelli.*] Curiously, only three specimens of *Worlandia* have been found at other sites, two from the Clarkforkian of the Clark's Fork Basin and one from the early Wasatchian of the central Bighorn Basin (Bown and Rose, 1979). The latter specimen is slightly larger than the Clarkforkian specimens and may warrant specific distinction when larger samples are known.

Almost the entire dental complement of *Worlandia inusitata* is known, although the homologies of the lower anterior teeth remain uncertain. The upper dentition includes a small canine, four premolars, and three molars; the upper incisors are unknown. In the dentary there are three molars and six antemolar teeth including at least three premolars and one enlarged incisor. Bown and Rose (1979) reported that $P_4$ is larger than $M_1$, but additional specimens now available reveal that this is variable, and in most of them $P_4$ is the same size as $M_1$ or

Table 11. Metrical data for cheek teeth of Clarkforkian *Worlandia inusitata.*

| | N | OR | $\overline{X} \pm$ SE | s | V |
|---|---|---|---|---|---|
| $P_3$L | 5 | 1.85-2.00 | 1.92 ± .03 | .057 | 3.0 |
| $P_3$B tal | 5 | 1.35-1.50 | 1.45 ± .04 | .079 | 5.4 |
| $P_4$L | 9 | 1.70-2.05 | 1.87 ± .03 | .103 | 5.5 |
| $P_4$B tri | 8 | 1.45-1.75 | 1.57 ± .04 | .113 | 7.2 |
| $P_4$B tal | 8 | 1.60-1.85 | 1.69 ± .03 | .088 | 5.2 |
| $M_1$L | 10 | 1.85-1.95 | 1.89 ± .01 | .034 | 1.8 |
| $M_1$B tri | 10 | 1.55-1.80 | 1.65 ± .03 | .080 | 4.8 |
| $M_1$B tal | 9 | 1.65-185 | 1.73 ± .02 | .061 | 3.5 |
| $M_2$L | 4 | 1.60-1.65 | 1.63 ± .01 | .029 | 1.8 |
| $M_2$B tri | 4 | 1.45-1.50 | 1.49 ± .01 | .025 | 1.7 |
| $M_2$B tal | 4 | 1.40-1.55 | 1.49 ± .03 | .063 | 4.2 |
| $P^3$L | 1 | 1.90 | | | |
| $P^3$B | 1 | 2.90 | | | |
| $P^4$L | 1 | 1.95 | | | |
| $P^4$B | 1 | 2.80 | | | |
| $M^1$L | 1 | 1.75 | | | |
| $M^1$B | 1 | 2.40 | | | |
| $M^2$L | 1 | 1.60 | | | |
| $M^2$B | 1 | 2.10 | | | |
| $M^3$L | 1 | 1.30 | | | |
| $M^3$B | 1 | 1.60 | | | |

Dimensions of upper teeth from Bown and Rose, 1979.

slightly smaller than $M_1$. The new specimens preserve $M_2$ and $M_3$, previously known only from their alveoli, revealed in radiographs, in UW 10158. UM nos. 69601 and 69602 confirm that the molars decrease in size from $M_1$ to $M_3$ and show that $M_2$ is essentially identical to $M_1$ except for having a slightly smaller paraconid. In $M_3$ (UM 69601), the paraconid is further reduced and the hypoconulid is larger than in $M_1$ and $M_2$, a condition also seen in *Plagiomene*. A second specimen preserving $P^4$ is now known (UM 71041) and, as in UM 69600, it is larger than $M^1$ (especially transversely) and has its paracone and metacone slightly more closely appressed. Only the single metastyle is well developed, but there is a small stylar cusp anterolabial to the metacone and a very weakly expressed parastyle. $P^3$ (UM 69600) has a large metastyle and a small, poorly defined parastyle.

Two specimens, UM nos. 71608 and 71610, are subadults, the former with $P_3$ in place and $P_4$ erupting, and the latter with both $P_3$ and $P_4$ unerupted in a very shallow dentary.

Several isolated incisors (UM 71044, Figure 18D) that are possibly referable to *Worlandia* have also been recovered by screen-washing at SC–188. A similar incisor, UM 67021, was found at SC–120 (*Plesiadapis cookei* Zone; Rose and Simons, 1977: text-figure 8). All these specimens have bilobate crowns closely resembling the incisors of *Plagiomene* (Rose, 1973) and an incisor from Bear Creek that may belong to *Planetetherium* (ANMH 22153; Rose, 1973; Rose and Simons, 1977). The mesiodistal length of the crowns in the Clarkforkian incisors is less than in *Plagiomene*. The root diameter is very close to that of the enlarged incisor in the holotype of *Worlandia inusitata* (Figure 18B,C), hence it seems quite possible that these are lower central incisors of *Worlandia.*

*Worlandia* is more specialized than *Plagiomene* in having reduced the number and size of its lower anterior teeth. It clearly belongs to a separate lineage, contemporary to the one represented by *Plagiomene*. Available evidence suggests that *Planetetherium* was more closely related to *Worlandia* than to *Plagiomene* but, as discussed above, its dental formula and, hence, its precise affinities, remain ambiguous.

The unusual predominance of *Worlandia inusitata* at one locality, SC–188, recalls the abundance of *Planetetherium* at Bear Creek. Most of the collection from SC–188 was acquired by screen-washing a gray clay bed at the tip of one knoll. It is possible that, if more washing were done at other sites, *Worlandia* would be found to have had a broad range in the Clarkforkian. However, the two specimens from other localities, as well as the holotype itself, were surface discoveries. Fossils in the size range of *Worlandia* are not uncommon surface finds in the overbank deposits of the Clark's Fork Basin. Moreover, thorough surface prospecting and screen-washing of the penecontemporary Paint Creek locality (SC–143) has failed to turn up any specimens of *Worlandia*. The prevalence of *Worlandia* at SC–188 thus seems to be peculiar to that site and may reflect particular conditions of its environment or of its depositional setting. Resolution of these factors will require more detailed paleoecological and sedimentological analyses than can be undertaken here.

### Order PRIMATES Linnaeus, 1758
### Suborder PLESIADAPIFORMES Simons and Tattersall, 1972
### Family Microsyopidae Osborn, 1892

Referral of the Microsyopidae to the Plesiadapiformes (and thus to the order Primates) still rests primarily on dental evidence (Bown and Rose, 1976; Bown, 1979). The primitive middle Paleocene genera *Palaechthon*, *Plesiolestes* (probably a synonym of *Palaechthon*), *Palenochtha*, and *Torrejonia* are closely allied plesiadapiforms that appear to be related to Eocene microsyopids. They may be members of the Microsyopidae (Bown and Rose, 1976; Gingerich, 1976b) or ancestors of the family (Bown and Gingerich, 1973); but in any case it is now clear that they are not members of the Paromomyidae as they have been generally regarded. The structure of their postcanine teeth is more primitive than in any other plesiadapiforms (except for *Purgatorius*), whereas true paromomyids are relatively specialized (Bown and Rose, 1976; Rose and Gingerich, 1976).

Szalay (1969a) has discussed the difficulty of distinguishing two genera for the species formerly included in the genera *Microsyops* and *Cynodontomys*. The problem is much the same as that in the genera *Pelycodus* and *Notharctus*. When poorly known, the genera were relatively easy to separate. As collecting intensified and more specimens were discovered, however, gaps between species and genera diminished and the boundaries between them became nebulous. The generic boundaries now must be drawn essentially arbitrarily, and the species on either side are more similar to each other than to stratigraphically more distant members of their own genus. For this reason, Szalay used a single genus, *Microsyops* (which includes *Cynodontomys*), a position I adopt here, following also Bown and Rose (1976) and Bown (1979).

Szalay (1969b) erected the Uintasoricinae as a subfamily of the Microsyopidae to accommodate the genera *Niptomomys* and *Uintasorex*. Dental morphology of these and other microsyopids was discussed by Bown and Rose (1976). The minute forms *Micromomys* and *Tinimomys* bear detailed resemblances in molar structure to uintasoricines and are similar to them in size; but they are not well enough known to allow definite subfamily assignment. Krishtalka (1978) recently transferred the Uintasoricinae to the Omomyidae, but this allocation cannot be sustained by the evidence. Detailed (and derived) dental similarities of uintasoricines to other undoubted microsyopids, for example in structure of the incisors and of the molar talonids, are compelling evidence of their microsyopid affinities (see detailed discussions by Szalay, 1969b; Bown and Gingerich, 1972; Bown and Rose, 1976).

## Subfamily Microsyopinae (Osborn, 1892)

## *Microsyops* Leidy, 1872

### *Microsyops simplicidens*, sp. nov.

Figure 20

*Holotype.*—UM 67214, right dentary with $P_2$ (part of crown missing), $P_{3-4}$, and root of enlarged incisor, and associated right $M_1$, collected by Robert G. Habetler at locality SC-137 (*Plesiadapis cookei* Zone).

*Hypodigm.*—Holotype and UM 66178, right dentary with $P_4$ (incomplete)-$M_{1-2}$.

*Horizon and Locality.*—Willwood Formation, Clarkforkian, lower *Plesiadapis cookei* Zone (SC-74: UM 66178; SC-137: holotype), Clark's Fork Basin, northern Bighorn Basin, Wyoming.

*Etymology.*—Latin *simplex*, simple, and *dens*, tooth, in allusion to the structure of $P_4$, and in analogy with other specific names in the genus, *M. angustidens* and *M. latidens*.

*Diagnosis.*—Oldest and most primitive known species of *Microsyops*. Slightly larger than *M. wilsoni*, but otherwise closely similar in most features. Differs from *M. wilsoni* and other species of *Microsyops* in simpler structure of $P_4$: paracristid extremely weak or absent; no trace of paraconid or metaconid; protoconid tall and inflated; talonid not at all basined, but simple with one relatively high, acute cusp; cristid obliqua short, not continuous onto postvallid; no ectocingulid on talonid. Trigonid of $M_1$ slightly more open than in *M. wilsoni*.

*Description.*—The holotype and referred specimen of *Microsyops simplicidens* are very similar to *M. wilsoni* in most features, differing significantly only in the more primitive construction of $P_4$. Large samples of *M. wilsoni* now available (YPM, UW, and UM collections) indicate that the Clarkforkian specimens are outside the range of variation exhibited by *M. wilsoni*. $P_4$ in *M. wilsoni* consistently bears a strong paracristid and a distinct fold of enamel (probably homologous with the protocristid) extending from the protoconid onto the postvallid. Its talonid, though simple, is more advanced than in *M. simplicidens*. It has either one cusp (probably the hypoconid, e.g. UW nos. 7194 and 8834) or two (the hypoconid and the entoconid, e.g. UW nos. 6984, 7172) in *M. wilsoni*. The talonid of $P_4$ in *M. wilsoni* is incipiently basined as a result of a well developed internal cingulum and a strong cristid obliqua. The cristid obliqua is notched at the base of the postvallid but continues onto it. Finally, a distinct ectocingulid is consistently present on the talonid of $P_4$ in *M. wilsoni*.

The lower dental formula of *M. simplicidens* can be determined from the two known specimens, and it is the same as in other species of *Microsyops*, 1.0.3.3. The holotype dentary contains the root of an enlarged anterior tooth, interpreted as $I_1$ as in other species of the genus. Behind it and separated by a short diastema is a robust one-rooted tooth interpreted as $P_2$ by previous authors, although it is larger than $P_3$. The crown of this tooth is damaged in the type but it preserves a tiny talonid cuspule. A shorter diastema separates the small, simple, single-rooted $P_3$ from $P_2$, but there is no diastema between $P_3$ and $P_4$. $P_4$ is much larger, two-rooted, and simple, as described in the diagnosis. $M_1$ and $M_2$ are essentially identical to those of *M. wilsoni*, except for their slightly larger size and the slightly more open trigonid of $M_1$ in *M. simplicidens*.

*Discussion.*—*Microsyops simplicidens* is the most primitive species of *Microsyops* and the first of the genus recorded from pre-Wasatchian sediments. Although the two known specimens are slightly larger than *M. wilsoni*, larger samples will be necessary to determine if its mean size is really greater.

The molars of *M. simplicidens* are morphologically extremely similar to those of Torrejonian *Plesiolestes*

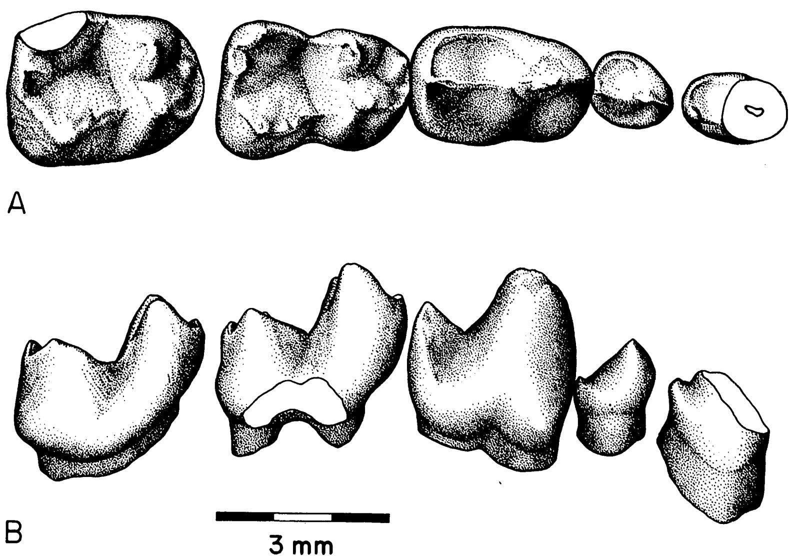

Figure 20. *Microsyops simplicidens*, sp. nov., composite right lower dentition based on UM 67214 (holotype, right dentary with $P_{2-4}$ and $M_1$, from SC–137) and UM 66178 (right dentary with $M_{1-2}$ and part of $P_4$, from SC–74). A, crown, and B, labial views.

*problematicus*, as well as to early Wasatchian *M. wilsoni*. The simple structure of $P_3$ and $P_4$, however, contrasts with the two-rooted $P_3$ and molariform $P_4$ of *Plesiolestes*. The Paleocene *Palaechthon-Plesiolestes* group may be related to *Microsyops* through common ancestry or perhaps direct ancestry, but the latter would have required a decrease in $P_4$ complexity from middle Paleocene to Clarkforkian and a subsequent increase in its complexity in the Eocene. When all the dental evidence is considered, this appears to be a reasonable hypothesis that is consistent with the known fossil record.

Two additional Clarkforkian specimens are referable to *Microsyops* but their specific identity is not certain; they may belong to either *M. simplicidens* or *M. wilsoni*. UM 69360, a left maxilla with $M^1$, and UM 71022, a fragmentary $I_1$, are both from upper Clarkforkian strata (SC–10 and SC–159, respectively, *Phenacodus-Ectocion* Zone). A third specimen, UM 68287, a right dentary fragment with $M_3$ (SC–143, *Plesiadapis cookei* Zone), may represent *Microsyops*. It is slightly smaller than *M. wilsoni* and differs from it in having a more lingual paraconid and a weaker mesoconid. Its precise identification must await recovery of more complete specimens.

Measurements of the holotype and other Clarkforkian specimens are: UM 67214, Holotype: $P_2L=1.90$, $B=1.20$; $P_3L=1.35$, $B=1.25$; $P_4L=2.95$, $B=2.05$; $M_1L=3.15$, $B=2.35$. UM 66178: $P_4L=3.25a$, $B=2.00a$; $M_1L=3.20$, $B=2.45$; $M_2L=3.30$, $B=2.65$. UM 69360: $M^1L=2.95$, $B=3.80$. UM 68287: $M_3L=2.90$, $B=1.80$.

### Subfamily Uintasoricinae Szalay, 1969
### *Niptomomys* McKenna, 1960
### *Niptomomys doreenae* McKenna, 1960

*Referred Specimens.*—UM nos. 65119, 66176, 66752, 71000.

*Occurrence.—Plesiadapis cookei* Zone (SC–119, 188); *Phenacodus-Ecotocion* Zone (SC–23, 77). Oldest record of *Niptomomys*.

*Discussion.*—The Clarkforkian specimens of *Niptomomys* consist only of isolated upper molars, except for UM 66752, a right dentary fragment with damaged $P_4$-$M_1$. They show no significant differences from specimens referred to this taxon by McKenna (1960) and Bown and Gingerich (1972). The upper molars have large, shallow trigon basins with widely separated paracone and metacone, characteristic features of *Niptomomys*. $P_4$ is robust and submolariform, with a tiny basal paraconid and a somewhat larger metaconid, and a broad talonid heel. This specimen (UM 66752) is larger than the holotype of *N. doreenae* but very close in size to YPM 27577.

Measurements of these specimens are: UM 66752: $P_4L=1.50$, $B=1.15$; $M_1$ (damaged) $L=1.85a$, $B=1.40a$. $M^1L=1.20-1.35$ (n=2), $M^1B=1.70-1.80$ (n=2), $M^2L=1.40$, $M^2B=1.70$.

### Microsyopidae, Subfamily uncertain
### *Tinimomys* Szalay, 1974
### *Tinimomys graybulliensis* Szalay, 1974

Figure 21

*Referred Specimens.*—UM nos. 71015, 71030.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–188). Oldest record of *Tinimomys.*

*Discussion.*—Two Clarkforkian specimens represent the oldest geological record of the diminutive rare microsyopid *Tinimomys graybulliensis.* UM 71030 is a fragmentary left maxilla with M$^2$ and incomplete M$^1$ and M$^3$ (Figure 21A). It is similar in size and structural details to previously reported upper dentitions of *T. graybulliensis*, PU 17899 (holotype, Szalay, 1974: figure 1) and UW 8956 (Bown, 1979). M$^1$ and M$^2$ in the Clarkforkian specimen, as in the early Wasatchian Princeton and Wyoming specimens, are transversely broad with low cusps. They have small but distinct conules with internal conule cristae. Prominent anterior and posterior cingula on the lingual half of each molar meet lingually in a prominent internal cingulum that gives rise to a small hypocone and pericone, traits characteristic of *Tinimomys.* A faint postprotocone fold joining the protocone and the hypocone can be discerned on the relatively unworn M$^2$.

UM 71015, a left M$_2$ (Figure 21B), has a relatively narrow trigonid, with the metaconid distinctly more lingual than the paraconid. The talonid is very broad and basined, with distinct hypoconid, hypoconulid, and entoconid. The hypoconulid is closer to the entoconid than to the hypoconid and is separated from the former by a shallow notch, a feature typical of most microsyopid molars. Just anterior to the hypoconid there is a slight constriction of the cristid obliqua, in front of which is a vaguely defined mesoconid. A prominent ectocingulid is present on the trigonid. UM 71015 closely resembles M$_2$ in early Wasatchian *T. graybulliensis* (UW nos. 6893 and 6894), differing only in having a slightly more acute hypoconulid and a slightly less lingual paraconid. It shows less detailed resemblances to late Tiffanian *Micromomys* (probably a close relative to *Tinimomys*), but differs from both *M. silvercouleei* Szalay (1973) and *M. vossae* Krause (1978) in having a broader talonid, shorter trigonid (i.e. its paraconid is closer to the metaconid), and more anteriorly-inclined postvallid.

*Tinimomys graybulliensis* was previously known only from the early Wasatchian of the Bighorn Basin. In addition to the specimens recorded here, *T. graybulliensis* is also known from the Clarkforkian "Big Multi Locality" in the Washakie Basin (Chapter V).

Measurements of the Clark's Fork Basin specimens are: UM 71015, M$_2$L=1.05, B trigonid=0.85, B talonid=0.95; UM 71030, M$^1$B=1.65, M$^2$L=1.00, M$^2$B=1.60, M$^3$L=0.85. (See Bown and Rose, 1976, for measurements of PU 17899, P$^4$-M$^2$, holotype of *T. graygulliensis.*)

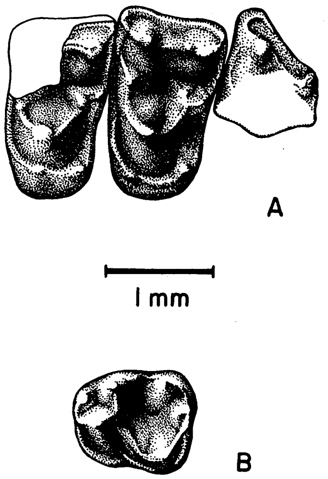

Figure 21. *Tinimomys graybulliensis* from SC–188. A, UM 71030, left maxilla with M$^{1-2}$ and part of M$^3$. B, UM 71015, left M$_2$, crown view.

### Family Plesiadapidae Trouessart, 1897
### *Plesiadapis* Gervais, 1877
### *Plesiadapis dubius* (Matthew, 1915)

Figure 22, Table 12

*Referred Specimens.*—UM nos. 63733, 67244, 67553, 67559, 68027, 68411, 68414, 68436, 69940, 71017–71021, 71305, 71307, 71312, 71614, 71821, and fragmentary teeth in UM nos. 63735, 65496, 66161, 66196, 66586, 67251, 68437.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–156, 171, 173, 179, 226, 250, 251); *Plesiadapis cookei* Zone (SC–143); *Phenacodus-Ectocion* Zone (SC–50, 72, 81, 102).

*Discussion.*—The new sample of *Plesiadapis dubius* from the Clark's Fork Basin doubles the number of specimens of this species known to Gingerich (1976b) only a few years ago. Most are fragmentary lower dentitions, and they do not add significantly to our knowledge of the morphology of *P. dubius*, except to reinforce the differences from *P. fodinatus*, such as the smaller mean size, narrower cheek teeth and lower incisors, smaller margoconid on the lower incisor, and consistent absence of P$_2$. One specimen, UM 71307, is a subadult with P$_3$ partially erupted and P$_4$ almost fully erupted. UM 71021 includes the crowns of three upper central incisors, of interest because only one upper incisor of this species was previously known. Each of the three Clarkforkian incisors bears three small bead-like mediocones, whereas Gingerich observed two in the incisor then known.

*Plesiadapis dubius* is very similar to late Tiffanian *P. fodinatus*, from which it was directly descended. *P.*

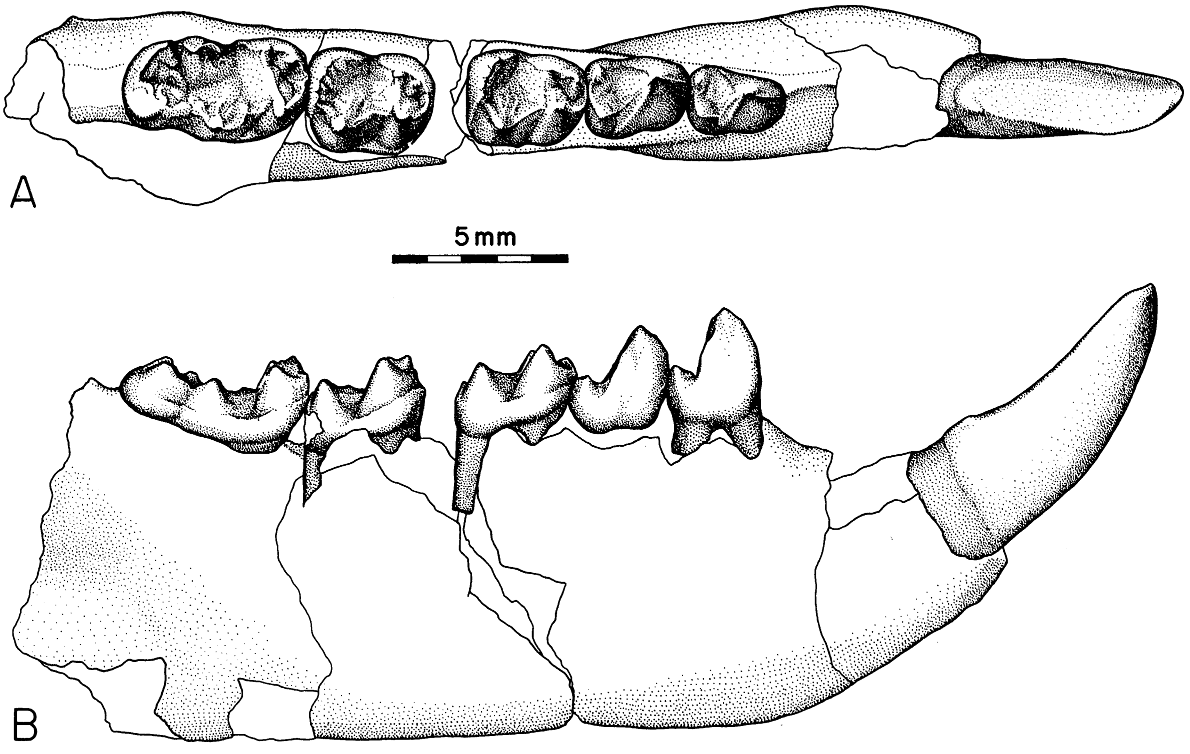

Figure 22. *Plesiadapis dubius*, UM 67244, from SC–143: right dentary with incisor and $P_3$-$M_3$. A, crown, and B, labial views.

Table 12. Metrical data for UM Clarkforkian teeth of *Plesiadapis dubius*.

| | N | OR | $\overline{X}$ ± SE | s | V |
|---|---|---|---|---|---|
| $I_1B$ | 5 | 2.10–2.20 | 2.16 ± .02 | .042 | 1.9 |
| $P_3L$ | 2 | 2.30–2.45 | 2.38 | | |
| $P_3B$ | 2 | 1.75–1.90 | 1.83 | | |
| $P_4L$ | 3 | 2.45–2.55 | 2.50 ± .03 | .050 | 2.0 |
| $P_4B$ | 3 | 1.90–2.10 | 2.02 ± .06 | .104 | 5.1 |
| $M_1L$ | 2 | 2.70–3.10 | 2.90 | | |
| $M_1B$ | 1 | 2.65 | | | |
| $M_2L$ | 6 | 2.95–3.25 | 3.10 ± .04 | .110 | 3.5 |
| $M_2B$ | 5 | 2.75–2.95 | 2.87 ± .04 | .084 | 2.9 |
| $M_3L$ | 4 | 4.55–5.00 | 4.76 ± .09 | .189 | 4.0 |
| $M_3B$ | 4 | 2.70–2.90 | 2.81 ± .05 | .103 | 3.7 |
| $P^4L$ | 1 | 2.50 | | | |
| $P^4B$ | 1 | 3.70 | | | |
| $M^1L$ | 2 | 3.05–3.15 | 3.10 | | |
| $M^1B$ | 2 | 4.20–4.50 | 4.35 | | |
| $M^2L$ | 3 | 3.10–3.50 | 3.25 ± .13 | .218 | 6.7 |
| $M^2B$ | 3 | 4.50–4.80 | 4.70 ± .10 | .173 | 3.7 |
| $M^3L$ | 3 | 3.00–3.10 | 3.03 ± .03 | .058 | 1.9 |
| $M^3B$ | 3 | 4.25–4.55 | 4.40 ± .09 | .150 | 3.4 |

*fodinatus* is common in the Princeton Quarry level and at some latest Tiffanian sites above Princeton Quarry (e.g. SC–165). In the interval between SC–165 and lowest Clarkforkian SC–179 are several sites that have yielded isolated teeth and tooth fragments more or less intermediate between *P. fodinatus* and *P. dubius*. Some teeth included in UM 68892 (SC–191, latest Tiffanian) are the size of *P. fodinatus*, whereas others are rather small for that species. A lower central incisor in this lot has a reduced margoconid characteristic of *P. dubius*, but is slightly larger and broader, as in *P. fodinatus*.

Wood (1967: 26) suggested that *P. dubius* might be a synonym of *P. fodinatus*, a conclusion that stemmed from his uncertainty of the provenance of the holotype of *P. dubius*, and the belief then held that *P. fodinatus* ranged from Tiffanian into early Wasatchian. Matthew (1915c) specified that the type of *P. dubius*, AMNH 16073, was from "Clark Fork beds at base of bluff northeast of Ralston," that is, the southern tip of Polecat Bench. It is probable that the specimen came from the vicinity of localities SC–76, 77, or 107, from upper Clarkforkian beds. Our present knowledge of the evolution of *Plesiadapis* indicates that *P. dubius* evolved directly from *P. fodinatus* just prior to the beginning of

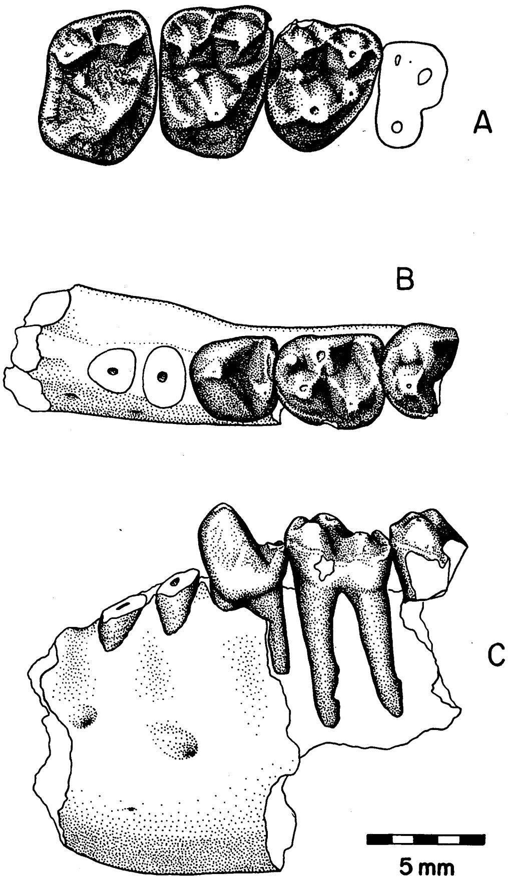

Figure 23. *Plesiadapis gingerichi*, sp. nov., Holotype, UM 68409, from SC–171: A, right maxilla with M$^1$ and root of P$^4$ and associated M$^{2-3}$; B and C, left dentary with P$_4$-M$_1$, trigonid of M$_2$, and roots of P$_3$, crown and labial views.

the Clarkforkian, hence *P. fodinatus* is restricted to the Tiffanian. As far as I am aware, only one specimen of *Plesiadapis* is known from the early Wasatchian: UW 6118 (*P. dubius*), from north of Emblem in the Bighorn Basin (T. M. Bown, personal communication). The distinctions between *P. fodinatus* and *P. dubius* are minor, nonetheless they reflect a more progressive stage achieved by the latter. It is both useful and important to recognize these distinctions.

### *Plesiadapis gingerichi*, sp. nov.

Figures 23, 24, Table 13

*Holotype.*—UM 68409, left dentary with P$_4$-M$_1$, M$_2$ trigonid, and roots of P$_3$, right maxilla with M$^1$ and roots of P$^4$, and associated right M$^2$ and M$^3$, from SC–171 (*Plesiadapis gingerichi* Zone).

*Hypodigm.*—Holotype and UM nos. 68421 (right M$_2$), 68734 (incomplete left P$_4$ and right P$^4$), 68741 (right dentary with M$_{1-3}$, M$_3$ lacking heel, and right maxilla with M$^1$ and part of M$^2$), 68742 (left dentary with M$_{1-3}$, M$_2$ lacking trigonid), 68743 (right dentary with M$_1$), 68758 (incomplete left M$_3$), 71682 (labial part of left upper molar), 71683 (incomplete crown of left I$_1$), 71794 (right P$_3$), and tentatively UM 71817 (right I$^1$).

*Horizon and Locality.*—Polecat Bench Formation, latest Tiffanian, *Plesiadapis gingerichi* Zone (SC–178: UM 68734; SC–181: UM 68758), and early Clarkforkian, *Plesiadapis gingerichi* Zone (SC–179: UM nos. 68741, 68742, 68743); and basal Willwood Formation, early Clarkforkian, *Plesiadapis gingerichi* Zone (SC–171: Holotype and UM nos. 68421, 71682; SC–226: UM

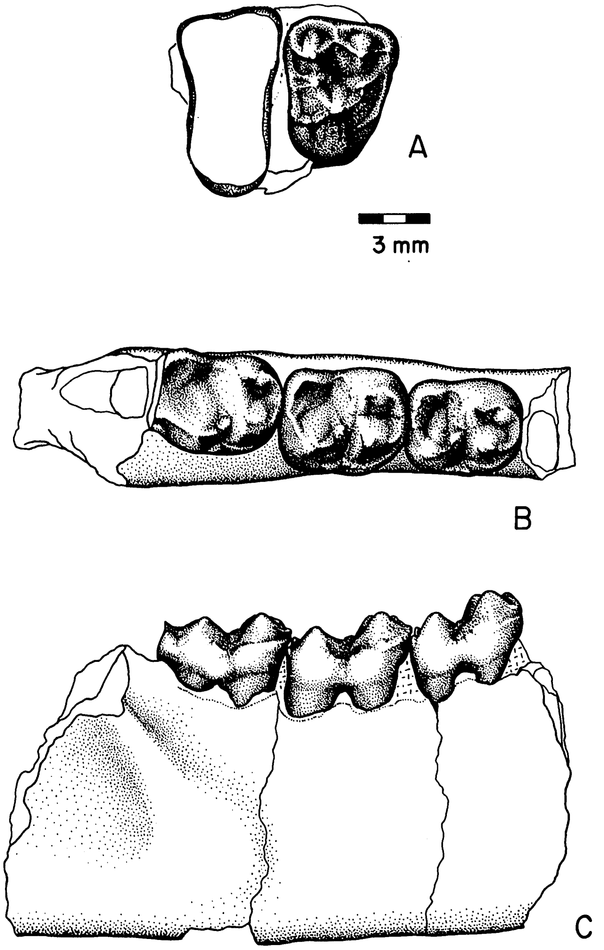

Figure 24. *Plesiadapis gingerichi*, sp. nov., UM 68741, from SC–179: A, right maxilla with $M^1$ and base of $M^2$; B and C, right dentary with $M_{1-3}$ (talonid of $M_3$ incomplete), crown and labial views.

71683; SC–248: UM 71794; SC–251: 71817); all Clark's Fork Basin, northern Bighorn Basin, Wyoming.

*Etymology.*—For Dr. Philip D. Gingerich, in recognition of his outstanding contributions to the study of early Tertiary mammals, particularly plesiadapid primates.

*Diagnosis.*—Intermediate in size between *Plesiadapis simonsi* and *P. cookei* but significantly different in size from both (about 20% larger than *P. simonsi* and 10–15% smaller than *P. cookei* in most dimensions); within upper part of size range of European *P. tricuspidens*. Morphologically very similar to these three species, but $P_3$ elongate, relatively narrow, and wedge-shaped as in *P. cookei* and in contrast to *P. tricuspidens*; $P_4$ relatively shorter and broader than in *P. cookei.*

*Description.*—The holotype and referred specimens of *P. gingerichi* are almost identical in structure to the slightly younger *P. cookei* from the same area. They differ significantly in size from *P. cookei* and the slightly older (late Tiffanian) *P. simonsi*, as far as can be tested from the small sample. A *t*-test comparing $M_1$ length in these species indicates that *P. gingerichi* differs from both *P. simonsi* and *P. cookei* at $p < .01$. (Mean length of $M_1$ in *P. cookei* was taken from Table 14. For the holotype of *P. simonsi*, the only specimen with $M_1$, I estimated the maximum length of $M_1$ to be 3.75 mm. Even using Gingerich's [1976b] measurement of 4.0, the test is significant at $p < .02$). UM 68741 has relatively narrower molars than in *P. cookei*, whereas UM 68421 has relatively broader molars than most specimens of *P. cookei.* These two specimens display the extremes in molar breadth observed in the sample of *P. gingerichi* and help to demonstrate the range of variation to be expected in this species. $P_4$ is complete only in the holotype, where it is short and very broad. Its talonid is relatively much broader than in most specimens of *P. cookei.* Except in size, the molars are essentially identical to those of *P. cookei.* In one specimen, UM 68741, $M_2$ and $M_3$ bear a strong mesoconid, but mesoconids are weak or absent in other specimens.

*P. gingerichi* is very similar to larger specimens of European *P. tricuspidens*, from Berru (Mouras Quarry) in the Paris Basin. It is virtually the same size, and I have been unable to detect any significant differences in molar morphology. The size and shape of $P_3$ in *P. gingerichi*, however, contrasts with that in *P. tricuspidens.* From the roots preserved in the holotype of *P. gingerichi* and from an isolated $P_3$ (UM 71794), we know that this tooth was elongate, wedge-shaped, and slightly longer than $P_4$. These are resemblances to *P. cookei.* $P_3$ in *P. tricuspidens* is a relatively short tooth and is smaller than $P_4$. *P. gingerichi* also appears to differ from *P. tricuspidens* and *P. cookei* in having a much shallower dentary (mean depth labially below $M_1$ in *P. gingerichi*=13.1 [n=4]; in *P. tricuspidens* mean depth=17.7 [n=9]; in *P. cookei* mean depth=17.5 [n=5], from Gingerich, [1976b]).

UM 71817, an isolated upper central incisor, may belong to *P. gingerichi.* It has a very large laterocone and a small mediocone and is very similar to $I^1$ of *P. cookei.* Like *P. cookei*, it lacks a centroconule, a feature present in the upper incisors of *P. tricuspidens.* The tooth is slightly larger than that of *P. tricuspidens* and is as large as that of *P. cookei* (and thus larger than might have been expected for *P. gingerichi*). Because of its low stratigraphic level, UM 71817 is here tentatively referred to *P. gingerichi.*

*Discussion.*—Although the sample size of *Plesiadapis gingerichi* is rather small, most of the dentition is known and it compares very closely with that of the younger *P.*

Table 13. Measurements of teeth and mandibles of *Plesiadapis gingerichi*, sp. nov.

| | UM 68409, holotype | UM 68421 | UM 68741 | UM 68742 | UM 68743 | UM 71794 | $\bar{X}$ ± SE |
|---|---|---|---|---|---|---|---|
| $P_3$L | | | | | | 4.30 | |
| $P_3$B | | | | | | 3.05 | |
| $P_4$L | 3.80 | | | | | | |
| $P_4$B | 3.80 | | | | | | |
| $M_1$L | 4.60 | | 4.50 | 4.75 | 4.75a | | 4.65 ± .06 |
| $M_1$B tri | 3.95 | | 3.90 | 4.10 | | | 3.98 ± .06 |
| $M_1$B tal | 4.25 | | 3.90 | 4.40 | | | 4.18 ± .15 |
| $M_2$L | | 5.00 | 5.00 | | | | 5.00 |
| $M_2$B tri | 4.30 | 4.55 | 4.40 | | | | 4.42 ± .07 |
| $M_2$B tal | | 4.70 | 4.25 | 4.70 | | | 4.55 ± .15 |
| $M_3$L | | | | 7.40 | | | |
| $M_3$B tri | | | 4.05 | 4.35 | | | 4.20 |
| $M_3$B tal | | | 4.20 | 4.60 | | | 4.40 |
| MD* | 13.5a | | 11.10 | 13.5a | 14.4a | | 13.13 ± .71 |
| $M^1$L | 4.80 | | 4.50 | | | | 4.65 |
| $M^1$B | 6.10 | | 6.00 | | | | 6.05 |
| $M^2$L | 5.20 | | | | | | |
| $M^2$B | 7.00 | | | | | | |
| $M^3$L | 4.85 | | | | | | |
| $M^3$B | 6.80 | | | | | | |

*Depth of dentary measured labially beneath $M_1$.

*cookei*. As already discussed, *P. gingerichi* is almost perfectly intermediate in size between late Tiffanian *P. simonsi* and middle Clarkforkian *P. cookei*, and it occurs in the stratigraphic interval between them (latest Tiffanian and early Clarkforkian). There can be no doubt that it is their phylogenetic intermediary.

Of particular interest is the very close similarity between *P. gingerichi* and larger specimens of *P. tricuspidens* from the Thanetian (late Paleocene) of the Paris Basin. There are minor differences in the shape and size of $P_3$ and in mandibular depth, but molar size and morphology in the two species are practically indistinguishable. Gingerich (1976b: 32) stated that "*Plesiadapis simonsi* is of about the same size as *Ples. tricuspidens* from Cernay and could eventually prove to be conspecific with it, the two possibly being regarded as geographic subspecies of the same species." Indeed, *P. simonsi* confirms closely in size and structure to the smaller specimens of *P. tricuspidens*, among which is the holotype. Thus *P. simonsi* and *P. gingerichi* closely parallel populations of *P. tricuspidens*. Gingerich (1974) demonstrated that *P. tricuspidens* specimens from Cernay are, on average, smaller than those from Berru. Although the two localities are usually considered to be of approximately the same age, stratigraphic data are not available to show this, and faunal evidence suggests that Berru is slightly younger than Cernay (Russell, 1975: 30). Thus the correspondence between the North American and European species of *Plesiadapis* appears striking indeed. Moreover, *P. tricuspidens* gave rise to a larger species, *P. russelli*, "closely resembling the contemporaneous *Ples. cookei* from North America" (Gingerich, 1976b: 40). The parallel between the lineages *P. simonsi*-*P. gingerichi*-*P. cookei* in North America and *P. tricuspidens* (Cernay)-*P. tricuspidens* (Berru)-*P. russelli* in the Paris Basin provides strong evidence that these faunas were closely allied and essentially contemporaneous. As they become better known, *P. simonsi* and *P. gingerichi* may prove to be successive geographic subspecies of *P. tricuspidens*.

At present, *P. gingerichi* is best interpreted as a species distinct from *P. tricuspidens*, although very closely related, because of minor differences that reflect a slightly divergent direction of evolution. *P. gingerichi*, with its elongate, wedge-shaped $P_3$ foreshadows *P. cookei*, whereas *P. tricuspidens*, with a shorter, relatively broader $P_3$ trends toward *P. russelli* and *Platychoerops*. (In *P. gingerichi*, the length:width ratio of $P_3$=1.41 [n=1]; in *P. cookei*, the ratio is 1.29 [n=4]; in *P. tricuspidens*, the ratio is 1.12 [n=25]; in *P. russelli*, the ratio is 1.11 [n=1]; all ratios except *P. gingerichi* based on measurements from Gingerich, 1976b).

The stratigraphic interval that yields *P. gingerichi* has been poorly known because it is the least fossiliferous in the entire Clark's Fork Basin sequence. With the discovery of *P. gingerichi* from lower Clarkforkian strata, it is now possible to refine Gingerich's (1975, 1976b) plesiadapid zonation by inserting a *P. gingerichi* Zone between the *P. simonsi* Zone and the *P. cookei* Zone. The age of the zone is defined by the total vertical range of *P. gingerichi* and is latest Tiffanian (above the Princeton Quarry level) and early Clarkforkian. At present, this zone has been recognized only in the Clark's Fork Basin, but its presence may be expected elsewhere as latest Tiffanian and early Clarkforkian beds are discovered and thoroughly searched for vertebrate remains.

### *Plesiadapis cookei* Jepsen, 1930

Figure 25, Table 14

*Referred Specimens.*—UM nos. 63284, 63288, 63289, 64999, 65006, 65008, 65009, 65014, 65016, 65028, 65031, 65035, 65041, 65049, 65050, 65053, 65533, 65662, 65720, 66125, 66179, 66326, 66701-66704, 66716, 66718, 66720, 66725, 66730, 66731, 66739, 66741, 66746, 66755, 66911, 66919, 67018, 67187, 67190, 67203, 67252, 68278, 68861, 68875, 69175, 69221, 69265, 69300, 69306, 69313, 69319, 69339, 69341, 69344, 69906, 69913, 69995, 71016, 71031, 71764, and miscellaneous isolated teeth.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–19, 20, 53, 58, 61, 62, 65, 74, 92, 115, 116, 117, 119, 120, 127, 136, 143, 166, 188, 189, 195, 201, 220).

*Discussion.*—Specimens of *Plesiadapis cookei* in the new collections from the Clark's Fork Basin more than double the size of all previously known samples of this species. Gingerich (1976b) listed more than 30 additional specimens collected earlier in the Clark's Fork Basin. The dental morphology of *P. cookei* has been well known, but the new specimens provide some minor additions to our knowledge. UM 67187 is the first specimen found that preserves both lower incisors in place (Figure 25B,C). UM 66731, a right maxilla with $P^3$-$M^2$, appears to lack any trace of an alveolus for $P^2$, thus suggesting an upper dental formula of 2.0.2.3. At least some individuals of *P. cookei*, then, lost $P^2$, a tooth retained in *P. tricuspidens*. Two specimens represent subadults. UM 67190 includes fragmentary dentaries with the $P_4$s partially erupted; however, no deciduous teeth are preserved. UM 71031 appears to be left $dP^4$ (Figure 25A) of *P. cookei* (L=4.40, B=5.70), the first deciduous upper tooth of *P. cookei* to be illustrated. It is fully molariform but smaller (especially transversely) than the molars.

Gingerich (1976b: figure 24) indicated a probable size increase through time in *Plesiadapis cookei*. The number of specimens available was only ten, and Gingerich's conclusion was based on the observation that three specimens from the Paint Creek locality (SC–143, then believed to be of latest Clarkforkian age) had a larger mean size than seven from the Sand Coulee area. The relationship of SC–143 to other Clarkforkian sites cannot be established stratigraphically, but faunal evidence clearly places it in the *P. cookei* Zone (middle Clarkforkian). The vertical stratigraphic range of *P. cookei* is now known to be more restricted than previously believed, and there is no evidence in the sample now available of any size trend during this interval.

*Plesiadapis cookei* is one of the most common and diagnostic fossils of the Clarkforkian. According to Jepsen (1930b), the holotype is from T.57 N., R.101 W., probably section 32, Park County, Wyoming. This location corresponds approximately to SC–92 or SC–136, low in the *P. cookei* Zone. In the Clark's Fork Basin, *P. cookei* is restricted to an interval about 200 m thick in the middle of the Clarkforkian. The limits of its range define the boundaries of the *P. cookei* Zone. Outside of the Bighorn Basin, *P. cookei* is now known from the Togwotee Pass area, La Barge area (Buckman Hollow), Shotgun Butte area (Gazin, 1971), and Washakie Basin, all in Wyoming (see Chapter V).

*P. cookei* is closely allied to *P. tricuspidens* of the Paris Basin and differs from it primarily in having larger cheek teeth and relatively broader molars and incisors. The upper central incisor of *P. cookei* differs from that of *P. tricuspidens* in having a slightly weaker mediocone and lacking the crest-like centroconule between the mediocone and the laterocone. *P. cookei* is even more similar to early Clarkforkian *P. gingerichi* which, as discussed above, closely parallels *P. tricuspidens*. The Clarkforkian collections now known appear to document the direct derivation of *P. cookei* from *P. gingerichi* through phyletic evolution, and they strengthen the probability of close relationship between the larger species of *Plesiadapis* from North America and Europe.

### *Chiromyoides* Stehlin, 1916

### *Chiromyoides potior* Gingerich, 1975

Figure 26A

*Referred Specimens.*—UM nos. 66135, 67184.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–66, 136).

*Discussion.*—Two incomplete incisors are referred to *Chiromyoides potior*. Both are from localities low in the *P. cookei* Zone, and they may represent about the latest occurrence of this species. UM 66135 (Figure 26A) is a partial upper central incisor that is essentially identical to the holotype of *C. potior* and somewhat smaller than *C. major*. UM 67184 is an incomplete left lower incisor

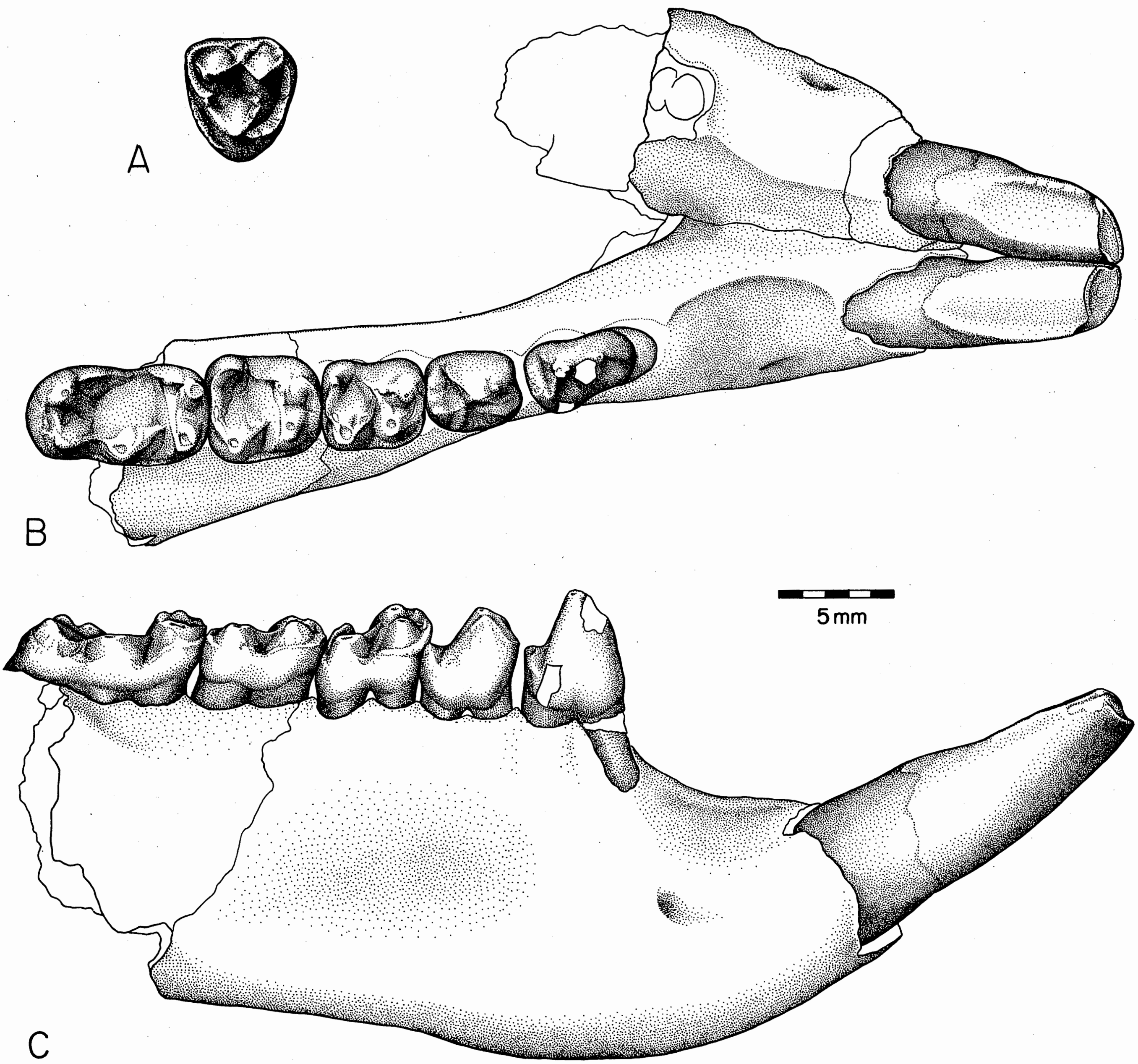

Figure 25. *Plesiadapis cookei.* A, UM 71031, from SC–143: left ?dP$^4$. B and C, UM 67187, from SC–136: dentaries with both lower incisors, right $P_4$ and $M_2$; $P_3$ and $M_1$ restored from UM 65720 (SC–62), and $M_3$ restored from UM 65049 (SC–20); crown and labial views.

that is slightly smaller but otherwise very similar to a lower incisor (PU 18348) of *C. potior* from Bear Creek; it is much smaller than the lower incisor of *C. major*. The tooth is laterally compressed and relatively short, in contrast to the long, broad lower incisor of *Plesiadapis cookei*, and it bears a small but distinct margoconid.

*C. potior* is known also from late Tiffanian beds in the Clark's Fork Basin (PU 19125) and elsewhere (Gingerich, 1976b). Two additional Clarkforkian specimens may be added to the hypodigm: PU 17895, an upper

Table 14. Metrical data for UM teeth of *Plesiadapis cookei*.

| | N | OR | $\bar{X}$ ± SE | s | V |
|---|---|---|---|---|---|
| $P_4L$ | 15 | 4.30-5.35 | 4.79 ± .07 | .284 | 5.9 |
| $P_4B$ | 14 | 3.80-4.60 | 4.13 ± .05 | .192 | 4.6 |
| $M_1L$ | 15 | 4.75-5.50 | 5.11 ± .06 | .221 | 4.3 |
| $M_1B$ | 15 | 4.25-5.30 | 4.84 ± .07 | .265 | 5.5 |
| $M_2L$ | 16 | 5.35-6.05 | 5.63 ± .06 | .229 | 4.1 |
| $M_2B$ | 17 | 4.90-6.00 | 5.41 ± .07 | .281 | 5.2 |
| $M_3L$ | 11 | 8.50-10.00 | 9.05 ± .13 | .438 | 4.8 |
| $M_3B$ | 11 | 4.75-5.55 | 5.25 ± .08 | .252 | 4.8 |
| $P^4L$ | 3 | 4.00-4.40 | 4.18 ± .12 | .202 | 4.8 |
| $P^4B$ | 3 | 5.90-7.05 | 6.48 ± .33 | .575 | 8.9 |
| $M^1L$ | 9 | 5.05-5.75 | 5.54 ± .08 | .243 | 4.4 |
| $M^1B$ | 9 | 6.75-7.55 | 7.13 ± .09 | .277 | 3.9 |
| $M^2L$ | 6 | 5.25-5.90 | 5.66 ± .11 | .273 | 6.3 |
| $M^2B$ | 6 | 7.30-8.70 | 7.98 ± .21 | .505 | 6.3 |
| $M^3L$ | 7 | 4.80-5.40 | 5.15 ± .08 | .212 | 4.1 |
| $M^3B$ | 6 | 6.90-8.55 | 7.78 ± .28 | .696 | 8.9 |

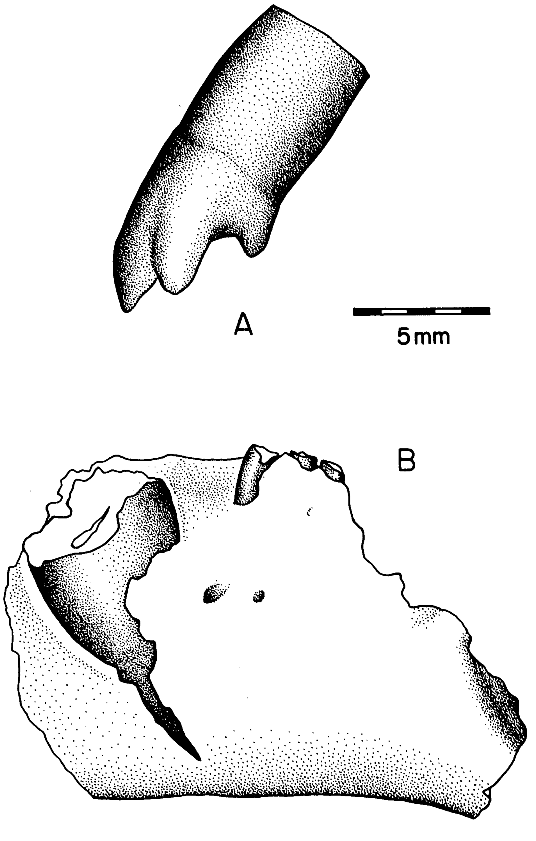

Figure 26. A, *Chiromyoides potior*, UM 66135, from SC-66: left $I^1$, lateral view. B, *Chiromyoides major*, UM 67245, from SC-143: left dentary with roots of incisor, $P_3$, and anterior root of $P_4$, lateral view.

incisor from the vicinity of SC-92 and SC-136, and PU 19522, a right $M_3$ from near SC-209. The latter tooth is broad and flat and very similar to $M_3$ in European *C. campanicus*, except for being slightly smaller.

Measurements: UM 67184, left $I_1$ breadth=2.80, depth=5.20. PU 19522, right $M_3L$=3.65, B=2.40. (Dimensions of $M_3$ in *C. campanicus* are L=3.95, B=2.60; measured from epoxy cast of the holotype.)

### *Chiromyoides major* Gingerich, 1975

Figure 26B

*Referred Specimens.*—UM nos. 67245, 67247.

*Occurrence.*—*Plesiadapis cookei* Zone (SC-143).

*Discussion.*—Two additional specimens of *Chiromyoides major* from its type locality are recorded here. Only incisors have been known previously from this site. UM 67245 is an edentulous left dentary containing the incisor root (Figure 26B). The size of the root is very similar to that of PU 21587, a complete lower incisor of *C. major* from SC-143, and is considerably larger than in *C. potior* (UM 67184). The dentary is short, robust, and very deep, even deeper than in *C. campanicus* from the late Thanetian of the Paris Basin. The diastema between the incisor and the anterior-most premolar is longer than in *C. campanicus*, and the roots of the premolar indicate a larger tooth than in *C. campanicus*. These features suggest that *C. major* may have retained only one lower premolar, but confirmation of this must await more complete specimens. The symphysis of the Clarkforkian dentary is very deep and almost vertically oriented to accommodate the very robust and laterally compressed root of the incisor. UM 67247 is an isolated right $M_2$. It is relatively broad and low crowned, but slightly narrower and longer than $M_2$ in *C. campanicus*.

*Chiromyoides* was only recently recognized in North American early Tertiary faunas (Gingerich, 1973), and it is still a rare element. Gingerich (1973, 1975) described four American species of the genus, distinguished mainly on the basis of upper incisor morphology and size. One additional species, *C. campanicus*, is known from Europe (late Thanetian of the Paris Basin). *C. major* is the youngest known species of *Chiromyoides*.

Measurements of the two new specimens of *C. major* are: UM 67245, symphysial depth=14.80; depth of dentary, lingually at most anterior tooth,=15.35; incisor depth=6.80; incisor breadth (at root)=4.20a. UM 67247, $M_2L$=3.05, B=2.75. (Dimensions of $M_2$ in *C. campanicus* are L=2.65, B=2.90; measured from epoxy cast of the holotype.)

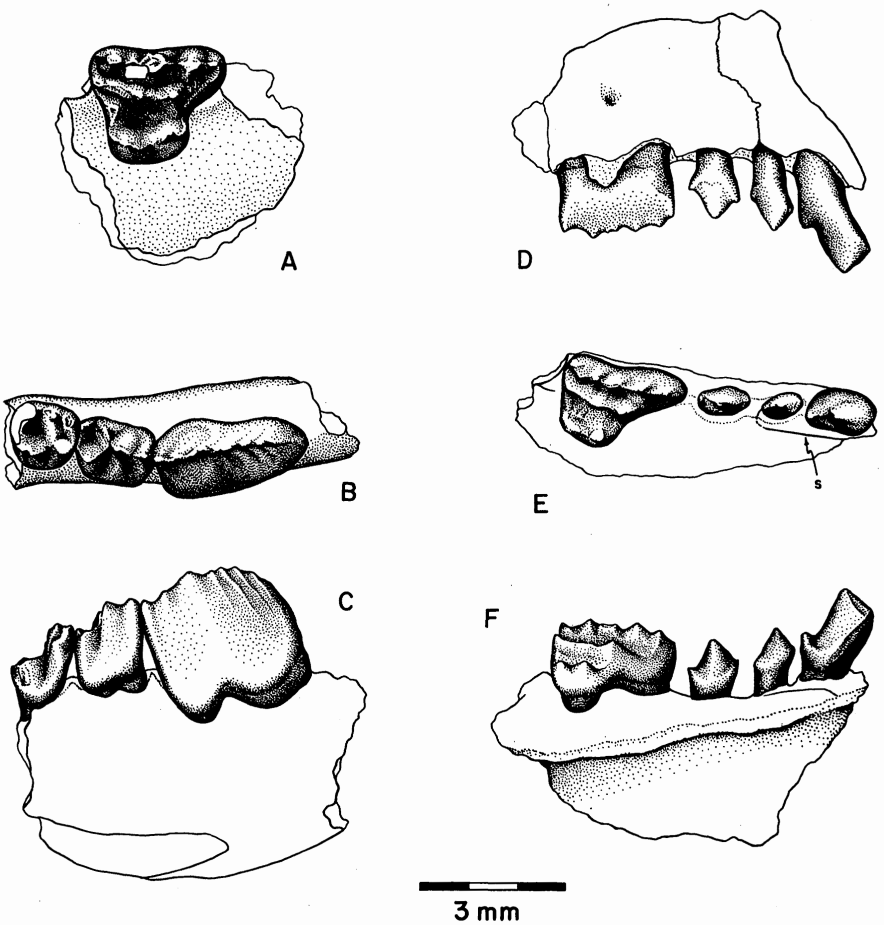

Figure 27. Carpolestidae. A, *Carpolestes dubius/nigridens* intermediate, UM 69251, from SC–199 (latest Tiffanian): right maxilla with $P^3$. B–F, *Carpolestes nigridens* from SC–188. B and C, UM 71004: right dentary with $P_4$-$M_2$, crown and labial views. D–F, UM 71002, right premaxilla and maxilla with ?$I^2$-?C-$P^{2-3}$, labial, crown, and lingual views. Premaxillary-maxillary suture is designated by *s*.

### Family Carpolestidae Simpson, 1935
### *Carpolestes* Simpson, 1928
### *Carpolestes nigridens* Simpson, 1928

Figure 27

*Referred Specimens.*—UM nos. 65033, 65254, 66909, 67556, 68289, 69338, 69943, 71001–71006, 71644, 71778.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–19, 53, 127, 143, 188); *Phenacodus-Ectocion* Zone (SC–29).

*Discussion.*—These are the latest well-documented records of the genus *Carpolestes.* These specimens conform closely to the morphology of *Carpolestes* as described by Rose (1975a), and $P^3$ (UM nos. 67556, 71002) displays an elongate anteroexternal spur, confirming their identity as *C. nigridens.*

In addition to the UM specimens here assigned to *C. nigridens*, two Princeton specimens may be added to the list: PU nos. 18169 and 21227, both from SC–143. Other Clarkforkian specimens of this species were cited by Rose (1975a). Locality data with PU 13284, Jepsen's (1930b) paratype of *Carpolestes dubius*, indicate that it comes from the *Plesiadapis cookei* Zone in the vicinity of SC–136 and SC–92. Thus it almost certainly represents *C. nigridens*, not *C. dubius.* (Also in the Princeton collection are two lower teeth, PU nos. 18102 and 20720, for which locality records indicate an early Wasatchian provenance in the vicinities of SC–161 and SC–2. No other evidence, however, corroborates the Wasatchian occurrence of *C. nigridens*; indeed, the species appears to be restricted to the Clarkforkian. Thus I suspect that the locality data for these Princeton specimens are erroneous and that they are actually from Clarkforkian strata.)

UM 71002, a right upper dentition including $P^3$ and three one-rooted teeth anterior to it, is the most complete upper anterior dentition of a carpolestid yet discovered (Figure 27D–F). $P^2$ is diminutive and laterally compressed, with one prominent cusp and low accessory cuspules in front and back. The tooth in front of $P^2$ (?canine) is smaller still, with a high cusp and only the faintest trace of a posterior accessory cuspule. In front of this tooth is a larger, higher-crowned one ($I^2$). The principal cusp of $I^2$ is preceded by a crest that inclines only slightly, giving the tooth a gently procumbent profile. A low cusp is situated at the base of the incisor behind the main cusp. The back of the alveolus for the enlarged central incisor is also preserved in UM 71002. The specimen includes parts of the maxilla and the premaxilla, and shows clearly that the premaxillary-maxillary suture, in lateral view (Figure 27D), meets the back of the alveolus of the ?canine. The palatal path of the suture is less definite but appears to run posterolaterally to the back of the same alveolus (Figure 27E). Thus it appears that the ?canine was held primarily in the premaxilla. Alternatively, it is just possible that the tooth is $I^3$, not C; but no other plesiadapiform is known to have had more than two upper incisors.

Rose (1975a, 1977) recently revised the Carpolestidae and provided evidence of the ancestral-descendant relationship between late Tiffanian *Carpolestes dubius* and Clarkforkian *C. nigridens*. Additional specimens now clarify this evolutionary transition. UM 71007, maxillary fragments with $P^{3-4}$ and $M^2$ from SC–165 (latest Tiffanian about 100 m above Princeton Quarry, see Figure 2), has a $P^3$ that is morphologically similar to that of *C. dubius*. A right $P^3$ from SC–199 (UM 69251, Figure 27A, very late Tiffanian about 50 m above SC–165) is almost perfectly intermediate between *C. dubius* and *C. nigridens* in the degree of projection of the anteroexternal spur. Thus it appears that the transition from *C. dubius* to *C. nigridens* occurred in latest Tiffanian time and was complete by the middle Clarkforkian.

Three specimens from the early Clarkforkian of the Badger Basin area (UM nos. 69540, 71306, 71309, from SC–171 and SC–226, *Plesiadapis gingerichi* Zone) may also be transitional between *C. dubius* and *C. nigridens*, or they may represent early individuals of *C. nigridens*. $P^3$ is not preserved intact in any of the specimens, and its morphology must be known to be certain of the specific identity. (UM 69540 contains parts of both $P^3$s, but both are damaged. The root of an extended anteroexternal spur appears to be present on the right side, but this interpretation is not certain.)

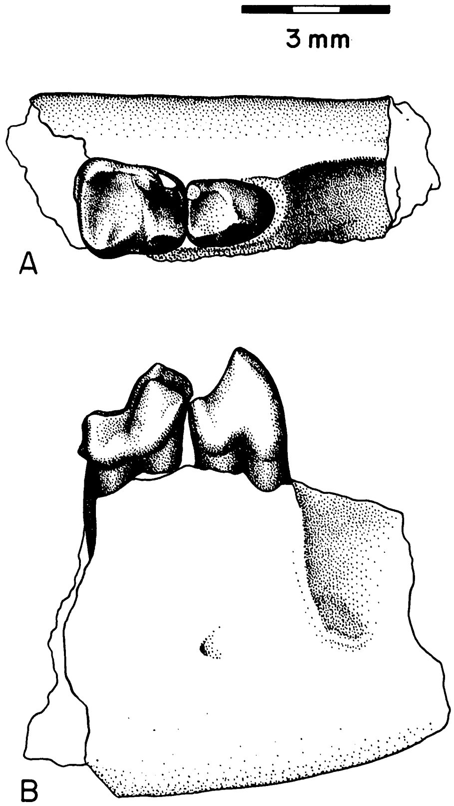

Figure 28. *Ignacius graybullianus*, UM 69877, from SC–214: right dentary with $P_4$-$M_1$. A, crown, and B, labial views.

Metrical data for the new specimens of *C. nigridens* are: $P_4L=2.85$–$3.35$ ($\bar{X}=3.16$, $n=9$), $P_4B=1.40$–$1.75$ ($\bar{X}=1.53$, $n=9$); $M_1L=1.65$–$1.90$ ($\bar{X}=1.77$, $n=9$), $M_1B=1.20$–$1.65$ ($\bar{X}=1.37$, $n=9$); $M_2L=1.40$–$1.60$ ($n=3$), $M_2B=1.30$–$1.50$ ($n=3$); $P^3L=2.50$–$3.20$ ($n=2$), $P^3B=1.90$–$2.40$ ($n=2$); $P^4L=1.90$–$2.30$ ($n=2$), $P^4B=1.70$–$2.10$ ($n=2$).

### Family Paromomyidae (Simpson, 1940)

### *Ignacius* Matthew and Granger, 1921

### *Ignacius graybullianus* Bown and Rose, 1976

Figure 28

*Referred Specimens.*—UM nos. 66771, 67016, 69687, 69877, 69998, 71025.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–120, 127, 188, 220); *Phenacodus-Ectocion* Zone (SC–214). First Clarkforkian record of the genus.

*Discussion.*—Several Clarkforkian specimens compare closely with previously known specimens of *Ignacius graybullianus* Bown and Rose (1976), from the early Wasatchian of the Bighorn Basin, except that $P_4$ in the Clarkforkian specimens is somewhat larger (but still markedly smaller than $M_1$). These specimens have relatively low and flat crowned molars, in which the cusps and crests are less well defined than in *Phenacolemur.*

Bown and Rose (1976) resurrected the genus *Ignacius* Matthew and Granger, 1921, which had for many years been considered a synonym of *Phenacolemur.* They provided an emended diagnosis designed to facilitate distinguishing between *Ignacius* and its close relative *Phenacolemur.* The distinctness of the genus was further indicated by cranial morphology described from an early Wasatchian specimen of *I. graybullianus* from the Clark's Fork Basin (Rose and Gingerich, 1976). Bown (1979) reported additional specimens of *I. graybullianus* from the early Wasatchian of the southeastern Bighorn Basin. In light of this new evidence, it will be useful to review the interrelationships and distinctions between *Ignacius* and *Phenacolemur.*

*Ignacius* appears to have been derived from a species of *Paromomys,* probably *P. depressidens* or a closely allied form. The oldest known representatives of *Ignacius* are of late Torrejonian age (*I.* cf. *fremontensis* from Rock Bench Quarry, see Table 38). *Phenacolemur pagei* from the late Tiffanian Princeton Quarry level is the oldest known species of *Phenacolemur.* Its ancestry is less clear than that of *Ignacius.* Bown and Rose (1976) speculated that *Phenacolemur* may have been derived independently from a different species of *Paromomys, P. maturus,* and that *Phenacolemur* and *Ignacius* thus represent distinct lineages that evolved in parallel. Paleocene species of *Ignacius* possess a reduced $P_4$ (characteristic of the genus), and they are therefore unlikely to be related to the ancestry of *Phenacolemur.* Some specimens of *Phenacolemur pagei* and of later species of the genus are similar to *Ignacius* in certain features, including some traits regarded as diagnostic of the latter genus by Bown and Rose (1976). However, *Ignacius* is characterized by a suite of features and, while occasional specimens of *Phenacolemur* resemble *Ignacius* in one or another aspect, adequate specimens can be readily distinguished.

Among the most characteristic features of *Ignacius* is its relatively small fourth premolar, always markedly smaller than the first molar. In early *Phenacolemur* (*P. pagei* and *P. praecox*) $P_4$ is variable in size and shape but is always much larger than $M_1$, whereas $P^4$ is about the same size or slightly smaller than $M^1$ but always relatively larger and more inflated than in *Ignacius.* In later species such as *P. jepseni* and *P. praecox citatus,* $P_4$ is somewhat smaller but still usually broader or longer than $M_1$, and it is comparatively larger than in *Ignacius.* In addition to the difference in relative size, $P^4$ of *Ignacius* differs from that of *Phenacolemur* in having a much weaker metacone.

Differences in molar morphology are, in some cases, rather subtle, making positive identification of isolated teeth very difficult (this is particularly true in late Tiffanian and Clarkforkian specimens). Nonetheless, thorough comparisons usually permit confident identification. The molars of *Ignacius* are lower and flatter crowned, and they have less acute cusps and crests and shallower basins than in *Phenacolemur.* These features are structural in nature and are not the result of wear. Molars of *Ignacius* are more squared, particularly at the posterior margin, whereas in *Phenacolemur* they are distinctly more rounded (convex) posteriorly. The trigonids of the lower molars of *Ignacius* are lower with respect to the talonids that in *Phenacolemur,* and the postvallids are more anteriorly inclined. Associated with this trait, the talonid notch is poorly defined or absent in *Ignacius,* but it is typically well marked in *Phenacolemur.* Upper molars of *Ignacius* have a deeply invaginated (V-shaped) centrocrista, in which the postparacrista is much longer than the premetacrista. Concomitant with this feature is reduction of the metacone, which is markedly smaller and lower than the paracone, usually more so than in *Phenacolemur.* Some specimens of *Phenacolemur pagei* and *P. jepseni* closely approach *Ignacius* in these characters, but they differ from *Ignacius* in the other aspects of molar morphology described above. The juncture of the postprotocone fold and the postcingulum is sharply angular in *Ignacius* but is gently rounded in *Phenacolemur.* Taken together, all these characters consistently separate *Ignacius* from *Phenacolemur* in all specimens I have examined. $M^3$ in *Ignacius* has a large, expanded posterointernal basin (Rose and Gingerich, 1976: plate 2), not significantly different from that in *Phenacolemur,* contrary to our earlier belief (Bown and Rose, 1976).

In addition to the details of dental morphology, the structure of the skull and dentary also appear to separate *Ignacius* and *Phenacolemur.* The dentary of *Ignacius* is relatively deeper than in *Phenacolemur* (Bown and Rose, 1976: figure 1c), a trait somewhat exaggerated by the lower crowned molars of *Ignacius.* Only one cranium of each species is known, but they demonstrate a difference in dental formula and configuration of upper teeth (Rose and Gingerich, 1976).

The available anatomical evidence, together with the phylogenetic interpretations regarding the derivations of *Ignacius* and *Phenacolemur*, justify recognition of both as valid genera. Robinson (1968a) recognized the distinction between the two taxa but used *Ignacius* as a subgenus. The evidence now available suggests that this was overly conservative.

*Phenacolemur* and *Ignacius* occur together at several localities in the Bighorn Basin (Rose and Gingerich, 1976; Bown, 1979). In the Clarkforkian and early Wasatchian of the Clark's Fork Basin, *Ignacius graybullianus* coexisted with *Phenacolemur pagei* (at SC–127, 188, both middle Clarkforkian) and *P. praecox* (at SC–54, very early Wasatchian), respectively. Although the molars of these taxa are approximately the same size, *Ignacius* can be consistently distinguished from *Phenacolemur* using the criteria outlined above.

The preceding discussion has concerned only *Ignacius* and *Phenacolemur* from western North America. Two species of *Phenacolemur* have been described from the early Eocene of France (Russell et al., 1967), and both are known only from small samples of isolated teeth. Some specimens of the European *Phenacolemur* resemble *Ignacius* in the form of the centrocrista of the upper molars. A $P_4$ referred to *P. fuscus* is much smaller than $M_1$s of that species, as in *Ignacius*, but serially associated $P_4$-$M_1$ are not yet known. The relationship of the French species to the North American lineages, therefore, is unclear, and it cannot be adequately assessed until larger samples and more complete specimens are known. However, it seems possible that some of the European specimens represent *Ignacius*, or that the European species belong to an endemic lineage. In addition to the French fossils, two species of paromomyids were recently reported from the Eureka Sound Formation of Ellesmere Island (West, Dawson, and Hutchison, 1977). Casts of some of these specimens were made available to me through the kindness of Dr. Dawson. The Eureka Sound paromomyids appear to be very specialized forms belonging to an undescribed genus that is more closely allied to *Ignacius* than to other paromomyids.

Measurements of the Clarkforkian specimens of *I. graybullianus* are: UM 67016, $P_4$L=2.25, B=1.95; UM 69687, $M_1$L=2.55, B=2.45; UM 69877, $P_4$L=1.90, B=1.45, $M_1$L=2.30, B=2.10; UM 69998, $M_1$L=2.40, B=2.25, $M_2$L=2.45, B=2.20; UM 71025, $M_1$ or $M_2$ L=2.25, B=2.00, $P^4$L=1.95, B=2.60. Mean dimensions of $M_1$ are L=2.42, B=2.27 (n=3).

### *Phenacolemur* Matthew, 1915

### *Phenacolemur pagei* Jepsen, 1930

Figures 29, 30, Table 15

Table 15. Metrical data for UM Clarkforkian teeth of *Phenacolemur pagei*.

| | N | OR | $\bar{X} \pm$ SE | s | V |
|---|---|---|---|---|---|
| $P_4$L | 11 | 2.80-3.35 | 3.09 ± .05 | .174 | 5.6 |
| $P_4$B | 10 | 1.75-2.20 | 2.00 ± .04 | .132 | 6.6 |
| $M_1$L | 11 | 2.10-2.50 | 2.34 ± .04 | .131 | 5.6 |
| $M_1$B | 9 | 1.90-2.20 | 2.05 ± .03 | .094 | 4.6 |
| $M_2$L | 4 | 2.25-2.40 | 2.35 ± .04 | .071 | 3.0 |
| $M_2$B | 4 | 2.05-2.15 | 2.09 ± .02 | .048 | 2.3 |
| $M_3$L | 3 | 2.95-3.20 | 3.10 ± .08 | .132 | 4.3 |
| $M_3$B | 3 | 1.70-1.80 | 1.77 ± .03 | .058 | 3.3 |
| $dP^4$L | 1 | 2.45 | | | |
| $dP^4$B | 1 | 2.35 | | | |
| $P^4$L | 1 | 2.00 | | | |
| $P^4$B | 1 | 2.65 | | | |
| $M^1$L | 3 | 2.05-2.40 | 2.22 ± .10 | .176 | 7.9 |
| $M^1$B | 3 | 2.90-3.30 | 3.05 ± .13 | .218 | 7.1 |
| $M^2$L | 1 | 1.70 | | | |
| $M^2$B | 1 | 2.75 | | | |

*Synonym.—Parapheliscus bjorni* Van Valen, 1967.

*Referred Specimens.*—UM nos. 64998, 65054, 65255, 66533, 66908, 67183, 67251, 67558, 68438, 68515, 69269, 69310, 69720, 69905, 69944, 71023, 71024, 71026, 71167, 71304, 71635, 71785, and miscellaneous isolated teeth.

*Occurrence.—Plesiadapis gingerichi* Zone (SC–174, 226); *Plesiadapis cookei* Zone (SC–19, 20, 62, 74, 99, 109, 127, 136, 143, 188, 197, 201, 238); *Phenacodus-Ectocion* Zone (SC–29, 176).

*Discussion.*—These specimens are very similar to the type sample of *Phenacolemur pagei* from the late Tiffanian Princeton Quarry, but they average slightly larger than that sample. (Measurements in Table 15 are smaller than those given by Simpson [1955] for *P. pagei* due to differences in measuring techniques. $P_4$ is difficult to measure consistently because of its variable shape.) Specimens from the Clarkforkian appear to show a gradual size increase from about the size of Princeton Quarry level *P. pagei* to the lower end of the range for *P. praecox* (Figure 30). Several specimens from the upper *Plesiadapis cookei* zone are intermediate in size between late Tiffanian samples of *P. pagei* and early Wasatchian samples of *P. praecox*. I have included most of them in *P. pagei* drawing the boundary between the species essentially arbitrarily in the lower *Phenacodus-Ectocion* Zone. The samples now available appear to document the gradual transition from *P. pagei* to *P. praecox* in the Clark's Fork Basin.

UM 71026 is a deciduous $P^4$ of *P. pagei*. It is fully molariform but differs from the molars in being longer than broad.

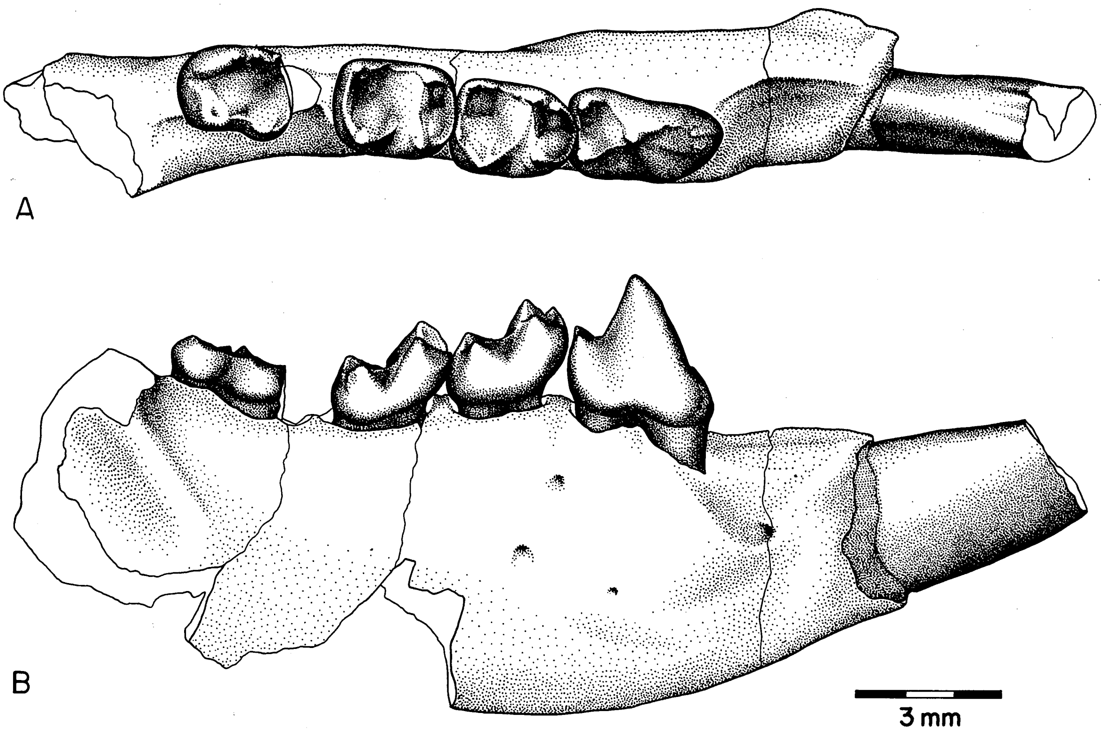

Figure 29. *Phenacolemur pagei*, UM 66908, from SC-127: right dentary with I, $P_4$-$M_3$ ($M_3$ trigonid missing). A, crown, and B, labial views.

The holotype and original sample of *P. pagei*, from Princeton Quarry (Jepsen, 1930b), were considered the best sample of any species of *Phenacolemur* by Simpson (1955). Since Simpson's study, several additional specimens from the same level at Schaff Quarry and in the vicinity of Princeton Quarry have increased this sample. *P. pagei* is very similar to *P. praecox* but is slightly smaller. Simpson found that the ratio of $P_4$ length to $M_1$ length is, on the average, greater in *P. pagei* than in *P. praecox*, but this is more evident in the Princeton Quarry sample than in that from the Clarkforkian. Simpson further observed that the Princeton Quarry specimens show "considerable variation" despite their homogeneity of origin. The Clarkforkian sample of *P. pagei* is also variable, especially in shape of $P_4$. Princeton Quarry specimens of *P. pagei* are readily separable from Wasatchian *P. praecox* but, as observed above, the Clarkforkian sample bridges the gap between the two species.

Delson (1971) transferred the holotype of Van Valen's (1967) *Parapheliscus bjorni* (AMNH 22244 from Bear Creek) to the genus *Phenacolemur* but suggested that it is "probably too small to represent the same population as the specimens of *P. pagei* from the slightly antecedent Silver Coulee Quarry [Princeton Quarry]" (Delson, 1971: 336). It is true that the specimen is slightly smaller than specimens of *P. pagei* from Princeton Quarry, and it is much smaller than *P. praecox*. In view of the variability observed in $P_4$ of *Phenacolemur*, AMNH 22244 is best considered as a small individual of *P. pagei* rather than as a representative of a distinct species. AMNH 22245, a right $P^4$ referred by Van Valen to *Parapheliscus bjorni*, almost certainly belings to *Phenacodaptes sabulosus*, not to *Phenacolemur*.

### *Phenacolemur praecox* Matthew, 1915

Figure 30, Table 16

*Referred Specimens.*—UM nos. 65106, 65528, 66307, 67236, 68211, 68217, 69284, 71027, 71028, 71029, and isolated teeth in UM nos. 66196, 67243, 68218.

*Occurrence.*—*Phenacodus-Ectocion* Zone (SC-24, 48, 50, 52, 81, 90, 138, 159, 203).

*Discussion.*—These specimens are indistinguishable from early Wasatchian specimens of *P. praecox* from the

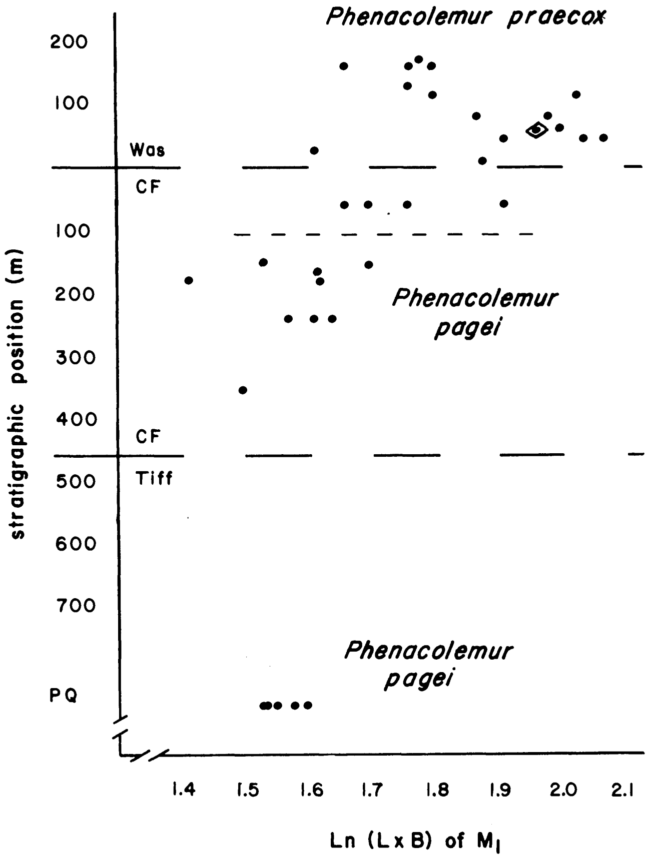

Figure 30. Stratigraphic plot of Clarkforkian and early Wasatchian *Phenacolemur pagei* and *P. praecox* of the Clark's Fork Basin. Natural logarithm of crown area of $M_1$ is plotted against stratigraphic level with respect to the Clarkforkian-Wasatchian boundary sandstone. A few specimens of *P. pagei* from Princeton Quarry (late Tiffanian) are shown for comparison. *P. pagei* and *P. praecox* are segments of the same evolving lineage which gradually increases in size through this section. The boundary between the species is drawn essentially arbitrarily in the late Clarkforkian (see text for further explanation). The holotype of *P. praecox* is indicated by a point enclosed in a diamond.

Clark's Fork Basin and elsewhere in the Bighorn Basin, although most of the Clarkforkian specimens are at the smaller end of the range of Wasatchian *P. praecox*. This sample, then, further demonstrates the gradual transition from *P. pagei* to *P. praecox* evidenced also by the earlier Clarkforkian specimens of *P. pagei*. The specimens here referred to *P. praecox* differ from Clarkforkian *P. pagei* only by being slightly larger, on average, but the smallest of them overlap with the largest *P. pagei*. Hence an arbitrary boundary between the species was drawn in the lower *Phenacodus-Ectocion* Zone, where available samples indicate that the known specimens all fall within the observed range of *P. praecox*.

Table 16. Metrical data for UM Clarkforkian teeth of *Phenacolemur praecox*.

| | N | OR | $\overline{X} \pm$ SE | s | V |
|---|---|---|---|---|---|
| $P_4L$ | 1 | 3.50a | | | |
| $P_4B$ | 1 | 2.60a | | | |
| $M_1L$ | 4 | 2.50-2.75 | 2.60 ± .06 | .122 | 4.7 |
| $M_1B$ | 4 | 2.10-2.45 | 2.24 ± .07 | .149 | 6.7 |
| $M_2L$ | 6 | 2.55-2.80 | 2.68 ± .04 | .108 | 4.0 |
| $M_2B$ | 6 | 2.30-2.40 | 2.32 ± .02 | .041 | 1.8 |
| $M_3L$ | 1 | 3.90 | | | |
| $M_3B$ | 1 | 2.25 | | | |
| $dP^4L$ | 1 | 2.70 | | | |
| $dP^4B$ | 1 | 2.60 | | | |
| $M^1L$ | 4 | 2.60-2.80 | 2.71 ± .05 | .103 | 3.8 |
| $M^1B$ | 4 | 3.35-3.60 | 3.50 ± .06 | .122 | 3.5 |

UM 71029 is a $dP^4$ of *P. praecox*. Like the $dP^4$ of *P. pagei* noted above, UM 71029 is molariform but is relatively longer and less transverse than the molars.

The holotype of *P. praecox*, AMNH 16102, a dentary with $P_4$-$M_2$, represents a relatively large individual. Granger's 1912 field notes indicate that the specimen was collected about "3 miles southeast of the mouth of Pat O'Hara Creek, Clark's Fork Basin," which is approximately in the vicinity of localities SC-139 (Gingerich and Simons, 1977) and SC-40 (sections 11 and 14, T.56 N., R.102 W., Park County). Exposures in this area are of earliest Wasatchian ("Sand Coulee") age, within the lower 75 m of Wasatchian age sediments. The sample referred here to *P. praecox* is the first record of the species from the Clarkforkian, but it is possible that late Clarkforkian specimens were included in Matthew's original sample.

*Phenacolemur* cf. *simonsi* Bown and Rose, 1976

*Referred Specimen.*—UM 71850.

*Occurrence.*—*Plesiadapis cookei* Zone (SC-65).

*Discussion.*—A single left $M^3$, UM 71850, is the only specimen of a very small paromomyid from the Clarkforkian of the Bighorn Basin. It is slightly smaller than the two known $M^3$s (including the holotype) of *Phenacolemur simonsi* and differs from $M^3$ in the holotype in having a slightly more oblique postprotocrista. In all other respects it is identical to $M^3$ in the type. The paracone is much larger than the metacone, and the posterointernal basin is greatly expanded.

An isolated lower molar from the Clarkforkian of the

Table 17. Metrical data for UM Clarkforkian teeth of *Thryptacodon* cf. *antiquus*.

| | N | OR | $\overline{X} \pm SE$ | s | V |
|---|---|---|---|---|---|
| $P_4$L | 1 | 5.80 | | | |
| $P_4$B | 1 | 3.10 | | | |
| $M_1$L | 1 | 6.25 | | | |
| $M_1$B tri | 1 | 3.95 | | | |
| $M_1$B tal | 1 | 4.60 | | | |
| $M_2$L | 5 | 5.70–6.55 | 6.09 ± .14 | .307 | 5.0 |
| $M_2$B tri | 5 | 4.90–5.85 | 5.26 ± .18 | .393 | 7.5 |
| $M_2$B tal | 5 | 5.25–6.10 | 5.55 ± .15 | .332 | 6.0 |
| $M_3$L | 2 | 6.10–6.15 | 6.13 | | |
| $M_3$B tri | 3 | 4.60–5.20 | 4.97 ± .19 | .321 | 6.5 |
| $M_3$B tal | 2 | 3.70–4.60 | 4.15 | | |
| $P^4$L | 2 | 4.80–5.40 | 5.10 | | |
| $P^4$B | 1 | 5.70 | | | |
| $M^1$L | 1 | 6.10 | | | |
| $M^1$B | 1 | 6.70 | | | |
| $M^2$L | 3 | 5.90–6.90 | 6.37 ± .29 | .503 | 7.9 |
| $M^2$B | 3 | 7.50–8.10 | 7.85 ± .18 | .312 | 4.0 |
| $M^3$L | 4 | 4.05–5.10 | 4.58 ± .24 | .484 | 10.6 |
| $M^3$B | 4 | 5.85–7.70 | 6.93 ± .39 | .788 | 11.4 |

Washakie Basin may belong to *P. simonsi* (Chapter V). All other specimens of *P. simonsi* are from early Wasatchian sediments of the Bighorn Basin.

The dimensions of UM 71850 are: $M^3L=1.50$, $M^3B=1.50$.

### Order CONDYLARTHRA Cope, 1881
### Family Arctocyonidae Murray, 1866
### *Thryptacodon* Matthew, 1915
### *Thryptacodon* cf. *antiquus* Matthew, 1915

Figure 31D, Table 17

*Referred Specimens.*—UM nos. 66208, 66312, 68028, 68215, 69179, 71241, 71557–71562, 71620, and isolated teeth in UM nos. 65112, 65529, 67459 , 68781, 68786, 71646.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–156, 179); *Plesiadapis cookei* Zone (SC–61, 84, 109, 117, 188, 195); *Phenacodus-Ectocion* Zone (SC–24, 52, 81, 90, 154, 159, 183, 184, 234).

*Discussion.*—*Thryptacodon* is moderately well represented in the Clarkforkian collection, and it is decidedly the most common arctocyonid. Although the sample is small, it shows considerable variability in size (Table 17) and morphology. $P_4$, preserved in one specimen (UM 71562), is relatively narrow and bears a thick metaconid ridge immediately lingual to the protoconid, but a cuspate metaconid is not developed. The lower molars are comparable in structure and proportions to those in the holotype of *T. antiquus* (AMNH 16162), but the lower teeth in the latter are not well preserved. The ectocingulids of the lower molars are variably developed but tend to be relatively weak. One specimen, UM 71560, has a prominent basal cusp (ectostylid of Van Valen, 1966; "protostyle on $M_2$" of Matthew, 1915a) on the cingulum at the hypoflexid, but this feature appears to be quite variable (Matthew, 1915a; Simpson, 1937c). The upper teeth do not differ significantly from those of *T. antiquus*. The cingula are very prominent and appear to be narrower than in *T. pseudarctos* from Bear Creek. The presence of a pericone is variable. It is usually distinct on $M^2$ (UM nos. 68215, 71241, 71559), is present on both $M^1$s in this sample (UM nos. 68028 and 71241), and is present in one $M^3$ (UM 66208) among four. Pericones are not discernible in the holotypes of either *T. pseudarctos* or *T. antiquus*, but they are present in the type of *T. olseni* (Matthew, 1915a). A small cingular hypocone is variably present on $M^3$ of the Clarkforkian specimens.

The evidence now available suggests that the Clark's Fork Basin specimens, although quite variable, probably all belong to one species. Several names are available, including *T. antiquus* Matthew (1915a), *T. olseni* Matthew (1915a), and *T. pseudarctos* Simpson (1928). Although minor differences separate the holotypes of these species, larger samples now known indicate that few if any of these differences are of specific magnitude. Hence the original diagnoses of the species appear to be inadequate to distinguish confidently between them. Both *T. antiquus* and *T. olseni* were described from the early Wasatchian ("Graybullian") of the Bighorn Basin (*T. antiquus* is from the Clark's Fork Basin). *T. pseudarctos*, from the Bear Creek local fauna, is the only species originally described from the Clarkforkian (although Bear Creek was then considered Tiffanian in age). In a review of the Clarkforkian fauna, Simpson (1937c) considered two specimens of *Thryptacodon* then known from the Sand Coulee area to be conspecific with early Wasatchian *T. antiquus*.

It is possible that *T. pseudarctos* is a valid name for some Clarkforkian specimens of *Thryptacodon*. The holotype, an isolated $M^1$ or $M^2$, appears to differ from *T. antiquus* by being slightly larger and having the trigon cusps set well in from the margins of the tooth, thereby having wider cingula. Simpson also noted the twinned metaconule of the type as a specific character. These features are variable, however, and in any case they are very difficult to judge objectively. Gingerich (1978) suggested that *T. pseudarctos* is characterized by its "larger size, metaconid on $P_4$, larger pericones on the upper molars, and less labiolingually compressed canine teeth," and he tentatively retained the species for a specimen from the Clarkforkian Buckman Hollow locality (see Chapter V). Van Valen and Sloan (1966), however, considered *T. pseudarctos* to be a synonym of *T. antiquus*.

Bown (1979) described a large sample of *Thryptacodon* from the early Wasatchian of the southeastern Bighorn Basin, comparing the sample with *T. antiquus*. He observed considerable variability in size and morphology, from which he inferred that two species might be present. An arctocyonid closest to *T. antiquus* was described from the Clarkforkian of the northeastern Bighorn Basin by Gingerich and Rose (1979). For the present, two species of *Thryptacodon* may be tentatively recognized from the Clarkforkian, *T. pseudarctos* and *T. antiquus* (the specimens from the Sand Coulee area probably representing *T. antiquus*), with the acknowledgment that additional evidence may prove them to be conspecific.

### *Tricentes* Cope, 1883
### cf. *Tricentes* sp.
Figure 31A,C

*Referred Specimens.*—UM nos. 69901, 71175, 71563, 71564.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–74, 136); *Phenacodus-Ectocion* Zone (SC–52, 234).

*Discussion.*—Four Clarkforkian specimens represent a small arctocyonid with cusps somewhat more acute than in *Thryptacodon*. They are most similar to undescribed specimens tentatively referred to *Tricentes* sp., from the late Tiffanian Princeton Quarry (e.g. PU nos. 13943, 13957, 14115, 14321; see Table 42). They also resemble *Metachriacus punitor* Simpson (1935) and *M. provocator* Simpson (1935; see illustrations in Simpson, 1937a). The latter two species were transferred to the genus *Tricentes* (Van Valen and Sloan, 1965; footnote 15), which is a senior synonym of *Metachriacus*.

The Clarkforkian specimens are very fragmentary consisting of only one or two teeth each, but they are sufficient to document the presence of a distinct species of small arctocyonid. The trigonid of the lower molars (UM nos. 69901 and 71175) is moderately high, its three cusps of about equal height and arranged in a tight triangle with the paraconid fully lingual. The talonid is deeply basined and the hypoconid is high and moderately acute. There is a well developed ectocingulid that continues onto the front and back of the tooth, where it is almost shelf-like. Two upper molars (UM 71563, left $M^1$ or $M^2$, and UM 71564, right $M^3$) are very primitive in aspect, with acute trigon cusps bordering a deep basin. The conules are small and there is no hypocone. Each tooth is encircled by prominent cingula, continuous all around but widest posterolingually.

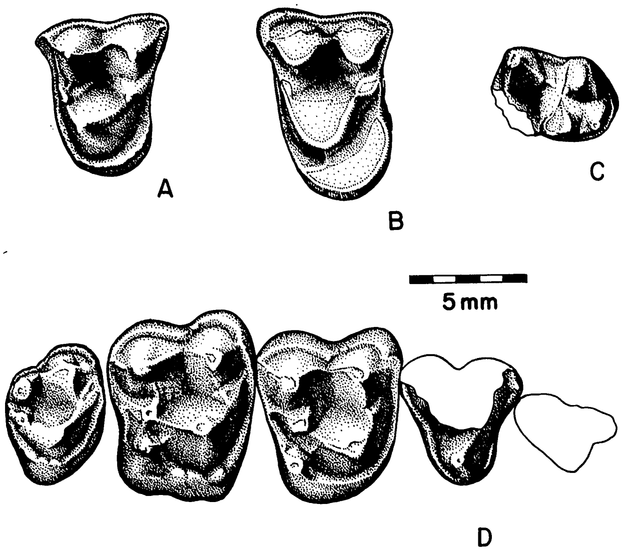

Figure 31. Arctocyonidae. A and C, cf. *Tricentes* sp., A, UM 71563, from SC–52: left ?$M^1$; C, UM 69901, from SC–136: left $M_1$ or $M_2$. B, ?"*Chriacus*" sp., UM 71574, from SC–19: left $M^1$ or $M^2$. D, *Thryptacodon* cf. *antiquus*, UM 71241, from SC–195: right side of snout, showing right $M^{1-3}$, part of $P^4$, roots of $P^3$. All in crown view.

Only UM 71563 is complete enough for accurate measurement: $M^1$ or $M^2$ L=5.65, B=6.50.

### *Chriacus* Cope, 1883
### ?"*Chriacus*" sp.
Figure 31B

*Referred Specimens.*—UM nos. 71565, 71566, 71574.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–19, 136); *Phenacodus-Ectocion* Zone (SC–155).

*Discussion.*—A complete upper molar (UM 71574, Figure 31B) and two upper molar fragments appear to represent a third arctocyonid from the Clarkforkian. They differ from both *Thryptacodon* and cf. *Tricentes* in having a very prominent continuous lingual cingulum that is exceptionally broad posterolingually. There is no distinct hypocone. In these features, they most closely resemble *Chriacus* as illustrated by Matthew (1915a, 1937) and Delson (1971). "*Chriacus*" may also occur at SC–143 (*Plesiadapis cookei* Zone, D. C. Parris, personal communication).

I have used the generic name *Chriacus* in quotation marks to reflect the uncertainty surrounding present understanding of this genus. There is no consensus concerning the proper generic assignments of many species originally allocated to *Chriacus*, and there is disagreement about the definition of *Chriacus*. Hence the assignment of the Clarkforkian teeth to this genus is tentative, pending revision of the Arctocyonidae.

### Family Phenacodontidae Cope, 1881

Phenacodontids are important elements of the Clarkforkian fauna, occurring at every well-sampled site and often comprising 40–50% of the sample. The Clarkforkian representatives are *Phenacodus* and *Ectocion*, both of which existed earlier and later than the Clarkforkian. Known collections now indicate that phenacodontids reached their acme during the Clarkforkian, and that they underwent an abrupt and severe decline immediately thereafter.

The UM Clarkforkian collection includes more than 600 catalogued jaws of phenacodontids, about three-quarters of them referable to *Ectocion osbornianus*. Hundreds of other jaw fragments and isolated teeth of phenacodontids are included in lots of miscellaneous teeth in the UM collection. The Princeton, American Museum, and Amherst collections also contain numerous phenacodontids from the Clarkforkian of the northern Bighorn Basin. A brief account of Clarkforkian phenacodontids of the Clark's Fork Basin is presented here, in order to record stratigraphic occurrences and to provide a general view of their evolution. However, this important collection merits a more thorough analysis than is possible here, and it should be studied in the context of other samples of phenacodontids.

In addition to *E. osbornianus*, at least three other species of phenacodontids are known from the Clarkforkian of the Clark's Fork Basin. *Ectocion parvus*, much smaller than *E. osbornianus*, is still known from only one Clarkforkian specimen from this area, although a few more have recently been collected from basal Wasatchian exposures there. At least two species of *Phenacodus* are known in the Clarkforkian, and they were referred to *P. primaevus* and *P. vortmani* by West (1976). Additional evidence that has accumulated since West made his study suggests that phenacodontid evolution is considerably more complex than he believed (West, 1976: figure 40), especially during the Wasatchian. Nevertheless, most Clarkforkian specimens of *Phenacodus* can be sorted into two groups, mainly on the criterion of size, and these sizes correspond to the ranges of *P. primaevus* and *P. vortmani* as used by West.

The abundance and omnipresence of phenacodontids in many Paleocene and early Eocene deposits give this group special potential for biostratigraphic and evolutionary studies. Previous research suggested that phenacodontid species are relatively static and of long duration (e.g. West, 1976), a conclusion borne out by preliminary observations presented below. More detailed studies are warranted, however, and they could prove enlightening in view of the rich fossil record and long duration of the Phenacodontidae.

### *Phenacodus* Cope, 1873

*Phenacodus* was very common in the Clarkforkian and has been found at virtually all important sites of this age. In the Clark's Fork Basin, it is recorded from more than 80% of all Clarkforkian localities (more than 100 sites). Almost 150 catalogued jaws and hundreds of isolated teeth and jaw fragments are included in the UM Clarkforkian collection, and many more jaws are housed at Princeton and the American Museum. The UM collection also contains postcranial remains of *Phenacodus*, but most of them require preparation before study; hence they will not be considered here.

West (1976: figure 40) viewed the evolution of late Tiffanian through Wasatchian *Phenacodus* as consisting of two essentially parallel lineages, distinguished by size and separate since earliest Tiffanian time. The smaller specimens he placed in *P. vortmani* and the larger ones in *P. primaevus* (having synonymized other contemporary nominal species with one or the other of these). (West and previous workers have placed earlier Tiffanian specimens of a large *Phenacodus* in *P. grangeri*. Van Valen [1978] regarded *P. grangeri* as a synonym of *P. primaevus*, thus further extending the range of this species. If Van Valen's view is adopted, together with a Bridgerian record of the species [West and Atkins, 1970], *P. primaevus* would have one of the longest ranges of any species of early Tertiary mammal, perhaps as much as 8 million years.) Most of the Clarkforkian specimens can be separated into two groups corresponding to West's segregation of *P. vortmani* and *P. primaevus*, but several early Clarkforkian specimens are intermediate in size and morphology between these two species, suggesting that evolution in Clarkforkian *Phenacodus* was more complex than West envisioned. This intermediate group I have called *Phenacodus* sp. Each of the size groups displays considerable variation in both size and morphology, hence it seems possible that each one may comprise more than one species (see also Simpson, 1937c; Bown, 1979) or that sexual dimorphism may be a factor.

Although large samples of *Phenacodus* have been available for some time, there has been no thorough study of dental variability in the genus. As a consequence, the extent and significance of intraspecific variation is poorly understood. It seems likely that as these aspects become better known, a more complex picture of evolution in the genus *Phenacodus* will emerge.

### *Phenacodus primaevus* Cope, 1873

Plates 2:2 and 3:3, Figure 33, Table 18

*Referred Specimens.*—UM nos. 63278, 64711, 64716, 65003, 65004, 65020, 65036, 65063, 65079. 65080, 65081, 65239, 65258, 65476, 65480, 65482, 65487, 65490, 65495, 65522, 65527, 65542, 65546, 65642, 65663, 66186, 66211, 66294, 66295, 66300, 66313, 66317, 66322, 66327, 66336, 66497, 66550, 66552, 66553, 66578, 66582, 66593, 66594, 66595, 66627, 66635, 66636, 66643, 66719, 66753, 66758, 66761, 66923, 67019, 67022, 67026, 67029, 67030, 67201, 67354, 67357, 67359, 68042, 68208, 68222, 68223, 68231, 68288, 68293, 68404, 68405, 68408, 68416, 68422, 68517, 68727, 68750, 68753, 68754, 68881, 69223, 69261, 69266, 69299, 69307, 69340, 69672, 69677, 69678, 69876, 69880, 69883, 69890, 69912, 71186, 71188, 71237, 71297, 71301, 71423, 71441, 71463, 71466–71469, 71473, 71480, 71632, 71797, 71805, 71807, and miscellaneous isolated teeth.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–82, 169, 171, 173, 177, 179, 215, 216, 217, 226, 249, 250); *Plesiadapis cookei* Zone (SC–19, 53, 58, 62, 65, 66, 74, 84, 92, 93, 108, 109, 110, 115, 116, 117, 119, 120, 127, 136, 137, 143, 188, 189, 190, 194, 195, 197, 200, 201, 222; SC–168, 208, 209, probably *P. cookei* Zone); *Phenacodus-Ectocion* Zone (SC–8, 9, 10, 11, 21, 22, 23, 24, 25, 28, 29, 48, 49, 50, 52, 55, 57, 71, 75, 80, 81, 90, 99, 100, 101, 102, 105, 107, 138, 149, 150, 152, 159, 162, 163, 164, 175, 176, 183, 184, 202, 203, 214, 230, 231, 233, 234.

*Discussion.*—*Phenacodus primaevus* is the most abundant species of this genus in the Clarkforkian. These specimens closely resemble early Wasatchian specimens of *P. primaevus* from the Bighorn Basin. The Clarkforkian sample shows considerable variation, particularly in the shape and size of $P_4$ and $M_3$, the expression of ectocingulids on the molars, the degree of crenulation of enamel and of inflation of the cusps, and the relative proportions of the trigonids and talonids. The talonid is usually broader than the trigonid in $M_1$ and narrower than the trigonid in $M_2$, but inconsistency in these relative proportions forced me to abandon an attempt to identify isolated molars by these criteria. Upper molars display variability in comparable features, including shape, crenulation of enamel, size of mesostyles, and development of internal cingula. In these and other aspects of morphology, and in overall size, I could detect no obvious trend in the Clarkforkian sample of *P. primaevus*.

Table 18. Metrical data for UM Clarkforkian lower cheek teeth of *Phenacodus primaevus*.

| | N | OR | $\bar{X} \pm$ SE | s | V |
|---|---|---|---|---|---|
| $P_4$L | 27 | 10.30–13.05 | 11.67 ± .15 | .776 | 6.6 |
| $P_4$B tri | 23 | 7.30–9.20 | 8.28 ± .11 | .509 | 6.1 |
| $P_4$B tal | 23 | 7.70–9.75 | 8.45 ± .12 | .574 | 6.8 |
| $M_1$L | 35 | 10.80–13.85 | 11.91 ± .11 | .630 | 5.3 |
| $M_1$B tri | 32 | 9.45–11.60 | 10.19 ± .10 | .560 | 5.5 |
| $M_1$B tal | 32 | 9.25–12.50 | 10.47 ± .13 | .713 | 6.8 |
| $M_2$L | 38 | 11.20–13.55 | 12.26 ± .10 | .591 | 4.8 |
| $M_2$B tri | 36 | 10.25–12.90 | 11.34 ± .10 | .573 | 5.1 |
| $M_2$B tal | 38 | 9.65–12.10 | 10.78 ± .10 | .600 | 5.6 |
| $M_3$L | 27 | 10.60–13.90 | 12.29 ± .13 | .673 | 5.5 |
| $M_3$B tri | 27 | 8.45–11.35 | 9.73 ± .13 | .655 | 6.7 |
| $M_3$B tal | 28 | 6.85–10.05 | 8.42 ± .12 | .658 | 7.8 |

See West (1976) for statistics on previously known samples of *Phenacodus primaevus*. Because of small sample size and uncertainty of distinguishing between first and second upper molars, statistics for upper teeth of *P. primaevus* are omitted here.

The precise horizon of the holotype of *P. primaevus* is not known, but its general provenance is clearly the Wasatchian of Wyoming (Cope [1884: 435] listed the locality as "Wasatch Eocene marl on Bear River, Wyoming" [Wasatch Formation near Evanston]). Cope, Granger (1915), Simpson (1937c), West (1976), and others, have used the name *Phenacodus primaevus* for the abundant large species of *Phenacodus* from early Eocene beds of the Bighorn Basin. Granger recognized two subspecies, *P. primaevus hemiconus* and *P. primaevus robustus*, for early Wasatchian ("Graybullian") variants, and a separate species, *P. intermedius*, for specimens smaller than typical *P. primaevus*. Simpson suggested that *P. primaevus robustus* be accorded full species rank. Aside from the latter form, Simpson observed that the larger "Graybullian" *Phenacodus* are extremely variable and not easily divisible into Granger's taxa. He remarked (Simpson, 1937c: 17–18):

> It is highly unlikely that such a distribution belongs to a single pure race. . . .[but] the subspecies cannot be distinguished in any natural way. It does not follow that they are synonymous, for the fact that they cannot be fully distinguished does not prove that they are the same thing.

With regard to the large specimens from the Clarkforkian, Simpson continued (1937c: 19):

> The biological conclusion is that the Clark Fork specimens are a nearly or quite homogeneous sample of one subspecies and that this subspecies may occur also in the Gray Bull (in which case it is probably *P. primaevus primaevus*) or may be distinct.

The Clarkforkian sample of *P. primaevus* now known includes specimens similar to all of Granger's taxa. It is much less homogeneous than the smaller sample that Simpson studied and, in fact, Simpson's remarks on "Graybullian" *Phenacodus* now seem equally appropriate to the Clarkforkian sample. Thus it seems entirely possible that more than one species or subspecies of large *Phenacodus* is present in the Clarkforkian, but I have used the name *Phenacodus primaevus* for all large specimens, pending more thorough study.

Several of the Clarkforkian specimens contain deciduous premolars (e.g. UM nos. 69912, 71441, 71469) or erupting permanent teeth (UM 66923). They conform closely to the deciduous premolars of *Phenacodus* as described by West (1971).

### *Phenacodus vortmani* Cope, 1880

Plates 2:1 and 3:2, Figure 33, Table 19

*Referred Specimens.*—UM nos. 64714, 65661, 65668, 66150, 66155, 66288, 66304, 66305, 66310, 66574, 66585, 66587, 66628, 66922, 67242, 67443, 68220, 71641, 71793, and miscellaneous isolated teeth.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–248); *Plesiadapis cookei* Zone (SC–58, 108, 117, 127, 143 [specimens in Princeton collection], 200, 201); *Phenacodus-Ectocion* Zone (SC–10, 11, 22, 59, 72, 81, 90, 101, 102, 103, 138, 153, 162, 176).

*Discussion.*—A medium-sized phenacodontid, here tentatively referred to *Phenacodus vortmani*, is moderately common in the Clarkforkian of the Clark's Fork Basin. It displays the same sort of variability as observed in *P. primaevus* above, particularly in relative breadth of the lower molars. Hence it would not be surprising if further study showed that these specimens represent more than one species.

The Clarkforkian sample of *P. vortmani* compares closely to *P. almiensis* Gazin (1942, 1956b; e.g. UM nos. 68364 and 71341 from Buckman Hollow, see Chapter V) from the Clarkforkian of Buckman Hollow, western Wyoming. They are closer in size to *P. copei* Granger (1915) than to *P. vortmani* Granger (1915) (*P. copei* is slightly larger). The holotype of *P. copei* is from the early Wasatchian ("Graybullian") of the Bighorn Basin, and Granger assigned specimens to this species from the "Sand Coulee" and "Lysite" beds of the Bighorn Basin and the Lysitean of the Wind River Basin. The holotype of *P. vortmani* is from the Lostcabinian of the Wind River Basin. Guthrie (1967) regarded *P. copei* as a synonym of *P. vortmani*, and West (1976) considered both *P. copei* and *P. almiensis* as synonyms of *P. vortmani*. Considering the variability observed in medium-sized phenacodontids and their long temporal duration, I am not convinced that these synonymies are correct and suspect that *P. almiensis* or *P. copei* is the proper name for the smaller Clarkforkian *Phenacodus*. However, pending further study, I have followed the most recent revision of the genus (West, 1976) and have used the name *P. vortmani*.

Table 19. Metrical data for UM Clarkforkian lower cheek teeth of *Phenacodus vortmani*.

| | N | OR | $\bar{X} \pm$ SE | s | V |
|---|---|---|---|---|---|
| $P_4$L | 5 | 9.05–9.55 | 9.20 ± .09 | .212 | 2.3 |
| $P_4$B tri | 4 | 5.60–6.00 | 5.79 ± .11 | .217 | 3.7 |
| $P_4$B tal | 4 | 5.85–6.30 | 5.99 ± .10 | .210 | 3.5 |
| $M_1$L | 9 | 8.50–9.60 | 9.08 ± .13 | .376 | 4.1 |
| $M_1$B tri | 9 | 7.30–8.55 | 7.72 ± .13 | .394 | 5.1 |
| $M_1$B tal | 11 | 6.95–8.35 | 7.68 ± .11 | .361 | 4.7 |
| $M_2$L | 11 | 8.50–9.50 | 9.00 ± .08 | .260 | 2.9 |
| $M_2$B tri | 10 | 7.35–8.90 | 8.00 ± .16 | .511 | 6.4 |
| $M_2$B tal | 10 | 7.00–8.40 | 7.68 ± .15 | .470 | 6.1 |
| $M_3$L | 11 | 8.35–9.75 | 9.15 ± .13 | .442 | 4.8 |
| $M_3$B tri | 12 | 5.95–7.65 | 6.84 ± .14 | .492 | 7.2 |
| $M_3$B tal | 11 | 5.65–6.50 | 6.15 ± .08 | .278 | 4.5 |

Patterson and West (1973) described a new phenacodontid, *Prosthecion major*, from the Clarkforkian of the Plateau Valley beds, northern Colorado. The large Clarkforkian samples now available demonstrate that features such as cingulum expression and premolar structure—characters used by Patterson and West in their diagnosis—are exceedingly variable in phenacodontids. *P. major* may be a valid taxon, and additional study of the UM Clarkforkian specimens may permit allocation of some of them to *P. major*. However, it seems quite possible that *P. major* is a local variant of what has been called *Phenacodus vortmani* in the Bighorn Basin and *Phenacodus almiensis* at Buckman Hollow. In the sample of *P. vortmani* from the Clark's Fork Basin, the parastyle and paraconule of $P^4$ are better developed than in the holotype of *Prosthecion major*, and the cingulum is not complete on any specimen of $P^4$, in contrast to the continuous cingulum completely encircling $P^4$ in the type of *P. major*. Lower teeth of the Clark's Fork Basin specimens are very similar to those of *P. major*. As in *P. major*, a small metaconid is present on $P_3$ of UM 66288, but the paraconid, robust in $P_3$ of *P. major*, is very weak (UM 66288) or absent (UM 66587). The significance of these minor differences is not known, hence I have tentatively retained the name *Prosthecion major* for the medium-sized phenacodontid from the Plateau Valley fauna (Chapter V).

### *Phenacodus* sp.

Plate 3:1, Figure 33

*Referred Specimens.*—UM nos. 69928, 71300, 71302, 71619, 71819, 71822.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–157, 179, 215, 226, 251).

*Discussion.*—Several specimens from the early Clarkforkian resemble *Phenacodus primaevus* morphologically but are smaller, intermediate in size between *P. primaevus* and *P. vortmani.* They fall closer to (perhaps within) the size range of *P. vortmani*, but differ from it in having broader, flatter crowned teeth with more rounded cusps. For these reasons they are separated here from the other samples of *Phenacodus*, although further collecting and study may prove them to be variants of *P. primaevus* or *P. vortmani.* It is also possible that the specimens considered here do not all represent the same species. This sample is particularly instructive in further exhibiting the broad range of variation present in Clarkforkian *Phenacodus*.

Measurements of these specimens are: $P_4$L=9.80–9.90, $P_4$B tri=6.70–6.75, $P_4$B tal=6.95–8.00 (n=2); $M_1$L= 9.60–10.05 (n=2), $M_1$B tri=8.25–8.80 (n=3), $M_1$B tal= 8.45–8.55 (n=2); $M_2$L=9.35–10.00 (n=4), $M_2$B tri= 8.50–9.50 (n=4), $M_2$B tal=7.95–8.70 (n=3); $M_3$L= 10.15–10.50 (n=2),$M_3$B tri=7.40–8.75 (n=2), $M_3$B tal=6.90 (n=1).

### *Ectocion* Cope, 1882

### *Ectocion osbornianus* Cope, 1882

Figures 32, 33, Tables 20, 21

*Referred Specimens.*—UM nos. 64707, 64710, 64712, 64715, 64717, 64719–64725, 64992, 64993, 64995–64997, 65005, 65007, 65012, 65017–65019, 65021–65023, 65025–65027, 65029, 65030, 65032, 65034, 65052, 65058, 65062, 65064, 65065, 65068, 65070, 65074, 65076, 65077, 65082, 65085–65087, 65089–65091, 65093–65097, 65100, 65103, 65105, 65107–65111, 65113–65116, 65126, 65128, 65235–65237, 65242, 65243, 65246, 65248, 65250–65253, 65257, 65259, 65260, 65474, 65475, 65477, 65479, 65486, 65488, 65489, 65518–65520, 65523–65526, 65532, 65535–65537, 65539, 65541, 65543, 65544, 65548, 65549, 65553, 65557, 65558, 65633, 65638, 65639, 65641, 65643, 65646, 65647, 65651, 65652, 65655, 65664, 65669, 65670, 65673–65678, 65717–65719, 65776, 65779, 65781, 65782, 66126, 66151, 66168, 66170, 66172, 66181, 66190–66192, 66197, 66203–66207, 66293, 66296, 66297, 66299, 66303, 66306, 66308, 66311, 66314, 66315, 66323, 66324, 66328–66331, 66333, 66498–66501, 66503, 66532, 66534, 66549, 66573, 66575–66577, 66579–66581, 66596, 66601, 66619, 66620, 66623–66626, 66637, 66638, 66640, 66641, 66698, 66699, 66708, 66710, 66711, 66713, 66714, 66717, 66722–66724, 66726–66729, 66733, 66738, 66743–66745, 66748, 66750, 66756, 66760, 66762, 66766, 66767, 66846, 66848, 66849, 66851, 66852, 66906, 66907, 66916, 66917, 66920, 67020, 67025, 67027, 67028, 67181, 67182, 67185, 67192–67195, 67197, 67198, 67202, 67204–67210, 67213, 67215–67219, 67222, 67224, 67225, 67228–67235, 67237–67241, 67259, 67352, 67353, 67441, 67447–67449, 67451, 67453, 67458, 67465, 67466, 67557, 68026, 68031, 68034, 68038, 68203, 68207, 68226, 68229, 68230, 68232–68235, 68240–68243, 68246, 68247, 68286, 68410, 68412, 68413, 68415, 68418, 68424, 68425, 68427, 68433, 68435, 68508, 68510, 68512, 68513, 68516, 68518–68521, 68749, 68751, 68752, 68782, 68783, 68785, 68862, 68880, 68882, 69173, 69176, 69226–69229, 69234, 69257, 69259, 69260, 69262, 69263, 69267, 69268, 69272, 69275, 69281–69283, 69286–69289, 69292–69294, 69302, 69304, 69311, 69315, 69318, 69320, 69322–69324, 69329, 69330, 69346, 69347, 69356, 69358, 69443, 69444, 69669, 69675, 69676, 69679, 69685, 69688, 69692–69695, 69697, 69873, 69875, 69878, 69879, 69881, 69882, 69886–69889, 69891–69893, 69895, 69900, 69902–69904, 69909–69911, 69915–69919, 69921, 69922, 69924, 69926, 69927, 69935, 69936, 69939, 69997, 71169, 71174, 71180, 71182, 71235, 71239, 71296, 71298, 71308, 71314, 71315, 71357, 71358, 71419–71422, 71425–71429, 71432, 71435–71437, 71442, 71444–71446, 71450–71452, 71454, 71456, 71461, 71462, 71470, 71472, 71478, 71479, 71486, 71488, 71494, 71613, 71616–71618, 71621, 71622, 71633, 71640, 71647, 71648, 71773, 71777, 71804, 71806, 71814, 71815, 71818, and miscellaneous isolated teeth and jaw fragments.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–78, 82, 83, 156, 157, 170, 171, 172, 173, 174, 177, 179, 215, 216, 217, 226, 227, 250, 251); *Plesiadapis cookei* Zone (SC–19, 20, 53, 58, 62, 65, 66, 74, 84, 91, 92, 93, 108, 109, 110, 115, 116, 117, 118, 119, 120, 127, 134, 136, 137, 143, 166, 188, 189, 190, 195, 197, 200, 201, 220, 222, 238; SC–208, probably, *P. cookei* Zone); *Phenacodus-Ectocion* Zone (SC–8, 9, 10, 11, 21, 22, 23, 24, 25, 28, 29, 48, 49, 50, 51, 52, 55, 56, 57, 59, 60, 70, 71, 72, 73, 75, 76, 77, 80, 81, 90, 99, 101, 102, 105, 106, 107, 138, 149, 150, 152, 153, 154, 155, 158, 159, 162, 163, 164, 175, 176, 183, 184, 202, 203, 204, 214, 230, 231, 233, 234, 235); SC–196, zone uncertain.

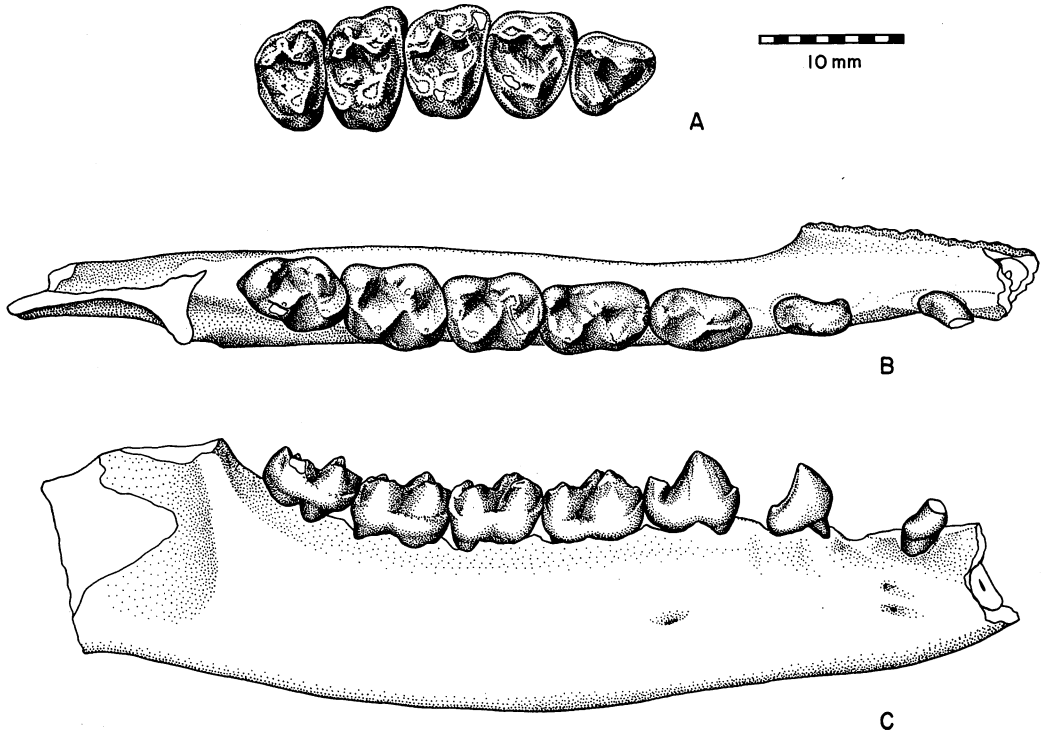

Figure 32. *Ectocion osbornianus*. A, UM 65253, from SC–29: associated right $P^3$-$M^3$, occlusal view. B and C, UM 71804, from SC–250: right dentary with $P_1$-$M_3$, occlusal and labial views.

*Discussion.—Ectocion* is by far the most common mammal known from the Clarkforkian, and it is represented by almost 500 catalogued jaws and hundreds of additional isolated teeth and jaw fragments in the UM collection. It is ubiquitous, occurring at more than 90% of the UM Clarkforkian sites in the Clark's Fork Basin and at almost every important Clarkforkian locality outside of the type area as well.

In his recent revision of the Phenacodontidae, West (1976) concluded that almost all specimens of late Tiffanian and Wasatchian *Ectocion* are referable to *E. osbornianus*. The Clark's Fork Basin sample of *E. osbornianus* shows considerable variability, particularly in shape and morphology of $P_4$, size and proportions of the molars, and relative size of $M_3$. Development of the paraconid, hypoconulid, and entoconid of $P_4$ are variable, and relative breadths of the trigonids and talonids of the molars are by no means constant. All these characters, however, appear to be within the realm of intraspecific variation, and there is no consistent, satisfactory means for subdividing the sample. This applies equally to the early Wasatchian sample of *Ectocion* from the Clark's Fork Basin, which is not significantly different from the Clarkforkian sample (means of most dimensions do not differ by more than 0.1 mm between the two samples, see Tables 20 and 21). Thus I follow West and allocate all the UM Clarkforkian specimens of *Ectocion* to *E. osbornianus*. (*T*-tests comparing the mean lengths of $P_4$, $M_1$, and $M_2$ in West's Polecat Bench and "Graybullian" samples of *E. osbornianus* suggest that the samples are significantly different [$p<.001$], although the ranges in length overlap considerably. West did not recognize the Clarkforkian in his study, and it is probable that Clarkforkian specimens were included in both his Polecat Bench and Willwood samples.)

Granger (1915) proposed three new species of *Ectocion*, distinguished mainly by size. Two of them, *E. ralstonensis* and *E. parvus*, were from Clarkforkian beds in the head of Big Sand Coulee, while the third, *E. superstes*, was from the Lostcabinian of the Wind River Basin. Simpson (1937c, 1943) rearranged Granger's species as temporal subspecies of a chronocline of

Table 20. Metrical data for UM Clarkforkian lower cheek teeth of *Ectocion osbornianus**

| | N | OR | $\overline{X} \pm SE$ | s | V |
|---|---|---|---|---|---|
| $P_4$L | 32 | 5.75–7.20 | 6.55 ± .07 | .397 | 6.1 |
| $P_4$B tri | 31 | 3.80–5.10 | 4.66 ± .05 | .266 | 5.7 |
| $P_4$B tal | 31 | 4.20–5.25 | 4.72 ± .05 | .273 | 5.8 |
| $M_1$L | 53 | 5.50–7.00 | 6.36 ± .05 | .347 | 5.5 |
| $M_1$B tri | 53 | 4.65–6.00 | 5.36 ± .04 | .286 | 5.3 |
| $M_1$B tal | 53 | 4.65–6.25 | 5.43 ± .04 | .310 | 5.7 |
| $M_2$L | 44 | 5.60–7.10 | 6.46 ± .05 | .326 | 5.0 |
| $M_2$B tri | 44 | 5.15–6.50 | 5.75 ± .05 | .356 | 6.2 |
| $M_2$B tal | 44 | 4.75–6.55 | 5.45 ± .06 | .379 | 7.0 |
| $M_3$L | 25 | 6.00–7.60 | 6.85 ± .09 | .435 | 6.4 |
| $M_3$B tri | 25 | 4.10–5.55 | 4.77 ± .07 | .352 | 7.4 |
| $M_3$B tal | 25 | 3.65–5.10 | 4.24 ± .08 | .377 | 8.9 |

*Sample includes UM nos. 65032, 65034, 65052, 65065, 65074, 65087, 65105, 65113, 65242, 65474, 65558, 65646, 65776, 66126, 66299, 66331, 66503, 66532, 66640, 66714, 66726, 66852, 67185, 67210, 67218, 67259, 68234, 68418, 68425, 68427, 68516, 68519, 68749, 69226, 69228, 69875, 69878, 69915, 69924, 71298, 71314, 71419, 71422, 71425, 71429, 71437, 71445, 71461, 71618, 71647, 71804, 71814, 71815, and 71818.

Table 21. Metrical data for UM Wasatchian lower cheek teeth of *Ectocion osbornianus**

| | N | OR | $\overline{X} \pm SE$ | s | V |
|---|---|---|---|---|---|
| $P_4$L | 11 | 6.40–7.00 | 6.65 ± .06 | .188 | 2.8 |
| $P_4$B tri | 10 | 4.00–4.80 | 4.54 ± .07 | .212 | 4.7 |
| $P_4$B tal | 10 | 4.25–4.90 | 4.62 ± .09 | .277 | 6.0 |
| $M_1$L | 14 | 6.00–6.65 | 6.28 ± .06 | .220 | 3.5 |
| $M_1$B tri | 14 | 5.00–5.60 | 5.30 ± .05 | .186 | 3.5 |
| $M_1$B tal | 14 | 5.00–5.70 | 5.44 ± .05 | .204 | 3.8 |
| $M_2$L | 12 | 6.10–6.70 | 6.42 ± .05 | .187 | 2.9 |
| $M_2$B tri | 12 | 5.50–6.25 | 5.77 ± .06 | .217 | 3.8 |
| $M_2$B tal | 12 | 5.25–5.95 | 5.56 ± .06 | .218 | 3.9 |
| $M_3$L | 9 | 6.35–6.95 | 6.69 ± .07 | .199 | 3.0 |
| $M_3$B tri | 9 | 4.65–5.30 | 4.90 ± .07 | .214 | 4.4 |
| $M_3$B tal | 9 | 4.25–4.60 | 4.43 ± .05 | .154 | 3.5 |

*Sample includes UM nos. 64585, 64973, 65131, 65160, 65173, 65348, 65381, 65382, 66342, 66367, 66374, 68147, 68570, 69476.

*Ectocion osbornianus*, apparently subsuming *E. parvus* into *E. osbornianus ralstonensis* (Simpson, 1943). Both Granger's and Simpson's classifications of *Ectocion* seem to be based on an assumption of increasing size in a single lineage of *Ectocion*, from *E. parvus* (or *E. osbornianus ralstonensis*) to *E. superstes*. Much new fossil evidence has come to light since the studies by Granger and Simpson, and it does not especially support either of their concepts. West (1976) considered both *E. parvus* and *E. superstes* to be valid species, and available evidence supports this. *E. parvus* was, however, a contemporary of *E. osbornianus* (which existed both earlier and later than *E. parvus*), and it is significantly smaller than the latter. *E. superstes* is based on a single specimen which is larger and comes from much younger deposits than any other member of the genus. There seems to be no evidence to support recognition of *E. ralstonensis* as a distinct species or as a subspecies of *E. osbornianus*. Although *E. osbornianus* is highly variable, it displays no clear trend toward size increase or decrease during the Clarkforkian and early Wasatchian of the Clark's Fork Basin. Indeed, it remains remarkably constant in size throughout this interval (Figure 33). Hence the concept of *E. ralstonensis* or *E. osbornianus ralstonensis*, of Clarkforkian age, as part of a lineage that is increasing in size is not supported by evidence now known. (*E. osbornianus* also commonly occurs in the late Tiffanian of the Polecat Bench area [Table 42], where it does not appear to differ significantly from the Clarkforkian and Wasatchian samples.)

The Clarkforkian collection includes a large number of juvenile and subadult individuals of *Ectocion osbornianus* with deciduous and erupting permanent teeth. They conform closely to descriptions of the deciduous dentition of *Ectocion* presented by West (1971). Additional discussions of the dental morphology of *Ectocion* have been provided by Granger (1915) and West (1976).

Tables 20 and 21 summarize metrical data for a small part of the Clarkforkian and Wasatchian samples of *Ectocion osbornianus* from the Clark's Fork Basin. Specimens were selected in order to include the most complete and least worn individuals and to maximize the stratigraphic distribution covered by the sample; in all other respects, the samples on which the tables are based are random.

### *Ectocion parvus* Granger, 1915

Figure 34 A

No additional specimens of this species have been discovered from Clarkforkian beds of the Clark's Fork Basin since Granger's description of the holotype more than sixty years ago. The type (AMNH 16080, Figure 34 A), a left dentary with $M_{1-3}$, clearly represents *Ectocion* and is considerably smaller than other species. $M_1$ approaches the size of the smallest individuals of *E. osbornianus*, but $M_2$ and $M_3$ are decidedly smaller than in even the smallest *E. osbornianus*. The type of *E. parvus* is from Clarkforkian strata in the head of Big Sand Coulee (Granger, 1915), and is therefore of late Clarkforkian age (*Phenacodus-Ectocion* Zone). It has been described and illustrated by Granger (1915) and West (1976).

West reported possible specimens of *E. parvus* from the Plateau Valley beds of Colorado and the Togwotee

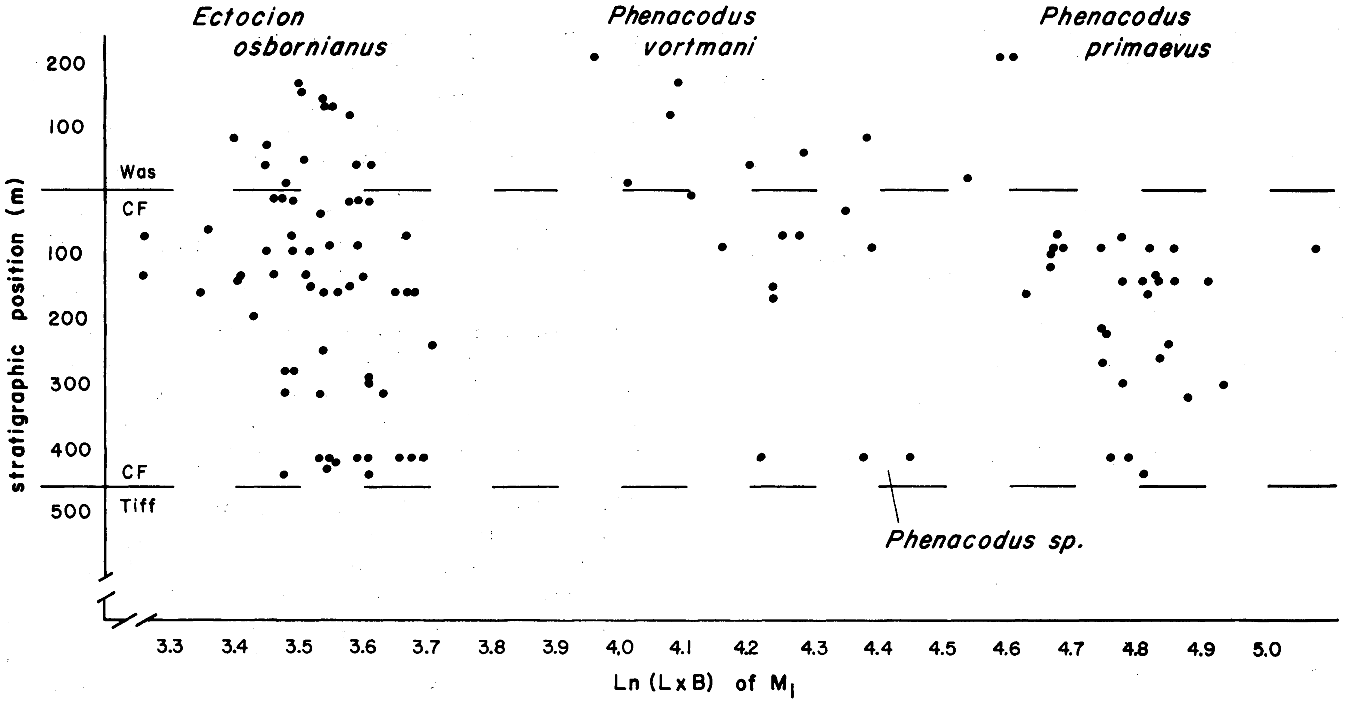

Figure 33. Stratigraphic plot of Clarkforkian and early Wasatchian Phenacodontidae from the Clark's Fork Basin. Natural logarithm of crown area of $M_1$ is plotted against stratigraphic level with respect to the Clarkforkian-Wasatchian boundary sandstone. The sample sorts generally into three size groups, increasing in size from *Ectocion osbornianus* to *Phenacodus vortmani* to *P. primaevus*. The rare *E. parvus*, not shown here, is smaller than any of these. Some early Clarkforkian specimens (here designated *Phenacodus* sp.) are near the size of *P. vortmani* but are morphologically closer to *P. primaevus*. No obvious size trends are evident in the Clark's Fork Basin phenacodontid sample, although there is some indication that all three species may have undergone a slight size reduction from the Clarkforkian into the early Wasatchian.

Pass area of Wyoming, both of probable Clarkforkian age. Additional specimens have been found in basal Wasatchian beds at the southern end of Polecat Bench (UM nos. 66138, 71769, 71770, all from SC–67, and PU 18153, from the vicinity of SC–67). The discovery of these specimens appears to confirm the validity of *E. parvus* as a diminutive species of *Ectocion* from the very early Eocene.

Measurements of the holotype are: $M_1L$=4.70, $M_1B$ tri=4.10, $M_1B$ tal=4.35; $M_2L$=5.10, $M_2B$ tri=4.40, $M_2B$ tal=4.20; $M_3L$=5.40, $M_3B$ tri=3.75, $M_3B$ tal=3.50.

### Family Meniscotheriidae Cope, 1882
### *Meniscotherium* Cope, 1874
### *Meniscotherium priscum* Granger, 1915

Figure 34 B

*Meniscotherium priscum* is still known from only one specimen, the holotype (AMNH 16145, left dentary with $dP_4$–$M_1$, Figure 34 B), found almost seventy years ago near the head of Big Sand Coulee. It is of late Clarkforkian age (*Phenacodus-Ectocion* Zone). Granger's original assessment of the specimen as a representative of *Meniscotherium* remains the most reasonable interpretation. *Meniscotherium priscum* resembles *Ectocion parvus* in size and in some aspects of morphology (Figure 34), but it differs from *E. parvus* (and resembles other species of *Meniscotherium*) in lacking a hypoconulid and in having a high entoconid, a large metastylid that projects more posteriorly than in *Ectocion*, and a very deep hypoflexid, with the cristid obliqua meeting the metaconid almost at the lingual border of the tooth. As in other species of *Meniscotherium*, the crests are relatively straight, not rounded as in *E. parvus*, and they form a sharp W-shaped pattern. Except for the holotype of *M. priscum*, *Meniscotherium* is unknown from the Bighorn Basin or from any other Clarkforkian faunas.

Measurements of the holotype are: $dP_4L$=5.80, $dP_4B$ tri=3.40, $dP_4B$ tal=3.75; $M_1L$=5.20, $M_1B$ tri=4.40, $M_1B$ tal=4.05.

### Family Hyopsodontidae Lydekker, 1889
### Subfamily Hyopsodontinae Trouessart, 1879

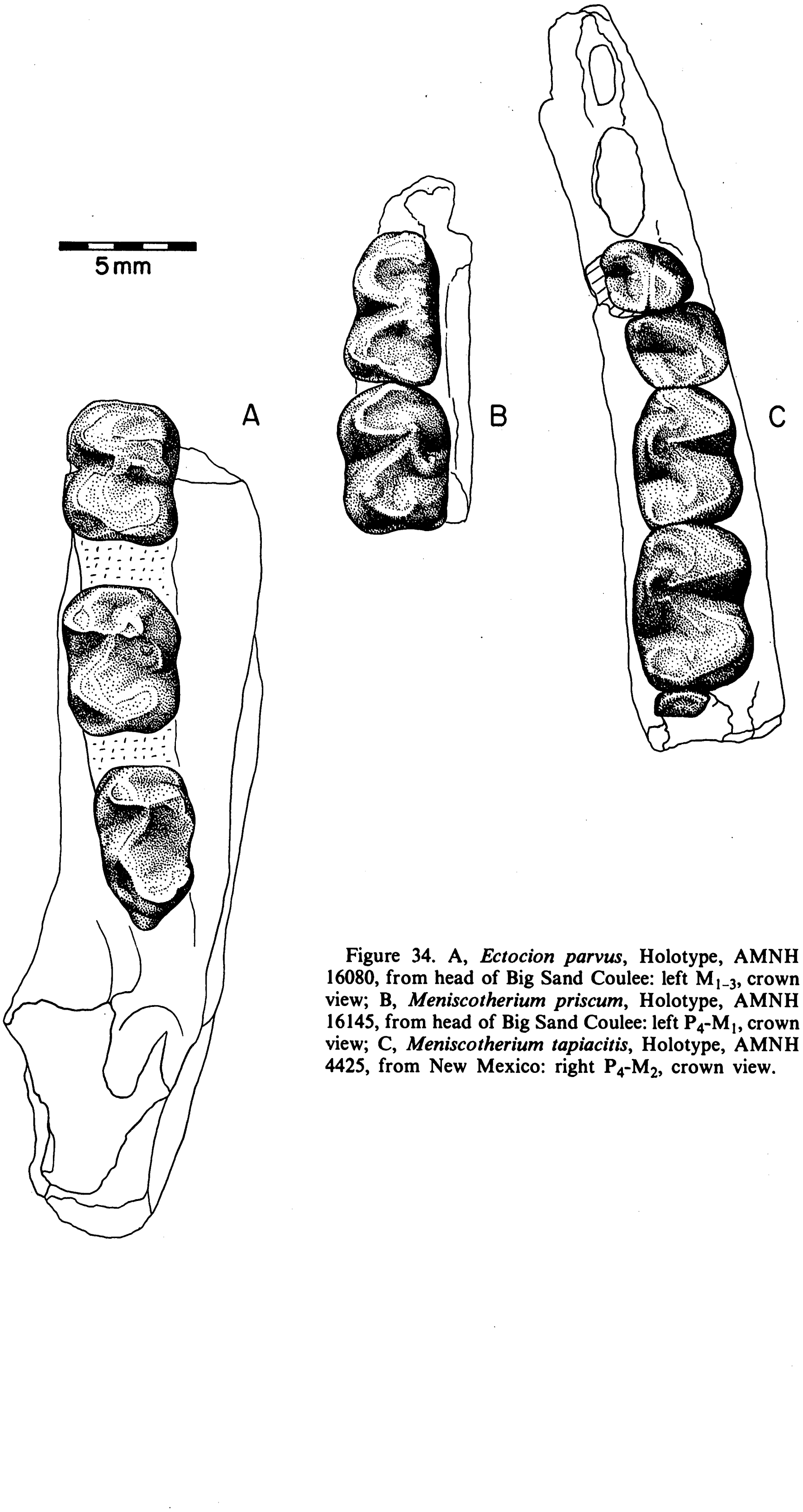

Figure 34. A, *Ectocion parvus*, Holotype, AMNH 16080, from head of Big Sand Coulee: left $M_{1-3}$, crown view; B, *Meniscotherium priscum*, Holotype, AMNH 16145, from head of Big Sand Coulee: left $P_4$-$M_1$, crown view; C, *Meniscotherium tapiacitis*, Holotype, AMNH 4425, from New Mexico: right $P_4$-$M_2$, crown view.

### *Aletodon* Gingerich, 1977
### *Aletodon gunnelli* Gingerich, 1977

Figure 35

*Referred Specimens.*—UM nos. 67444, 68285, 68291, 68509, 69290, 71171, 71233, 71430. (17 additional UM specimens and 5 Princeton specimens were previously reported by Gingerich.)

*Occurrence.*—*Plesiadapis cookei* Zone (SC–74, 108, 143; previously recorded also from SC–136); *Phenacodus-Ectocion* Zone (SC–153, 176, 203, 231; previously recorded also from SC–21, 55, 70, 72, 76, 90, 149, 155).

*Discussion.*—This characteristic Clarkforkian species was first described very recently (Gingerich, 1977), although specimens were known earlier (but unrecognized) in the Princeton collection. The additional specimens here referred to *Aletodon gunnelli* do not add significantly to our knowledge of its morphology, nor do they extend its stratigraphic range. Both of these aspects are discussed and specimens are illustrated by Gingerich. Gingerich provided specific locality numbers for only a couple of the specimens, thus I have listed all Clarkforkian localities in the Clark's Fork Basin that have yielded *A. gunnelli.* Gingerich provided metrical data for all previously known specimens.

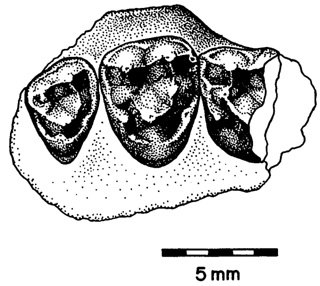

Figure 35. *Aletodon gunnelli*, UM 63307, from SC-149: right maxilla with $M^{1-3}$, crown view.

### *Hyopsodus* Leidy, 1870
### *Hyopsodus* sp.

Figure 36 A, B

*Referred Specimens.*—UM nos. 71049, 71050.

*Occurrence.*—Upper *Phenacodus-Ectocion* Zone (SC–57, 153). Oldest North American record of the genus.

*Discussion.*—Four field seasons of intensive collecting in the Clarkforkian of the northern Bighorn Basin have resulted in discovery of only two specimens of *Hyopsodus*, which is abundant in early Wasatchian deposits of the area. No other Clarkforkian specimens of *Hyopsodus* are known from North America, thus these specimens are significant in recording for the first time the existence of *Hyopsodus* in pre-Wasatchian sediments. UM 71049, a right $M_3$ (Figure 36 B), is from SC–153, at the top of the Clarkforkian sequence (within 10 m of the Clarkforkian-Wasatchian boundary). UM 71050, a dentary fragment with right $P_4$ (Figure 36 A), comes from SC–57, which is stratigraphically somewhat lower, about 80 m below the boundary. Both specimens conform closely in size and morphology to earliest Wasatchian (early "Graybullian") *Hyopsodus* from neighboring strata in the Clark's Fork Basin.

UM 71050 resembles $P_4$ in specimens of *Hyopsodus* from basal Wasatchian sites, such as SC–6 and SC–4. It may be slightly more primitive in having a low paracristid with a poorly expressed paraconid, and a smaller metaconid, but both features may be the result of heavy abrasive wear in this tooth. UM 71049 is slightly larger than basal Wasatchian *Hyopsodus* and is essentially identical in size and morphology to specimens from about 100 m above the Clarkforkian-Wasatchian boundary (e.g. SC–46 and SC–161, early Wasatchian). While there is no doubt as to the generic reference of these Clarkforkian specimens, their fragmentary nature makes specific assignment premature.

The appearance of *Hyopsodus* in the late Clarkforkian was unexpected. It is, however, extremely rare, hence it remains an excellent indicator of the initiation of Wasatchian time in the Bighorn Basin.

The immediate ancestry of *Hyopsodus* is unknown. Thus it is of considerable interest that *Hyopsodus* has recently been discovered at Tsagan Khushu, Mongolia (Naran Bulak equivalent; Dashzeveg, 1977). The fauna of the Mongolian deposits suggests that it is approximately correlative with the North American Clarkforkian or earliest Wasatchian (see Chapter V).

Measurements of the two Clarkforkian teeth of *Hyopsodus* are: UM 71049, $M_3L=3.55$, $M_3B$ trigonid=3.25, $M_3B$ talonid=2.35; UM 71050, $P_4L=2.90$, $P_4B=2.10$.

### *Haplomylus* Matthew, 1915
### *Haplomylus simpsoni*, sp. nov.

Figures 37, 38, Tables 22, 23

*Holotype.*—UM 65249, left dentary with $P_4$–$M_3$, from locality SC–29 (*Phenacodus-Ectocion* Zone).

*Hypodigm.*—Holotype and UM nos. 65069 (right dentary with $dP_4$–$M_{1-2}$), 65104 (left dentary with $P_4$–$M_2$), 65121 (right dentary with $M_{1-3}$), 65124 (right dentary with $M_{1-2}$), 66160 (right dentary with $M_3$), 66584 (left

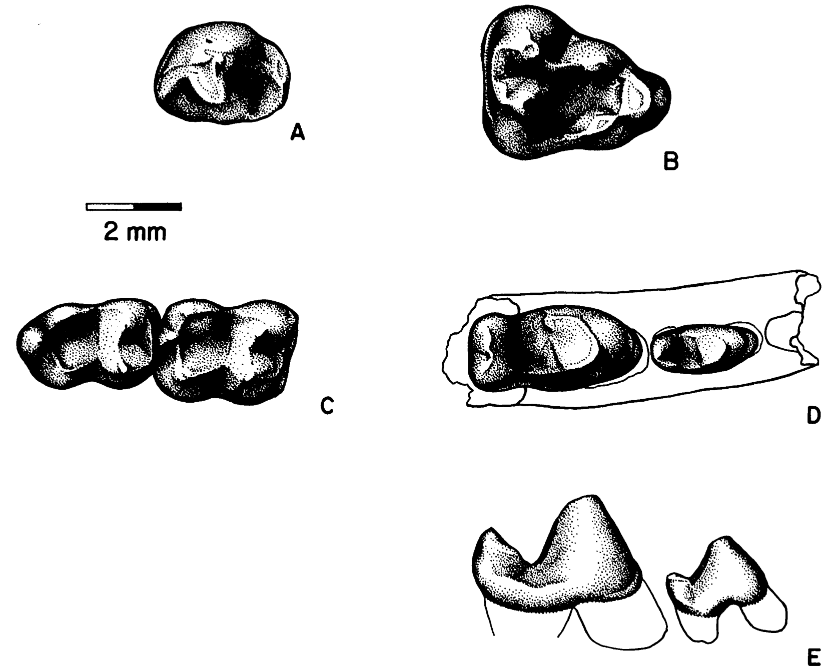

Figure 36. Hyopsodontidae. A and B, *Hyopsodus* sp. A, UM 71050, from SC-57: right $P_4$, crown view. B, UM 71049, from SC-153: right $M_3$, crown view. C-E, *Apheliscus nitidus*. C, UM 66630, from SC-108: right dentary with $M_{2-3}$, crown view. D and E, UM 66502, from SC-48: right dentary with $P_{3-4}$, crown and labial views.

$M_2$), 66847 (left dentary with $M_{1-2}$), 66910 (right dentary with $P_4$-$M_3$, right $P^3$-$M^2$, and left maxilla with $M^2$), 67200 (left $M_2$), 67461 (right dentary with $M_{1-2}$ and left dentary with $M_1$), 68035 (left $M_2$), 68210 (right $M^2$), 68239 (right and left dentaries with $M_{1-3}$), 68434 (right $M^1$, $M^3$), 69178 (left dentary with $M_{1-2}$), 69233 (left $M_1$), 69285 (right $M_1$), 69445 (left dentary with $P_4$, $M_{2-3}$), 69894 (right dentary with $P_4$), 71475 (left dentary with $M_2$ talonid-$M_3$), 71567 (right dentary with $M_1$), 71568 (right $P_4$, $M_2$, $M_3$), 71569 (right dentary with $M_2$), 71570 (left dentary with $M_1$), 71571 (left $M_2$ and $M^2$), 71572 (right dentary with $dP_4$, associated right $M_2$, $P^4$ fragment), 71573 (right and left $M^2$), and isolated teeth in UM nos. 65011, 65529, 66127, 66153, 66161, 66177, 66319, 66535, 66631, 68036, 68218, 68224, 68514, 68781, 68786, 69342, 69999, 71779; and AMNH nos. 16072, 16074, and 21868.

*Horizon and Locality.*—Willwood Formation, Clarkforkian, *Plesiadapis gingerichi* Zone (SC-173: UM 68434); *Plesiadapis cookei* Zone (SC-19: UM 65011; SC-53: UM 69342; SC-65: UM 66127; SC-127: UM nos. 66910 and 71568; SC-136: UM nos. 67200 and 69233; SC-137: UM 69445; SC-188: UM 71779; SC-195: UM 69178; SC-197: UM 71567; SC-220: UM 69999; SC-108: UM 66631); *Phenacodus-Ectocion* Zone (SC-10: UM 71569; SC-22: UM 65069; SC-23: UM nos. 65121, 65124, and 71571; SC-24: UM 65104; SC-29: Holotype; SC-52: UM 65529; SC-70: UM 66847; SC-72: UM nos. 66153, 66160, 66161; SC-77: UM 66177; SC-81: UM 71572; SC-90: UM 66319; SC-99: UM 66535; SC-102: UM 66584; SC-153: UM 71573; SC-155: UM nos. 67461, 71570; SC-158: UM nos. 68035, 68036; SC-159: UM nos. 68210, 68218; SC-162: UM 68224; SC-164: UM 68239; SC-176: UM 68514; SC-183: UM 68781; SC-184: UM 68786; SC-203: UM 69285; SC-214: UM 69894; SC-234: UM 71475); all Clark's Fork Basin, northern Bighorn Basin, Wyoming.

*Etymology.*—For Dr. George Gaylord Simpson, who

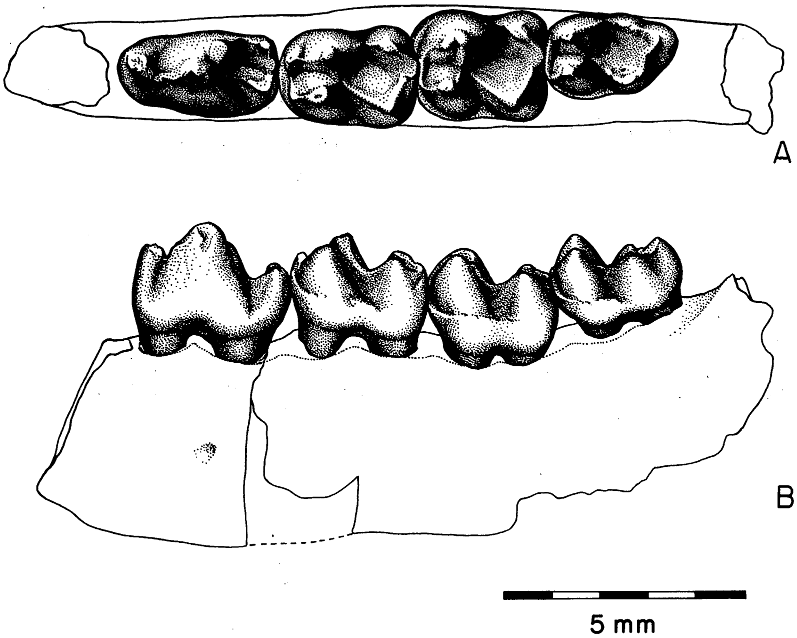

Figure 37. *Haplomylus simpsoni*, sp. nov., Holotype, UM 65249, from SC–29: left dentary with $P_4$-$M_3$, crown (A) and labial (B) views.

foresaw the possibility that the Clarkforkian *Haplomylus* were distinct from early Wasatchian *H. speirianus*; in recognition of his contributions to our knowledge of the Clarkforkian fauna.

*Diagnosis.*—Morphologically like *H. speirianus* but significantly larger (means 15–20% larger than *H. speirianus*).

*Description.*—*Haplomylus simpsoni* is very similar morphologically to *H. speirianus* from the early Wasatchian (see Matthew, 1915b, for description and illustrations of *H. speirianus*). Like the latter, *H. simpsoni* has an elongate, semimolariform $P_4$ with a high protoconid, a somewhat lower but prominent paraconid set well forward of the protoconid, a small metaconid immediately posterolingual to the protoconid, and a small, basined talonid. The hypoconid and entoconid are well defined on $P_4$, and in little worn specimens such as the holotype a small hypoconulid can be discerned. Deciduous $P_4$ (UM nos. 65069, 71572) is longer and narrower than permanent $P_4$. It possesses all the molar cusps, but the crown is more drawn out anteroposteriorly than that of $M_1$. Its trigonid is long, basined, and trapezoidal, the corners of the trapezoid formed by the three trigonid cusps and a sharply angled paracristid (anteroexternally). The talonid of $dP_4$ is slightly longer and narrower than in $M_{1-2}$ but is otherwise similarly constructed. The lower molars are relatively broad and bunodont and they frequently show pronounced abrasive wear on the cusps. As in *H. speirianus*, a distinct paraconid exists only on $M_1$; it is represented only by a low paracristid on $M_{2-3}$. $M_2$ tends to be the largest molar (particularly, the broadest), and its talonid is usually broader than its trigonid. In *H. speirianus*, the talonid of $M_2$ is often narrower than the trigonid. In both species $M_3$ and $M^3$ are substantially smaller than the first two molars. Upper teeth are not well represented in the sample of *H. simpsoni*, but as far as known, they do not differ from *H. speirianus* except in size.

The primary distinction between *H. simpsoni* and *H. speirianus* is, then, one of size. In all tooth dimensions examined (Tables 22–24), *H. simpsoni* is significantly larger in mean size than *H. speirianus*. Lengths of $P_4$, $M_1$, $M_2$, and $M_3$ differ by about four standard deviations from the means in *H. speirianus*. Student's *t*-tests were performed on dimensions of $P_4$-$M_3$, and in each case they demonstrated that *H. simpsoni* is significantly larger than *H. speirianus* ($p<.001$), except for breadth of $M_3$, which is significantly larger at $p<.01$. Consultation of the tables reveals that there is no overlap in dimensions of $P_4$, almost no overlap in dimensions of $M_3$, and a small degree of overlap in dimensions of $M_1$ and $M_2$.

Table 22. Measurements of teeth of *Haplomylus simpsoni*, sp. nov.

| | UPPER DENTITION | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Number | $P^4L$ | $P^4B$ | $M^1L$ | $M^1B$ | $M^2L$ | $M^2B$ | $M^3L$ | $M^3B$ |
| UM 66177 | | | | | 3.00 | 4.60 | | |
| UM 66319 | | | | | 2.95 | | 2.25 | 2.65 |
| UM 66631 | | | | | | | 2.15 | 2.80 |
| UM 66910 | 2.60 | 2.90 | 2.75 | 3.20 | 2.75 | 3.90 | | |
| UM 69999 | | | | | 2.85 | 4.40 | | |
| UM 68210 | | | | | 3.10 | 4.10 | | |
| UM 68434 | | | | | | | 2.40 | 3.00 |
| UM 71571 | | | | | 3.10 | 4.70 | | |
| UM 71573 R | | | | | 3.00 | 4.50 | | |
| UM 71573 L | | | | | 3.10 | 4.40 | | |

| | LOWER DENTITION | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Number | $P_4L$ | $P_4B$ | $M_1L$ | $M_1B$ | $M_2L$ | $M_2B$ | $M_3L$ | $M_3B$ |
| UM 65249 holotype | 3.05 | 1.85 | 2.60 | 2.15 | 2.60 | 2.30 | 2.40 | 1.80 |
| UM 65069 | 3.60* | 1.65* | 2.55 | 2.25 | | | | |
| UM 65104 | 3.20 | 2.10 | 2.80 | 2.55 | 2.80 | 2.70 | | |
| UM 65121 | | | 2.75 | 2.50 | 2.90 | 2.90 | 2.80 | 2.25 |
| UM 65124 | | | | 2.50 | 3.10 | 2.90 | | |
| UM 66127 | | | | | 2.70 | 2.65 | | |
| UM 66153 | | | 2.70 | 2.30 | | | | |
| UM 66160 | | | | | | | 2.70 | 2.20 |
| UM 66161 | 2.85 | 2.00 | | | | | | |
| UM 66535 | | | | | 2.50 | 2.30 | | |
| UM 66584 | | | | | 3.00 | 2.90 | | |
| UM 66631 | 2.90 | 1.90 | | | | | | |
| UM 66847 | | | 2.65 | 2.45 | 2.65 | 2.60 | | |
| UM 66910 | 2.75 | 1.90 | 2.20a | | 2.30a | 2.30a | 2.20 | 1.80 |
| UM 67461 R | | | 2.70 | 2.35 | 2.70 | 2.65 | | |
| UM 67461 L | | | 2.65 | 2.40 | | | | |
| UM 68035 | | | | | 2.90 | 3.10 | | |
| UM 68036 | | | | | 2.75 | 2.80 | | |
| UM 68239 | | | 2.65 | 2.20 | 2.80 | 2.60 | 2.60 | 2.20 |
| UM 68514 | | | | | 2.65 | 2.70 | | |
| UM 69178 | | | 2.45 | 2.15 | 2.55 | 2.50 | | |
| UM 69233 | | | 2.35 | 2.10 | | | | |
| UM 69285 | | | 2.65 | 2.45 | | | | |
| UM 69445 | 2.90 | 2.10 | | | 2.50 | 2.50 | 2.40 | 1.90 |
| UM 71475 | | | | | | | 2.45 | 1.85 |
| UM 71567 | | | 2.50 | 2.30 | | | | |
| UM 71568 | | | | | | | 2.25 | 1.85 |
| UM 71569 | | | | | 2.60 | 2.50 | | |
| UM 71570 | | | 2.90 | 2.65 | | | | |
| UM 71571 | | | | | 3.15 | 3.15 | | |
| UM 71572 | 3.70* | 1.80* | | | 2.75 | 2.60 | | |
| UM 71779 | 3.00 | 1.90 | | | | | | |
| AMNH 16072 | | | | | 2.75 | 2.65 | 2.50 | 1.95 |
| AMNH 16074 | 2.80 | 1.90 | 2.50 | 2.40 | | | | |
| AMNH 21868 | | | 2.85 | 2.45 | 2.70 | 2.70 | | |

*Deciduous $P_4$

The overlap in $M_1$ and $M_2$ sizes occurs between early Clarkforkian specimens of *H. simpsoni* (which are smaller than later Clarkforkian specimens) and earliest Wasatchian specimens of *H. speirianus*.

Table 23. Metrical data for teeth of *Haplomylus simpsoni*, sp. nov.

| | N | OR | $\overline{X} \pm SE$ | s | V |
|---|---|---|---|---|---|
| $P_4L$ | 8 | 2.75–3.20 | 2.93 ± .05 | .146 | 5.0 |
| $P_4B$ | 8 | 1.85–2.10 | 1.94 ± .03 | .082 | 4.2 |
| $M_1L$ | 17 | 2.20–2.90 | 2.61 ± .04 | .178 | 6.8 |
| $M_1B$ | 17 | 2.10–2.65 | 2.36 ± .04 | .156 | 6.6 |
| $M_2L$ | 21 | 2.30–3.15 | 2.73 ± .04 | .203 | 7.4 |
| $M_2B$ | 21 | 2.30–3.15 | 2.67 ± .05 | .235 | 8.8 |
| $M_3L$ | 9 | 2.20–2.80 | 2.48 ± .07 | .197 | 7.9 |
| $M_3B$ | 9 | 1.80–2.25 | 1.98 ± .06 | .186 | 9.4 |
| $P^4L$ | 1 | 2.60 | | | |
| $P^4B$ | 1 | 2.90 | | | |
| $M^1L$ | 1 | 2.75 | | | |
| $M^1B$ | 1 | 3.20 | | | |
| $M^2L$ | 8 | 2.75–3.10 | 2.98 ± .05 | .128 | 4.3 |
| $M^2B$ | 7 | 3.90–4.70 | 4.37 ± .11 | .281 | 6.4 |
| $M^3L$ | 3 | 2.15–2.40 | 2.27 ± .07 | .126 | 5.6 |
| $M^3B$ | 3 | 2.65–3.00 | 2.82 ± .10 | .176 | 6.2 |

Includes all UM Clarkforkian specimens that could be accurately measured, and also AMNH nos. 16072, 16074, and 21868; all from the Clarkforkian of the Clark's Fork Basin.

Table 24. Metrical data for lower teeth of early Wasatchian *Haplomylus speirianus**

| | N | OR | $\overline{X} \pm SE$ | s | V |
|---|---|---|---|---|---|
| $P_4L$ | 7 | 2.45–2.65 | 2.56 ± .03 | .079 | 3.1 |
| $P_4B$ | 7 | 1.55–1.80 | 1.68 ± .04 | .099 | 5.9 |
| $M_1L$ | 15 | 2.10–2.50 | 2.27 ± .02 | .092 | 4.1 |
| $M_1B$ | 15 | 1.70–2.20 | 1.98 ± .03 | .112 | 5.7 |
| $M_2L$ | 15 | 2.00–2.50 | 2.29 ± .03 | .122 | 5.3 |
| $M_2B$ | 15 | 1.95–2.45 | 2.18 ± .03 | .117 | 5.4 |
| $M_3L$ | 10 | 2.10–2.25 | 2.17 ± .02 | .048 | 2.2 |
| $M_3B$ | 10 | 1.65–1.85 | 1.76 ± .02 | .061 | 3.5 |

*Sample includes AMNH 4190 (holotype of *H. speirianus*) and UM nos. 63271, 64672, 64700, 64825, 64856, 64956, 65172, 65697, 65781, 66409, 66423, 66446, 66488, 67130, 67376, 68064, 68068, 68071, 68120, 69761.

*Discussion.—Haplomylus* is one of the most common mammals of the Wyoming early Eocene, especially the early Wasatchian (Matthew, 1915b; McKenna, 1960; Gingerich, 1976a; Bown, 1979). Matthew described and illustrated specimens of *H. speirianus* from the Bighorn Basin, and recorded its occurrence in "Graybullian," "Sand Coulee," and Clarkforkian beds. Simpson (1937c) studied all the Bighorn Basin specimens of *Haplomylus* and inferred size trends similar to those that emerged from the present study (Figure 38). He had only three Clarkforkian specimens and, although he observed that they were "large in comparison with the Gray Bull specimens," the sample size was insufficient to demonstrate statistically different populations. Simpson predicted, however, that a larger Clarkforkian sample might substantiate the differences from early Wasatchian ("Graybullian") *Haplomylus*. His remarks are of interest here:

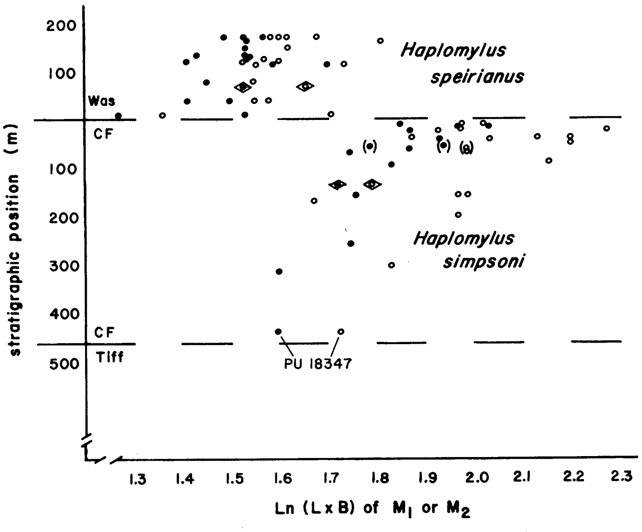

Figure 38. Stratigraphic plot of Clarkforkian and early Wasatchian *Haplomylus* of the Clark's Fork Basin. Natural logarithm of the crown area of $M_1$ (solid circles) and $M_2$ (open circles) is plotted against stratigraphic level with respect to the Clarkforkian-Wasatchian boundary sandstone. Both the Clarkforkian and early Wasatchian populations show a gradual increase in size through time, but the trend is not continuous from Clarkforkian *H. simpsoni* to early Wasatchian *H. speirianus*. The holotype specimens of each species are indicated by points within diamonds. Points enclosed in parentheses are Simpson's Clarkforkian specimens of *Haplomylus*. PU 18347 is a specimen of *H.* cf. *simpsoni* from Bear Creek (stratigraphic level uncertain but believed to be early Clarkforkian).

> The Sand Coulee specimens, although their range overlaps (but is not entirely included in) that of the Gray Bull specimens, average smaller, and the difference in size is decisively significant. . . . The three Clark Fork specimens, however, more closely resemble those from the Gray Bull, and not those from the Sand Coulee as one would expect from their ages. They are relatively large, even for the Gray Bull series, but could be three random specimens drawn from the same subspecies or race as that occurring in the Gray Bull. They cannot be exactly the same race as that in the Sand Coulee. (Simpson, 1937c: 22)

Much larger samples are now known from the Clarkforkian and the early Wasatchian (including "Sand Coulee" level, which is earliest Wasatchian), and they generally bear out Simpson's observations. The Clarkforkian specimens, especially those from the late Clarkforkian, are larger than early Wasatchian ("Graybullian") specimens, and the earliest Wasatchian specimens are the smallest. There is a clear trend toward larger size in both the Clarkforkian and early Wasatchian samples (also indicated in early Wasatchian studies of Gingerich, 1976a, and Bown, 1979), but the trend is not continuous from Clarkforkian into Wasatchian. Rather, a sharp break in the trend of gradual size increase is evident at the Clarkforkian-Wasatchian boundary, above which appear the smallest specimens, as small or smaller than those from the early Clarkforkian. These data confirm Simpson's suggestion that the Clarkforkian sample cannot be the same "race" as that from the earliest Wasatchian ("Sand Coulee").

Delson (1971) concluded that no size trend could be detected in *Haplomylus*; but his analysis suffered by grouping all Bighorn Basin specimens from different horizons (including those from the Clarkforkian), a procedure he justified because precise stratigraphic levels of many specimens were then unknown. He wrote (Delson, 1971: 349–350): "the large 'Clark Fork' specimens noted by Simpson are offset by the smaller ones from the Sand Coulee (often from the same localities)." There is now no doubt that Simpson's Clarkforkian and "Sand Coulee" specimens were not from the same localities, but were, in fact, from successive stratigraphic levels, as Simpson stated. Thus Simpson correctly anticipated the discontinuous size trends that are now documented by much larger samples.

The statistical difference in tooth dimensions and the clearly different size trends between Clarkforkian and early Wasatchian *Haplomylus* justify separation of the Clarkforkian specimens as a new species, *H. simpsoni.* Although most specimens of *H. simpsoni* can be distinguished from *H. speirianus* by their larger size, the smallest ones, particularly those from lower strata in the Clarkforkian, overlap in size with early Wasatchian *H. speirianus*; and confusion may arise if provenance of specimens is not known. Simpson (1943) dealt with this problem in some detail:

> If two specimens cannot be distinguished, except by trivial variations admittedly less than can occur within a subspecies, how can one maintain that they are taxonomically distinct? If a fossil can only be identified when its horizon is known, what becomes of the whole basis of paleontological correlation of horizons by the identification of their fossils? Both objections are based on the fallacious tendency to compare *individuals* when the correct comparison is of *groups*. The groups as such are here readily distinguishable even though some individuals are not. Valid inference of group characters requires some homogeneity as to time, and hence some specification as to horizon. (Simpson, 1943: 175)

Simpson wrote this in a discussion of Clarkforkian and Wasatchian *Ectocion*, but it is even more appropriate now with reference to *Haplomylus*. Indeed, Clarkforkian and early Wasatchian *Haplomylus* provide an excellent example of evolutionary trends and differences that are obscured by grouping all specimens from different horizons and considering them as one highly variable species. (Other pertinent examples have been presented in several studies by Gingerich, notably 1976a.) As noted above, McKenna, Gingerich, and Bown have reported the presence of very small specimens of *Haplomylus* from various very early Wasatchian faunas. In addition, Gazin (1962) reported specimens of *Haplomylus* smaller than typical *H. speirianus* from the Wasatch Formation ("Knight" Formation) of southern Wyoming.

The precise locality and horizon of the holotype of *H. speirianus* are unknown. Cope (1880) initially reported that it had come from the Wind River Basin but later emended the record to read Bighorn Basin (Cope, 1884). There is now considerable evidence supporting Cope's correction, that the type is from early Wasatchian deposits of the Bighorn Basin (Matthew, 1915b; Delson, 1971).

In the absence of the Clarkforkian sample of *Haplomylus* now known, Gingerich (1976a) detected a single trend toward gradual size increase in early Eocene *Haplomylus*, and he posited that the Clarkforkian specimens mentioned by Simpson (1937c) and Matthew (1915b) were actually from Wasatchian (late "Graybullian") strata. Both labels and field notes for these specimens (which are now known to be highly reliable) indicate that two of them are clearly from the late Clarkforkian: AMNH nos. 16072 and 16074 are from the head of Big Sand Coulee (*Phenacodus-Ectocion* Zone). AMNH 21868 is recorded to be from north of Ralston, in the "Clark Fork Formation." These data are ambiguous but probably also indicate a late Clarkforkian provenance. In his figure 6, Gingerich showed the smallest specimen of *Haplomylus* as a Clarkforkian one. The specimen in question is UM 27242 from UM locality Sub-Wy 2 in the Hoback Basin. Faunally this locality is clearly Wasatchian, not Clarkforkian (Dorr, 1978; see Chapter V). UM 27242 is as small as the smallest specimens of *H. speirianus* now known from the earliest Wasatchian in the Clark's Fork Basin (Gingerich, personal communication, 1979). The only pre-Wasatchian specimen of *Haplomylus* from the Hoback Basin is UM 34761, a left $P_4$ from UM locality Sub-Wy 7 (Dorr, 1958b). It falls at the smallest end of the size range of *H. simpsoni* and may represent this species.

In addition to the Clarkforkian specimen from the Hoback Basin, specimens of a large species of *Haplomylus*, probably *H. simpsoni*, are known from the Purdy Basin Clarkforkian of the Togwotee Pass area, Wyoming (AMNH nos. 57282 and 88166; see Chapter V). The species possibly occurs also at Bear Creek and in the Plateau Valley Clarkforkian (Chapter V).

The abrupt shift in size of *Haplomylus* at the Clarkforkian-Wasatchian boundary evokes several questions. Did *H. simpsoni* undergo sudden extinction at this boundary? Did it emigrate from the Clark's Fork Basin? Is there a temporal hiatus at this boundary and, if so, could *H. simpsoni* have experienced a gradual size decrease toward the size of *H. speirianus* during such an interval? Known evidence is not yet conclusive, but it suggests that the first alternative is the most likely. One may then ask about the origin of *H. speirianus*. If it did not evolve gradually from *H. simpsoni* in the Bighorn Basin, what was its ancestry? The abrupt appearance of small *H. speirianus* in the earliest Wasatchian suggests that it was an immigrant that entered the Bighorn Basin at about the same time as *Pelycodus*, *Hyracotherium*, and *Diacodexis*. One may postulate that a population of small *Haplomylus* (at the lower end of the size range of *H. simpsoni*) became isolated in a neighboring basin in the early Clarkforkian. Perhaps this population did not undego size increase through time, and its descendants returned to the Clark's Fork Basin at the beginning of the Wasatchian, giving rise to *H. speirianus*. Until larger samples are known from the Clarkforkian outside of the Clark's Fork Basin, the precise relationship between *H. simpsoni* and *H. speirianus* will remain obscure. The sample described here demonstrates that distinctive populations of *Haplomylus* characterized the Clarkforkian and the early Wasatchian of the Clark's Fork Basin, and that they are best recognized as different species.

### Subfamily Apheliscinae (Matthew, 1918)
### *Apheliscus* Cope, 1875
### *Apheliscus nitidus* Simpson, 1937

Figures 36 C–E, 39, Table 25

*Referred Specimens.*—UM nos. 65092, 66147, 66156, 66302, 66325, 66332, 66502, 66630, 67199, 67220, 67249, 67250, 67468, 68744, 69279, 69938, 69941, 71046, 71047, 71048, 71183, and miscellaneous isolated teeth.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC-179); *Plesiadapis cookei* Zone (SC-74, 92, 108, 136, 137, 143); *Phenacodus-Ectocion* Zone (SC-10, 24, 48, 70, 72, 90, 155, 176, 202, 203, 231).

*Discussion.*—Simpson (1937c) proposed *Apheliscus nitidus* for a Clarkforkian specimen (AMNH 15849, left maxilla with $P^4$–$M^1$) that had been questionably referred to *A. insidiosus* by Matthew (1918). The specimen is

Table 25. Metrical data for Clarkforkian teeth of *Apheliscus nitidus*

| | N | OR | $\bar{X} \pm$ SE | s | V |
|---|---|---|---|---|---|
| $P_4$L | 3 | 3.10-3.20 | 3.13±.03 | .058 | 1.9 |
| $P_4$B | 3 | 1.70-1.90 | 1.77±.07 | .115 | 6.5 |
| $M_1$L | 5 | 2.35-2.70 | 2.49±.07 | .152 | 6.1 |
| $M_1$B | 4 | 1.85-2.00 | 1.90±.04 | .071 | 3.7 |
| $M_2$L | 13 | 2.75-3.15 | 2.92±.03 | .115 | 3.9 |
| $M_2$B | 13 | 2.05-2.50 | 2.25±.04 | .131 | 5.8 |
| $M_3$L | 4 | 2.35-3.10 | 2.76±.15 | .309 | 11.2 |
| $M_3$B | 4 | 1.90-2.35 | 2.04±.10 | .210 | 10.3 |
| $P^4$L | 3 | 2.15-3.00 | 2.57±.25 | .425 | 16.5 |
| $P^4$B | 3 | 2.75-3.50 | 3.10±.22 | .377 | 12.2 |
| $M^1$L | 2 | 2.60-2.95 | 2.78 | | |
| $M^1$B | 2 | 2.75-3.20 | 2.98 | | |
| $M^2$L | 0 | | | | |
| $M^2$B | 0 | | | | |
| $M^3$L | 2 | 2.60-2.75 | 2.68 | | |
| $M^3$B | 2 | 2.80-2.95 | 2.88 | | |

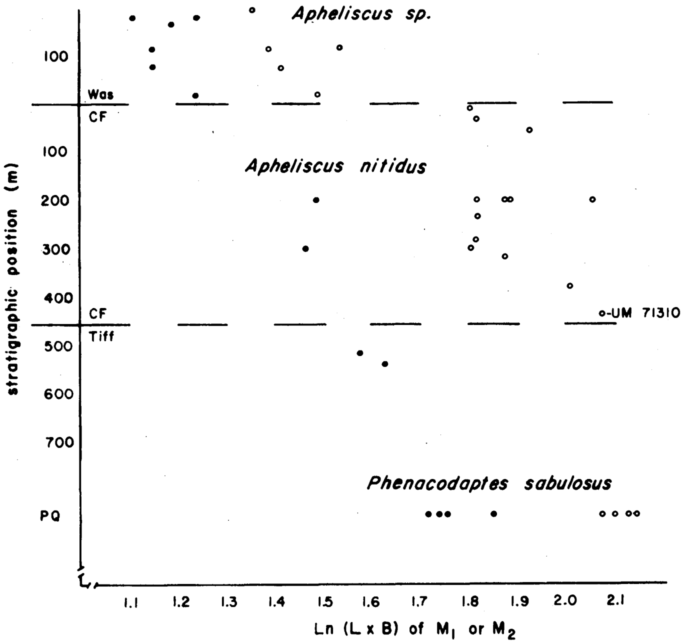

Figure 39. Stratigraphic plot of late Tiffanian *Phenacodaptes sabulosus* and Clarkforkian and early Wasatchian *Apheliscus* of the Clark's Fork Basin. Natural logarithm of crown area of $M_1$ (solid circles) and $M_2$ (open circles) is plotted against stratigraphic level with respect to the Clarkforkian-Wasatchian boundary sandstone. UM 71310 and two late Tiffanian specimens are intermediate between *P. sabulosus* and *A. nitidus*. Although the number of data points is small, *A. nitidus* appears to remain relatively static in size and is distinctly larger than early Wasatchian *Apheliscus* sp. The transition between the two species occurs abruptly at the Clarkforkian-Wasatchian boundary, suggesting that *Apheliscus* sp. was an immigrant and did not evolve directly from late Clarkforkian *A. nitidus*.

Table 26. Comparative data for lower cheek teeth of early Wasatchian *Apheliscus* sp. and late Tiffanian *Phenacodaptes sabulosus*.

| | *Apheliscus* sp.[1] | | | *Phenacodaptes sabulosus*[2] | | |
|---|---|---|---|---|---|---|
| | N | OR | $\bar{X}$ | N | OR | $\bar{X}$ |
| $P_4$L | 5 | 2.35-2.80 | 2.53 | 4 | 3.20-3.35 | 3.31 |
| $P_4$B | 5 | 1.20-1.50 | 1.35 | 4 | 1.90-2.10 | 2.00 |
| $M_1$L | 6 | 2.10-2.20 | 2.13 | 4 | 2.60-2.70 | 2.66 |
| $M_1$B | 6 | 1.45-1.65 | 1.53 | 4 | 2.15-2.35 | 2.20 |
| $M_2$L | 5 | 2.30-2.40 | 2.34 | 4 | 2.90-3.15 | 2.99 |
| $M_2$B | 5 | 1.70-1.95 | 1.81 | 4 | 2.70-2.85 | 2.78 |
| $M_3$L | 2 | 2.20-2.40 | 2.30 | 3 | 2.60-2.75 | 2.68 |
| $M_3$B | 2 | 1.50-1.65 | 1.58 | 3 | 2.25-2.30 | 2.27 |

[1] *Apheliscus* sp. sample includes UM nos. 65267, 65441, 65589, 66379, 66420, 66875, 68299, and 69477, all from early Wasatchian of the Clark's Fork Basin.

[2] *Phenacodaptes sabulosus* sample includes PU nos. 13302 (holotype), 13391, 13932, and 14398, all from the late Tiffanian Princeton Quarry.

from exposures in the head of Big Sand Coulee (late Clarkforkian, *Phenacodus-Ectocion* Zone). The new specimens here referred to *A. nitidus* include upper teeth that conform closely in size and morphology to the holotype, as well as lower teeth that can be confidently assigned to the same species.

Like other apheliscines, these specimens of *Apheliscus nitidus* have bunodont molar cusps and a small paraconid on $M_1$, but only a low paracristid (with no distinct paraconid) on $M_2$ and $M_3$. The lower molars have well developed anterior cingulids and the remnants of ectocingulids in the hypoflexids. The upper molars are roughly triangular, with prominent posterior and external cingula and a somewhat weaker anterior cingulum. The hypocone is moderately well developed on $M^1$ and $M^2$. $P^4$ and $P_4$ are large and distinctive, $P_4$ with single high trigonid cusp and sharply defined talonid heel, and $P^4$ with a large, inflated external cusp and a lower and smaller internal cusp.

*A. nitidus* is consistently larger than early Wasatchian *Apheliscus* sp. from the Clark's Fork Basin (Tables 25 and 26) and from the southeastern Bighorn Basin (*Apheliscus* cf. *insidiosus* in Bown, 1979). It has more prominent postcingula and larger hypocones on $M^1$ and $M^2$ than in Wasatchian *Apheliscus*. In other respects it is similar to early Wasatchian *Apheliscus*, and it also closely resembles *Phenacodaptes sabulosus*, described from the late Tiffanian Princeton Quarry (Jepsen, 1930b). In most tooth dimensions, *A. nitidus* is consistently slightly smaller than *P. sabulosus*, particularly in the breadths of the last premolar and the molars (Tables 25 and 26). *A. nitidus* also differs from *P. sabulosus* in having slightly smaller hypocones on $M^1$ and $M^2$ and a more labially oriented cristid obliqua on $P_4$, both features of resemblance to Wasatchian *Apheliscus*. The nature of dental wear in apheliscines is highly distinctive (see also McKenna, 1960), with large shearing (phase I) and grinding (phase II) facets well developed and $P_4$ displaying heavy postvallid wear. Wear patterns in *A. nitidus* seem somewhat more like those in early Wasatchian *Apheliscus* than in *Phenacodaptes*.

In morphology and size, as well as stratigraphic occurrence, *A. nitidus* is essentially intermediate between *Phenacodaptes sabulosus* and *Apheliscus* sp. of the early Wasatchian; and it appears almost certain that *P. sabulosus* was the immediate progenitor of *A. nitidus* (see also Gazin, 1959). Several specimens in the UM collection are so perfectly intermediate in morphology (and stratigraphic level) between *Phenacodaptes* and *A. nitidus* that their taxonomic assignment is equivocal (e.g., UM 71310, right dentary with $M_2$ and unassociated $M^2$, from SC–226, *Plesiadapis gingerichi* Zone). In contrast, the transition from *A. nitidus* to early Wasatchian *Apheliscus* sp. is not gradual (Figure 39); rather, an abrupt shift to smaller size occurs at the beginning of the Wasatchian. Clarkforkian *A. nitidus* shows no apparent trend in size.

*Apheliscus* remains a problematical taxon primarily for two reasons: disagreement over its precise relationships to other early Tertiary mammals, and nomenclatural confusion within the genus *Apheliscus*.

Gazin (1959) suggested that the Apheliscinae are most closely related to the Torrejonian Pentacodontinae, because of resemblances in premolar and molar talonid structure. McKenna (1960) discussed the affinities of *Apheliscus* at some length and proposed that the Apheliscinae be included as a subfamily of the Hyopsodontidae. This position was also adopted by Van Valen (1967) and Delson (1971). Recently Bown (1979) returned to Gazin's view and included *Apheliscus* in the Pentacodontidae. I agree with McKenna and others that apheliscines possess significant resemblances to hyopsodontids, and only superficial ones to pentacodontids. As McKenna observed, molar structure in pentacodontids is quite unlike that in apheliscines. Moreover, numerous middle Paleocene hyopsodontids exhibit suites of features of molar and premolar morphology that foreshadow those seen in *Apheliscus* and *Phenacodaptes*. McKenna selected *Promioclaenus* as showing particular similarity, while Van Valen mentioned *Promioclaenus* and especially *Haplaletes*. To these may be added *Litomylus dissentaneus*, which differs from *Phenacodaptes* primarily in its longer $P_2$ and $P_3$ and larger molar hypocones. $P_4$–$M_3$ in *L. dissentaneus* bear remarkable resemblance to those of *Phenacodaptes*, except that the latter normally lacks a paraconid and a metaconid on $P_4$. PU 13932, a well preserved right dentary of *Phenacodaptes* from Princeton Quarry, has a tiny basal paraconid and a moderately expressed metaconid, giving it a very close resemblance to *Litomylus*.

Nomenclatural difficulties within the genus *Apheliscus* stem primarily from problems of synonymy. *A. nitidus* is a valid species name, but it should be applied only to the relatively large Clarkforkian form. Delson (1971) referred early Wasatchian *Parapheliscus wapitiensis* Van Valen (1967) to *Apheliscus* and considered it a junior synonym of *A. nitidus*, a synonymy accepted by Bown (1979). Delson acknowledged the difference in size between these two, but cited specimens from the early Wasatchian Four Mile fauna (McKenna, 1960) that bridge the gap in size as justification for this synonymy. The UM collection of *Apheliscus* from the Clark's Fork Basin is the only large sample of the genus for which precise stratigraphic data are available through the Clarkforkian and early Wasatchian, and it does not support synonymy of *A. nitidus* and *A. wapitiensis* at the species level. *A. wapitiensis* may be a valid name for small early Wasatchian *Apheliscus*.

Wasatchian *Apheliscus* have often been assigned to *A. insidiosus* Cope (1874), following Matthew's (1918) allocation of Wasatchian specimens from the Bighorn Basin to this species. Cope's holotype of *A. insidiosus* was from the Wasatchian of New Mexico and no more specimens of *Apheliscus* have been found there. Unfortunately, Cope's type was lost more than 60 years ago. His description and illustration (Cope, 1877: 146–147 and plate 45, figure 18) are not very precise but indicate a form congeneric with Matthew's specimens and with others subsequently allocated to *Apheliscus*. It may not be possible now, however, to determine if any Wyoming *Apheliscus* represent the same species as Cope's *A. insidiosus*, and the early Wasatchian specimens almost surely do not. As aforementioned, the Wasatchian specimens belong to a different species from Clarkforkian *A. nitidus*. Here I refer to them as *Apheliscus* sp., but the name *A. wapitiensis* is available and, as I have noted, may be the proper one.

Imprecise or questionable locality data associated with some specimens have also contributed to the problem of species identification in *Apheliscus*. A dentary of a small *Apheliscus* with $P_4$–$M_3$ (PU 21176) is recorded as coming from "?Sec. 18, T.56 N., R.100 W." in the Clark's Fork Basin. These data suggest a locality in the lower Clarkforkian, but there are no UM localities in the immediate area. The specimen is unlike any other Clarkforkian *Apheliscus* but closely resembles early Wasatchian *Apheliscus* from the Clark's Fork Basin. Thus it seems probable that the locality data for PU 21176 are in error and that the specimen is actually from the Wasatchian. AMNH 15696, a specimen referred to *A. insidiosus* by Matthew (1918), is larger than most specimens of early Wasatchian *Apheliscus* and is within the size range of *A. nitidus*. Matthew reported that the specimen was from the "Upper Gray Bull," and Granger's field notes for 1911 indicate that it is indeed from Wasatchian beds. However, AMNH 15696 differs from *A. nitidus* and resembles other Wasatchian *Apheliscus* in the configuration of $P^4$ and $P_4$ and in having narrower molars and weaker postcingula on $M^1$ and $M^2$. A second relatively large early Wasatchian specimen, PU 13025, is recorded from southwest of Otto in the central Bighorn Basin, which appears to confirm Matthew's record. These specimens may be merely large individuals of the small Wasatchian species of *Apheliscus*, but they suggest the possibility that *A. nitidus* survived into the early Wasatchian in the central Bighorn Basin.

Close similarities between *A. nitidus* and *Phenacodaptes sabulosus* have been discussed above. A case could be argued either for transfer of *A. nitidus* to the genus *Phenacodaptes* or for synonymy of the latter genus under *Apheliscus*. Intermediate specimens from the Clark's Fork Basin were noted above. In addition, undescribed specimens collected from the Clarkforkian Purdy Basin localities (Togwotee Pass area) by McKenna also appear to be intermediate between *Phenacodaptes sabulosus* and *Apheliscus nitidus* (Chapter V). Pending further studies, I maintain both genera but emphasize their close resemblance and relationship.

### Order MESONYCHIA Van Valen, 1969
### Family Mesonychidae Cope, 1875
### *Dissacus* Cope, 1881
### *Dissacus praenuntius* Matthew, 1915

*Referred Specimens.*—UM nos. 65002, 65067, 65098, 66175, 66188, 66597, 66634, 66854, 67360, 69305, 71178, 71590, 71675, 71676, and isolated teeth in UM nos. 66196, 68786, 69180.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–19, 66, 74, 109, 134, 189, 195); *Phenacodus-Ectocion* Zone (SC–22, 24, 70, 77, 80, 81, 105, 150, 184); and specimens in the Princeton collection from *Plesiadapis gingerichi* Zone (vicinity of SC–156 or SC–157); *Plesiadapis cookei* Zone (vicinity of SC–136 and of SC–209 or SC–135); *Phenacodus-Ectocion* Zone (vicinity of SC–23).

*Discussion.*—A medium-sized species of *Dissacus* is moderately common in the Clarkforkian collection. Most specimens consist of only isolated teeth or fragments of teeth, but some exceptionally complete specimens are also included. They are very similar in size and morphology to the holotype (and only previously known specimen), AMNH 16069, collected by Walter Granger from outcrops in the head of Big Sand Coulee (late Clarkforkian). Among the new Clarkforkian specimens is a nearly complete skull and mandible with almost the entire dentition (UM 69305), from the quarry at SC–195. It is the first known skull of this primitive mesonychid. The specimen will be described elsewhere after further preparation. The Princeton collection also includes several noteworthy Clarkforkian specimens of *Dissacus praenuntius*: PU nos. 13294, 13295, 13309, 17991, 18711, 19597, and 22314. PU 13294 is a left dentary with $dP_{3-4}$–$M_1$. Three others, PU nos. 13295, 18711, and 19597, include relatively complete dentaries, maxillae, or both. Of the latter, PU 18711, from the latest Clarkforkian, is relatively small and possibly represents a different species, *D. navajovius longaevus* (see below).

Matthew (1915a) recognized three species of *Dissacus* from North America, distinguished by size, relative size of $M_1$, and development of molar paraconids. *D. saurognathus* Wortman and *D. navajovius* Cope, both originally described from the Torrejonian of New Mexico, are the largest and smallest species, respectively. They differ substantially in size and there is no reason to question their validity. Matthew proposed *D. praenuntius* for a Clarkforkian form intermediate in size between the two Torrejonian species (see Simpson, 1937c, for illustrations of the holotype). In addition to size, *D. praenuntius* was defined by its more reduced paraconids and vestigial metacone on $M^3$.

In the UM sample of *D. praenuntius*, the paraconids are generally very reduced, but this is clearly variable. $M^3$ is preserved only in UM 69305, and its metacone is smaller than on $M^1$ or $M^2$ but does not appear to be more reduced than in the Torrejonian species. In other details, these specimens are clearly distinct from the Torrejonian species. They exceed the size of *D. navajovius* but are significantly smaller than *D. saurognathus* (in UM 69305, $M_{1-3}$ length=43.5; in *D. navajovius*, $M_{1-3}$ length=33.0, and in *D. saurognathus* $M_{1-3}$ length=57.0 [Matthew, 1915a]). As in both Torrejonian species, $M_1$ in *D. praenuntius* is slightly smaller than $M_2$. $M_3$ is the smallest molar and its talonid is somewhat reduced (as in *D. saurognathus* but in contrast to *D. navajovius*). The metaconids are small but distinct on all the lower molars. Additional morphological details will be available when preparation of UM 69305 has been completed.

Matthew (1915a) also named *D. navajovius longaevus*, from the early Wasatchian of the Bighorn Basin, as a variant of the New Mexican species ($M_{1-3}$ length=38.0). According to Matthew, its other distinguishing features include larger molar paraconids, equal-sized $M_1$ and $M_2$, and a reduced talonid on $M_3$. These features contrast with those of *D. navajovius* from the Torrejonian, hence it is not at all certain that the Wasatchian form is conspecific with *D. navajovius*. It seems more probable that it is a derivative of Clarkforkian *D. praenuntius*, but whether it merits specific distinction from the latter requires further investigation.

In addition to the sample referred above to *D. praenuntius*, there are several Clarkforkian specimens referable to *Dissacus* but not certainly to *D. praenuntius*. Two of them, UM 65555 (SC–50, *Phenacodus-Ectocion* Zone) and UM 67191 (SC–136, *Plesiadapis cookei* Zone) are smaller and have narrower cheek teeth than all other Clarkforkian specimens. PU 18711 is slightly larger than these two Clarkforkian specimens, but (as noted above) it is smaller than other specimens referred here to *D. praenuntius* ($M_{1-3}$ length=38.4). These specimens fall within the size range of Matthew's *D. navajovius longaevus*, but it seems likely that they are small individuals of *D. praenuntius*. Other specimens of *Dissacus* in the Clarkforkian collection that are too fragmentary for definite species assignment include: UM nos. 66169 (SC–75, *Phenacodus-Ectocion* Zone), 66198 (SC–82, *Plesiadapis gingerichi* Zone), 67212 (SC–137, *Plesiadapis cookei* Zone), 68423 (SC–171, *Plesiadapis gingerichi* Zone), 68870 (SC–188, *Plesiadapis cookei* Zone), 68745 (SC–179, *Plesiadapis gingerichi* Zone), and 69898 (SC–197, *Plesiadapis cookei* Zone). A small species of *Dissacus* (*D.* cf. *navajovius*: PU 16135, $M_{1-3}$ length=36.0) occurs at the late Tiffanian Princeton Quarry (Table 42).

Outside of North America, *Dissacus* has been reported from the late Paleocene of Europe (Russell, 1964) and the early Tertiary (?Clarkforkian equivalent) of Naran Bulak, Mongolia (Dashzeveg, 1976; see Chapter V). The Mongolian species, *D. indigenus* Dashzeveg, is much smaller than *D. praenuntius*, nearer the size of *D. navajovius*. Specimens of questionable reference to *Dissacus* have been reported from China by several authors, and recently a new species of *Dissacus* from the Paleocene of Anhui, China, was described (Yan and Tang, 1976).

Measurements of complete teeth in the Clarkforkian sample are presented below. (Isolated first and second molars have been grouped because of the difficulty in differentiating them when not serially associated.) Dimensions of the teeth in UM 69305 are: $P_3L$=14.15, $P_4L$=15.15, $M_1L$=14.65, $M_2L$=16.10, $M_3L$=13.65, $P^4L$=12.70, $M^1L$=14.65, $M^2L$=14.20, $M^3L$=8.90 (other measurements cannot be made until preparation of the specimen is completed). Metrical data for isolated teeth are: $M_1$ or $M_2L$=13.60–14.90 ($\bar{X}$=14.31, n=9); $M_1$ or $M_2B$=6.10–7.15 ($\bar{X}$=6.73, n=8); $M_3L$=12.85 (n=1); $M_3B$=5.80 (n=1); $P^4L$=12.15–12.90 (n=2); $P^4B$=9.80–10.15 (n=2); $M^1$ or $M^2L$=13.10–13.90 ($\bar{X}$=13.50, n=3); $M^1$ or $M^2B$=12.90–14.15 (n=2). Measurements of the two small specimens are: UM 65555, $P_4L$=12.60, B=5.15; UM 67191, $P_4L$=12.40, B=5.50.

## Order TAENIODONTA Cope, 1876
## Family Stylinodontidae Marsh, 1875
## Subfamily Stylinodontinae Schlosser, 1911
## *Lampadophorus* Patterson, 1949
## cf. *Lampadophorus* sp.

Figure 40

*Referred Specimens.*—UM nos. 67186, 69996, 71801, and tooth fragments (?canine) in UM nos. 66586 and 66639.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–250); *Plesiadapis cookei* Zone (SC–109, 136, 220); *Phenacodus-Ectocion* Zone (SC–102).

*Discussion.*—The specimens at hand are very fragmentary, consisting of isolated teeth or fragments of teeth. The three separately catalogued specimens include one or more complete cheek teeth and are sufficient to document the presence of a stylinodontine taeniodont in the Clarkforkian of the Clark's Fork Basin. They are very similar to specimens of *Lampadophorus lobdelli* (Simpson, 1929b) from the Clarkforkian at Bear Creek and appear to conform to the diagnosis of *Lampadophorus* presented by Patterson (1949a). Incomplete material of taeniodonts is often difficult to identify accurately, however, hence a precise taxonomic assignment of the Clark's Fork Basin specimens should await recovery of better specimens. *Lampadophorus* is the only taeniodont so far reported from the Tiffanian or the Clarkforkian, consequently allocation of the specimens to this genus is inescapable at present.

Of the new Clarkforkian specimens, only UM 69996 is not heavily worn (Figure 40). It is an isolated cheek tooth with enamel still covering the entire crown. UM

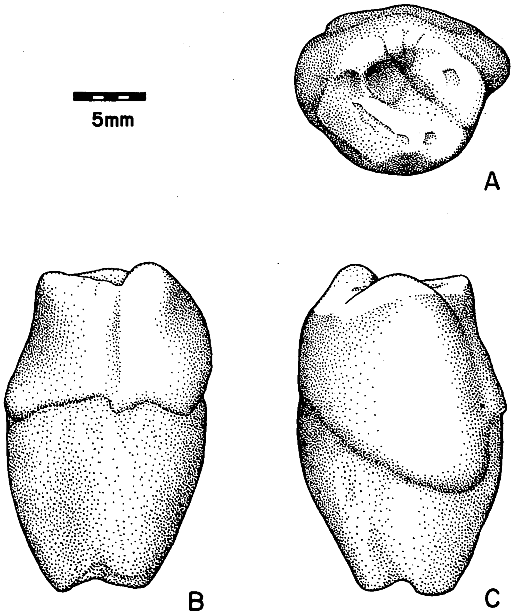

Figure 40. Cf. *Lampadophorus* sp., UM 69996, from SC–220: cheek tooth, crown (A) and end (B,C) views.

nos. 67186 and 71801 each include several associated cheek teeth in which the enamel is completely or almost completely worn off the occlusal surfaces. The best preserved teeth have cement at the base of the crowns and enamel encircling the crowns; there is no development of enamel-free bands anteriorly or posteriorly. These features agree with Patterson's definition of *Lampadophorus*. Some of the teeth preserve the root intact, and this single root is cylindrical and tapering and only very faintly bilobate. In this regard, it resembles the root of AMNH 22234, the holotype of *L. lobdelli.*

The Princeton collection contains several specimens of *Lampadophorus* from the Clarkforkian of the Bighorn Basin. Three specimens are from early Clarkforkian localities in the Badger Basin part of the Clark's Fork Basin (PU nos. 18863, 18994, and 21498, all *Plesiadapis gingerichi* Zone), and one is from the *Plesiadapis cookei* Zone (PU 19548 from the vicinity of SC–136). Two specimens (PU nos. 14678 and 18052) are from exposures at the southern tip of Polecat Bench. Locality data with these specimens are insufficient to ascertain whether they are of late Clarkforkian or early Wasatchian age; if they are of Wasatchian age they may represent *Ectoganus* rather than *Lampadophorus*. Of particular note is a specimen that includes more than 30 associated teeth of *Lampadophorus* from the Foster Gulch Oil Well site in the northeastern Bighorn Basin (PU 20864, see Chapter V).

Patterson (1949b) considered *Lampadophorus* to be restricted to the Tiffanian (he included Clarkforkian within the Tiffanian). *L. lobdelli* is now known to be of Clarkforkian age, whereas *L. expectatus* Patterson (1949a), from the Plateau Valley beds of Colorado, is probably latest Tiffanian in age (see Chapter V). I formerly considered *Lampadophorus* to be restricted to the Clarkforkian (Rose, 1977), a view based partly on my earlier belief that the Princeton Quarry level was of earliest Clarkforkian age. In the revised concept of the Clarkforkian presented herein, Princeton Quarry is clearly late Tiffanian in age. Several specimens of *Lampadophorus* are known from the environs of Princeton Quarry (PU nos. 18910, 18954, 18982, and 21499). Thus the range of *Lampadophorus* includes both Tiffanian and Clarkforkian, and appears to be restricted to those ages.

### Order PANTODONTA Cope, 1873
### Family Coryphodontidae Marsh, 1876
### *Coryphodon* Owen, 1845
### *Coryphodon* sp.
Plate 4: 3

*Referred Specimens.*—UM nos. 65037, 65040, 65485, 65531, 65650, 66149, 66162, 66600, 66622, 66737, 66921, 68277, 68279, 68784, 68872, 68876, 69277, 69301, 69332, 69691, 71236, 71575, and miscellaneous isolated teeth and tooth fragments.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–83, 226); *Plesiadapis cookei* Zone (SC–19, 20, 53, 58, 62, 66, 84, 98, 108, 109, 115, 116, 117, 119, 120, 127, 136, 166, 188, 189, 197, 205, 220, 238); *Phenacodus-Ectocion* Zone (SC–8, 11, 21, 22, 29, 49, 55, 57, 73, 81, 99, 105, 106, 149, 150, 153, 164, 175, 176, 184, 202, 203, 214, 234).

*Discussion.*—*Coryphodon* is common and widespread in the middle and upper Clarkforkian of the Clark's Fork Basin, as it is in many Wasatchian beds of the Western Interior. The UM sample of *Coryphodon* consists primarily of isolated teeth and fragments of teeth, but several more complete specimens are also included. Notable among them are UM 66149 (a left maxilla with $dP^{1-4}$), UM 68279 (partial palatal dentition and associated postcranial elements), and UM 66162 (a well preserved mandible including the symphysis, both canines, lower incisors, and complete right cheek tooth series, and associated maxillary fragments and postcrania, including atlas and axis vertebrae). The deciduous upper premolars conform in all respects to those described and illustrated by Simons (1960: 43–44 and figure 4) and Bown (1979).

In addition to the UM specimens, Simpson (1937c) reported one Clarkforkian specimen of *Coryphodon* (AMNH 16078). Granger (1912 field catalogue) recorded its locality as "northwest side Clark's Fork, between Little Rocky Creek and Line Creek," which is in the vicinity of Sugarloaf Butte, near locality SC–166. The Princeton collection includes numerous Clarkforkian specimens of *Coryphodon* from various sites in the Bighorn Basin. PU nos. 18092, 18718, 18767, 18769, 20781, and 20989, are from the Clark's Fork Basin. PU 20781 is a well preserved skull with most of the dentition, which was extracted from sandstone in the vicinity of locality SC–209.

*Coryphodon* is large and distinctive, consequently it is one of the easiest early Tertiary mammals to recognize and identify at the generic level. Its specific taxonomy, however, is among the most poorly known of any early Eocene mammal, mainly because no systematic revision of North American representatives of the genus has appeared since before 1900. As a result, most recent authors have been compelled to leave their specimens without specific assignment. Simons (1960) determined that 28 species of *Coryphodon* have been proposed; but how many and which of them are valid is unknown, and their distinguishing characters are poorly understood. Only one of them, *C. proterus* Simons (1960), has been described from sediments of Clarkforkian age. Its holotype, PU 13400, a lower jaw, is from exposures along the Beartooth Front, 3 miles southwest of Bear Creek, Montana. The locality is in an isolated outcrop and cannot be precisely stratigraphically correlated with Polecat Bench and Willwood strata of the rest of the Clark's Fork Basin, but it appears to be of approximately early Clarkforkian age (D. C. Parris, personal communication). (In 1977, a UM field party revisited this locality and discovered a fragmentary right $P_1$ [UM 68282], possibly belonging to the holotype.)

Preliminary study of the UM Clarkforkian sample of *Coryphodon* reveals differences between these specimens and the holotype of *C. proterus*, primarily in molar talonid structure. UM 66162 (the most complete lower dentition in the collection; from SC–73, *Phenacodus-Ectocion* Zone) has shallowly basined talonids lingual to the cristid obliqua, rather than having this part of the talonid planar and higher than the buccal part of the talonid as in *C. proterus*. $M_3$ is larger than $M_1$ and $M_2$ but is not relatively so large as in *C. proterus*, nor does it exhibit the distinctive talonid structure of this species, i.e. the hypoconulid-entoconid crest equal in length to the hypoconulid-hypoconid crest. In UM 66162, the entoconid is distinctly closer to the hypoconulid than is the hypoconid. The significance of these differences is uncertain. If the UM sample is referable to *C. proterus*, some of the features that Simons considered diagnostic of the species would have to be ascribed to individual (intraspecific) variation. Pending revision of the genus *Coryphodon*, the UM sample is designated *Coryphodon* sp.

*Coryphodon* was first described from the Eocene of Europe. West et al. (1977) have recently reported *Coryphodon* from the Eocene of Ellesmere Island, Canada. Asian specimens of the genus have been reported from the Nemegt Basin of Mongolia (Reshetov, 1976) and from China (Zhai, 1978). When available samples of *Coryphodon* are thoroughly studied and the distinctions between species better understood, it seems likely that *Coryphodon* will play an important role in biostratigraphic correlation and investigation of mammalian dispersal.

Measurements of UM 66162 are: $P_1L$=13.75, $P_1B$=9.00; $P_2L$=22.10, $P_2B$=14.70; $P_3L$=23.40, $P_3B$=17.90; $P_4L$=24.00, $P_4B$=19.20; $M_1L$=28.50, $M_1B$ trigonid=22.40, $M_1B$ talonid=20.40; $M_2L$=33.65, $M_2B$ talonid=25.75; $M_3L$=43.00, $M_3B$ trigonid=29.60, $M_3B$ talonid=26.50 (all measurements taken as described by Simons, 1960: 73; lengths measured on buccal side).

### Family Cyriacotheriidae Rose and Krause, 1981*

### *Cyriacotherium* Rose and Krause, 1981*

### *Cyriacotherium psamminum* Rose and Krause, 1981*

Figure 41

*Referred Specimens.*—UM nos. 68040 (holotype), 65775, 68039, 68202, 68214, 69274, 71439, and PU 18824.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–62); *Phenacodus-Ectocion* Zone (SC–159, 202, 234; PU 18824 from vicinity of SC–48).

*Discussion.*—Specimens referable to this genus have been known for nearly three decades, but they remained undescribed until very recently. With one exception, all specimens known prior to the UM explorations in the Clark's Fork Basin belong to a single species of late Tiffanian age, *Cyriacotherium argyreum*. Most of the new material of this genus found by UM collectors represent a smaller, more advanced species, *C. psamminum* of Clarkforkian age.

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*Note added in proof: Publication of Rose and Krause (1981) has been delayed until 1982. These names are used as *nomina nuda* pending valid publication in the Proceedings of the American Philosophical Society.

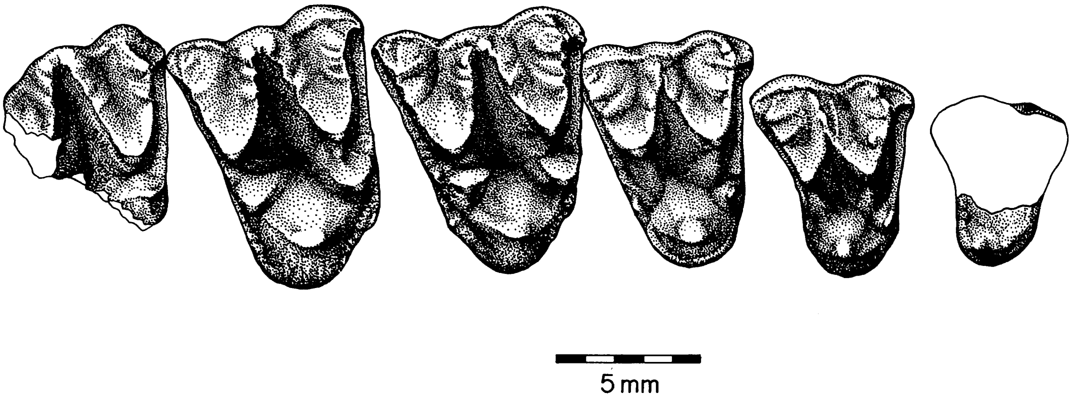

Figure 41. *Cyriacotherium psamminum*, Holotype, UM 68040, from SC-159: right maxilla with $P^3$-$M^2$ and incomplete $P^2$ and $M^3$.

*Cyriacotherium* is characterized by pronounced dilambdodonty, large upper molar conules, molariform posterior premolars, crenulated enamel, and small size relative to other North American pantodonts. It appears to be most closely allied to *Pantolambda*, a primitive small to moderate sized pantodont from the Torrejonian of western North America. Clarkforkian *C. psamminum* is about 25% smaller than *C. argyreum* and has a more dilambdodont $P^3$ than *C. argyreum*. Rose and Krause (1981) provide diagnoses and descriptions of both species and a discussion of the phylogenetic relationships of *Cyriacotherium*.

### Order TILLODONTIA Marsh, 1875
### Family Esthonychidae Cope, 1883
### Subfamily Esthonychinae Zittel and Schlosser, 1911
### *Esthonyx* Cope, 1874

In the 25 years since Gazin's (1953) review of the Tillodontia, a large number of new specimens have been collected. They contribute substantially to our knowledge of this unusual order and particularly of the genus *Esthonyx*. Much of the new material of *Esthonyx* is from the Clarkforkian and Wasatchian of the Bighorn Basin, and it constitutes the major source of new data for a revision of the genus by Gingerich and Gunnell (1979). These authors provided emended diagnoses, descriptions, and measurements of the Clarkforkian species, obviating the need for detailed discussion here. For completeness in the present survey, brief accounts are presented below.

Both Simpson (1937c) and Gazin (1953) reported three species of *Esthonyx* from the Clarkforkian: two large species (*E. grangeri* and *E. latidens*) and one small species (designated *E. ?bisulcatus* by Simpson and *E.* cf. *spatularius* by Gazin). The UM collection of *Esthonyx* from the Clark's Fork Basin is large and well documented stratigraphically, and it affords new insights concerning the systematics and phylogeny of Clarkforkian *Esthonyx*. Gingerich and Gunnell also recognize three species, but only one is among the three previously recognized; two are new. *E. grangeri* is the largest species of the genus, occurring in late Clarkforkian and early Wasatchian strata. *E. latidens* is a junior synonym of *E. grangeri*. The earliest species of the genus, *E. xenicus*, is from early and early middle Clarkforkian beds. It is near the size of early Wasatchian *E. spatularius*, and includes the specimen (AMNH 16065) assigned questionably to *E. bisulcatus* by Simpson and compared to *E. spatularius* by Gazin. *E. ancylion* is intermediate in size between *E. xenicus* and *E. grangeri* and occurs in the stratigraphic interval between them. The three Clarkforkian species appear to be parts of a single, rapidly-evolving lineage, quite distinct from the lineage (or lineages) present in the Wasatchian. Because we now have a good fossil record of *Esthonyx* in the Clarkforkian, the boundaries between the nominal species in this evolving continuum must be largely arbitrary (see Gingerich and Gunnell, 1979, for details). This is an

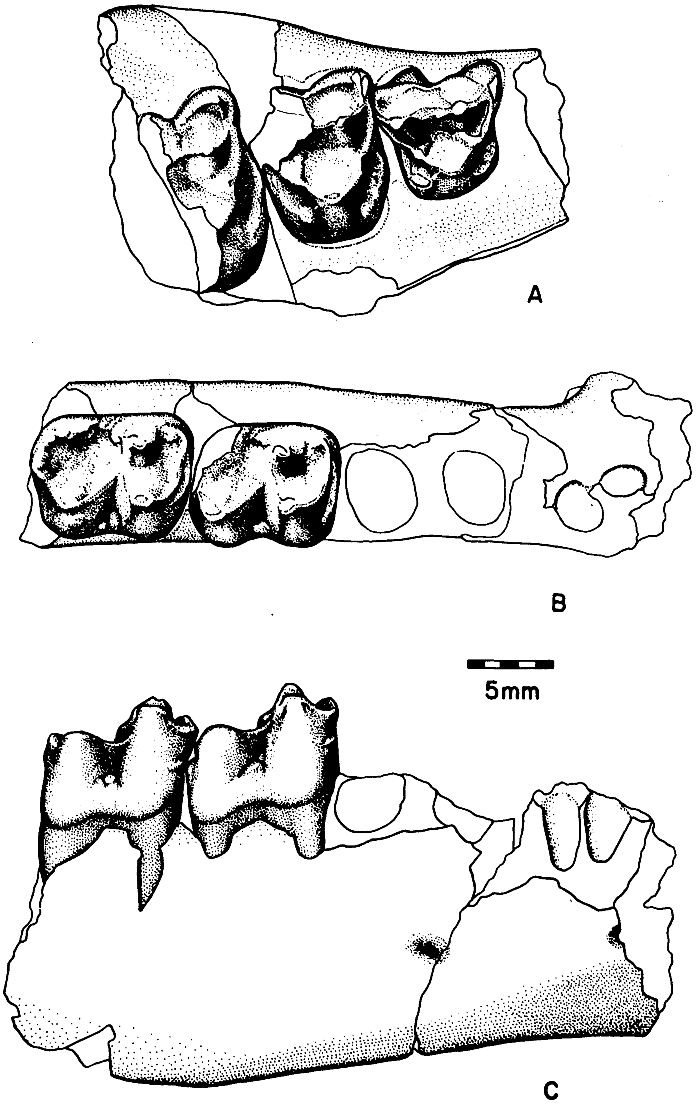

Figure 42. *Esthonyx xenicus*, Holotype, UM 66166, from SC–74. A, right maxilla with dP$^4$-M$^1$ and part of M$^2$. B and C, right dentary with M$_{1-2}$, crown and labial views.

evolutionary situation analogous to that observed in the Wasatchian primate *Pelycodus* (Gingerich and Simons, 1977).

The study by Gingerich and Gunnell demonstrates the importance and special utility of stratigraphic data for understanding and interpreting evolution in closely related species of mammals.

### *Esthonyx xenicus* Gingerich and Gunnell, 1979

Figure 42

*Referred Specimens.*—UM nos. 66166 (holotype), 66320, 67179, 71234, 71303, 71576 (formerly included in UM 71191), and a molar trigonid in UM 71185.

*Occurrence.—Plesiadapis gingerichi* Zone (SC–83, 226); lower *Plesiadapis cookei* Zone (SC–74, 91, 135).

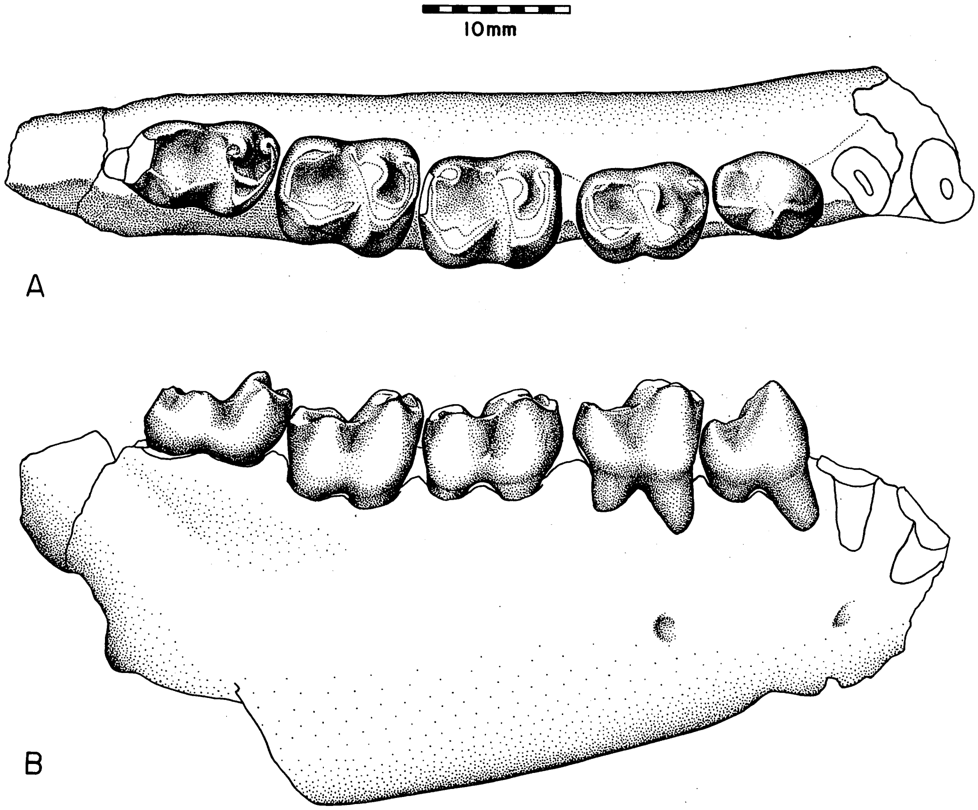

Figure 43. *Esthonyx ancylion*, UM 71455, from SC–234: right dentary with $P_3$-$M_3$. A, crown, and B, labial views. (From Gingerich and Gunnell, 1979).

*Discussion.*—As mentioned above, this early species of *Esthonyx* was previously confused with the early Wasatchian species *E. spatularius* and *E. bisulcatus* before its provenance and distinctive traits were clearly known. *E. xenicus* differs from the Wasatchian species in having a two-rooted $P_2$ and in lacking symphysial fusion. Gingerich and Gunnell listed additional specimens of *E. xenicus* from the Clark's Fork Basin that are in the Princeton collection.

As noted above, a small Clarkforkian specimen of *Esthonyx* (AMNH 16065) was known to both Simpson and Gazin. It is a well preserved dentary with $P_2$-$M_3$. Granger (1912 field catalogue) listed its locality as "bluff NE of Ralston, on Fisher's contact line" (see Figure 1), which leaves no doubt that it came from near UM locality SC–74, about on the boundary between the *Plesiadapis gingerichi* and *Plesiadapis cookei* Zones. It is clearly referable to *E. xenicus.*

The holotype of *E. xenicus* (UM 66166, Figure 42), from SC–74, includes incomplete dentaries and maxillae. The right maxilla preserves $dP^4$, which is fully molariform but longer and narrower than $M^1$.

### *Esthonyx ancylion* Gingerich and Gunnell, 1979

Figure 43

*Referred Specimens.*—UM nos. 65010, 65051, 65774, 65780, 66633, 66732, 66912, 67189, 68225, 68236, 68245, 68511 (holotype), 68874, 69264, 69298, 69309, 71455, 71464, 71474, and isolated teeth or tooth fragments in UM nos. 65722, 66639, 66734, 68514, 69230, 71646.

*Occurrence.—Plesiadapis cookei* Zone (SC–19, 20, 62, 109, 117, 127, 136, 188, 189, 197, 201); lower *Phenacodus-Ectocion* Zone (SC–163, 164, 176, 234).

*Discussion.—Esthonyx ancylion* is intermediate in tooth size, dentary depth, and stratigraphic position between *E. xenicus* and *E. grangeri*; and it is surely the phylogenetic intermediary between them. In addition to the UM sample, four specimens in the Princeton collection were noted by Gingerich and Gunnell. Collections available to previous students apparently did not include any specimens of this species. The holotype (UM 68511) is a skull and dentaries with most of the dentition. It is the first known skull of *Esthonyx.*

*E. ancylion* is a characteristic fossil of the middle Clarkforkian. Most specimens are from the *Plesiadapis*

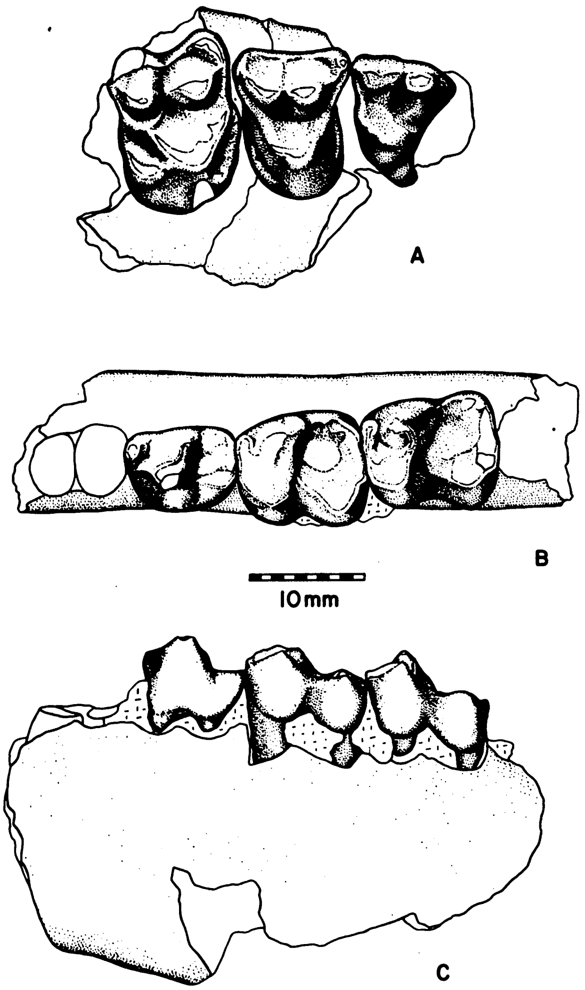

Figure 44. *Esthonyx grangeri.* A, UM 66289, from SC-90: right maxilla with $P^{3-4}$-$M^1$. B and C, UM 66154, from SC-72: left dentary with $P_4$-$M_2$, crown and labial views.

*cookei* Zone, but a few that are clearly below the size range of *E. grangeri* (including the holotype of *E. ancylion*) are from the lowest part of the *Phenacodus-Ectocion* Zone. The transition from *E. ancylion* to *E. grangeri* is relatively gradual and continuous, and the largest specimens of *E. ancylion* closely approach the size of *E. grangeri.*

McKenna has collected specimens of *Esthonyx* from the Clarkforkian of the Purdy Basin (Togwotee Pass area, Wyoming), where they are associated with *Plesiadapis cookei.* AMNH 86834 (right dentary with $M_3$) and AMNH 56130 (left dentary with $P_3$-$M_3$, somewhat smaller than AMNH 86834) both appear to be referable to *E. ancylion* (see Chapter V).

### *Esthonyx grangeri* Simpson, 1937

Figure 44

*Synonym.—Esthonyx latidens* Simpson, 1937.

*Referred Specimens.*—UM nos. 65072, 65099, 65261, 65644, 66154, 66158, 66187, 66289, 66316, 67227, 67351, 67454, 67456, 68204, 68780, and isolated teeth or tooth fragments in UM nos. 64709, 64718, 65073, 65078, 66189, 66196, 66586, 67355, 67361, 67467, 68786, 69897, 71355.

*Occurrence.—Phenacodus-Ectocion* Zone (SC-8, 10, 22, 24, 25, 29, 55, 72, 80, 81, 90, 102, 138, 149, 150, 153, 154, 155, 159, 183, 184, 214, 230).

*Discussion.—Esthonyx grangeri* is the largest species of *Esthonyx* and the largest esthonychine except for the late Wasatchian ("Lostcabinian") *Megalesthonyx* Rose (1972). In the Clarkforkian, it occurs only in the *Phenacodus-Ectocion* Zone, but it is also present in earliest Wasatchian (early "Graybullian") beds in the Clark's Fork Basin (Gingerich and Gunnell, 1979), the southern Bighorn Basin (Bown, 1979), and the central Bighorn Basin (Schankler, 1980).

The holotype of *E. grangeri,* AMNH 16067, was collected by Walter Granger from sediments in the head of Big Sand Coulee (vicinity of SC-102). The holotype of *E. latidens,* AMNH 16066, is from 3 miles east of the mouth of Pat O'Hara Creek (approximately SC-159, 162, or 90). Hence the two specimens are from very nearly the same horizon, about 70-80 m below the Clarkforkian-Wasatchian boundary. They are similar in size, and their minor morphological differences can now, in the light of larger samples, be confidently ascribed to intraspecific variation. There can be little doubt that they are conspecific.

Other Clarkforkian specimens of *E. grangeri* from the Clark's Fork Basin include AMNH 16123 and PU nos. 13239, 13341, and 18147.

## Order DINOCERATA Marsh, 1873

## Family Uintatheriidae Flower, 1876

### *Probathyopsis* Simpson, 1929

### *Probathyopsis praecursor* Simpson, 1929

Plate 4: 1-2, Tables 27, 28

*Synonyms.—Probathyopsis successor* Jepsen, 1930; *Prouintatherium hobackensis* Dorr, 1958.

*Referred Specimens.*—UM nos. 63279, 65042, 65071, 65478, 65556, 65660, 66134, 66146, 66334, 66539, 66544, 66763, 66769, 67023, 67457, 67460, 68030, 68206, 68244, 68419, 68439, 69668, 69670, 69696, 69937, 71184, 71440, 71677, 71796, and miscellaneous isolated teeth and tooth fragments.

*Occurrence.—Plesiadapis gingerichi* Zone (SC-78, 157, 171, 174, 215, 249); *Plesiadapis cookei* Zone

Table 27. Measurements of UM Clarkforkian teeth of *Probathyopsis praecursor*.

| | UM 65071 | UM 65660 | UM 66769 | UM 67460 | UM 68244 | UM 69696 | UM 71440 |
|---|---|---|---|---|---|---|---|
| $M_1L$ | 11.10 | | | | | | |
| $M_1B$ | 7.65 | | | | | | |
| $M_2L$ | 15.75 | | | 16.15 | | | |
| $M_2B$ | 10.40 | | | 12.60 | | | |
| $M_3L$ | | 22.75 | | | 20.65 | | |
| $M_3B$ | | 16.0a | | | 13.10 | | |
| $P^2L$ | | | | | | 10.00 | |
| $P^2B$ | | | | | | 9.40 | |
| $P^3L$ | 10.40 | | | | | 10.00 | |
| $P^3B$ | 12.55 | | | | | 11.90 | |
| $P^4L$ | 11.00 | | | | | 10.70 | |
| $P^4B$ | 13.80 | | | | | 13.75 | |
| $M^1L$ | 11.45 | | | | | 11.50 | |
| $M^1B$ | 11.35 | | | | | 11.50 | |
| $M^2L$ | 15.60 | 16.30 | | 15.40 | | 14.55 | |
| $M^2B$ | | 17.50 | | | | 15.20 | |
| $M^3L$ | | 19.65 | 17.15 | | | 16.80 | 17.80 |
| $M^3B$ | | 19.95 | 17.65 | | | 16.75 | 18.65 |

Lengths of upper premolars measured along buccal margin; lengths of upper molars taken at midline of tooth, from anterior to posterior cingulum. Breadths of upper teeth measured from base of protocone to ectocingulum buccal to centrocrista notch.

(SC–19, 20, 58, 66, 74, 92, 119, 120, 135, 143, 208); *Phenacodus-Ectocion* Zone (SC–8, 22, 29, 48, 50, 55, 57, 70, 100, 154, 155, 159, 164, 176, 233, 234).

*Discussion.*—The primitive uintathere *Probathyopsis* is well represented in the Clarkforkian collection. Many of the specimens consist of isolated teeth, but some relatively complete dentitions are known as well (e.g. UM nos. 65071, left dentary with $P_4$–$M_3$ and right maxilla with $P^3$–$M^2$, from SC–22; 69696, left upper canine and right maxilla with $P^1$–$M^3$, from SC–19). The Princeton and American Museum collections also include several Clarkforkian specimens of *Probathyopsis.* In size and morphology all of the specimens from the Clark's Fork Basin appear to be indistinguishable from *P. praecursor.* Simpson (1929c) discussed the dental morphology of *Probathyopsis* in detail and, to avoid repetition, the reader is referred to his description.

When naming *Probathyopsis successor*, Jepsen (1930a) observed that it "has many characters in common with both *Probathyopsis praecursor* and *Prodinoceras martyr*, and differs only slightly from each." Jepsen cited three distinctive traits of *P. successor*: $P^2$ different in shape from (but similar morphologically to) that of *P. praecursor*, upper molars with a prominent ridge descending posteriorly from the middle of the metaloph (present in $M^3$ of *P. praecursor*), and back of $M_3$ talonid "wider, more rounded, and smoother" than in *P. praecursor.* From the larger samples of Clarkforkian *Probathyopsis* now available, it is apparent that these features may vary intraspecifically; hence in size and morphology, *P. praecursor* and *P. successor* appear to be conspecific (Table 28).

The provenances of the holotypes of *P. praecursor* and *P. successor* also provide compelling evidence in support of their synonymy. The type of *P. praecursor* was collected from beds in the head of Big Sand Coulee. Jepsen recorded the type locality of *P. successor* as "Lower Gray Bull beds, Lower Eocene, T55N, R101W, Sec.2, Park County, Wyoming," but (although not previously stated) this is precisely the location of the head of Big Sand Coulee. Most of the outcrops in section 2 are of later Clarkforkian age (*Phenacodus-Ectocion* Zone), but at the extreme western edge of the section and topographically higher are the basal Wasatchian localities SC–94, 104, and 182. The UM project has yielded common remains of *Probathyopsis* from the Clarkforkian, but no evidence of *Probathyopsis* from Wasatchian beds. Hence it is almost certain that the types of both species came from very nearly the same stratigraphic level in late Clarkforkian strata. (The type of *P. praecursor*, AMNH 16786, was collected in 1913 by William Stein. Stein's field catalogue indicates that the specimen is from "upper beds" in the head of Big Sand Coulee. Other specimens bearing this locality designation suggest that Stein—unaware of the age boundary in this area—may have mixed specimens from the latest Clarkforkian and the earliest Wasatchian exposures in the head of Big Sand Coulee. Judging from associated

Table 28. Comparative measurements of *Probathyopsis* and "*Prouintatherium hobackensis*."

| | AMNH 16786, Holotype, *Probathyopsis praecursor* | PU 13234, Holotype, *Probathyopsis successor* | UM 27249, Holotype, *Prouintatherium hobackensis* | UM 27250 *Prouintatherium hobackensis* |
|---|---|---|---|---|
| $M_1L$ | | | 10.80 | |
| $M_1B$ | | | 8.50 | |
| $M_2L$ | 16.00a | | 16.60 | |
| $M_2B$ | | | 12.20 | |
| $M_3L$ | 20.25 | | 21.60 | |
| $M_3B$ | 12.25 | | 13.90 | |
| $P^2L$ | 10.25 | 10.20 | 11.25 | 10.40 |
| $P^2B$ | 9.60 | 9.35 | 10.55 | 9.70 |
| $P^3L$ | | | | 9.90 |
| $P^3B$ | | | | 12.40 |
| $P^4L$ | | 11.45 | | 10.05 |
| $P^4B$ | | 13.70 | | 12.50 |
| $M^1L$ | | 12.05 | 11.65 | 10.00 |
| $M^1B$ | | 12.35 | 11.20 | 10.10 |
| $M^2L$ | 15.35 | 15.45 | 17.00 | 15.40 |
| $M^2B$ | 15.50 | 16.00 | 17.25 | 14.30 |
| $M^3L$ | | 17.80 | 18.40 | 17.85 |
| $M^3B$ | | 17.75 | 18.15 | 16.20 |

specimens and UM records of *Probathyopsis*, it is highly probable that the type of *P. praecursor* was from strata below the Clarkforkian-Wasatchian boundary. Granger's collections of 1911–1912 from the head of Big Sand Coulee appear to be from Clarkforkian beds only.)

$M^1$ in the holotype of "*P. successor*" (PU 13234) and in other specimens (e.g. UM nos. 65071 and 69696) is clearly smaller than $P^4$ and $M^{2-3}$. This is a characteristic of *P. praecursor*. ($M_1$ is smaller than $P_4$ and $M_{2-3}$ also.) $P^4$ and $M^1$ of *P. praecursor*, as restored by Simpson (1929c: figure 1) from AMNH 16984, are actually $M^1$ and $M^2$. This is now clear from the relative sizes of the teeth and the presence of a hypocone on both; $P^4$ in *Probathyopsis* lacks a hypocone. This is important because the "relatively large first molar" was considered diagnostic of *P. praecursor* (Wheeler, 1961) and, therefore, a distinction from *P. successor*. Jepsen (1930a) had considered the crest descending from the metaloph of upper molars to be an additional distinctive trait of *P. successor*, but this is extremely variable in specimens now known. It ranges from very prominent to indistinct or absent (absent on $M^1$, UM 69937; weak on $M^2$, UM 65478; present on $M^1$ but absent on $M^3$, UM 66539). With the clarification of these features of Clarkforkian *Probathyopsis*, there now seems little doubt that *P. praecursor* and *P. successor* are the same.

Jepsen (1930a) and Wheeler (1961) referred PU 13378, a specimen from Clarkforkian beds near the mouth of Little Sand Coulee, to *Probathyopsis* sp., and regarded it as older and more primitive than *P. praecursor* and *P. successor*. This view now seems untenable, and the specimen should be assigned to *P. praecursor*.

Contrary to our previous understanding (Gingerich and Rose, 1977: table 1), *Probathyopsis* did not make its initial appearance during the Clarkforkian. Several specimens are known from the late Tiffanian of the Clark's Fork Basin (PU nos. 18837, 18838, 18844, 18866, 18869, 19106). Further study is required to determine if they are conspecific with *P. praecursor*. *Probathyopsis newbilli* Patterson (1939), from the Plateau Valley beds of Colorado, also appears to be of Tiffanian age.

*Prouintatherium hobackensis* Dorr (1958a) appears to be dentally indistinguishable from *P. praecursor* (Table 28; Dorr, 1952, initially assigned it to *P. successor*). The holotype has a very prominent inframandibular flange, much larger than in the holotype of *P. praecursor*, but this difference may result from sexual dimorphism, which is known to be pronounced in uintatheres (Dorr, 1958a; Wheeler, 1961). (UM 69668, a specimen of *Probathyopsis* from SC-208 in the Clark's Fork Basin, preserves part of a large and robust inframandibular flange.) The type locality of *Prouintatherium hobackensis*, UM-Sub-Wy 7 (Hoback Basin, Wyoming), was first believed to be of Wasatchian age but is now considered to be probably Clarkforkian (Dorr, 1978; Chapter V). Thus, *Prouintatherium* is almost certainly congeneric with *Probathyopsis*, and *Prouintatherium hobackensis* is probably a junior synonym of *Probathyopsis praecursor.*

Kelley and Wood (1954) described *Probathyopsis lysitensis* from the Wasatchian of the Wind River Basin. If the generic allocation is correct, this is the latest occurring species of *Probathyopsis*. These authors noted, however, that *P. lysitensis* approaches *Bathyopsis* in some features. Schankler (1980) also recorded *P. lysitensis* from the late Wasatchian of the Bighorn Basin.

Closely related to *Probathyopsis* is *Bathyopsoides harrisorum* Patterson (1939), found at the same locality as the holotype of *P. newbilli* in the Plateau Valley beds and thus of probable late Tiffanian age. Patterson noted some minor differences in dental morphology between *Bathyopsoides* and *Probathyopsis*; but other differences, such as large canines, a longer canine-$P_2^3$ diastema, and a larger inframandibular flange, suggest that the holotype of *B. harrisorum* is a male *Probathyopsis* (Gazin, 1956b). A Princeton specimen, PU 14991, has been identified on labels as *B. harrisorum*. It is from the SE¼, SE¼, Sec. 35, T.53 N., R.94 W., Bighorn County, Wyoming (age uncertain: Clarkforkian or possibly late Tiffanian). Gazin (1956b) described two upper premolars from Buckman Hollow, Clarkforkian of western Wyoming, and assigned them questionably to *Probathyopsis*. They are larger than their counterparts in *P. praecursor*, and Gazin observed that they are closer in size to *Bathyopsoides harrisorum.*

Uinthatheres have been discovered in fair numbers and diversity in the early Tertiary of Mongolia (Matthew et al., 1929; Flerov, 1957) and China (e.g. Tong, 1978). Among them, *Prodinoceras* and *Mongolotherium* are very similar to *Probathyopsis* and are clearly closely related to it. *Prodinoceras martyr* differs from the North American genus only "in details of $P^2$, heel of $M_3$, and other minor features" (Matthew et al., 1929: 11). Initially described from the Gashato fauna, Mongolia, *Prodinoceras* is now known also from the Turfan Basin of Sinkiang, China (Chow, 1960; Tong, 1978). These occurrences appear to be approximately correlative with the North American Clarkforkian (Chapter V). The similarities between *Prodinoceras* and *Probathyopsis* are so close that it seems probable that they are congeneric. A new species questionably referred to *Probathyopsis* was described from the "early Eocene" of China by Chow and Tung (1962). Thus evidence is increasing that mammalian faunas of the early Eocene (including Clarkforkian) of North America and Asia included many of the same genera, or closely allied genera, suggesting considerable faunal interchange between the two continents (see Table 37).

Figure 45. *Arctostylops steini*, UM 65024, from SC-19: right dentary with $P_3$. A, crown, and B, lingual views.

### Order NOTOUNGULATA Roth, 1903
### Family Arctostylopidae Schlosser, 1923
### *Arctostylops* Matthew, 1915
### *Arctostylops steini* Matthew, 1915

Figures 45, 46, Table 29

*Referred Specimens.*—UM nos. 65024, 66707, 68863, 69280.

*Occurrence.*—*Plesiadapis cookei* Zone (SC-19, 116, 188); *Phenacodus-Ectocion* Zone (SC-203).

*Discussion.*—Four new specimens of the rare North American notoungulate *Arctostylops* have been found in Clarkforkian beds of the Clark's Fork Basin. They consist of a left dentary fragment with heavily worn ?$M_2$ and right dentary fragment with $P_3$ (UM 65024, Figure 45), a right dentary fragment with $M_1$ and the back of $M_2$ (UM 66707, Figure 46), a right $M_2$ (UM 68863), and a right $P_3$ (UM 69280). These teeth are morphologically identical to those in the holotype (AMNH 16830, see Matthew, 1915c) but are slightly larger (though probably not significantly so). Although these specimens do not preserve any teeth not known in the holotype (a left

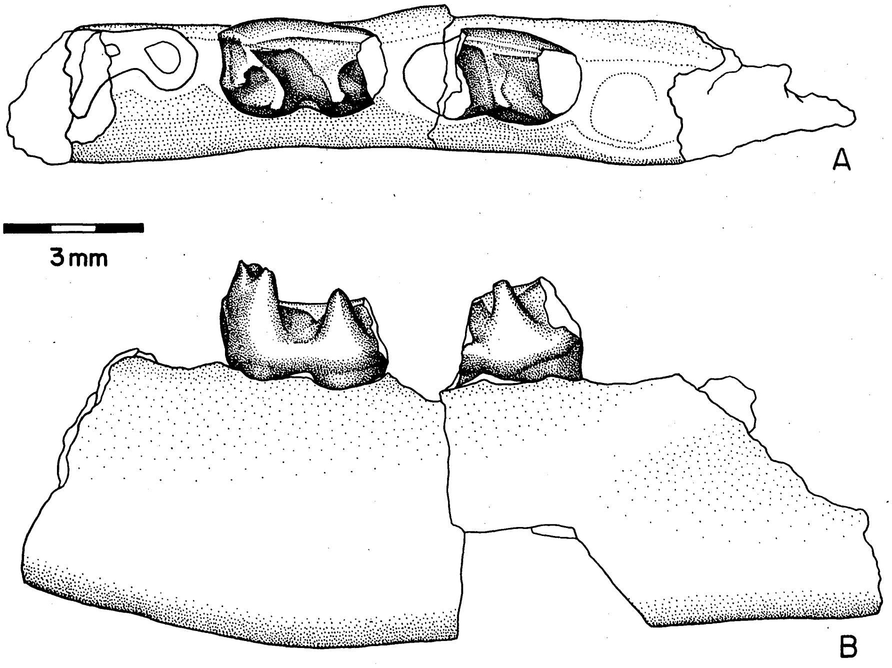

Figure 46. *Arctoctylops steini*, UM 66707, from SC–116: right dentary with $M_{1-2}$ (incomplete). A, crown and B, lingual views.

Table 29. Measurements of lower teeth of Clarkforkian *Arctostylops steini.*

| | UM 65024 | UM 66707 | UM 68863 | UM 69280 | AMNH 16830, Holotype |
|---|---|---|---|---|---|
| $P_3$L | 3.55 | | | 3.60 | 3.10 |
| $P_3$B | 2.05 | | | 1.70 | 1.65 |
| $P_4$L | | | | | 3.20 |
| $P_4$B | | | | | 1.75 |
| $M_1$L | 3.85 | 3.65a | | | 3.70 |
| $M_1$B | 2.25 | 2.25 | | | 2.20 |
| $M_2$L | | | 3.40 | | 3.30 |
| $M_2$B | | | 2.20 | | 2.20 |
| $M_3$L | | | | | 2.95 |
| $M_3$B | | | | | 1.85 |

dentary with $P_3$–$M_3$), they are important in further confirming the presence in North America of this peculiar form, previously known from only two specimens (the second specimen, from the late Tiffanian, was recorded by Jepsen and Woodburne, 1969).

Matthew (1915c) gave the provenance of the holotype of *A. steini* as "Lower Gray Bull beds, Clark Fork Basin." The specimen was collected in 1913 by William Stein, and his field notes indicate that it came from "the head of Big Sand Coulee (upper beds)." Most localities in this area are in the late Clarkforkian (*Phenacodus-Ectocion* Zone) and it is probable that, like the UM specimens of *Arctostylops*, the holotype is from the Clarkforkian (see additional discussion of the age of Stein's locality under *Probathyopsis*). *Arctostylops* is known also from the later Tiffanian on the west side of Polecat Bench, about 6 miles northeast of the Clarkforkian occurrences. A poorly preserved skull and jaws (PU 20397, Jepsen and Woodburne, 1969) was found near Princeton Quarry in 1966, and a very well preserved partial skull and jaws with nearly complete dentition (MCZ 20004) was discovered about 5 m from Princeton Quarry in 1977 (C. R. Schaff, personal communication, 1977).

The presence of the Notoungulata—often considered a basically South American group—in North America has sparked widespread interest. The origin and precise relationships of *Arctostylops* are matters of considerable importance and debate. In addition to the new North American specimens of *Arctostylops*, other evidence bearing on these problems has come to light recently. *Arctostylops* is most closely allied with Asian *Palaeostylops*, two species of which were described from the

Gashato fauna of Mongolia (Matthew and Granger, 1925; Matthew et al., 1929). *Palaeostylops* has more recently been reported from Naran Bulak (Gradzinski et al., 1969; Dashzeveg, *in litt.*, 1976) and Bumbin Nuru (Dashzeveg, 1968), both in the Nemegt Basin of Mongolia. Gingerich and Rose (1977) suggested that Gashato and Naran Bulak are at least in part correlative with the Clarkforkian of North America, an hypothesis adopted by Dashzeveg and McKenna (1977; see also Chapter V herein). *Arctostylops* is very similar in size and morphology to *Palaeostylops iturus* and somewhat less so to *P. macrodon.* The resemblances are so close that the two genera may prove to be congeneric.

In addition to the Mongolian forms, several new primitive notoungulates have been described recently from the early Tertiary of China (Chow et al., 1976; Tang and Yan, 1976; Zhai, 1978). Consideration of notoungulate origins must take into account these discoveries.

The notoungulates underwent their most successful and diverse radiation in South America, where several families were already in existence in the Riochican (Simpson, 1948, 1967; Paula Couto, 1970). The similarities of *Arctostylops* to many of the South American notoungulates are so numerous that its notoungulate affinities cannot be denied; nevertheless, it is not demonstrably allied with any one particular South American family. Compared to the Riochican and Casamayoran Henricosborniidae, perhaps the most primitive notoungulates, arctostylopids are more specialized in some features but possibly more primitive in others (Simpson, 1948). Matthew (1915c) allocated *Arctostylops* questionably to the Isotemnidae, and Patterson (1934) also mentioned resemblances to this family. Arctostylopids also display interesting similarities to some notostylopids (but these characters may be primitive), as well as to other South American families. Simpson (1948) united the arctostylopids with the Henricosborniidae and the Notostylopidae in the suborder Notioprogonia, which he defined (admittedly and intentionally) chiefly on primitive characters.

Considerable evidence now demonstrates that early notoungulates were quite widely distributed geographically. When more thoroughly analyzed, they may have important bearing on the origin of the order and on mammalian dispersal during the early Tertiary.

### Order CARNIVORA Bowdich, 1821
### Family Miacidae Cope, 1880
### Subfamily Viverravinae Matthew, 1909

A study of the subfamily Viverravinae (Gingerich, Schankler, and Winkler, in preparation) nearing completion will include emended diagnoses, descriptions, and measurements of the Clarkforkian species. For this reason, the Clarkforkian specimens will not be described in detail here, but brief accounts of each species are presented to record the Clarkforkian specimens and their occurrences.

A new genus of viverravine, *Pappictidops*, has recently been reported from the Paleocene of China (Chiu and Li, 1977; Wang, 1978). From published illustrations, it appears to be similar to both *Viverravus* and *Protictis* and provides further evidence of close affinity between the early Tertiary faunas of eastern Asia and western North America.

### *Didymictis* Cope, 1875
### *Didymictis protenus proteus* Simpson, 1937

Figure 48

*Referred Specimens.*—UM nos. 64708, 65013, 65057, 65084, 65101, 65129, 65241, 65245, 65247, 65256, 65654, 65656, 65658, 65665, 65667, 65671, 65777, 66157, 66171, 66194, 66209, 66318, 66504, 66543, 66712, 66715, 66764, 66915, 67017, 67446, 67450, 67452, 68205, 68216, 68227, 68248, 68249, 68865, 69177, 69225, 69316, 69317, 69325, 69869, 69874, 69885, 71181, 71433, 71438, 71453, 71458, 71460, 71585–71588, 71606, 71636, 71637, and miscellaneous teeth.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–19, 53, 58, 62, 66, 74, 84, 91, 109, 115, 116, 117, 118, 120, 127, 143, 188, 195, 197, 201, 205, 238); *Phenacodus-Ectocion* Zone (SC–8, 11, 21, 23, 24, 25, 29, 48, 50, 52, 57, 59, 72, 75, 80, 81, 90, 100, 149, 153, 154, 155, 158, 159, 163, 164, 175, 176, 184, 202, 203, 214, 230, 233, 234, 235).

*Discussion.*—*Didymictis* is very common and widespread in the Clarkforkian (indeed, much more so than in the early Wasatchian of the Clark's Fork Basin), exceeded in the number of sites at which it occurs by only *Ectocion osbornianus* and *Phenacodus primaevus.* Except for a few specimens from the early and early middle Clarkforkian, all Clarkforkian fossils of *Didymictis* are referable to *D. protenus proteus.* There is no obvious size trend in the middle and late Clarkforkian sample of *D. protenus proteus* (Figure 48). These specimens conform closely in size and structure to the holotype, AMNH 16071, from late Clarkforkian deposits in the head of Big Sand Coulee.

Simpson (1937c) distinguished *D. protenus proteus* from typical *D. protenus* (originally described from the Wasatchian of New Mexico) by the size of $M_2$, which is longer and slightly broader than in early Wasatchian *Didymictis.* In comparison with early Wasatchian *D. protenus* from the Clark's Fork Basin and the southeastern Bighorn Basin (Bown, 1979), this distinction appears to hold true. However, the size of $M_2$ displays considerable variation. Further study is necessary to assess whether the Clarkforkian sample is conspecific with the early Wasatchian sample or is better considered a distinct species; thus I have maintained Simpson's designation here.

The holotype of *D. protenus proteus* (AMNH 16071) was initially assigned (Matthew, 1915a) to *D. leptomylus* Cope (1880), which Matthew considered to be a subspecies of *D. protenus*. It is possible that *D. protenus proteus* is a junior synonym of *D. leptomylus*. Cope initially reported the type locality of *D. leptomylus* as the Wind River Basin, but it is more probable that it is the early Wasatchian of the Bighorn Basin, in the same area that yielded the holotypes of *Esthonyx spatularius* and *Haplomylus speirianus* (Gazin, 1953: 23; Matthew, 1915a: 20, 1915b: 314). As Simpson observed, *D. leptomylus* is smaller than most specimens of Clarkforkian *D. protenus proteus* and has narrower molars. In the absence of an adequate, stratigraphically-documented sample of *D. leptomylus*, its affinities remain ambiguous. None of the Clarkforkian specimens appear to be referable to this species in any case, hence the best available name for them at present is *Didymictis protenus proteus*.

### *Didymictis*, ?undescribed species

Figures 47, 48

*Referred Specimens.*—UM nos. 68428 (edentulous right dentary with alveoli for C–$M_1$), 68432 (left dentary with C, $P_1$, $P_3$–$M_1$, right dentary with $P_{3-4}$, associated right C, $M_{1-2}$, left $P^4$–$M^2$, right $M^1$, etc.), 69907 (left dentary with $P_{3-4}$, left $M_2$ trigonid, right dentary with $P_3$, $M_1$ talonid-$M_2$, right $M^1$), 71589 (left $M_1$, two fragmentary $M_1$s), 71792 (left $M_1$), 71802 (left $M_1$), and a damaged $M_1$ in UM 71313; questionably UM 66201 (left $M_1$).

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–156, 172, 173, 226, 248, 250; UM 66201 from SC–83); lower *Plesiadapis cookei* Zone (SC–136).

*Discussion.*—Several specimens of *Didymictis* from earlier Clarkforkian beds are decidedly smaller and have narrower $M_1$ and $M_2$ than those from higher stratigraphic levels, referred above to *D. protenus proteus* (Figure 48). They are very similar in most respects to an undescribed form from the late Tiffanian Princeton Quarry (e.g. PU 13937), differing from it in having a much larger, broader $M_2$, and slightly longer upper molars. In these features, the Clarkforkian specimens foreshadow *D. protenus proteus*. In UM 68428, the dentary is slender and shallow, and the configuration of the roots of the cheek teeth matches exactly that in PU 13937, thus indicating a shorter and smaller jaw than in *D. protenus proteus* and later forms. This is also evident in UM 68432 (Figure 47). These specimens are clearly very closely allied with the form from Princeton Quarry and may be the same species, however the contrast in proportions of $M_2$ may justify separation at the species level. At present, the late Tiffanian and Clarkforkian forms from the Clark's Fork Basin appear to belong to a single lineage.

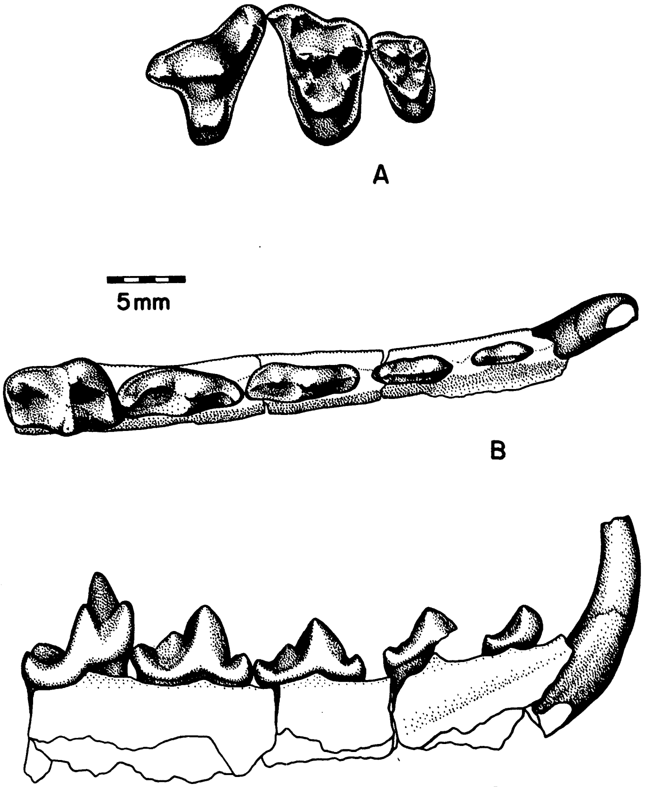

Figure 47. *Didymictis*, ?undescribed species, UM 68432, from SC–173: A, left $P^4$-$M^2$. B and C, left dentary with C–$P_{1-4}$-$M_1$, crown and lingual views.

The early Clarkforkian specimens of *Didymictis* also bear close resemblance to the holotype of *D. leptomylus* in both size and structure, but seem to differ by having a deeper hypoflexid on $M_1$ (i.e. the cristid obliqua meets the postvallid more lingually) than in *D. leptomylus*. The type of *D. leptomylus* is too incomplete to permit further comparison (it consists of only $M_{1-2}$). As discussed earlier, that specimen is probably of early Wasatchian age; hence it is unlikely that the early Clarkforkian specimens belong to *D. leptomylus*.

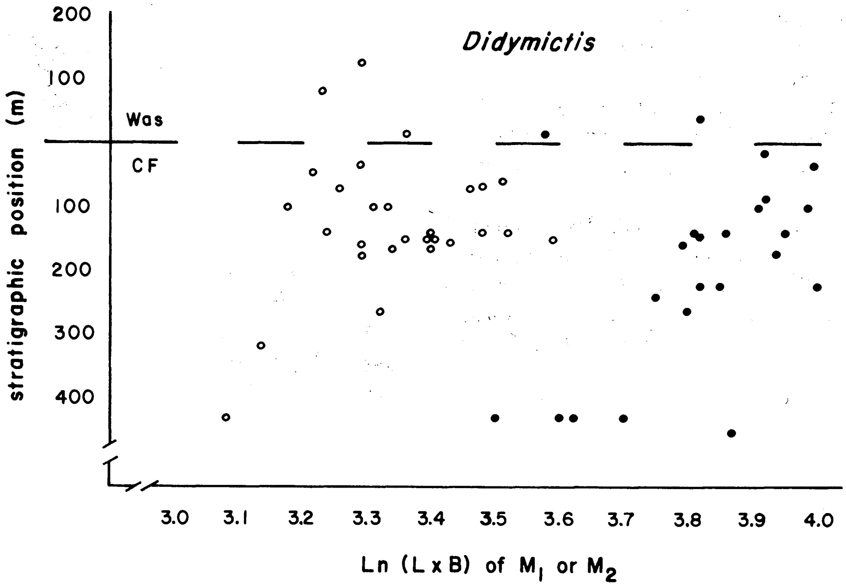

Figure 48. Stratigraphic plot of Clarkforkian and early Wasatchian *Didymictis* of the Clark's Fork Basin. Natural logarithm of crown area of $M_1$ (solid circles) and $M_2$ (open circles) is plotted against stratigraphic level with respect to the Clarkforkian-Wasatchian boundary sandstone. Early Clarkforkian *Didymictis* sp. (specimens at 300 m or more below the sandstone) are smaller than later Clarkforkian *D. protenus proteus*, which appears to show a gradual size increase through time. See text for further discussion.

Interpretation of the evolution of the genus *Didymictis* is no simple matter. As Simpson (1937c: 16) remarked, "the Clark Fork to Lost Cabin specimens do not form a single linear sequence." Bown (1979) found two size groups of *Didymictis* co-existing in early Wasatchian sediments of the southeastern Bighorn Basin, both of which he included in *D. protenus*. The smaller of them is about the size of the holotype of *D. leptomylus* and of early Wasatchian specimens of *Didymictis* from the Clark's Fork Basin; the larger one exceeds the size of any Clark's Fork Basin *Didymictis*. Size variability occurs in the Clarkforkian sample of *Didymictis*, but the smallest individuals are restricted to the lower part of the Clarkforkian section, and at any one time only one species appears to have been in existence.

### *Viverravus* Marsh, 1872

### *Viverravus acutus* Matthew, 1915

Figure 49

*Referred Specimens.*—UM nos. 69270, 69336, 69923, 71577, and a trigonid of $M_1$ in UM 66196.

*Occurrence.—Plesiadapis gingerichi* Zone (SC–215); *Plesiadapis cookei* Zone (SC–195, 197, 201); *Phenacodus-Ectocion* Zone (SC–81). Oldest record of the species.

*Discussion.*—Unlike *Didymictis*, *Viverravus acutus* is rare in the Clarkforkian but relatively common in the early Wasatchian of the Clark's Fork Basin. The holotype of *V. acutus* is from 3 miles southeast of the mouth of Pat O'Hara Creek (the same locality as the holotype of *Phenacolemur praecox*) and is therefore of earliest Wasatchian age (so-called "Sand Coulee" level). McKenna (1960) reported *V. acutus* from the early Wasatchian Four Mile fauna. The larger specimens in Bown's (1979) sample of *Viverravus* from the southeastern Bighorn Basin probably represent *V. acutus*, whereas the smaller ones may be referable to an undescribed new species.

Only one of the Clarkforkian specimens, UM 69336 (left dentary with $P_2$–$M_2$, Figure 49), is relatively complete, and it is indistinguishable in comparable parts from the holotype. The other Clarkforkian specimens allocated here appear to be closer to *V. acutus* than to any other species of the genus. UM 69923, a right dentary fragment with $M_2$ and the talonid of $M_1$, has slightly smaller and narrower teeth than the other specimens (including the type). It is the only specimen of a

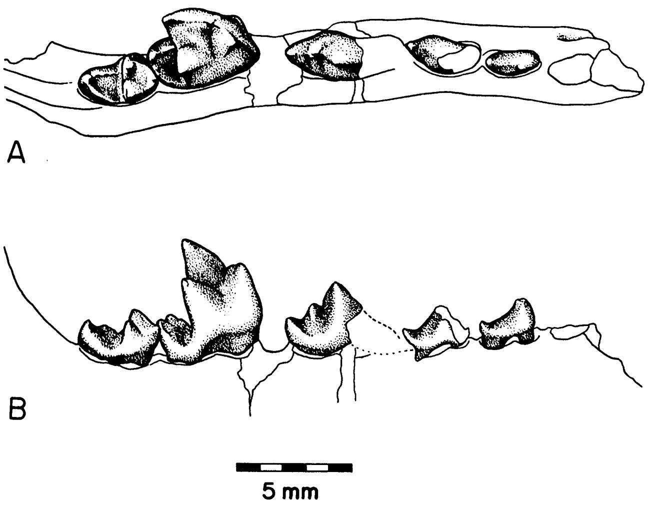

Figure 49. *Viverravus acutus*, UM 69336, from SC-195: left dentary with $P_{2-4}$-$M_{1-2}$ ($P_{3-4}$ incomplete). A, crown, and B, lingual views.

small *Viverravus* known from the early Clarkforkian and could be a small, early individual of *V. acutus*, or possibly a representative of the new species discussed next.

### *Viverravus*, undescribed new species

*Referred Specimens.*—UM nos. 64713, 71578, 71579, and labial part of $P^4$ in UM 71646.

*Occurrence.—Plesiadapis cookei* Zone (SC-188); *Phenacodus-Ectocion* Zone (SC-10).

*Discussion.*—Gingerich, Schankler, and Winkler (in preparation) have distinguished a second small early Wasatchian species of *Viverravus*, not yet described, that is slightly smaller than *V. acutus* and has a more open trigonid on $M_1$. It is contemporaneous and sympatric with *V. acutus*, and fragmentary specimens are very difficult to separate. However, there is evidence from other collections, as well, that samples previously referred to *V. acutus* may include two closely allied species (e.g., Gazin, 1962; Bown, 1979). The Clarkforkian specimens listed here are somewhat smaller than *V. acutus* and may represent this new species. All of them are very fragmentary: left dentary fragment with $M_1$ talonid and roots of $P_4$ (UM 64713), left $M_2$ (UM 71578), left $P_3$ and C (UM 71579), and incomplete $P^4$ (in UM 71646).

### *Viverravus politus* Matthew, 1915
Figure 50

*Referred Specimens.*—UM nos. 65088, 65118, 65125, 65127, 65653, 66618, 66853, 68748, 69884, 71580, 71581, and fragmentary teeth in UM nos. 65011 and 67467.

*Occurrence.—Plesiadapis gingerichi* Zone (SC-179), *Plesiadapis cookei* Zone (SC-19); *Phenacodus-Ectocion* Zone (SC-23, 24, 50, 52, 57, 70, 107, 155, 214).

*Discussion.— Viverravus politus* is relatively well represented in the Clarkforkian collection, although the majority of specimens come from the late Clarkforkian. The specimens from the lower two zones are the oldest records of this species to date. *V. politus* is markedly larger than *V. acutus* and the undescribed species just discussed, the only contemporaneous species of the genus. Its size is very close to that of the contemporaneous miacine *Uintacyon*, but the latter retains $M^3_3$, lost in the Viverravinae. *V. politus* further differs from *Uintacyon* in structure of $P_{3-4}$ and $M_{1-2}$, thus there is little danger of confusing the two. Both $P_3$ and $P_4$ are relatively longer and more trenchant than in *Uintacyon*, each possessing an anterior basal cusp and two cusps behind the high main cusp. $M_1$ has a very distinctive open trigonid, the angle formed by the paracristid and protocristid being larger than in miacines. Both $M_1$ and $M_2$ are comparatively elongate and have basined talonids, unlike the molars of *Uintacyon*. The talonids of *V. politus* are more broadly basined than in Wasatchian *Miacis* but less so than in *Vulpavus*. The hypoconid and the hypoconulid are clearly present, but the entoconid is indistinct.

Matthew's holotype of *V. politus* (AMNH 16113) was reported to be from "Sand Coulee beds in Clark Fork Basin." Granger's 1912 field notes indicate that it is from the "point of bluff north of Ralston, upper strata," i.e. the southern end of Polecat Bench. Without more precise data, it is not certain if the type comes from late Clarkforkian beds or basal Wasatchian beds, both of which outcrop at the southern end of Polecat Bench. However, Granger also collected *Hyracotherium* and *Pelycodus* (Wasatchian index fossils) at the same locality on the same day, strongly suggesting that the type is of earliest Wasatchian age. The UM collection contains additional early Wasatchian specimens of *V. politus*, and Bown (1979) reported the species from the early Wasatchian of the southern Bighorn Basin. *V. politus* has not been recorded from outside the Bighorn Basin.

Upper teeth of miacids of the size of *V. politus* have not been clearly distinguished by previous authors and are therefore very difficult to differentiate if not found in association with lower teeth. Among the Clarkforkian specimens are a number of isolated upper teeth that belong to either *V. politus* or *Uintacyon rudis*. They include UM nos. 71424 (SC-230), 71477 (SC-233), and

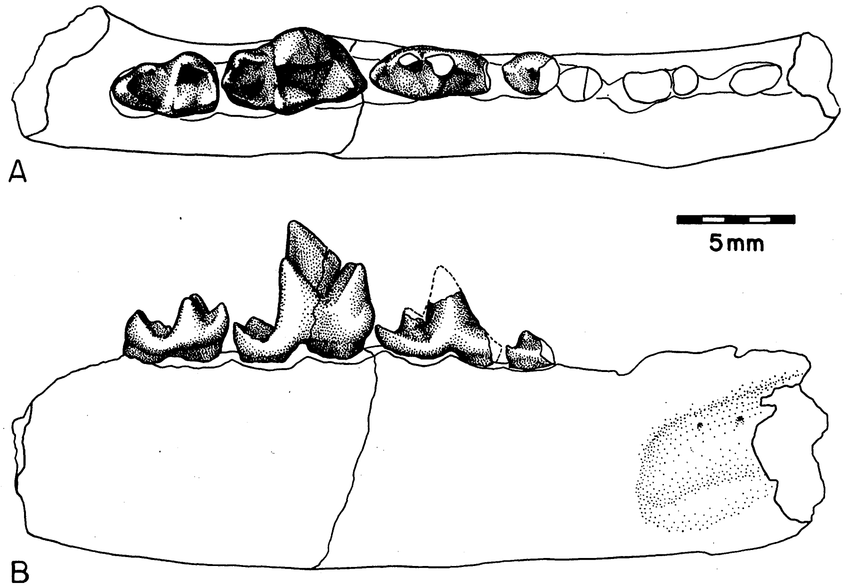

Figure 50. *Viverravus politus*, UM 65118, from SC–23: left dentary with $P_4$-$M_2$ and part of $P_3$. A, crown, and B, lingual views.

isolated teeth or tooth fragments in UM nos. 66196 (SC–81), 67455 (SC–153), 68250 (SC–164), 68522 (SC–175), 68786 (SC–184), and 69291 (SC–203).

*Viverravus politus* appears to have evolved directly from a slightly smaller form (as yet undescribed) that is fairly well represented in the late Tiffanian Princeton Quarry and Schaff Quarry local faunas (e.g. PU nos. 17848, 17849, 18318, 19365; see Table 42).

### Subfamily Miacinae (Cope, 1880)
### *Uintacyon* Leidy, 1871
### *Uintacyon rudis* Matthew, 1915

Figures 51, 52, Table 30

*Referred Specimens.*—UM nos. 65066, 65234, 65473, 66298, 66918, 68868, 69314, 69872, 69896, 71482, 71582, 71583, 71584, and isolated $M_1$ trigonids in UM nos. 66319, 68877.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–127, 188, 189, 201); *Phenacodus-Ectocion* Zone (SC–22, 28, 48, 57, 90, 150, 214, 233). Oldest record of the genus.

*Discussion.*—Several Clarkforkian specimens represent a small species of *Uintacyon*, *U. rudis*. Matthew (1915a) regarded *U. rudis* as a subspecies of *U. massetericus*, but its distinctions from the latter justify its elevation to species rank. *U. rudis* is smaller than *U. massetericus* but has a relatively larger $M_3$ and relatively narrower molar talonids. The talonids in *U. rudis* are slightly basined (particularly in $M_1$), whereas in Wasatchian *U. massetericus* they are somewhat trenchant and not at all basined. The Clarkforkian specimens have a weakly developed entocristid (bearing a small entoconid on $M_1$) that, together with the higher, trenchant cristid obliqua, encloses a shallow basin. In some specimens the trigonid of $M_1$ is slightly more compressed anteroposteriorly than in *U. massetericus*. All of these characters demonstrate, not surprisingly, that *U. rudis* is more primitive than *U. massetericus*. Matthew stated that *U. rudis* has a smaller $M_2$ with a higher trigonid and a smaller talonid than in *U. massetericus*; however, larger samples now available indicate that these features are variable: in fact, $M_2$ is often relatively larger in *U. rudis* than in *U. massetericus*.

$P_4$ of *U. rudis* bears a variably developed anterobasal cusp (well developed in UM 65234, weaker in UM 65066), also observed in specimens of *U. massetericus* from the southern Bighorn Basin (Bown, 1979). $P_3$ and $P_4$ are shorter and have a higher, more pointed main cusp than in the similar-sized, contemporaneous *Viverravus politus*. Bown reported differences in jaw depth in his sample of *Uintacyon*, which he interpreted as possible reflections of sexual dimorphism. The Clarkforkian sample includes only a few specimens that reveal

Table 30. Measurements of UM teeth of *Uintacyon rudis.*

| | UM 65066 | UM 65234 | UM 65473 | UM 66298 | UM 68868 | UM 69314 | UM 69872 | UM 71482 | UM 71582 | UM 71583 |
|---|---|---|---|---|---|---|---|---|---|---|
| LOWER DENTITION | | | | | | | | | | |
| $P_3L$ | 3.90 | | | | 4.15 | | | | | |
| $P_3B$ | 1.80 | | | | 1.90 | | | | | |
| $P_4L$ | 5.00 | 5.55 | | | | | | 4.75 | | |
| $P_4B$ | 2.40 | 2.65 | | | | | | 2.10 | | |
| $M_1L$ | 6.0a | 6.1a | 6.20 | | | 6.0a | | 5.75 | 5.50 | |
| $M_1B$ tri | | 4.25 | 4.40 | | 4.00 | | | 3.70 | 3.65 | |
| $M_1B$ tal | 3.05 | 3.00 | 3.25 | | | 3.00 | | 2.70 | 3.00 | |
| $M_2L$ | 4.10 | | 4.25 | | 4.40 | 4.30 | 4.40 | | | 4.90 |
| $M_2B$ tri | 3.10 | | 3.05 | | | 2.90 | 3.20 | | | 3.55 |
| $M_2B$ tal | 2.40 | | 2.40 | | | 2.25 | 2.2a | | | 3.00 |
| $M_3L$ | | | 2.85 | 3.0a | | | | | | |
| $M_3B$ tri | | | 2.10 | 2.50 | | | | | | |
| UPPER DENTITION | | | | | | | | | | |
| $P^4L$ | | | | | 6.95 | | | | | |
| $P^4B$ | | | | | 7.50* | | | | | |
| $M^1L$ | | | | 4.65 | 5.35 | | | | | |
| $M^1B$ | | | | 7.90 | 7.70 | | | | | |
| $M^2L$ | | | | | 3.05 | | | | | |
| $M^2B$ | | | | | 5.60 | | | | | |

*$P^4$ breadth measured as longest dimension of posterior border of tooth.

the depth of the dentary and they, too, suggest sexual dimorphism. Two specimens from the later Clarkforkian have robust and deep jaws (UM 69896, depth labially beneath $M_2$=10.0a; UM 65234, depth=12.1), whereas two others from the late Clarkforkian and one from the middle Clarkforkian have more slender, shallower jaws (UM 65066, depth=7.8; UM 65473, depth=8.65; UM 68868, depth=7.85). The cheek teeth in these specimens show no appreciable size difference.

Upper teeth of *U. rudis* have not previously been reported. UM 68868 (SC–188; Figure 51 A) and UM 66298 (SC–90) include upper teeth in association with lowers of *U. rudis.* UM 66918 consists of several incomplete upper teeth (right and left $P^4$, left $M^1$) closely resembling those of UM 68868. $M^1$ and $M^2$ of *U. rudis* are smaller and relatively shorter anteroposteriorly than in *U. masseterіcus.* The paracone is markedly larger than the metacone, and $M^1$ has a small hypocone shelf. The stylar shelf is broad and the parastylar region large, both of these to a greater degree on $M^1$ than $M^2$. The preparacrista of $M^1$ is separated from the paracone by a distinct notch, and the parastyle has a hooklike anteriorly-projecting process.

Two specimens from the late Clarkforkian (UM 71583 and UM 71584) are somewhat larger than others in the sample, and they approach *U. masseterіcus* in size.

Matthew (1915a) described a partial right dentary with $M_{1-2}$ (AMNH 16855) as the type of *U. masseterіcus rudis,* here elevated to species rank. He gave its locality as "Sand Coulee horizon in Clark Fork Basin." Like the holotypes of *Probathyopsis praecursor* and *Arctostylops steini,* AMNH 16855 was collected in 1913 by William Stein at the "head of Big Sand Coulee (upper beds)," and is almost certainly from late Clarkforkian exposures (see discussion under *Probathyopsis*). The type specimen of *U. masseterіcus* (AMNH 4250) is from the Wasatchian of the Bighorn Basin.

*Uintacyon* is closely related to Eocene *Miacis.* The primitive nature of *U. rudis* more closely approaches the morphology of *Miacis* than does *U. masseterіcus. U. rudis* is the oldest known miacine from North America. These facts strongly suggest that *Uintacyon* and *Miacis* shared a close common ancestor that was morphologically more like *Miacis* than like *U. masseterіcus.*

## Order CREODONTA Cope, 1875
## Family Oxyaenidae Cope, 1877

Oxyaenids are diverse and one of the dominant groups of carnivorous mammals in the Clarkforkian. Fossils of the Oxyaenidae first become prevalent in North America in beds of Clarkforkian age. That the family originated somewhat earlier is indicated by a few specimens representing different taxa from Tiffanian beds of the Bighorn Basin. Tooth fragments of a large oxyaenid (PU 17948), possibly *Dipsalodon,* are known from late Tiffanian strata southeast of Princeton Quarry (locality of PU 17948: sec. 27, T.57 N., R.100 W.), and a specimen of a

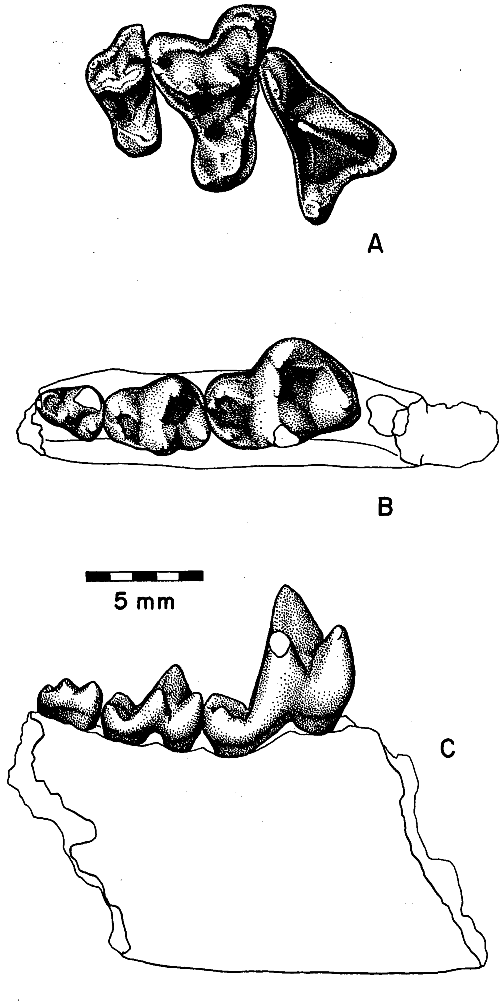

Figure 51. *Uintacyon rudis.* A, UM 68868, from SC–188: right maxilla with $P^4$-$M^2$ (specimen also includes dentaries). B and C, UM 65473, from SC–48: left dentary with $M_{1-3}$, crown and lingual views.

smaller species, cf. *Oxyaena transiens* (PU 18961) comes from north of Princeton Quarry in sec. 21, T.57 N., R.100 W. Van Valen (1966) reported a Tiffanian specimen of *Oxyaena* from beds above Mason Pocket, Ignacio, Colorado (this specimen is possibly Clarkforkian in age). Finally, a very small, primitive oxyaenid *Tytthaena parrisi* is present at the middle Tiffanian Cedar Point Quarry (Table 40); it is the oldest known member of the family.

A number of specimens in the UM Clarkforkian collection are too fragmentary for positive determination below the family or subfamily level. A few of particular interest are noted in the discussions below. Other specimens include UM nos. 66199 (SC–83), 66768 (SC–120), 66924 (SC–127), 68873 (SC–189), 69276 (SC–202), 69908 (SC–136), and fragments of teeth in UM miscellaneous numbers from SC–19, 62, 74, 93, 109, 117, 120, 189, 190, 194, 197 (all *Plesiadapis cookei* Zone) SC–25, 50, 70, 102, 138, 175, 214 (*Phenacodus-Ectocion* Zone). Most of these are probably referable to *Oxyaena.*

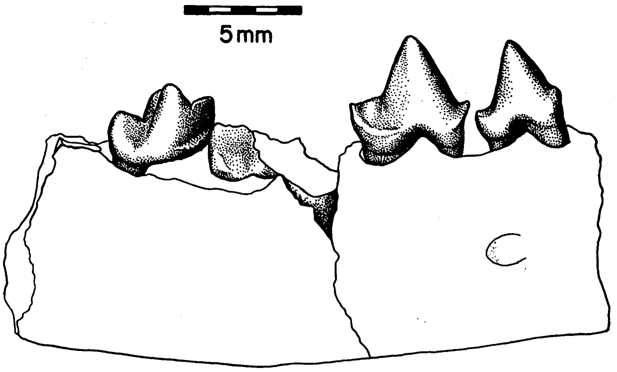

Figure 52. *Uintacyon rudis,* UM 65066, from SC–22: right dentary with $P_{3-4}$, $M_2$, and base of $M_1$, labial view.

### Subfamily Oxyaeninae (Cope, 1877)
### *Oxyaena* Cope, 1874
### *Oxyaena aequidens* Matthew, 1915

Figure 53, Table 31

*Referred Specimens.*—UM nos. 65038, 65039, 66700, 67024, 68869, 68871, 68879, 69326, 71465.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–19, 115, 120, 188, 189, 190, 205); lower *Phenacodus-Ectocion* Zone (SC–234).

*Discussion.*—Matthew (1915a) described several new species of the genus *Oxyaena,* but this is the only one he knew to be of Clarkforkian age. The holotype, AMNH 16070 (right $P_4$-$M_2$), came from Clarkforkian beds "between Little and Big Sand Coulees" (1912 field catalogue), but its precise location is unknown. *O. aequidens* is distinguished by relatively wide trigonids and relatively large talonids, subequal $M_1$ and $M_2$, and a robust $P_4$ (Matthew, 1915a). It is slightly larger and more robust than *O. transiens* ($M_{1-2}$ length=26.6 in *O. aequidens* [Denison, 1938]). Denison postulated that *O. aequidens* was the ancestor of Wasatchian *O. intermedia.*

The specimens here referred to *O. aequidens* compare closely in size and morphology with the holotype, particularly in being somewhat larger than *O. transiens* and having more robust premolars and broader molar trigonids. UM 67024, a right dentary with $P_{2-4}$ and the trigonid of $M_2$, also includes a heavily worn canine with a massive root. An exceptionally well preserved specimen, PU 19544 (left dentary with C–$M_2$, from SC–136), is somewhat more gracile but appears to be closest to *O. aequidens*. Its teeth are almost exactly the same length as in the holotype and UM 67024, but they are slightly narrower, the dentary is more slender, and the canine is less robust. These characteristics suggest that the specimen may be a female of *O. aequidens* (see also discussion under *Palaeonictis peloria*).

Specimens in this Clarkforkian sample include the first ones that show the morphology of the lower premolars anterior to $P_4$. These teeth are slightly longer and broader than in *O. transiens* but are otherwise similar to those in other species of *Oxyaena* (see illustrations in Matthew, 1915a, and Denison, 1938). $P_2$ and $P_3$ are two-rooted and have well developed heels, as in $P_4$, but they lack any trace of an anterior basal cusp. $P_1$ is a high-crowned unicuspid tooth with a single robust root.

Upper teeth probably referable to this species include UM nos. 65038 (incomplete right $M^1$), 68871 (maxillae with right $P^3$–$M^2$, Figure 53), and 71465 ($P^4$). UM 68871 is similar to upper teeth of *O. transiens* but is larger, thus resembling *O. aequidens*. $P^3$ has an internal root that supports a lingually-projecting lobe, but there is no lingual cusp. $P^4$ is incomplete but appears to be essentially identical to that of *O. transiens*. The molars are not substantially different from those of other species of the genus; the conules are well developed and there is a distinct internal cingulum continuous with the anterior and posterior cingula. AMNH 55499, incomplete $P^4$–$M^1$ from beds above Mason Pocket (later Tiffanian or Clarkforkian) near Tiffany, Colorado, may also represent this species (Van Valen, 1966).

*Oxyaena* is the most common and diverse genus of creodont during the Clarkforkian. *O. aequidens* is clearly a very primitive species of the genus. Most of the large specimens of *Oxyaena* from the Clarkforkian can be separated into two groups that correspond to Matthew's species *O. aequidens* and the slightly smaller, more gracile *O. transiens*. The differences between these species are relatively minor, however, and specimens that appear to be intermediate between them are known (e.g. PU 19544; see also Bown, 1979). The possibility cannot be excluded that the two are synonymous (e.g. sexual dimorphism should be considered), but better samples will be needed to investigate this.

Measurements of the upper teeth of *O. aequidens* (UM 68871) are: $P^3L=10.20$, $P^3B=8.00$; $P^4L=13.80$, $P^4B=13.90$; $M^1L=13.65$, $M^1B=15.85$; $M^2L=7.20$, $M^2B=14.25$ (breadths are the maximum dimension from the midpoint of the buccal border to the base of the protocone). Measurements of lower teeth are presented in Table 31.

### *Oxyaena transiens* Matthew, 1915

Figures 54, 55, Table 32

*Referred Specimens.*—UM nos. 66180, 69331, 69549, 71679, 71775, and a molar talonid in UM 66148; tentatively UM nos. 65123, 66309, 71680.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–171); *Plesiadapis cookei* Zone (SC–62, 74, 195); *Phenacodus-Ectocion* Zone (SC–70, 72; tentatively referred specimens from SC–23, 50, 90).

*Discussion.*—These specimens compare closely with the holotype of *O. transiens*, AMNH 16118, from the early Wasatchian ("Sand Coulee level") three miles southeast of the mouth of Pat O'Hara Creek (1912 field catalogue). Unfortunately, the type is not well preserved (the crowns of most of the teeth being damaged), making detailed comparisons difficult. This problem is compounded by the close similarity to the slightly larger *O. aequidens* and to the slightly smaller *Dipsalidictides amplus*, resemblances that will be further discussed below.

*O. transiens* has been characterized as a small oxyaenid (length $M_{1-2}=22.5$), slightly smaller than *O. aequidens* and with $M_1$ smaller than $M_2$ and the premolars more slender than in *O. aequidens* (Matthew, 1915a; Denison, 1938). By these features it is possible to distinguish the specimens listed above from *O. aequidens*. In UM 66180 (left dentary with $P_2$, incomplete $P_3$, $P_4$–$M_2$, and associated left lower canine), $P_3$ is slightly shorter than in the holotype of *O. transiens*, but in other ways the specimen agrees perfectly with the type. UM 69331, from the middle Clarkforkian quarry at SC–195, is one of the most complete known specimens of an early species of *Oxyaena*. It includes a nearly complete skull with most of the upper dentition (Figure 54) and both lower jaws with left $P_1$–$M_2$ (Figure 55) and right $P_2$–$M_2$. Detailed description of this specimen must be deferred until preparation is completed, but some features may be discussed here. The lower dentition is essentially identical to that in the holotype of *O. transiens*, except that the molars in UM 69331 are very slightly longer. The premolars are morphologically like those of *O. aequidens* described above, except that the anterior basal cusp of $P_4$ is weak (e.g. UM 66180) or absent (e.g. UM 69331). The lower molars (particularly the talonid) are narrower than in *O. aequidens*. In comparison to PU 19544 (tentatively allocated to *O. aequidens*), the teeth in UM 69331 are slightly shorter but not appreciably narrower. The upper teeth in UM nos. 69331 and 71679 are

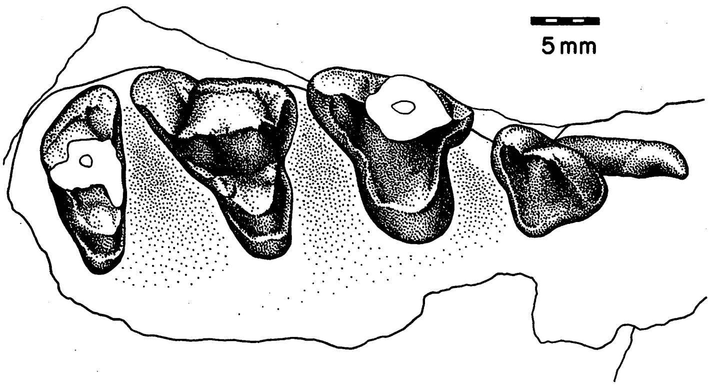

Figure 53. *Oxyaena aequidens*, UM 68871, from SC–189: right maxilla with $P^3$-$M^2$.

Table 31. Measurements of lower teeth of Clarkforkian *Oxyaena aequidens*.

| | AMNH 16070, Holotype, *O. aequidens* | UM 65039 | UM 67024 | UM 68869 | UM 68879 | UM 69326 | PU 19544 |
|---|---|---|---|---|---|---|---|
| C a-p* | | | 13.85 | 11.75 | | | 11.25 |
| C m-d* | | | 9.75 | 8.75 | | | 8.30 |
| $P_1L$ | | | | | | | 3.65 |
| $P_1B$ | | | | | | | 3.75 |
| $P_2L$ | | | 6.25a | | | | 6.50 |
| $P_2B$ | | | 5.20 | | | | 4.85 |
| $P_3L$ | | | 9.60 | 8.25 | 8.25 | | 8.15 |
| $P_3B$ | | | 6.40 | 6.00 | 6.15 | | 6.00 |
| $P_4L$ | 11.90 | 12.45 | 12.90 | 12.35 | | 13.00 | 11.95a |
| $P_4B$ | 7.80 | 8.05 | 8.50 | 7.60 | | 8.60 | 6.95 |
| $M_1L$ | 12.85 | | | | | | 12.10a |
| $M_1B$ tri | 7.55 | 7.20 | | | | | 7.40 |
| $M_1B$ tal | 5.95 | | | | | | 6.55 |
| $M_2L$ | 13.55 | 14.25 | | 13.85 | 13.70 | | 12.50a |
| $M_2B$ tri | 8.40 | 7.70 | 8.65 | 7.95 | 8.35 | | 8.50 |
| $M_2B$ tal | 5.95 | 5.75 | | 5.60 | 5.85 | | 5.75 |

*Canine measurements are anteroposterior diameter (a-p) and mesiodistal diameter (m-d), both measured at base of crown.

comparable to those in the holotype of *O. transiens*. They are smaller than in *O. aequidens* and longer but less transverse than in *Dipsalidictides amplus*.

When described by Matthew (1915a), *O. transiens* was known only from the early Wasatchian ("Sand Coulee beds") and *O. aequidens* only from the Clarkforkian. Specimens fitting his descriptions of both species are now known from the same intervals in the Clarkforkian and, as I have noted above, it is not definite that two different taxa are represented. Matthew (1930) himself believed it unlikely that two closely related species of the same genus would live "together at the same time, within the same area, and with the same habitat" (a variation of what has been called Cabrera's Law, see Simpson, 1937a: 64). In view of the variability now apparent among the larger specimens of *Oxyaena* from the Clarkforkian, and the existence of specimens that appear to be intermediate between *O. aequidens* and *O. transiens*, it is reasonable to ask whether Matthew would have recognized two different species had both then been known from the same level.

The specimens assigned here to *O. transiens* also bear close resemblance to early Wasatchian *Dipsalidictides amplus* (Jepsen, 1930a). The two species are almost exactly the same size (Table 32). $P_1$ in *D. amplus* is two-rooted (Van Valen, 1966), and $P_3$ in *O. transiens* is

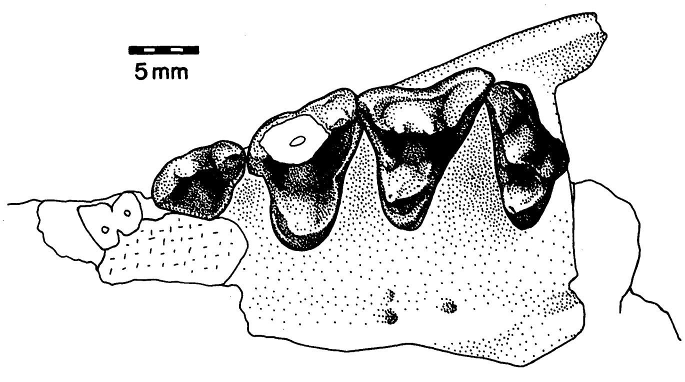

Figure 54. *Oxyaena transiens*, UM 69331, from SC–195: left maxilla with $P^3$-$M^2$; same individual as in Figure 55.

slightly larger than in the type (and only known specimen) of *D. amplus*, PU 13153. Minor differences in the upper teeth were noted above (see also Denison, 1938). Whether these differences merit generic distinction for *D. amplus* seems unlikely, and the specific separation of *D. amplus* and *O. transiens* may also be questioned. Previous authors have (apparently universally) recognized *D. amplus* as a valid genus and species (Denison, 1938; Simpson, 1945; Van Valen, 1966; Bown, 1979), however. The two specimens of upper teeth discussed above differ from the type of *D. amplus* and resemble the type of *O. transiens*, but it is unclear whether the minor differences observed could be attributed to intraspecific variation. Lower dentitions, even when nearly complete, are almost impossible to separate; but this may be more a consequence of the incomplete nature of the two holotypes than of a lack of specific differences. UM 66309, a right dentary with $M_1$ and erupting $P_4$, differs from other specimens referred here to *O. transiens* in having a shorter $M_1$ with a more closed trigonid. Perhaps it represents *D. amplus*, but the crown of $M_1$ is not preserved in the type of that species. Pending revision of the Oxyaenidae, I tentatively maintain both species but consider only *O. transiens* to be present in the Clarkforkian.

### *Oxyaena platypus* (Matthew, 1915)

Figure 56

*Referred Specimen.*—UM 71678.

*Occurrence.*—*Phenacodus-Ectocion* Zone (SC–214).

*Discussion.*—UM 71678 is a fragmentary left $M_1$ or $M_2$ from a small oxyaenid of the size of *O. platypus*. Although it does not add to our knowledge of the morphology of the species, it is important as a late Clarkforkian record. The precise provenance of the holotype (AMNH 15857) is unknown. It is recorded from "Clark Fork beds, 3 miles north of Ralston, Big Horn Basin" (Matthew, 1915a), and Granger's field notes (1911) add the designation "blue beds," which he seems to have used only for Clarkforkian localities. The locality is surely in exposures along the southern end of Polecat Bench, but it could be in either the middle (*Plesiadapis cookei* Zone) or late (*Phenacodus-Ectocion* Zone) Clarkforkian. Similar specimens of *O. platypus* have been found in beds of earliest Wasatchian age at the southern tip of Polecat Bench (see below), hence the possibility cannot be excluded that the holotype is from the earliest Wasatchian, not the Clarkforkian. Van Valen (1966) referred a $P_4$ and associated molar trigonids (AMNH 18667) to *O. platypus*, but he observed that its size ($P_4L=10.7$) more nearly conforms to that of *O. transiens*. I believe the specimen is better referred to the latter species.

In addition to the type and UM 71678, a third Clarkforkian specimen of *O. platypus* is known. PU 21215, including both lower jaws with most of the teeth (Figure 56) and a left maxilla with $P^4$ and parts of $M^1$ and $M^2$, is from section 14, T.56 N., R.101 W. (*Plesiadapis cookei* Zone, the same locality as the holotype of *Dipsalodon matthewi*). The specimen is virtually identical to the holotype of *O. platypus*, thus affirming the existence of this small oxyaenid in the middle Clarkforkian. All of the lower teeth from the canine through $M_2$ are present on one side or the other. $P_1$ is single-rooted and the other premolars are two-rooted. $P_4$ has a minute anterior basal cuspule, relatively smaller than that in *O. aequidens* and about as expressed in *O. transiens* (UM 66180). There is no anterior basal cusp on $P_2$ or $P_3$. In other regards, the premolars are similar in structure to those in other

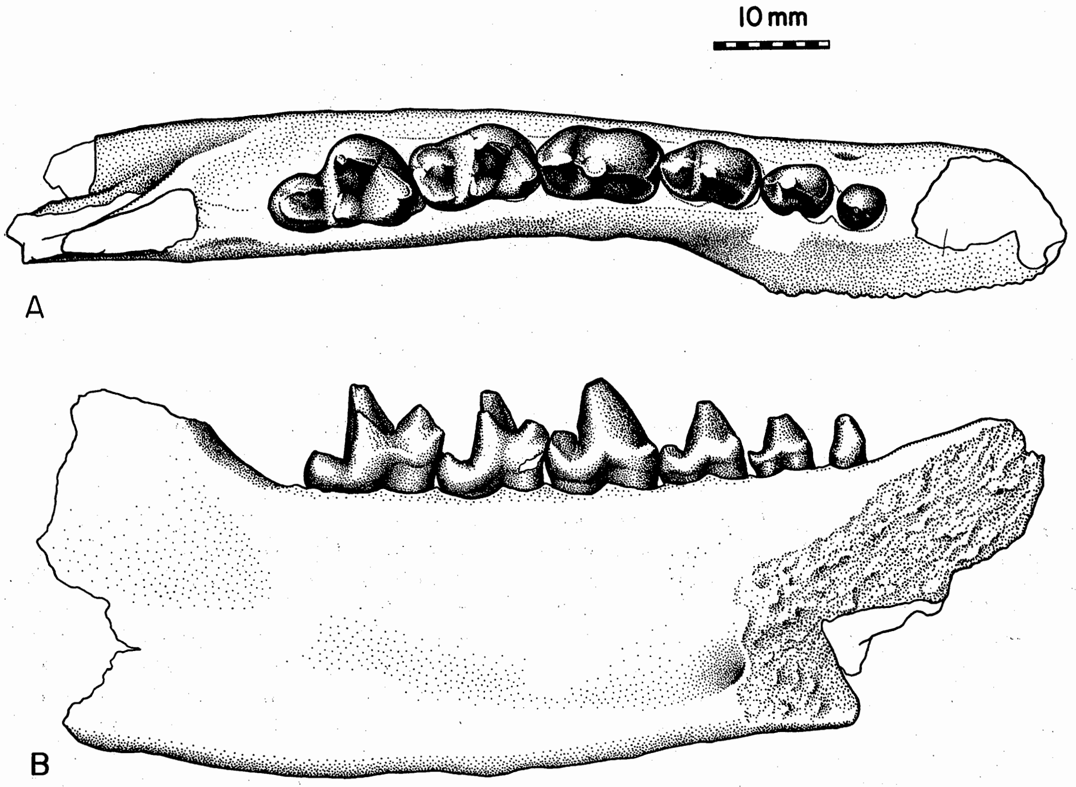

Figure 55. *Oxyaena transiens*, UM 69331, from SC–195: left dentary with $P_{1-4}$-$M_{1-2}$, crown and lingual views. Specimen also includes right dentary and partial skull.

Table 32. Measurements of *Oxyaena transiens* and *Dipsalidictides amplus*.

| | AMNH 16118, Holotype, *O. transiens* | UM 66180, *O. transiens* | UM 69331 (left) *O. transiens* | PU 13153 Holotype, *D. amplus* | UM 66309, ?*O. transiens* |
|---|---|---|---|---|---|
| $P_1L$ | | | 3.90 | | |
| $P_1B$ | | | 3.60 | | |
| $P_2L$ | | 6.05 | 5.60 | | |
| $P_2B$ | | 3.90 | 4.20 | | |
| $P_3L$ | 8.40 | 7.25a | 7.60 | 6.85 | |
| $P_3B$ | 4.90 | 4.60 | 5.40 | 4.00 | |
| $P_4L$ | 10.80 | 10.35 | 9.70 | 10.30 | |
| $P_4B$ | 6.30 | 6.25 | 6.50 | 5.60 | |
| $M_1L$ | 10.70 | 11.40 | 10.90 | 9.60a | 10.15 |
| $M_1B$ tri | 6.55 | 6.10 | 6.45 | | 6.10 |
| $M_1B$ tal | 5.75 | 5.30 | 6.20 | | 5.85 |
| $M_2L$ | 11.75 | 12.75 | 12.70 | 11.50 | |
| $M_2B$ tri | 7.25 | 7.25 | 7.25 | 7.15 | |
| $M_2B$ tal | 5.05 | 5.20 | 4.85 | 4.95 | |

Dimensions of teeth in holotypes of *O. transiens* and *D. amplus* were measured from epoxy casts.

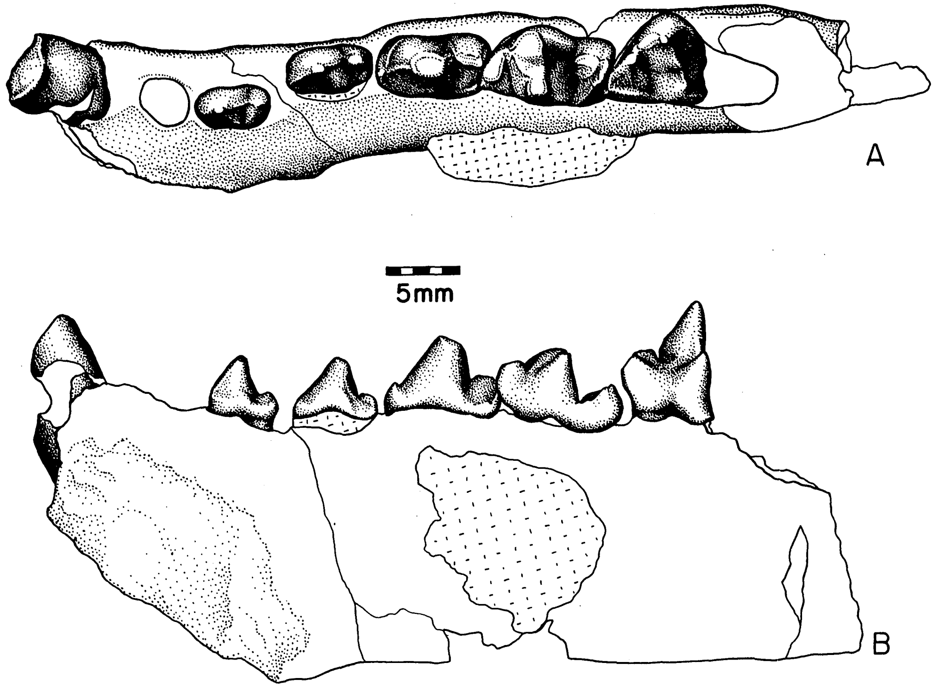

Figure 56. *Oxyaena platypus*, PU 21215, from sec. 14, T.56 N., R.101 W., Park County: right dentary with C, $P_{2-4}$-$M_1$ and $M_2$ trigonid. A, crown, and B, lingual views. Specimen also includes left dentary.

Clarkforkian species of *Oxyaena*. $M_1$ is slightly smaller than $M_2$.

As aforementioned, *O. platypus* is known also from the basal Wasatchian (SC–67), within a few meters of the Clarkforkian-Wasatchian boundary at the southern tip of Polecat Bench. UM 66137 includes a right dentary with $M_{1-2}$ and a right maxilla with $M^{1-2}$ which are closely comparable to the holotype and other specimens described above.

Matthew (1915a) allocated this species to his genus *Dipsalidictis*, but subsequent authors transferred it to *Oxyaena* (Denison, 1938; Van Valen, 1966). Denison regarded *O. platypus* as the ancestor of *O. transiens*, which remains a plausible view based on morphology. Both are now known from middle and upper Clarkforkian beds, and *O. transiens* appears to be present also in the early Clarkforkian and possibly the late Tiffanian (see above)—i.e., earlier than *O. platypus*. Thus it appears more likely that they represent two parallel lineages.

Measurements of PU 21215 are: C–$M_2$L=52.7; $M_{1-2}$L=19.0a; C buccolingual diameter=6.3, mesiodistal diameter=4.9; $P_1$L=2.5, $P_1$B=3.1; $P_2$L=5.0, $P_2$B=2.7; $P_3$L=5.6, $P_3$B=3.7; $P_4$L=8.0, $P_4$B=4.3; $M_1$L=8.5, $M_1$B trigonid=5.3, $M_1$B talonid=4.3; $M_2$L=10.0a, $M_2$B trigonid=5.8, $M_2$ talonids not preserved. (See Matthew, 1915a: 66–67, for measurements of the holotype of *O. platypus*.)

### *Oxyaena*? *lichna*, sp. nov.

Figures 57, 58

*Holotype.*—UM 71170, left dentary with $P_4$ and roots of $P_{2-3}$, and asssociated $M_1$ and talonid of $M_2$, collected by David W. Krause at SC–74 (*Plesiadapis cookei* Zone).

*Hypodigm.*—Holotype and UM 71803; possibly UM 71681.

*Horizon and Locality.*—Uppermost Polecat Bench Formation (near Polecat Bench-Willwood contact), middle Clarkforkian (lower *Plesiadapis cookei* Zone), SC–74; UM 71803 from SC–250 (*Plesiadapis gingerichi* Zone); UM 71681 from SC–127 (*Plesiadapis cookei* Zone).

*Etymology.*—Greek *lichnos*, translated either as greedy or dainty, in allusion to the small size and the inferred carnivorous habits of this diminutive oxyaenid.

*Diagnosis.*—Very small oxyaenid, smallest species of

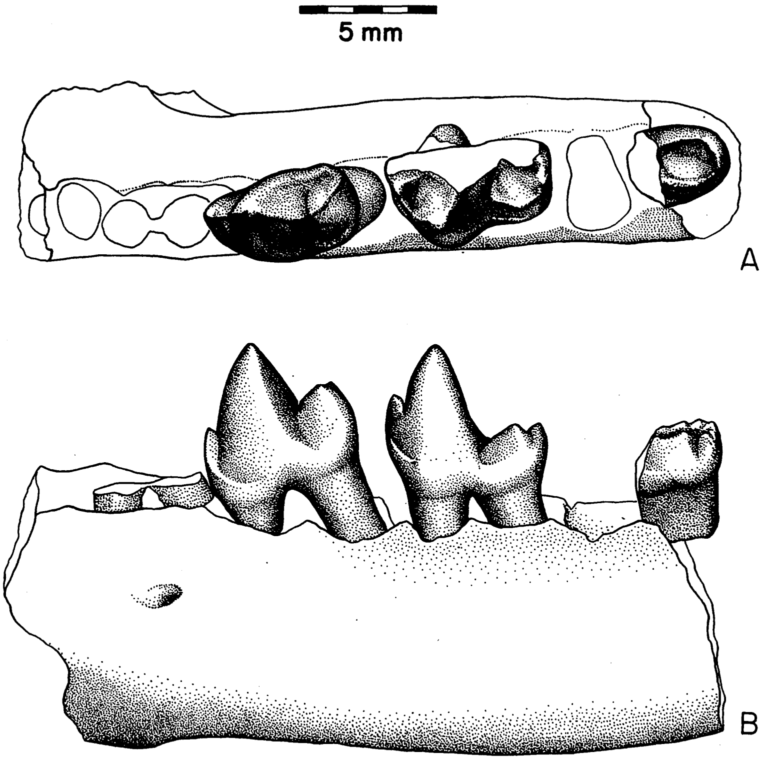

Figure 57. *Oxyaena*? *lichna*, sp. nov., Holotype, UM 71170, from SC–74: right dentary with $P_4$ and associated $M_1$ and talonid of $M_2$ (shown here replaced in dentary). A, crown, and B, labial views.

*Oxyaena*, about two-thirds the size of *O. platypus*. $P_4$ shorter than molars, with small but distinct anterior basal cusp and large, trenchant talonid; talonid with internal cingulum extending to base of protoconid. Molars relatively narrow, with elongate, basined talonids. Three talonid cusps distinct on $M_1$; hypoconid and postcristid distinct on $M_2$ but hypoconulid and entoconid poorly defined. Dentary relatively shallow and slender.

*Description.*—Only $P_4$–$M_2$ are known in *O.*? *lichna*, but their morphology shows clear affinity with the Oxyaenidae, and the size indicates a form quite distinct from any previously described.

$P_4$ in the holotype (Figure 57) is partly dislodged from its alveolus. It is a trenchant tooth, closer in structure to that of *Oxyaena* than of any other oxyaenid. It is noticeably shorter than the molars and bears a small, acute anterior basal cusp. The prominent talonid has two minute, twinned cusps. An arcuate crest (internal cingulum) runs from the back of the trigonid to the base of the protoconid.

$M_1$ and $M_2$ are incomplete in the type and, although found in association with the jaw and certainly belonging with it, have no precise contacts to the dentary. The lingual side of $M_1$ is damaged, but it is clear that the metaconid was of approximately the same size as the paraconid. The talonid of $M_1$ bears three distinct cusps, and the hypoconid and hypoconulid are separated by a shallow notch; the hypoconulid and the entoconid appear to be more closely appressed. Only the talonid of $M_2$ is preserved in the type. It is narrow and slightly longer than that of $M_1$, and its hypoconulid and entoconid are less well defined than on $M_1$. The hypoconid and the postcristid are distinct.

The dentary is shallow relative to that of other oxyaenids. A single mental foramen is situated below $P_3$.

UM 71803 is a right lower molar in which the paraconid and metaconid are subequal in size, as would be expected in $M_1$. Its trigonid is much broader than its talonid, and the posterior root is long and laterally compressed, as in $M_2$ of other oxyaenids. The tooth is here tentatively identified as $M_2$ (Figure 58). UM 71803 is

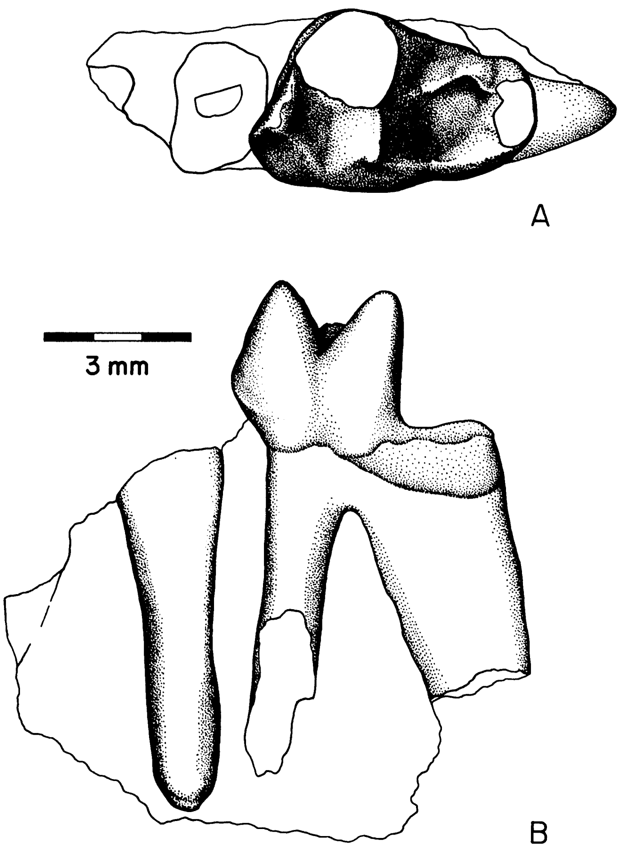

Figure 58. *Oxyaena*? *lichna*, sp. nov., UM 71803, from SC-250: right dentary with ?$M_2$, crown and lingual views.

distinctive in having an ectocingulum, faint on the talonid, but sharply expressed at the hypoflexid and continuing forward to join an anterior cingulum.

UM 71681 consists of fragments of dentaries with the talonid of left $M_2$. It is too incomplete for positive determination but is the right size for *O.*? *lichna* and resembles the other two specimens, as far as they can be compared. Alternatively, it may belong to *Palaeosinopa*.

*Discussion.*—Although rare and fragmentary, these specimens clearly represent an oxyaenid smaller than any other one known from the Clarkforkian or later. The only other oxyaenid of comparable size is *Tytthaena parrisi* (Gingerich, 1980a) from the middle Tiffanian Cedar Point Quarry (Table 40). Among known oxyaenids, *O.*? *lichna* most closely resembles the species of *Oxyaena*, but its small size and rather trenchant $P_4$ suggest that it may warrant separate generic status. In the absence of more complete specimens, I here assign it tentatively to the genus *Oxyaena*. Its precise relationships to other species of the genus are unclear, and a proper assessment must await more complete material.

UM 66644 (left $P_4$ and associated fragments from SC-110, *Plesiadapis cookei* Zone) resembles the holotype of *O.*? *lichna* but is larger; it may represent a closely related species.

Measurements of *O.*? *lichna* are: UM 71170, holotype: $P_4L=5.55$, $P_4B=3.15$; $M_1L=6.00$ ($M_1B$ cannot be accurately measured); $M_2B$ talonid=2.70. UM 71803, ?$M_2L=6.10$, B trigonid=3.70, B talonid=2.75.

### Subfamily Palaeonictinae Denison, 1938
### *Dipsalodon* Jepsen, 1930
### *Dipsalodon matthewi* Jepsen, 1930

*Referred Specimen.*—UM 66167.

*Occurrence.*—*Plesiadapis cookei* Zone (SC-74).

*Discussion.*—Only one specimen in the new Clarkforkian collections appears to represent *Dipsalodon matthewi*. UM 66167 consists of a few small fragments of the skull, part of the right dentary with $M_2$ and roots of $M_1$, $P_2$ and $P_3$, and associated $P_4$ and canine fragments. It conforms well in size with the holotype of *D. matthewi* (PU 13152), the roots of $M_1$ in UM 66167 indicating a slightly larger tooth than $M_2$, and the premolars being relatively large. The incomplete $P_4$ bears a small entoconid, as in the holotype, but it is a more slender tooth than in the latter. PU 21225, left $P_{3-4}$ from SC-143, appears to represent *D. matthewi*, but these teeth, too, are narrower than in the type. Other Princeton specimens probably referable to *D. matthewi* are PU nos. 13311 (right $P_4$, from vicinity of SC-209, probably lower *Plesiadapis cookei* Zone), 14995 (right dentary with $P_1$-$M_1$, from sec. 34, T.53 N., R.94 W., Bighorn Basin, zone uncertain), and 19890 (right $P_3$ and associated fragments, SC-143, *Plesiadapis cookei* Zone). Two other UM specimens are possibly *D. matthewi* but are too incomplete for positive identification: UM nos. 69671 (SC-108, *Plesiadapis cookei* Zone) and 71189 (SC-223, late Tiffanian, south side of Polecat Bench).

The holotype of *D. matthewi* consists of both lower jaws with nearly complete right dentition, and it remains the most complete specimen of this rare species. It is from sec. 14, T.56 N., R.101 W., in the *Plesiadapis cookei* Zone. The specimen was described and illustrated by Jepsen (1930b).

### *Dipsalodon churchillorum*, sp. nov.

Figure 59, Table 33

*Holotype.*—PU 17846, left $P_4$-$M_2$, fragmentary left $P_3$, right $P_3$ and canine, left $P^4$, associated jaw fragments,

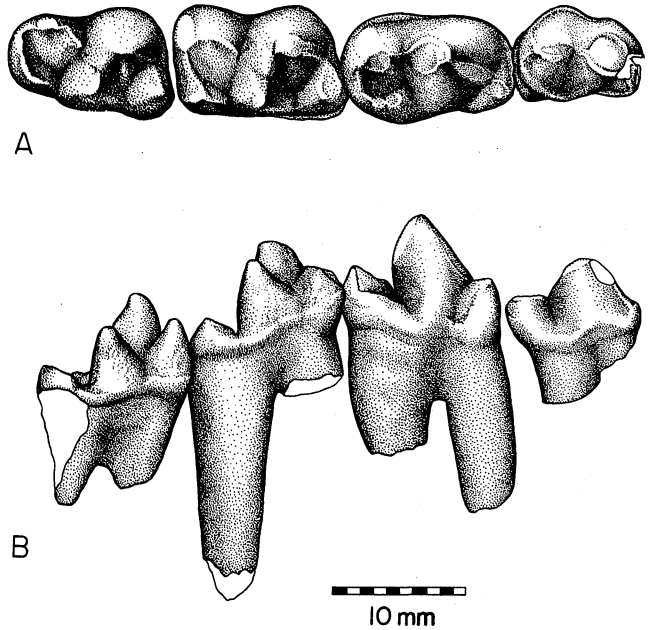

Figure 59. *Dipsalodon churchillorum*, sp. nov., Holotype, PU 17846, from Storm Locality, sec. 21, T.57 N., R.100 W., Park County (late Tiffanian): left $P_{3-4}$-$M_{1-2}$. A, crown, and B, lingual views. Specimen also includes canine and left $P^4$.

Table 33. Measurements of lower teeth of *Dipsalodon churchillorum*, sp. nov., and *Dipsalodon matthewi* Jepsen

| | PU 17846, type, *D. churchillorum* | AMNH 56137, *D. churchillorum* | PU 13152, type, *D. matthewi* |
|---|---|---|---|
| $P_3L$ | 10.00a | 10.00 | 14.85 |
| $P_3B$ tal | 6.95 | 5.90 | 7.80 |
| $P_4L$ | 11.40 | | 15.20 |
| $P_4B$ tal | 7.75 | | 10.10 |
| $M_1L$ | 12.30 | 12.95 | 14.20 |
| $M_1B$ tri | 7.85 | 7.70 | 9.55 |
| $M_1B$ tal | 7.55 | 7.10 | 8.85 |
| $M_2L$ | 12.00 | 11.80 | 13.40 |
| $M_2B$ tri | 7.50 | 7.50 | 9.80 |
| $M_2B$ tal | 5.80 | 6.20 | 7.15 |

and doubtfully associated right $M_2$, collected by F. Goto, from the late Tiffanian Storm Locality.

*Hypodigm.*—Holotype and AMNH 56137, left $P_3$-$M_2$, and possibly AMNH 86865, left $P_3$.

*Horizon and Locality.*—Polecat Bench Formation, "Silver Coulee beds," late Tiffanian, Storm Locality, sec. 21, T.57 N., R. 100 W., Park County, Wyoming. (AMNH 56137 from Lower Red Creek, Purdy Basin, Teton County, Wyoming; Clarkforkian, *Plesiadapis cookei* Zone.)

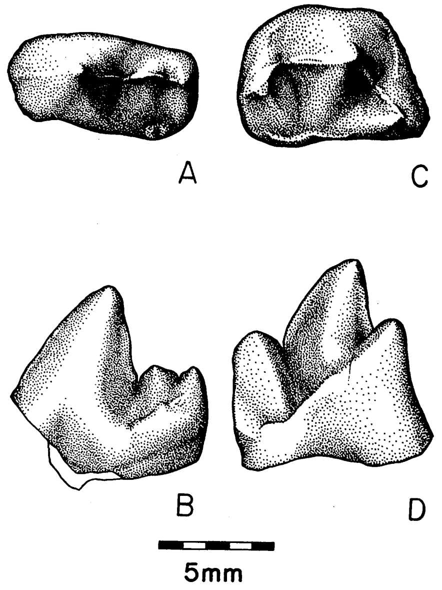

Figure 60. Cf. *Dipsalodon* sp., ?undescribed species, UM 71172, from SC–74: A, right $P_3$ or $P_4$ in crown view; B, same in lingual view. C, right $M_1$ trigonid in crown view; D, same in lingual view.

*Etymology.*—In honor of the Churchill family of Powell, Wyoming; in appreciation for their many years of generous help to paleontologists from Princeton, the University of Michigan, Yale, and many other institutions.

*Diagnosis.*—About 20% smaller than *D. matthewi.* Premolars relatively much shorter than in *D. matthewi.*

*Description.*—*Dipsalodon churchillorum* is similar morphologically to *D. matthewi*, differing mainly in its smaller size and its relatively shorter $P_3$ and $P_4$. $P_3$–$M_2$ are both shorter and narrower than in *D. matthewi.*

$P_3$ bears a low, faint lingual crest on the talonid. There is no lingual cuspule as is present in *D. matthewi.* A lingual cuspule (?entoconid) is present on the talonid of $P_4$, but it is situated somewhat anterior to the posterior border of the tooth, in contrast to its more posterior orientation in *D. matthewi.* $M_2$ is slightly smaller than $M_1$ but is otherwise structurally similar. In both molars, the paraconid and metaconid are subequal in size (the paraconid of $M_1$ shows heavy wear, as in the type of *D. matthewi*), and the talonids are relatively large and basined. As in *D. matthewi*, $M_2$ has a distinct hypoconid and a well developed postcristid, but the hypoconulid and entoconid are poorly defined. The associated $P^4$ does not differ significantly from its counterpart in other oxyaenids, except that it is comparatively broad transversely.

*Discussion.*—*D. churchillorum* is decidedly smaller and less robust than *D. matthewi.* It appears to be closely related to *D. matthewi.* The smaller overall size, shorter premolars, and greater antiquity of the holotype suggest that *D. churchillorum* lies in or near the immediate ancestry of *D. matthewi.*

Only the holotype is known from the Clark's Fork Basin, and it is of late Tiffanian age. *D. churchillorum* occurs also in the Clarkforkian, as indicated by AMNH 56137 and possibly AMNH 86865, both from the Purdy Basin area near Togwotee Pass (collected under the direction of Dr. M. C. McKenna, who has kindly permitted me to include them here). The Clarkforkian age of AMNH 56137 is verified by its mutual occurrence with *Plesiadapis cookei* at the Lower Red Creek locality (see Chapter V).

### cf. *Dipsalodon*, ?undescribed species

Figure 60

*Referred Specimen.*—UM 71172.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–74).

*Discussion.*—UM 71172, consisting of a partial right $P_4$ or $P_3$, right $M_1$ trigonid, and associated tooth and jaw fragments, appears to represent a medium-sized palaeonictine not otherwise known in the collection. The premolar is much smaller, especially in breadth, than in both species of *Dipsalodon.* It bears two distinct talonid cusps aligned anteroposteriorly on the trenchant talonid crest. A faint crest runs from the more posterior cusp to the lingual border of the tooth, turning anteriorly at that point and bearing two very minute cuspules. The structure of this tooth is closer to that of $P_3$ or $P_4$ in *Dipsaldon* than in any other oxyaenid. The molar trigonid is compressed transversely and widely open anteroposteriorly. The metaconid is larger and higher than the paraconid, indicating that the tooth represented is $M_1$. The trigonid is narrower than in other species of *Dipsalodon* but resembles them in being more open than in *Oxyaena.*

UM 71172 almost certainly pertains to an as yet undescribed oxyaenid, probably belonging to the genus *Dipsalodon.* It is, however, inadequate to serve as a type specimen, and formal description must await discovery of better specimens.

UM 66644 (SC–110, *Plesiadapis cookei* Zone), mentioned above in connection with *Oxyaena*? *lichna*, includes a left $P_4$ (or possibly $P_3$) and ?associated fragments of dentary that may belong to a form near that represented by UM 71172. It also resembles *O.*? *lichna* but is about 30% larger (UM 66644, $P_4L=6.85$). The premolar bears a small anterior basal cusp and a slightly basined talonid. There is a small talonid cusp at the back of the trenchant talonid crest. From this cusp a crest descends anterolingually to the talonid notch and, from there, ascends onto the lingual face of the protoconid. The precise affinities of this enigmatic specimen are uncertain, but it is probably an oxyaenid. It may represent yet another species of oxyaenid from the Clarkforkian.

### *Palaeonictis* De Blainville, 1842
### *Palaeonictis peloria*, sp. nov.

Figure 61, Table 34

*Holotype.*—PU 18077, left dentary with $P_3$-$M_2$, and associated lower left canine, collected by R. Eckler, from near SC–55 (*Phenacodus-Ectocion* Zone).

*Hypodigm.*—Holotype and UM nos. 65640 (right $dP_4$ and $M_1$[?]), 67445 (fragments of juvenile dentaries with left ?$dP_3$ and erupting $M_1$).

*Horizon and Locality.*—Willwood Formation, late Clarkforkian (*Phenacodus-Ectocion* Zone); Holotype from NW¼, sec. 6, T.55 N., R.100 W., Park County, Wyoming (approximately SC–55); UM 65640 from SC–55; UM 67445 from SC–153.

*Etymology.*—Greek *peloros*, monstrous, terrible.

*Diagnosis.*—Largest species of the genus, $M_{1-2}$ length=29.4 mm, about 50% greater than in *P. gigantea*, 20% greater than in *P. occidentalis.* $M_2$ larger relative to $M_1$ (length $M_1$/length $M_2$=1.14) than in *P. occidentalis.* Dentary deep and very robust.

*Description.*—This is the largest known Clarkforkian oxyaenid. It is decidedly larger than *Palaeonictis gigantea* from the Sparnacian of the Paris Basin and is also larger than *P. occidentalis* from the early Wasatchian of the Bighorn Basin (Tables 34, 35). In all tooth dimensions the holotype of *P. peloria* exceeds the mean for 11 specimens of *P. occidentalis* by more than two standard deviations (more than five standard deviations for $M_2$ length and more than eight standard deviations for $P_3$ length). *T*-tests comparing tooth dimensions in the two species are highly significant for most cases (e.g., $p<.001$ for lengths of $P_3$ and $M_2$).

The canine is large and the root exceptionally robust. A pronounced, deep groove is present on the posterolabial surface, caused by occlusion with the upper canine; striations can be clearly discerned on this wear surface. $P_3$-$M_2$ are larger, both longer and broader than in the other two species of *Palaeonictis*, but otherwise are very similar to them morphologically. A small but distinct entoconid occurs on $P_4$, somewhat anterior to the posterior margin of the tooth, and the talonid is noticeably broader than the trigonid. $M_1$ and $M_2$ in the holotype show considerable wear from shearing and abrasion, rendering the talonid cusps indistinct, particu-

Table 34. Measurements of lower cheek teeth of Clarkforkian *Palaeonictis peloria*, sp. nov., and Wasatchian *Palaeonictis occidentalis*.

| | PU 18077, type, *P. peloria* | AMNH 110, type, *P. occidentalis* | AMNH 15212 *P. occidentalis* | AMNH 15213 *P. occidentalis* | AMNH 15214 *P. occidentalis* | AMNH 15726 *P. occidentalis* | AMNH 16117 *P. occidentalis* | PU 14677 *P. occidentalis* | PU 16140 *P. occidentalis* | PU 17842 *P. occidentalis* | PU 17845 *P. occidentalis* | PU 19901 *P. occidentalis* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $P_3$L | 15.2 | 11.7 | | 11.6 | | 11.2 | 11.0 | | 11.9 | 11.4 | 12.1 | 12.0 |
| $P_3$B | 10.4 | 8.5 | | 8.2 | | 8.5 | 8.2 | | 8.1 | 8.7 | 8.6 | 8.9 |
| $P_4$L | 15.6 | 12.5 | 12.1 | 13.3 | | 15.0 | | 13.9 | 14.5 | 12.7 | 13.2 | 14.4 |
| $P_4$B tal | 12.7 | 9.6 | 8.5 | 9.0 | | 10.7 | | 9.4 | 10.0 | 9.8 | 9.3 | 10.0 |
| $M_1$L | 16.6 | 13.4 | 14.2 | 12.9 | | 14.9 | | 15.0 | 14.7 | 13.8 | 13.7 | 13.0 |
| $M_1$B tri | 10.5 | 8.6 | 8.0 | 7.8 | | 9.2 | | 9.0 | 8.9 | 8.3 | 8.6 | 8.9 |
| $M_1$B tal | 9.4 | 7.8 | 7.5 | 7.0 | | 8.7 | | 8.1 | 8.4 | 6.8 | 7.3 | 7.5 |
| $M_2$L | 14.5 | 10.4 | 9.9 | 10.8 | 11.5 | 11.7 | 10.5 | 10.5 | | 11.1 | 11.5 | 11.7 |
| $M_2$B tri | 10.2 | 7.3 | 6.8 | 6.7 | 7.7 | 8.1 | 6.7 | 7.4 | | 7.0 | 7.6 | 8.0 |
| $M_2$B tal | 7.1 | 6.0 | 5.3 | 4.5 | 5.6 | 7.0 | 4.7 | 5.8 | | 4.5 | 5.8 | 5.8 |
| MD* | 42.5 | 30.4 | 25.5 | 34.5 | 43.5a | | 29.7a | 34.4 | 39.8 | | 31.5 | 39.0 |

*Mandibular depth, measured labially beneath $M_1$.

Table 35. Metrical data for lower teeth of Wasatchian *Palaeonictis occidentalis*.

| | N | $\overline{X}\pm SE$ | s | V |
|---|---|---|---|---|
| $P_3$L | 7 | 11.6±.14 | .39 | 3.4 |
| $P_3$B | 7 | 8.5±.10 | .28 | 3.3 |
| $P_4$L | 9 | 13.5±.33 | 1.00 | 7.4 |
| $P_4$B tal | 9 | 9.6±.21 | .64 | 6.7 |
| $M_1$L | 9 | 14.0±.26 | .79 | 5.6 |
| $M_1$B tri | 9 | 8.6±.16 | .47 | 5.5 |
| $M_1$B tal | 9 | 7.7±.21 | .63 | 8.2 |
| $M_2$L | 10 | 11.0±.20 | .63 | 5.7 |
| $M_2$B tri | 10 | 7.3±.16 | .52 | 7.1 |
| $M_2$B tal | 10 | 5.5±.25 | .78 | 14.2 |

larly on $M_2$. On $M_1$, only the hypoconid has been heavily worn and it is still possible to distinguish the hypoconulid and the entoconid. The talonids of both molars are markedly smaller than the trigonids, a condition more pronounced in $M_2$ than $M_1$. The metaconid of $M_2$ is broken but was apparently relatively larger than in *P. occidentalis*. $M_2$ is reduced with respect to $M_1$, but less so than in *P. occidentalis*, the relative proportions of $M_1$ to $M_2$ more closely approximating those in *P. gigantea*.

The dentary of *P. peloria* is deep and massive. The articular condyle in the holotype is cylindrical and transversely very broad, not unlike that in many recent Carnivora.

Two juvenile oxyaenid specimens from the late Clarkforkian appear to represent *P. peloria*. UM 67445 (dentaries with part of ?$dP_3$, erupting $M_1$, and the roots of $P_2$ and ?$dP_4$ on the left side) and UM 65640 (right ?$dP_4$-$M_1$) are palaeonictine in morphology. The proportions of the premolars and the structure of the talonid of $M_1$ appear to conform more closely with those features in the type of *P. peloria* than with their counterparts in *Dipsalodon matthewi*, the only other oxyaenid of comparable size. The ?$dP_3$ is somewhat shorter and narrower than $P_3$ in the holotype, as would be expected for the deciduous premolar. $M_1$ is only partly erupted and completely unworn in UM 67445, but it appears to be of the same size and morphology as in the holotype. Its trigonid is relatively narrow but wide open, as in *Palaeonictis* but in contrast to *Oxyaena*. The talonid is basined, smaller than the trigonid, and bears three distinct talonid cusps. The dentary of UM 67445 is relatively shallow and more slender than in the type, a characteristic of juvenile specimens. The ?$dP_4$ of UM 65640 is slightly shorter and narrower than $M_1$ in UM 67445, but otherwise resembles the molar rather than permanent $P_4$. $M_1$ in UM 65640 is badly damaged, only part of the crown remaining, but it appears to have been similar to that in UM 67445 and in the holotype.

A left $P_2$ from SC-48 (UM 66505, *Phenacodus-Ectocion* Zone) may be referable to *P. peloria* or to *Dipsalodon matthewi*.

*Discussion.*—*P. peloria* is larger than *P. occidentalis*, but it is more primitive in having a less reduced $M_2$ and a larger metaconid on $M_2$. In this regard it is more like the European *P. gigantea* and also approaches the closely allied *Dipsalodon matthewi*. *P. peloria* is older than *P.*

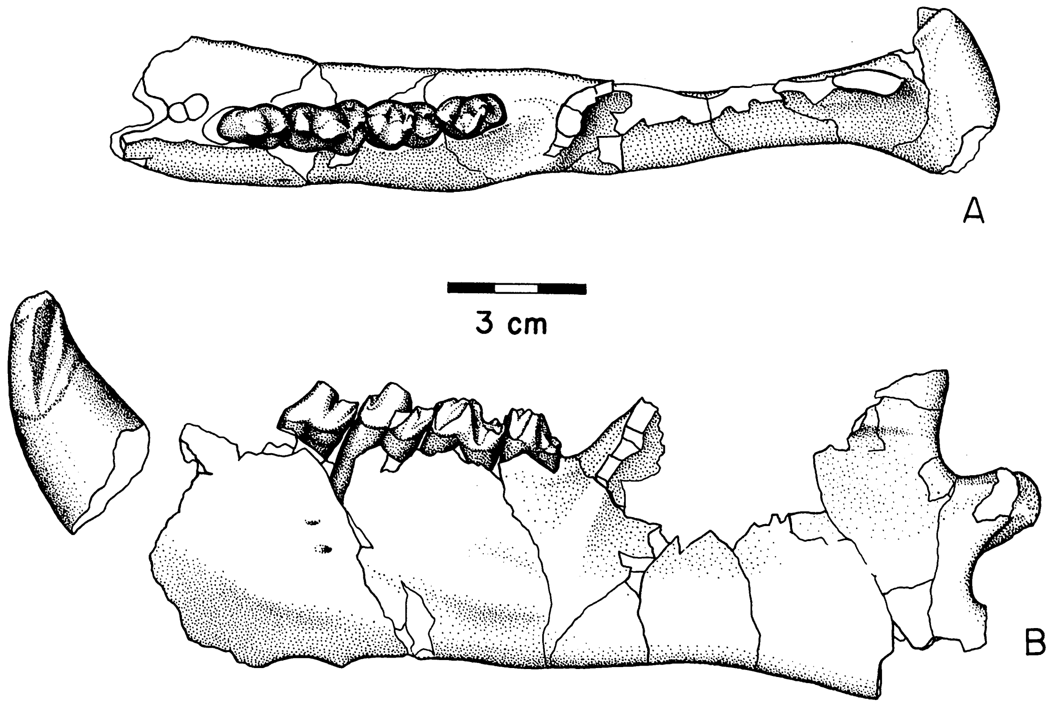

Figure 61. *Palaeonictis peloria*, sp. nov., Holotype, PU 18077, from vicinity of SC–55: left dentary with $P_3$-$M_2$ and associated canine. A, crown, and B, labial views.

*occidentalis*, which is known only from the early Wasatchian of the Bighorn Basin (Osborn, 1892; Matthew, 1915a; Denison, 1938; Bown, 1979).

*Ambloctonus priscus* Matthew (1915a) is a synonym of *P. occidentalis* (Denison, 1938). Matthew's type of *A. priscus* is from the early Wasatchian of the Bighorn Basin. His two paratypes, AMNH nos. 16116 and 16117, were reported to be from the Clarkforkian, but their locality data read "Sand Coulee beds, 3 miles southeast of mouth of Pat O'Hara Creek," now known to be in earliest Wasatchian beds (="Sand Coulee level," same locality as the holotypes of *Phenacolemur praecox* and *Viverravus acutus*; see also Simpson, 1937c: 13). Both *Hyracotherium* and *Pelycodus*, Wasatchian index fossils, were collected at this locality during the same field season. Hence there exists no well documented record of *P. occidentalis* from the Clarkforkian.

Denison (1938) used the subfamily Palaeonictinae (an emendation of Osborn's [1892] Palaeonictidae) for *Palaeonictis*, *Ambloctonus*, *Dipsalodon* and, provisionally, *Paroxyaena*, an arrangement followed by Van Valen (1966). The structural, temporal, and geographic proximity of *Palaeonictis peloria* and *Dipsalodon matthewi* suggest that the two genera evolved from a common ancestor in this area, perhaps not before the late Paleocene. *Palaeonictis* differs from *Dipsalodon* primarily in having relatively broader cheek teeth and a relatively smaller $M_2$, thus it is reasonable to postulate that *Palaeonictis* was derived directly from an early species of *Dipsalodon*.

The depth of the dentary is quite variable in specimens of *P. occidentalis* examined (Table 34), and it seems possible that oxyaenids were sexually dimorphic. In AMNH 15214, the depth approaches that in *P. peloria*, but $M_2$ (the only tooth preserved) is much smaller than in the latter and comparable to other specimens of *P. occidentalis*; it may represent a male. AMNH 15726 is an exceptionally large individual (a male?), if properly referred to *P. occidentalis*. Its locality data read "Big Horn, Shoshone River," which, although imprecise, suggest an early Wasatchian age. In dimensions of $P_3$ and $M_2$ (the teeth that differ most between *P. peloria* and *P. occidentalis*), the specimen conforms well to *P. occidentalis*.

*P. peloria* is the largest carnivorously-adapted mammal known from the Clarkforkian, even exceeding *Dissacus praenuntius* and *Dipsalodon matthewi* in the breadth of the cheek teeth and the depth and robustness of the jaw. Its teeth are well adapted for crushing and shearing, although the latter function is somewhat less developed than in *Oxyaena* (see Denison, 1938, and Van Valen, 1966, for discussions of dental function in *Palaeonictis*). *P. peloria* must have been a formidable predator.

## Order RODENTIA Bowdich, 1821

### Family Paramyidae Miller and Gidley, 1918

Paraymid rodents are abundant in the Clarkforkian and are constituents of nearly all known Clarkforkian faunas. In the Clark's Fork Basin, they are common fossils throughout the stratigraphic sequence, first appearing at the base of the Clarkforkian. Indeed, their initial occurrence is important in recognizing the Tiffanian-Clarkforkian boundary.

Until recently, only one species of rodent was known to come from rocks older than Wasatchian. This form, *Paramys atavus* Jepsen (1937), was reported exclusively from the Bear Creek locality, a site at which multituberculates have not been found. This early record of rodents at a site lacking multituberculates led Jepsen (1949: 489) to suggest that the two groups were in direct competition and that "the expansion of rodents was principally responsible for the decline and disappearance of multituberculates." McKenna (1960, 1961) observed that in the early Wasatchian of northwestern Colorado, both groups occurred together at some sites, but where one was common the other was rare, further supporting Jepsen's deduction. Multituberculates are, in general, not common in post-Tiffanian sediments; however, at least one Clarkforkian site (SC–188) yields remains of rodents and multituberculates, both of which are common.

Van Houten (1944) reported a single rodent incisor from the Clarkforkian of the Sand Coulee area, and for nearly 20 years this remained the only other record of Clarkforkian rodents besides the Bear Creek specimens. In 1962, Wood described *Franimys amherstensis* from the Clark's Fork Basin and gave its horizon as "basal Gray Bull beds" (earliest Wasatchian). From the same locality he identified an isolated $M_2$ as *Microparamys* species A (there is some reason to doubt the presence of this genus in the Clarkforkian, see below). We now know that the locality that yielded Wood's specimens corresponds to UM locality SC–119 and lies in the middle Clarkforkian *Plesiadapis cookei* Zone. (Wood, 1974: 17, recognized that these specimens are older than he initially reported, and he subsequently [Wood, 1977] identified their age as Clarkforkian.)

The UM Clarkforkian collection contains three species of rodents, and perhaps more. Two of them are new records for the Clarkforkian. At many localities, two or perhaps more species have been found together. Unfortunately, most of the specimens consist only of isolated teeth, predominantly incisors, which are difficult or impossible to identify specifically. In the following section, some incisors are tentatively assigned to species when their size and morphology compare closely to incisors in more complete specimens. In many cases, however, no specific identification was attempted. In order to reflect accurately the widespread occurrence of rodents in the Clarkforkian, I list here the localities from which unidentified rodent teeth are known. Most specimens are included among miscellaneous teeth from these sites; a few catalogued specimens are also noted.

*Plesiadapis gingerichi* Zone: SC–172 (UM 68426), SC–179 (UM 71615), SC–215 (UM 69925), SC–250 (UM 71810).

*Plesiadapis cookei* Zone: SC–66, 84, 93, 99, 110, 118, 119 (UM 66757), 120, 136, 143, 188, 194, 195, 200, 201; SC–168, probably *P. cookei* Zone.

*Phenacodus-Ectocion* Zone: SC–29, 81, 175, 176, 205, 234, 235.

Zone uncertain: SC–196.

Measurements of paramyids have been taken following the method prescribed by Wood (1962: 6).

### *Paramys* Leidy, 1871

### *Paramys atavus* Jepsen, 1937

Figure 62, Table 36

*Referred Specimens.*—UM nos. 65244, 68747, 69219, 69871, 71173, 71605, 71848, 72057, and miscellaneous isolated teeth.

*Occurrence.*—*Plesiadapis gingerichi* Zone (SC–179); *Plesiadapis cookei* Zone (SC–74, 108, 135, 188, 197, 201); *Phenacodus-Ectocion* Zone (SC–29, 50, 105, 153, 159, 162, 184, 214).

*Discussion.*—A very small paramyid that appears to be identical to *Paramys atavus* is found throughout the Clarkforkian. *P. atavus* was originally based on a lower molar ($M_2$) and several isolated incisors from Bear Creek, Montana (Jepsen, 1937). The only additional specimen of *P. atavus* that has been reported is an isolated upper cheek tooth from Bear Creek (McKenna, 1961). Five of the UM specimens are dentaries (UM nos. 65244, 69219, 69871, 71173, and 71605), three of which preserve cheek teeth (UM 65244: $P_4$-$M_3$; UM 69871: $P_4$-$M_2$ [Figure 62]; UM 71173: $M_{1-2}$). All are similar in structure to the holotype molar but are slightly smaller. The incisors in these jaws and the isolated incisors assigned here are almost identical in size and shape to those from Jepsen's sample, and they show the same very restricted distribution of enamel. Enamel covers the

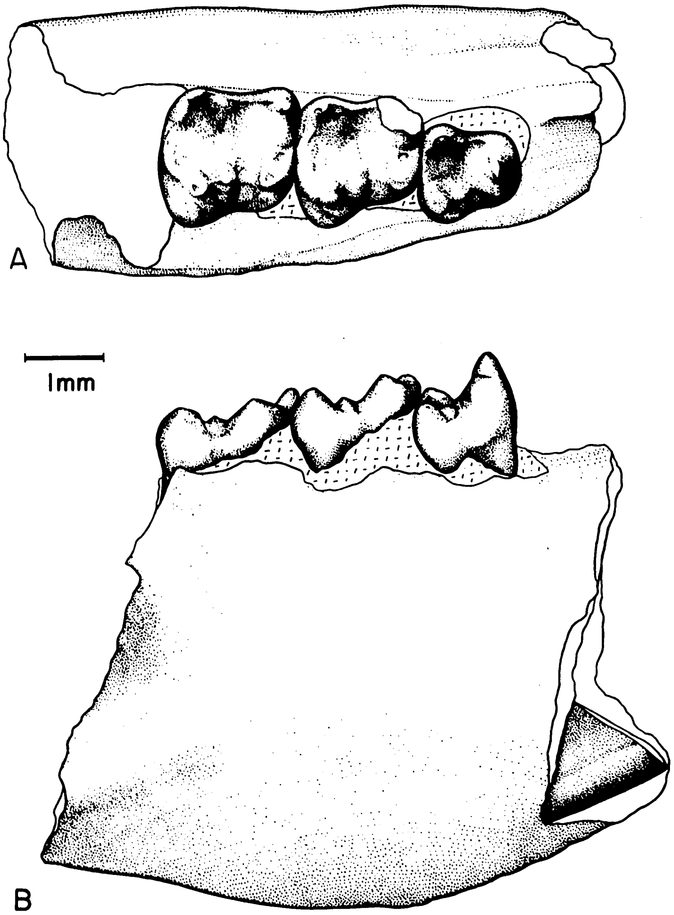

Figure 62. ***Paramys atavus***, UM 69871, from SC-214: right dentary with $P_4$-$M_2$ and base of incisor. A, crown, and B, labial views.

anterior (labial) surface and a narrow band on the lateral surface; there is almost no extension onto the medial surface.

As noted above, all the lower cheek teeth are represented in the Clarkforkian specimens now known. $P_4$ is noticeably smaller than the molars. Its metaconid is large and high and the protoconid is a small, low cusp closely appressed to the metaconid (UM 69871), much as Wood (1962) described in $P_4$ of *Franimys amherstensis.* The talonid of $P_4$ is fully molariform, although the hypoconulid is less distinct than in the molars. While $P_4$ resembles that of *Franimys*, it is only slightly more than half as big.

The molars are very primitive, showing no cresting or crenulation of enamel. The metaconid is high and situated far forward. The trigonid is more or less basined and opens anteriorly. The talonid basin is large and broad. A shallow notch separates the large entoconid from the hypoconulid, hence the posterior cingulum is not well defined. There is a prominent mesoconid. Although these teeth are within the size range of *Microparamys*, the posterior borders of the molars are more arcuate than in most specimens of that genus. $M_1$ is very slightly larger than $M_2$, but in other respects $M_1$ and $M_2$ are essentially identical. $M_3$ is preserved only in UM 65244, but the specimen is worn and poorly preserved, and it provides little information.

Several isolated upper molars are among teeth recovered by screen-washing at SC-188. They are of appropriate size and morphology to belong to *P. atavus*, but they have a larger hypocone and broader anterior cingulum than in AMNH 22195, illustrated and described by McKenna (1961). They further differ from that specimen by having a small mesostyle and slightly weaker conules. These differences suggest that McKenna's tooth is a $P^4$.

The specimens described here are placed in *P. atavus*, but inadequacy of the type material of the species makes positive identification uncertain. In morphological details, the UM specimens are closest to the *Paramys excavatus* species group, as designated by Wood (1962), of which *P. atavus* is a member (this conclusion is shared by Drs. Mary Dawson and John Wahlert, personal communication). (UM 71605, a dentary edentulous except for the incisor, may belong to a smaller species; its incisor is somewhat smaller than others here allocated to *P. atavus.*)

Wood (1962: 160-161) designated an isolated lower molar (ACM 10997, from SC-119) as *Microparamys* species A. From Wood's published illustration, this tooth appears to agree in all details with the UM specimens here assigned to *P. atavus*. Wood noted that in some characters the tooth resembles *Paramys francesi*, a member of the *P. excavatus* species group, and he stated that it "could be referred equally well either to the *Paramys excavatus* species group or to *Microparamys*." It is possible that more than one taxon of very small paramyids existed in the Clarkforkian, but at present there is no compelling evidence to support this. Until undoubted specimens of *Microparamys* are found in Clarkforkian sediments, I propose to include Wood's specimen and other very small Clarkforkian paraymids in *Paramys atavus*.

### *Paramys* cf. *excavatus* Loomis, 1907

Figure 63

*Referred Specimens.*—UM nos. 65055, 65117, 65120, 66185, 66210, 66754, 69335, 69950, 71849, and miscellaneous teeth.

Table 36. Measurements of lower teeth of *Paramys atavus*.

| | UM 65244 | UM 68747 | UM 69219 | UM 69871 | UM 71173 | UM 71848 | PU 14200, Holotype |
|---|---|---|---|---|---|---|---|
| I a-p diam[1] | | 2.30 | 2.1a | 2.2a | | 2.30 | |
| I tr diam[1] | | 1.00 | 1.00 | 1.05 | | 1.00 | |
| $P_4L$ | 1.10 | | | 1.30 | | | |
| $P_4B$ tri | 0.85 | | | 0.85 | | | |
| $P_4B$ tal | 1.00 | | | 1.20 | | | |
| $M_1L$ | 1.6a | | | 1.60 | | | |
| $M_1B$ tri | 1.30 | | | 1.30 | | | |
| $M_1B$ tal | 1.4a | | | 1.60 | 1.50 | | |
| $M_2L$ | 1.70 | | | 1.70 | 1.65 | | 1.90[2] |
| $M_2B$ tri | 1.30 | | | 1.50 | 1.45 | | 1.60[2] |
| $M_2B$ tal | 1.35a | | | 1.70 | 1.70 | | 1.70[2] |
| $M_3L$[3] | 1.70 | | | | | | |

[1] Incisor measurements are anteroposterior diameter (a-p) and transverse or mesiodistal diameter (tr).

[2] Measurements of holotype taken from epoxy cast.

[3] Because of damage to $M_3$ in UM 65244 breadth dimensions cannot be measured accurately.

*Occurrence.—Plesiadapis cookei* Zone (SC–20, 84, 119); *Phenacodus-Ectocion* Zone (SC–23, 48, 80, 184).

*Discussion.*—Several jaws and isolated teeth are very similar to *Paramys excavatus*, a species widespread in early Eocene (Wasatchian) deposits. UM 65117, a dentary with $P_4$-$M_3$, demonstrates that the cheek teeth increase in size progressively from front to back. $P_4$ in this specimen is heavily worn, obscuring the morphology of its trigonid, but it is evident that the trigonid is markedly narrower than the talonid, and that $P_4$ is smaller than $M_1$. The molar metaconids are high and, as in *P. excavatus*, the trigonids are open both anteriorly and posteriorly (the metalophid is discontinuous). There is a broad talonid basin, flanked by a large entoconid and hypoconid and the somewhat smaller but distinct mesoconid and hypoconulid. Wood (1962: 53) reported that the posterior cingulum (posterolophid) in *P. excavatus* "is continuous from the hypoconid to the entoconid," but in the UM specimens, the posterior cingulum is broken by shallow notches setting off the hypoconulid from the other cusps. (This is less apparent in worn individuals.) The enamel of the incisors in the Clarkforkian specimens is distributed as in *P. atavus*, with almost no extension of enamel onto the medial surface.

The linear dimensions of the cheek teeth in the Clarkforkian specimens are slightly smaller than in any of Wood's subspecies of *P. excavatus*, but the incisors appear to be larger and more robust than in most specimens of early Wasatchian *P. excavatus taurus* from the Clark's Fork Basin. In other respects, including details of tooth morphology, these specimens conform closely to *P. excavatus*.

Two maxillary fragments contain upper molars very similar to those of *P. excavatus*. UM 69335, a palatal fragment with right $M^3$ (SC–195), and UM 69950, a right maxilla with $M^{1-3}$ (SC–214, figure 63A), probably belong to the same species as the lower dentitions described above. UM 66210, a poorly preserved snout with the left upper incisor, may also be referable here. The incisor is larger, particularly in its labiolingual diameter, than the incisors in *P. excavatus taurus* (e.g. UM 69780, a well preserved snout from SC–213, early Wasatchian).

Several large isolated incisors are very similar to the upper incisor in UM 66210: UM nos. 65000, 65015, 72058, 72059, 72060 (Figure 64), and uncatalogued teeth, from the *Plesiadapis cookei* Zone (SC–19, 62, 120) and the *Phenacodus-Ectocion* Zone (SC–57, 90, 105, 138). They are larger in labiolingual and mesiodistal dimensions, and are more curved, than lower incisors here assigned to *Paramys* cf. *excavatus*; hence they are probably upper incisors. These teeth are distinctly larger than upper incisors of *P. excavatus taurus* and are as large or larger than incisors of *P. copei major*. They may be upper incisors of the Clarkforkian species here designated *P.* cf. *excavatus* (as suggested to me by Dr. Mary Dawson, 1978). If these specimens do represent that species, then Clarkforkian *P.* cf. *excavatus* is distinguished from Wasatchian populations by having larger, more robust incisors, but slightly smaller cheek teeth, than *P. excavatus taurus*. When better samples are known, it may prove useful to recognize these distinctions taxonomically.

Measurements of the Clarkforkian specimens referred to *Paramys* cf. *excavatus* are: UM 65117, lower incisor

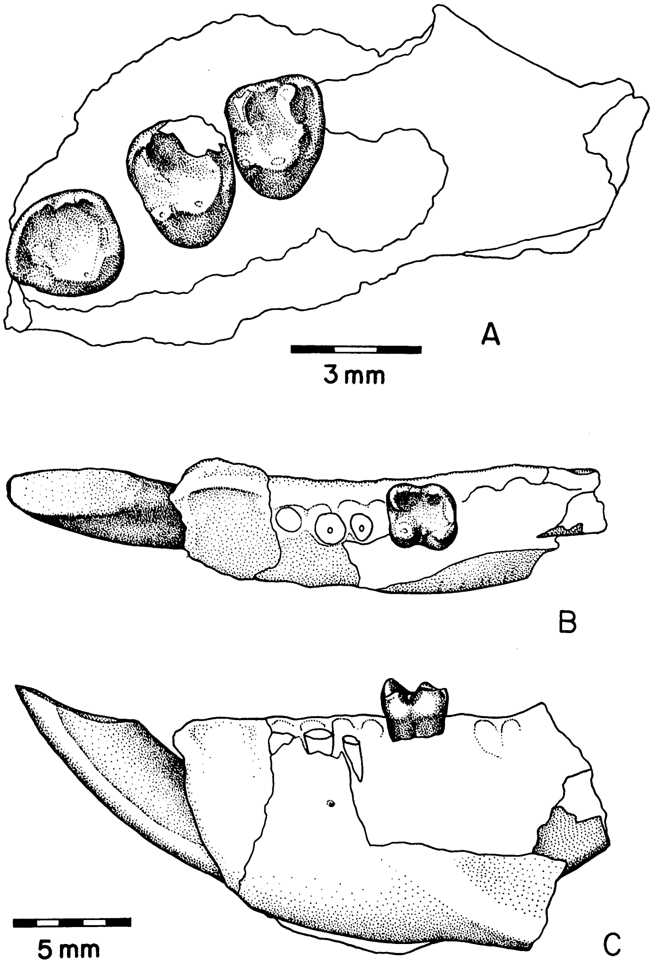

Figure 63. *Paramys* cf. *excavatus*. A, UM 69950, from SC-214: right maxilla with $M^{1-3}$. B and C, UM 65120, from SC-23: left dentary with incisor and $M_1$, crown and labial views.

mesiodistal diameter=2.20, $P_4L$=2.05, $P_4B$ trigonid=1.65, $P_4B$ talonid=1.95, $M_1L$=2.40 (breadth measurements cannot be made), $M_2L$=2.60, $M_2B$ trigonid=2.40, $M_2B$ talonid=2.70, $M_3L$=3.20, $M_3B$ trigonid=2.50, $M_3B$ talonid=2.50. UM 65120, lower incisor mesiodistal diameter=2.10, incisor labiolingual diameter=3.70, $M_2L$=2.70, $M_2B$ trigonid=2.60, $M_2B$ talonid=2.70. UM 65055, lower incisor mesiodistal diameter=1.90, labiolingual diameter=3.95. UM 66210, upper incisor mesiodistal diameter=2.0a, labiolingual diameter=4.2a. UM 69950, $M^1L$ =2.30, $M^1B$=2.65, $M^2L$=2.30, $M^2B$=2.65, $M^3L$=2.80, $M^3B$=2.40. Dimensions of the upper incisors discussed above are: mesiodistal diameter=2.20–2.80 ($\bar{X}$=2.48, n=5), labiolingual diameter=4.90–5.70 ($\bar{X}$=5.19, n=5).

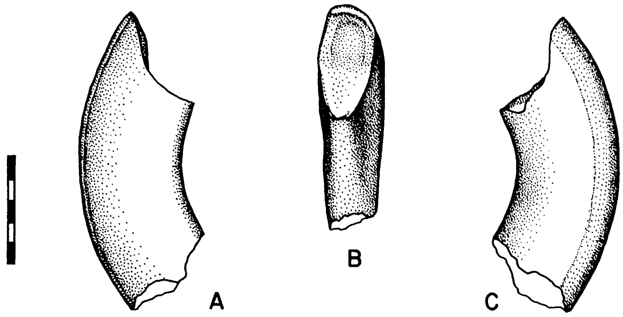

Figure 64. Paramyid, possibly *Paramys* cf. *excavatus*, UM 72060, from SC-138: left upper incisor, medial (A), crown (B), and lateral (C) views. Scale is 5 mm.

### *Paramys annectens*, sp. nov.

Figure 65

*Holotype.*—PU 19526, right dentary with $P_4$-$M_3$ and part of incisor, and left dentary with $M_{2-3}$, parts of $M_1$ and incisor, collected by Philip D. Gingerich, at SC-209 (probably lower *Plesiadapis cookei* Zone).

*Hypodigm.*—Holotype and UM 71177 (left dentary with $M_{1-2}$, roots of $P_4$, and part of incisor).

*Horizon and Locality.*—Uppermost Polecat Bench Formation or lowermost Willwood Formation (near contact), Clarkforkian, lower *Plesiadapis cookei* Zone (?). The label with the holotype reads "SE¼, NE¼, sec. 31, T. 57 N., R. 101 W., Park County, Wyoming," but Dr. Gingerich remembers collecting the specimen from the NW¼ of sec. 31, in exposures now designated as UM locality SC-209. (This discrepancy is at most ½ mile in an odd-sized section 1½ miles wide; stratigraphically there is little difference between the two locations.) UM 71177 is from SC-74 (lower *Plesiadapis cookei* Zone).

*Etymology.*—Latin *annectens*, linking, in allusion to the intermediate size and probable phylogenetic position between primitive *P. atavus* and the slightly more advanced *P. excavatus*.

*Diagnosis.*—Cheek tooth row 10–20% smaller than in *P. excavatus*, about the same length as in *P. francesi*, and about 50% larger than in *P. atavus*. Lower incisor much more slender than in *P. excavatus*, more similar to *P. atavus*, and with enamel distribution as in *P. atavus*. Differs from *Franimys amherstensis* in having more laterally-compressed lower incisor and larger protoconid on $P_4$; angular process of dentary not markedly lateral to incisive alveolus, in contrast to *Franimys*. Dentary

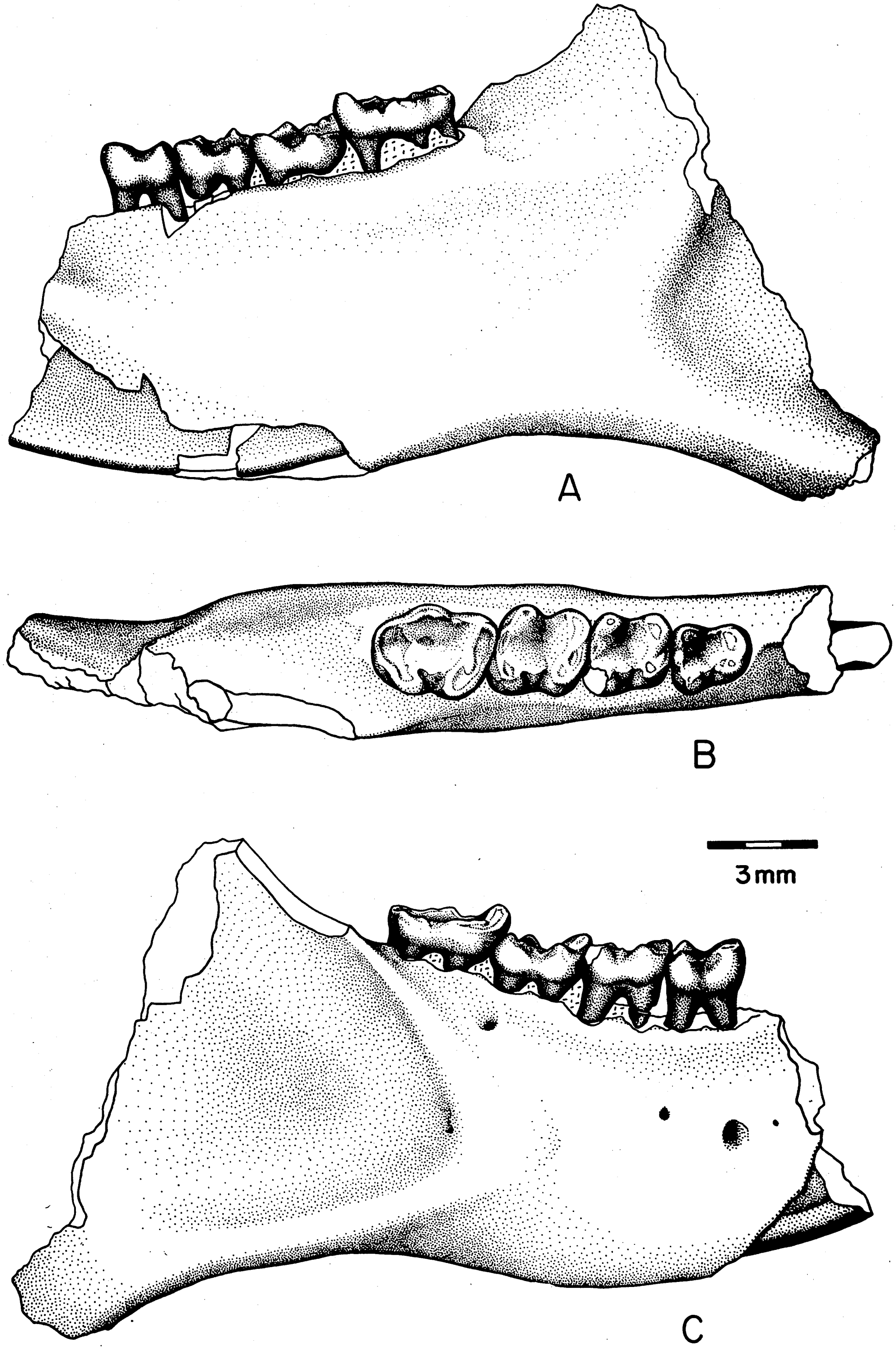

Figure 65. *Paramys annectens*, sp. nov., Holotype, PU 19526, from vicinity of SC–209: right dentary with $P_4$-$M_3$ and part of incisor. A, lingual, B, crown, and C, labial views. Specimen also includes left dentary with $M_{2-3}$.

shallower and less robust than in *P. excavatus*. Cheek tooth morphology as in *P. excavatus*.

*Description.*—Except for the smaller size of the cheek teeth and the much smaller size of the incisors, *P. annectens* is very similar to *P. excavatus*. $P_4$ is noticeably smaller than $M_1$, in contrast to $P_4$ in *P. francesi*, but it is relatively larger than in *P. atavus*. It is preserved only in the right dentary of the holotype, where the protoconid (though worn) appears to be larger than in *P. atavus* and *Franimys amherstensis*.

The mesoconid and the hypoconulid are well defined on all the cheek teeth, and the metaconid is high and anteriorly situated. The trigonids have small basins. In $M_1$ and $M_2$ of the holotype, which are worn, the trigonid basins open anteriorly, whereas the trigonid of $M_3$ appears to be closed anteriorly by a low anterior cingulum (anterolophid). The metalophids of $M_{1-3}$ are each continuous but dip slightly midway between the protoconid and the metaconid. $M_1$ and $M_2$ of UM 71177 show little wear, and their trigonids have distinct basins that are closed anteriorly by a shallow anterolophid. Posteriorly, the metalophid has a well developed valley between the protoconid and the metaconid, but it still provides a shallow wall separating the trigonid and talonid basins. These details are apparently obscured by wear, as in the holotype. The morphology of the molar trigonids in *P. annectens* is, in many respects, intermediate between that of *P. atavus* and that of *P. excavatus*, but it clearly foreshadows that of *P. excavatus*.

The talonids are large and primitive, with smooth enamel. The posterior cingulum is continuous in worn teeth, but shallow notches setting off the hypoconulid can be discerned in unworn teeth. They show no distinctive differences from those of *P. excavatus*, except in size.

The incisors of *P. annectens* are decidedly smaller, especially in mesiodistal diameter, than those of *P. excavatus*. Associated with the smaller incisors is a shallower and more gracile dentary than in *P. excavatus*. The enamel of the incisors is restricted to the labial surface and a narrow strip on the lateral surface; as in *P. atavus* there is essentially no expansion onto the medial surface.

*Discussion.*—*P. annectens* is intermediate in size and in some morphological features between *P. atavus* and *P. excavatus*, more closely approaching the latter. It is almost certainly the lineal ancestor of *P. excavatus* and must have evolved from a form similar to *P. atavus*. The form described earlier as *Paramys* cf. *excavatus* may represent an intermediate stage between *P. annectens* and early Wasatchian *P. excavatus*, but the relatively robust incisors of Clarkforkian *P.* cf. *excavatus* cast uncertainty on this possibility. *P. annectens* has only slightly smaller cheek teeth than in *P.* cf. *excavatus*, but the conspicuous difference in incisor size between the two enables them to be readily distinguished. This difference is more than occurs between most species and, coupled with the intermediate condition of the trigonids in *P. annectens*, it supports the specific distinction of *P. annectens*.

*P. annectens* is similar in size to the referred lower jaw of *Franimys amherstensis* (Wood, 1962: figure 49a), but it appears to differ in $P_4$ structure, incisor size, and mandibular form. The specimens described here as *P. annectens* are clearly in the *P. excavatus* species group, as observed independently by D. Parris, M. Dawson, and J. Wahlert (personal communication).

Measurements of *P. annectens* are: PU 19526, Holotype, right side: $P_4L=2.00$, $P_4B$ trigonid=1.50, $P_4B$ talonid=1.80; $M_1L=2.20$, $M_1B$ trigonid=1.90, $M_1B$ talonid=2.15; $M_2L=2.35$, $M_2B$ trigonid=2.30, $M_2B$ talonid=2.45; $M_3L=3.10$, $M_3B$ trigonid=2.30, $M_3B$ talonid=2.40; Incisor mesiodistal diameter=1.15, labiolingual diameter=3.3a; left side: $M_2L=2.30$, $M_2B$ trigonid=2.25, $M_2B$ talonid=2.40; $M_3L=3.10$, $M_3B$ trigonid=2.25, $M_3B$ talonid=2.40. UM 71177: $M_1L=2.25$, $M_1B$ trigonid=1.90, $M_1B$ talonid=2.15; $M_2L=2.40$, $M_2B$ trigonid=2.25, $M_2B$ talonid=2.40; Incisor mesiodistal diameter=1.30, labiolingual diameter=3.2a.

### *Franimys* Wood, 1962
### *Franimys amherstensis* Wood, 1962

No additional material definitely referable to this species has been found since Wood's description. The holotype is a partial skeleton including parts of the skull and dentary (ACM 10524, from SC-119, *Plesiadapis cookei* Zone). Of the dentition, only upper teeth are known in the type, but Wood referred a dentary with lower teeth from the Early Wasatchian of the Bighorn Basin to this species. The locality of the holotype given by Wood (1962:147) was incorrect and was subsequently corrected (Wood, 1974: 17). Wood (1962) listed the locality of the referred dentary (ROM 2180, left jaw with $P_4$-$M_2$) as "SW ¼, sec. 1, T. 50 N., R. 74 W., southwest of Basin, Wyoming," but he undoubtedly meant R. 94 W. Assignment of this specimen to *Franimys* was tentative since lower teeth are lacking in the holotype, making direct comparison impossible.

From Wood's figures and descriptions, I am unable to find any characters of the dental anatomy, except for those of $P_4^4$, which differentiate *Franimys* from the *Paramys excavatus* species group. New paramyid

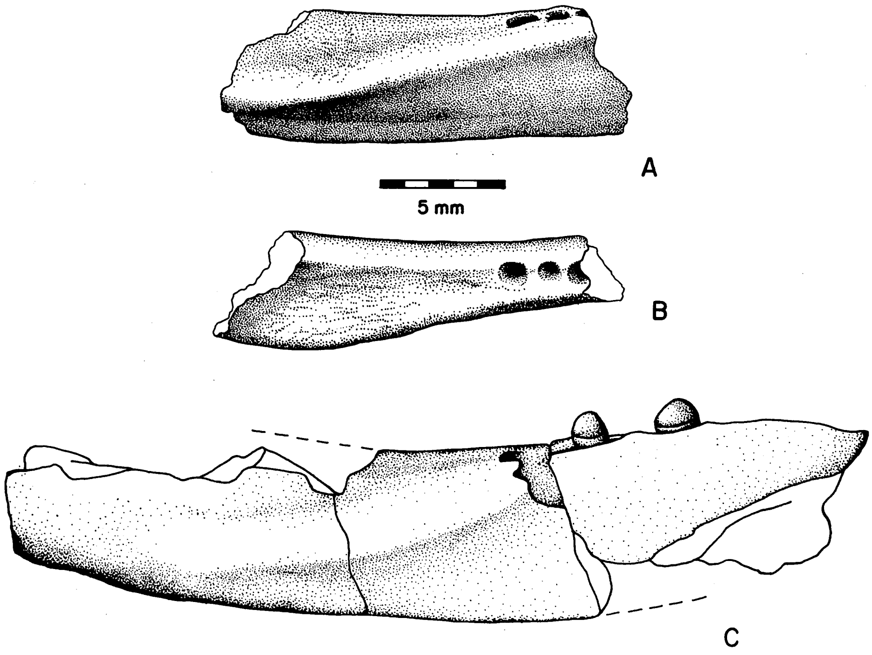

Figure 66. *Palaeanodon*. A and B, *Palaeanodon ?parvulus*, UM 71431, from SC–233: left dentary fragment, lingual and dorsal views, showing three most posterior postcanine alveoli. C, *Palaeanodon* cf. *ignavus*, UM 66243, from SC–87 (early Wasatchian): left dentary with third and fourth postcanines and alveolus for fifth postcanine, lingual view (from Rose, 1978b).

specimens described above show that $P_4$ in *Paramys atavus* is similar to that of *Franimys*, suggesting that this morphology represents a very primitive condition of $P_4$. Wood (1975) proposed a new infraorder of rodents, Franimorpha, for *Franimys*, based on its incipient indications of hystricognathy; but the overall similarity of *Franimys* to other primitive paramyids suggests that it is equally reasonable to consider it as a member of the *Paramys excavatus* species group.

Order Uncertain
Suborder PALAEANODONTA Matthew, 1918
Family Metacheiromyidae Wortman, 1903
*Palaeanodon* Matthew, 1918
*Palaeanodon ?parvulus* Matthew, 1918
Figure 66A, B

*Referred Specimens.*—UM nos. 67554, 67555, 71034, 71431.

*Occurrence.*—*Plesiadapis cookei* Zone (SC–143; SC–99, upper *P. cookei* Zone?); *Phenacodus-Ectocion* Zone (SC–233).

*Discussion.*—Matthew (1918) named *Palaeanodon parvulus* for a small number of associated postcranial elements from the head of Big Sand Coulee (AMNH 15859, holotype). He distinguished it from the Wasatchian *P. ignavus* by its smaller size ("one-fourth less than *P. ignavus*") and more slender aspect. The four Clarkforkian specimens reported here are fragments of the dentary, an element not preserved in the holotype (and only previously known specimen of the species). All four are, however, distinctly smaller and more gracile than Matthew's referred mandibular fragments of *P. ignavus* (AMNH nos. 15698 and 15699) and specimens in the Yale sample of Wasatchian *Palaeanodon*, probably also referable to *P. ignavus*.

Two specimens, UM nos. 71431 and 71034, preserve the ramus forward to the last two postcanine alveoli. The alveoli are markedly smaller and more closely spaced than in early Wasatchian specimens of *Palaeanodon* from the Bighorn Basin (UM nos. 63611 and 66243, Rose, 1978b: text-figures 3 and 4; Rose, 1979: figures 1 and 2; also YPM nos. 30574 and 34396). UM 71034 is broken longitudinally, revealing that the alveoli are tapered.

All the Clarkforkian specimens possess the prominent medial buttress characteristic of the dentary of *Palaeanodon*. The buttress forms a posteriorly-descending shelf that gradually broadens behind the last postcanine alveolus. Its dorsal surface is rugose, perhaps as an adaptation for lodging a corneous plate (Matthew, 1918). The internal mandibular groove is well defined in UM 71431 (Figure 66A).

The range of variation in size is considerable in Wasatchian *Palaeanodon*, but only the smallest specimens approach the size of those from the Clarkforkian. Rose (1978b) discussed the possibility that some of the size variability in palaeanodonts might be explained by sexual dimorphism. This hypothesis should be examined as larger samples of *Palaeanodon* become known. All of the Clarkforkian specimens are very small, however, suggesting that a diminutive species of *Palaeanodon* existed in the Clarkforkian; the name *P. parvulus* is available for it.

In a previous study (Rose, 1978b: 669), I made note of a shallow, slender dentary (UM 63287) from the early Wasatchian (SC–7). It is slightly smaller than the Clarkforkian specimens and may also belong to *P. parvulus*. The other early Wasatchian specimens in the UM collection are smaller than typical *P. ignavus* but not as small as the Clarkforkian jaws (Figure 66C). They may represent intermediates between *P. parvulus* and *P. ignavus*, but sample sizes are still very small and testing of this hypothesis must await further collecting.

Until recently, *Palaeanodon* was the oldest known metacheiromyid, and its origin was not at all clear. Discovery of a more primitive late Tiffanian metacheiromyid, *Propalaeanodon schaffi* from the Polecat Bench sequence (Rose, 1979), contributes toward solution of this problem. The Tiffanian genus possesses certain features intermediate between epoicotheriids and the more specialized *Palaeanodon*, thus indicating that metacheiromyids were derived from the Epoicotheriidae. *Propalaeanodon* itself is a plausible ancestor for *Palaeanodon*.

The Palaeanodonta are a unified group (Rose, 1978b, 1979), but the ordinal affinities of the suborder are uncertain. Evidence has been adduced by various authors to support palaeanodont relationship to the Xenarthra, the Pholidota, or both (in the latter case, revitalizing the concept of the Edentata). It appears that additional evidence will be needed before a confident ordinal assignment can be made.

## V

# CLARKFORKIAN MAMMALIAN FAUNAS OUTSIDE THE CLARK'S FORK BASIN

THE CLARKFORKIAN FAUNA was, until recently, defined and based principally on collections from the Clark's Fork Basin, Wyoming, and this limited geographic range may have been one of the reasons why doubt arose about the validity of the Clarkforkian as a land-mammal age. Aside from these collections, only two other samples were recognized as Clarkforkian in age when first described. A fauna from Buckman Hollow in western Wyoming was described by Gazin (1942, 1956) and it is, as Gazin indicated, "beyond doubt a Clarkforkian assemblage" (Gazin, 1956: 3). Morris (1966) described a small collection of fossil mammals from Baja California that he considered of probable Clarkforkian age.

Two other faunas of Clarkforkian age were described decades ago but were not recognized as being Clarkforkian until very recently. These are the Bear Creek fauna of the northern Clark's Fork Basin (southern Montana) and the Plateau Valley fauna of Colorado (partly Clarkforkian in age).

In this chapter, collections from outside of the type area are reviewed in order to determine the geographic range of Clarkforkian faunas and to assess the utility of the Clarkforkian as a North American Land-Mammal Age. As a result of studies summarized here, it is now possible to identify several Clarkforkian faunas in Wyoming, southern Montana, and Colorado, as well as questionable Clarkforkian faunas from Baja California and Texas (Figure 67; Rose, 1977; Gingerich and Rose, 1977). All these faunas are discussed briefly below.

## BIGHORN BASIN, WYOMING

In addition to the Clark's Fork Basin, several parts of the northern Bighorn Basin in Wyoming have yielded Clarkforkian assemblages of lesser significance. The most important sites are Rough Gulch (=UM locality SC–196), Foster Gulch (two localities), and the Ries Locality. Collections from these localities are mainly at Princeton University, but some specimens from Rough Gulch are housed at the American Museum of Natural History and the University of Michigan. With one exception (?*Bathyopsoides harrisorum* from the Ries Locality), all taxa in these small collections are also represented in the Clarkforkian fauna from the Clark's Fork Basin. The stratigraphic positions of the sites are uncertain, but *Plesiadapis cookei* has been found at Rough Gulch and at Foster Gulch (Cleopatra Reservoir), indicating that they are middle Clarkforkian. Faunal lists for these sites have been modified from compilations prepared by D. C. Parris, who has kindly allowed them to be presented here.

### Rough Gulch

The Rough Gulch Locality (SC–196), on the southwest side of McCullough Peak south of Ralston (secs. 17 and 18, T.53 N., R.100 W.), was discovered by Sinclair and Granger (1912), who believed that the fossils came from near the top of the "Fort Union" Formation. Van Houten (1944) later confirmed that they were from that horizon, by then called the Polecat Bench Formation. Sinclair and Granger included a faunal list, but only one element (*Phenacodus*) was confidently identified to the generic level. Subsequent work at this site by Princeton and the University of Michigan has added to the fauna, and the following taxa are now recorded from Rough Gulch:

- Order PRIMATES
  - Family Plesiadapidae
    - *Plesiadapis cookei*[1]
  - Family Carpolestidae
    - *Carpolestes nigridens*
- Order CONDYLARTHRA
  - Family Phenacodontidae
    - *Phenacodus* sp., probably *P. primaevus*
    - *Ectocion osbornianus*
- Order MESONYCHIA
  - Family Mesonychidae
    - *Dissacus* sp.
- Order DINOCERATA
  - Family Uintatheriidae
    - *Probathyopsis praecursor*

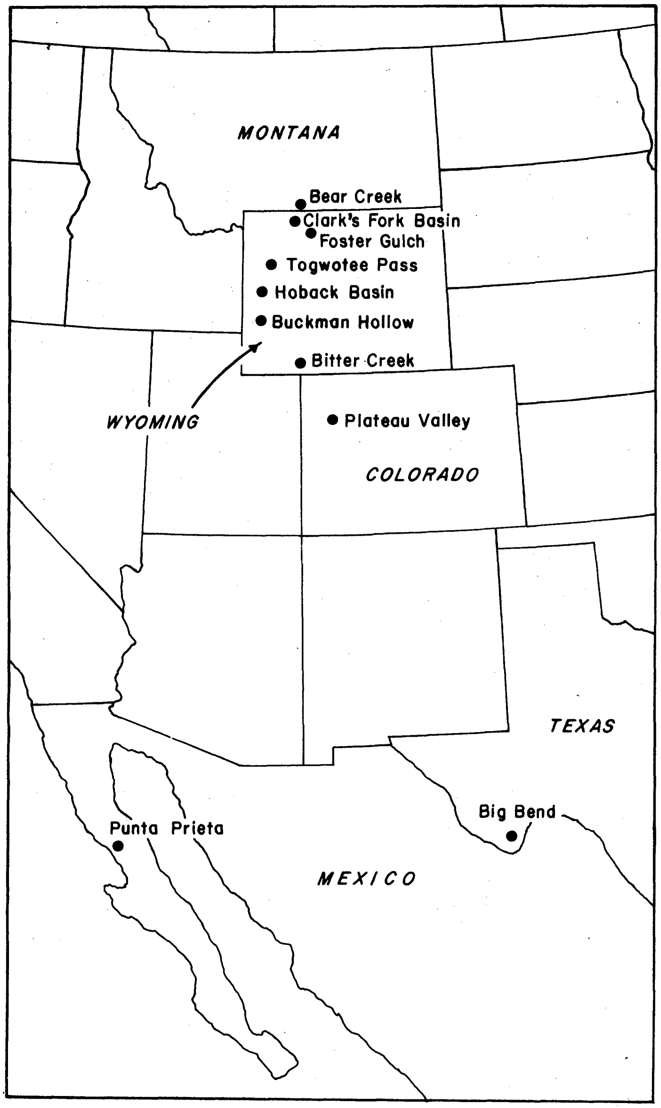

Figure 67. Clarkforkian localities in western North America.

Order CARNIVORA
  Family Miacidae
    *Didymictis protenus proteus*
Order RODENTIA
  Family Paramyidae
    cf. *Paramys*, probably two species

Note, Rough Gulch:
[1] PU 17973, right dentary with $P_4$–$M_1$, cited by Gingerich (1976b).

### Foster Gulch Oil Well No. 1

This locality, situated about 10 miles northwest of Emblem (NE¼ sec. 17 and NW¼ sec. 16, T.54 N., R.96 W., Big Horn County), was discovered in 1970 by a Princeton field crew under the direction of the late Dr. G. L. Jepsen. A faunal list was recently published by Gingerich and Rose (1979), and the mammals are relisted here:

Order CONDYLARTHRA
  Family Phenacodontidae
    *Phenacodus* sp.
    *Ectocion osbornianus*
  Family Arctocyonidae
    cf. *Thryptacodon antiquus*[1]
Order PANTODONTA
  Family Coryphodontidae
    *Coryphodon* sp.
Order TAENIODONTA
  Family Stylinodontidae
    *Lampadophorus expectatus*[2]
Order RODENTIA
  Family Paramyidae
    *Paramys* sp.

Notes, Foster Gulch Oil Well No. 1:
[1] PU 20853, snout and lower jaws described and figured by Gingerich and Rose (1979).
[2] PU 20864, about 30 associated teeth.

### Foster Gulch: Cleopatra Reservoir Locality

This small assemblage was collected about 4 miles north-northeast of the Foster Gulch oil well site (sec. 12, T.54 N., R.96 W., Big Horn County) by David C. Parris and assistants. The components of the fauna are:

Order PROTEUTHERIA
  Family ?Pantolestidae
    ?*Palaeosinopa* sp.
Order PRIMATES
  Family Plesiadapidae
    *Plesiadapis cookei*[1]
    *Plesiadapis* cf. *dubius*
  Family Carpolestidae
    *Carpolestes* cf. *nigridens*
Order CONDYLARTHRA
  Family Phenacodontidae
    *Phenacodus* sp.
    cf. *Ectocion osbornianus*
  Family Hyopsodontidae
    hyopsodontid, unident.
Order PANTODONTA
  Family Coryphodontidae
    *Coryphodon* sp.
Order CARNIVORA
  Family Miacidae
    *Didymictis protenus proteus*

Note, Cleopatra Reservoir Locality:
[1] PU 17825, right maxilla with $dP^{3-4}$, cited by Gingerich (1976b).

### Ries Locality

The Ries Locality east of Powell (secs. 20 and 21, T.55 N., R.98 W., Park County) was discovered by Princeton field parties directed by Dr. Jepsen, and it was worked periodically by them from the 1930s through 1950s. Its mammalian fauna includes:

Order CONDYLARTHRA
  Family Phenacodontidae
   *Ectocion osbornianus*
Order TILLODONTIA
  Family Esthonychidae
   *Esthonyx* sp.
Order PANTODONTA
  Family Coryphodontidae
   *Coryphodon* sp.
Order DINOCERATA
  Family Uintatheriidae
   ?*Bathyopsoides harrisorum*[1]
Order TAENIODONTA
  Family Stylinodontidae
   *Lampadophorus* sp.
Order RODENTIA
  Family Paramyidae
   paramyid, unident.

Note, Ries Locality:

[1] PU 16444, an edentulous dentary with an enlarged inframandibular process. Identified by Dr. Jepsen as belonging to this species, otherwise known only from the Plateau Valley fauna. It is possible that this specimen represents a large male *Probathyopsis praecursor*.

## Bear Creek, Montana

Bear Creek is situated in southern Carbon County, Montana (northern Clark's Fork Basin), about 12 miles north of the Wyoming state line. Discovered in 1926 and first published two years later, the mammalian fauna from Bear Creek was among the first Clarkforkian assemblages to be described; but it was not considered Clarkforkian until much later (Van Valen and Sloan, 1966). Both Simpson (1929b) and Jepsen (1930b), however, remarked on the close similarity between the Bear Creek and Clark's Fork Basin faunas. Most of the fauna was described by Simpson (1928, 1929a, b) and Jepsen (1937), and minor additions or discussions have been presented by several authors (see references cited in notes following the faunal list). The Bear Creek fauna is now generally recognized as Clarkforkian (Sloan, 1969; Rose, 1975a, 1977; Gingerich, 1976b). The fossiliferous zone has been included in the Fort Union Formation (Simpson, 1928) but should be considered in the Polecat Bench Formation.

The Bear Creek assemblage is one of the few large collections of small Clarkforkian mammals. It has been widely regarded as an atypical fauna because of the abundance of the dermopteran *Planetetherium* (rarely known elsewhere) and the absence of multituberculates, and because of its unusual geological occurrence. Nearly all the fossils come from a thin carbonaceous clay just above coal vein number 3 in the roof of the Eagle Mine. Some specimens have been obtained from the same horizon in the nearby Foster Mine, but all taxa from there are also known from the Eagle Mine. The fauna bears similarities to that from locality SC-188 (but is probably slightly older), suggesting that the Bear Creek fauna may not be such an unusual assemblage after all. Certain species (e.g., *Plesiadapis dubius* together with *Carpolestes nigridens*, *Paramys atavus*, and *Haplomylus simpsoni*) clearly indicate that the fauna is of Clarkforkian age, and is not a Tiffanian "Silver Coulee" equivalent as previously believed. An early Clarkforkian age seems indicated by the mutual occurrence of *Chiromyoides potior*, *Phenacodaptes sabulosus*, and *Paramys atavus*, and the absence of *Plesiadapis cookei*. The Bear Creek assemblage is clearly size-sorted: only four species (known only from isolated teeth) are from medium-sized or large animals.

The most recent review of the Bear Creek fauna was by Van Valen and Sloan (1966: 272–273) who, however, did not revise the fauna. Russell (1967) included their faunal list, with minor emendations, in his summary of the North American continental Paleocene. The revised faunal list presented below is based on my own study of the entire Bear Creek collections (about 200 specimens) in the American Museum of Natural History, the Carnegie Museum of Natural History, and Princeton University. It contains about 20 species, an increase over the 16 listed by Van Valen and Sloan, and includes many changes and additions. Several isolated incisors and tiny dentary fragments could not be identified, although some may belong to species already identified in the fauna. Relative abundances of the Bear Creek taxa are presented in Table 52 (Chapter VII).

The Bear Creek local fauna, as now known, comprises the following taxa:

Order POLYPROTODONTA
  Family Didelphidae
   cf. *Peradectes* sp.[1]
Order PROTEUTHERIA
  Family Pentacodontidae
   *Protentomodon ursirivalis*[2]
   ?*Aphronorus* sp.[3]
  Family Pantolestidae
   cf. *Palaeosinopa didelphoides*[4]
  Family Apatemyidae
   *Apatemys kayi*[5]
Order LIPOTYPHLA[6]
  Family Erinaceidae

*Leipsanolestes siegfriedti*[7]
Order DERMOPTERA
Family Plagiomenidae
*Planetetherium mirabile*[8]
Order PRIMATES
Family ?Microsyopidae
?microsyopid, indet.[9]
Family Plesiadapidae
*Plesiadapis dubius*[10]
*Chiromyoides potior*[11]
Family Carpolestidae
*Carpolestes nigridens*[12]
Family Paromomyidae
*Phenacolemur pagei*[13]
Order CONDYLARTHRA
Family Arctocyonidae
*Thryptacodon pseudarctos*[14]
Family Phenacodontidae
*Phenacodus* cf. *primaevus*[15]
Family Hyopsodontidae
*Haplomylus* cf. *simpsoni*[16]
cf. *Phenacodaptes sabulosus*[17]
Order MESONYCHIA
Family Mesonychidae
*Dissacus* sp.
Order TAENIODONTA
Family Stylinodontidae
*Lampadophorus lobdelli*
Order CARNIVORA
Family Miacidae
?*Viverravus* sp.[18]
Order RODENTIA
Family Paramyidae
*Paramys atavus*[19]

Notes, Bear Creek:

[1] New record, CM 11548, left dentary with one molar.

[2] The affinities of *Protentomodon* are unclear. I follow Van Valen and Sloan (1966) and Van Valen (1967) in placing it tentatively in the Pentacodontidae; but molar structure also shows resemblances to that of apatemyids, a similarity independently recognized by Bown (1979). This taxon is known only from Bear Creek.

[3] Two isolated upper molars, CM 11683 and AMNH 22222, belong to a species not otherwise represented in the collection. The affinities of these teeth are unclear. They show some resemblances to *Aphronorus*, but are significantly younger than all other records of the genus.

[4] AMNH nos. 22175, 22198, 22221, CM nos. 11535, 11684, 11685, and one uncatalogued Princeton specimen (all isolated teeth) belong to a pantolestid near *Palaeosinopa didelphoides* (see also Van Valen, 1967: 222), or perhaps *P. simpsoni*. AMNH 22175 was allocated by Simpson (1928) to ?*Pentacodon* cf. *inversus* and was subsequently transferred to *Palaeosinopa* by Van Valen and Sloan (1966). AMNH 22198, an upper molar, differs from *Palaeosinopa* in the closer proximity of its paracone and metacone, hence it may not belong to this genus. CM 11535, a left lower molar, is probably a pantolestid but is smaller than both *P. didelphoides* and *P. lutreola* (CM 11535 L=2.5).

[5] This species was originally placed in the genus *Labidolemur* and was transferred to *Apatemys* by McKenna (1960). West (1973c) synonymized *Apatemys kayi* with *A. bellus*, but I follow Bown and Schankler (1980) in maintaining *A. kayi* as a valid species. See Jepsen (1934) and McKenna (1963) for other discussions of the Bear Creek specimens.

[6] Russell (1967: 79) listed *Mckennatherium ladae* in the Bear Creek fauna, but it does not appear to be represented there.

[7] *Leipsanolestes siegfriedti* was placed in the genus *Leptacodon* (as a subgenus) by Simpson (1929a), in *Entomolestes* by McKenna (1960) and Van Valen and Sloan (1966), and in *Talpavus* by Robinson (1968b). I follow Russell et al. (1975) and Krishtalka (1976a), who retain *Leipsanolestes* as a valid genus, and I tentatively accept Krishtalka's reference of it to the Erinaceidae. Forms near or identical to this species are known from the Clarkforkian of the Clark's Fork Basin, Washakie Basin, and Togwotee Pass area.

[8] This is the most common species in the fauna, accounting for a third of all the specimens. Szalay (1969a: figure 7) illustrated the best maxilla known, CM 11671. Rose and Simons (1977) noted a possible record of *Planetetherium mirabile* from the Clark's Fork Basin, but it is more likely that the specimen represents the closely allied *Worlandia inusitata* (Bown and Rose, 1979). The only other possible specimen of *Planetetherium* from elsewhere than Bear Creek is an isolated tooth from the Togwotee area.

[9] Two upper incisors, AMNH nos. 22152 and 22227E, may belong to a microsyopid. They display morphology believed to characterize microsyopid upper incisors (Gingerich 1976b: figure 38). AMNH 22152 was illustrated by Simpson (1928: figure 12).

[10] AMNH 22154, a left $M_3$, was allocated to *Plesiadapis* by Simpson (1928) and was considered to belong to *Paromomys* or *Phenacolemur* by Van Valen and Sloan (1966). Gingerich (1976b) identified it as *Plesiadapis dubius*, an assignment with which I agree. Incisors of *P. dubius* are included in AMNH 22227 (specimens G, J, and possibly B).

[11] PU 18348, right lower incisor (Gingerich, 1976b).

[12] *Carpolestes nigridens* is a senior synonym of *C. aquilae* Simpson, 1929b (see Rose, 1975a). All carpolestids from Bear Creek are referable to the same species.

[13] AMNH 22244, right $P_4$, and isolated incisors in AMNH 22227. AMNH 22244 is the holotype of Van Valen's (1967) *Parapheliscus bjorni* ("undescribed genus of apheliscine hyopsodonts" in Van Valen and Sloan, 1966), recognized as a tooth of *Phenacolemur* by Delson (1971). Although somewhat smaller than most specimens of *P. pagei*, it is best referred to that species.

[14] Considered a synonym of *T. antiquus* by Van Valen and Sloan (1966) but tentatively recognized as valid by Gingerich (1978).

[15] Only two teeth of *Phenacodus* are known from Bear Creek: AMNH 22197 and PU 17713. Surprisingly, *Ectocion*, normally abundant in the Clarkforkian, has not been found at Bear Creek.

[16] AMNH numbers 22172 (left $P_4$), 22227I (talonid of right lower molar), 22218 (left $M_1$ or $M_2$ catalogued with a specimen of *Planetetherium*), PU 18347 (right dentary with $M_{1-3}$), and CM 11663 (left dentary with $M_{2-3}$), represent *Haplomylus* and are probably small specimens of *H. simpsoni*. Their small size is consistent with the inferred early Clarkforkian age of Bear Creek (see Figure 38). CM 11663 is of questionable reference. It is mounted in plaster and is labelled *Leipsanolestes siegfriedti* (conceivably it is a Graybullian specimen that became mixed with Bear Creek material many years ago).

[17] AMNH nos. 22181, 22245, 22246, and CM 11669 represent *Phenacodaptes sabulosus* or an intermediate between it and *Apheliscus nitidus*. Van Valen and Sloan (1966) suggested that AMNH 22181 might belong to *Haplaletes*, but this is unlikely. AMNH 22245 was referred to *Parapheliscus bjorni* by Van Valen (1967), but it is not conspecific with the holotype of that species (which is itself referable to *Phenacolemur*). Delson (1971) first reported *Phenacodaptes* from Bear Creek, but he included AMNH 22172 (*Haplomylus*, see note 16) in his sample of that genus.

[18] AMNH 22220 and CM 11530, an $M_1$ and an $M_1$ trigonid, respectively. The former was identified as a hyaenodontid or a palaeoryctid (Van Valen and Sloan, 1966), and notations on its label suggest oxyaenid or miacid affinities. My comparisons indicate that both specimens belong to a small miacid, probably *Viverravus*.

[19] First described by Jepsen (1937); additional records by McKenna (1961) and Wood (1962).

## TOGWOTEE PASS, WYOMING

One of the largest and most diverse Clarkforkian assemblages from outside the Bighorn Basin has been collected from the "lower variegated sequence" in the Purdy Basin near Togwotee Pass, under the direction of Dr. Malcolm McKenna. A preliminary faunal list was published by McKenna (1972a), but it includes all fossil mammals from the "lower variegated sequence," a unit spanning latest Tiffanian, Clarkforkian, and early Wasatchian time. Dr. McKenna kindly allowed me to study these collections and to include a list of the mammals now known from the more than 30 Clarkforkian localities in the sequence. A tabulation of mammalian occurrences in the Purdy Basin prepared by Earl Manning has been of assistance during my study of the Togwotee collections.

Precise stratigraphic relationships of the Purdy Basin sites are unknown, partly because of the area's structural complexity, but relative positions of certain sites can be determined. No attempt is made here to subdivide the Purdy Basin Clarkforkian. *Plesiadapis cookei* occurs throughout the Clarkforkian part of the sequence, however, suggesting that only the middle Clarkforkian is represented. It is possible that there was no deposition here during the subsequent *Phenacodus-Ectocion* Zone, or that beds of this zone are present but have not yet produced fossils (McKenna, personal communication). Alternatively, it may be that *P. cookei* persisted longer in the Togwotee area than in the Clark's Fork Basin, but no particular evidence supports this at present. Hence, the Purdy Basin Clarkforkian localities are here tentatively considered to date from the middle Clarkforkian only (*Plesiadapis cookei* Zone).

The Purdy Basin fauna contains at least one, and possibly five, species not present in the Clarkforkian of the type area. These are *Dipsalodon churchillorum*, sp. nov. (known also from the late Tiffanian of the northern Bighorn Basin), and possibly the following: *Anacodon*? *nexus* (known from the late Tiffanian of the Bighorn Basin and the Clarkforkian of Buckman Hollow), *Phenacodaptes sabulosus* (known from the late Tiffanian of the Bighorn Basin and possibly the Clarkforkian at Bear Creek), *Planetetherium mirabile* (known from the Clarkforkian at Bear Creek), and *Paramys excavatus* (known from the Wasatchian of the Bighorn Basin). All other species present are also found in the *Plesiadapis cookei* Zone of the Clark's Fork Basin.

The mammalian fauna of the Purdy Basin Clarkforkian consists of the following taxa:

- Order LIPOTYPHLA
  - Family Erinaceidae
    - cf. *Leipsanolestes siegfriedti*[1]
- Order DERMOPTERA
  - Family Plagiomenidae
    - cf. *Planetetherium mirabile*[2]
- Order PRIMATES
  - Family Plesiadapidae
    - *Plesiadapis cookei*
    - *Plesiadapis dubius*
  - Family Carpolestidae
    - *Carpolestes* cf. *nigridens*
  - Family Paromomyidae
    - *Phenacolemur pagei*
- Order CONDYLARTHRA
  - Family Arctocyonidae
    - ?*Chriacus* sp.
    - *Anacodon*? *nexus*[3]
  - Family Phenacodontidae
    - *Phenacodus primaevus*[4]
    - *Phenacodus vortmani*[4]
    - *Ectocion osbornianus*
    - ?*Ectocion parvus*[5]
  - Family Hyopsodontidae
    - *Aletodon gunnelli*
    - *Haplomylus simpsoni*
    - *Phenacodaptes sabulosus* (lower level only)[6]
    - *Apheliscus nitidus* (upper level only)[6]
- Order MESONYCHIA
  - Family Mesonychidae
    - *Dissacus* sp.
- Order TILLODONTIA
  - Family Esthonychidae
    - *Esthonyx* cf. *ancylion*
- Order PANTODONTA
  - Family Coryphodontidae
    - *Coryphodon* sp.
- Order TAENIODONTA
  - Family Stylinodontidae
    - stylinodontine, indet.
- Order NOTOUNGULATA
  - Family Arctostylopidae
    - *Arctostylops steini*[7]
- Order CREODONTA
  - Family Oxyaenidae
    - *Oxyaena transiens*
    - *Oxyaena platypus*
    - *Dipsalodon churchillorum*[8]
    - palaeonictine, ?*Dipsalodon matthewi*a1[9]
    - small oxyaenid?, unident.
- Order CARNIVORA
  - Family Miacidae
    - *Didymictis protenus proteus*
    - *Viverravus politus*[10]
    - ?*Viverravus acutus*[11]
- Order RODENTIA
  - Family Paramyidae
    - *Paramys* cf. *atavus*
    - *Paramys* cf. *excavatus*
    - paramyids, unident. (possibly one or two additional species)

Notes, Purdy Basin:

[1] AMNH 86745, slightly larger than Bear Creek specimens of *Leipsanolestes siegfriedti.*

[2] AMNH 86869, left $P_3$, slightly larger than its counterpart in Bear Creek *Planetetherium mirabile*.

[3] An uncatalogued $M^1$ (AMNH) represents an arctocyonid larger than *Thryptacodon*; it is closest in structure to $M^1$ of *Anacodon*? *nexus*.

[4] Two sizes of *Phenacodus* are present and are tentatively referred to the same species recognized in the Clark's Fork Basin.

[5] West (1976) listed two specimens (AMNH nos. 57208 and 57286) of *E. parvus* in the Togwotee Pass sample. It is possible that they are small individuals of *E. osbornianus*.

[6] Both *Phenacodaptes sabulosus* and *Apheliscus nitidus* appear to be present, but they do not coexist. *P. sabulosus* comes from the Lower Red Creek locality (e.g., AMNH 56270), and *A. nitidus* is known from the Middle Red Creek locality (e.g., AMNH 56268). Specimens intermediate between these two species are also present (e.g., AMNH nos. 86726 and 86889). The two species appear to be segments of a single lineage, and there is no evidence that more than one species existed at any given time.

[7] An incomplete lower molar is the first record of this rare notoungulate from outside the Clark's Fork Basin.

[8] AMNH nos. 56137 and possibly 86865 are the only Clarkforkian records of this new species. The holotype (the only other specimen) is from the late Tiffanian of the Clark's Fork Basin; see Chapter IV.

[9] AMNH 57284, a trigonid of a left lower molar, is similar in size and form to that of *D. matthewi*.

[10] AMNH 57207, a trigonid of $M_1$.

[11] Specimen not seen.

## HOBACK BASIN, WYOMING

Several small assemblages of early Eocene mammals have been reported from the Hoback Basin by Dorr and others (Dorr, 1952, 1958b, 1978; Dorr and Steidtmann, 1970; Dorr, Spearing, and Steidtmann, 1977) and have been considered to be of early Wasatchian or, possibly, Clarkforkian age. Most were initially reported to come from the upper Hoback Formation but more recently have been listed from the Chappo Member of the Wasatch Formation. These include collections from localities UM-Sub-Wy 2, 4, 7, 10, 16, 20, and 29.

UM-Sub-Wy 2, 4, and 16 are at about the same stratigraphic level and have yielded *Coryphodon*, *Pelycodus*, *Diacodexis*, *Hyracotherium*, and *Hyopsodus*, as well as seeds of the hackberry *Celtis*. Although the possibility was entertained that these faunas are of Clarkforkian age (Dorr et al., 1977), the combination of taxa present indicates clearly that they are early Wasatchian (Dorr, 1952, 1978).

UM-Sub-Wy 7, 10, and 20 are approximately equivalent in age and lie stratigraphically somewhat below UM-Sub-Wy 2, 4, and 16. They have produced *Phenacodus* (two species), *Probathyopsis*, *Coryphodon*, and *Haplomylus* cf. *simpsoni* (UM 34761, $P_4$, formerly identified as cf. *Haplomylus speirianus* by Dorr, 1958b, 1978). The presence of these taxa, the lower stratigraphic level, and the absence of typical early Wasatchian taxa such as those found at UM-Sub-Wy 2, combine to suggest strongly that these localities are Clarkforkian in age, as Dorr (1978) indicated.

Dorr and Steidtmann (1970) described a small fauna, including *Pelycodus*, *Meniscotherium*, *Hyracotherium*, and *Haplomylus*, from UM-Sub-Wy 29. They considered its age to be probably early or middle "Graybullian," but included the possibility that it might prove to be Clarkforkian. As subsequently stated by Dorr (1978), it is almost certainly "Graybullian" (= early Wasatchian).

## BUCKMAN HOLLOW, WESTERN WYOMING

The Buckman Hollow local fauna is one of the few mammalian assemblages that was initially recognized as Clarkforkian. Gazin (1942, 1956b) described the U. S. National Museum collection from Buckman Hollow, which is the largest. During the 1977 and 1978 field seasons, parties under the direction of Dr. Philip Gingerich made collections from Buckman Hollow for the University of Michigan Museum of Paleontology. The faunal list presented below is based on the collections of both institutions. All fossil vertebrates are from the Chappo Member of the Wasatch Formation (Oriel, 1962; =Almy Formation of Gazin).

Some of the taxa from Buckman Hollow occur in both late Tiffanian and Clarkforkian beds in the Clark's Fork Basin, whereas *Anacodon*? *nexus* and *Titanoides* sp. are unknown later than the Tiffanian there, although the former has been found in other Clarkforkian localities. *Plesiadapis cookei* occurs at Buckman Hollow, hence it may be tentatively considered middle Clarkforkian.

A detailed account of the Buckman Hollow fauna is in preparation by Gingerich and Dorr. The mammalian fauna now known includes:

- Order MULTITUBERCULATA
  - Family Ptilodontidae
    - ?*Prochetodon* sp.[1]
- Order PRIMATES
  - Family Plesiadapidae
    - *Plesiadapis dubius*[2]
    - *Plesiadapis cookei*
  - Family Carpolestidae
    - *Carpolestes* sp.
- Order CONDYLARTHRA
  - Family Arctocyonidae
    - *Thryptacodon pseudarctos*[3]
    - *Anacodon*? *nexus*[4]
  - Family Phenacodontidae
    - *Phenacodus almiensis*[5]
    - *Phenacodus primaevus*[5]
    - *Ectocion osbornianus*
  - Family Hyopsodontidae

*Apheliscus nitidus*
Order MESONYCHIA
  Family Mesonychidae
    *Dissacus* sp.
Order PANTODONTA
  Family ?Titanoideidae
    cf. *Titanoides* sp.[6]
Order DINOCERATA
  Family Uintatheriidae
    *Probathyopsis* sp.[7]
Order TAENIODONTA
  Family Stylinodontidae
    *Lampadophorus* sp.
Order CARNIVORA
  Family Miacidae
    ?*Viverravus* sp.[8]
Order RODENTIA
  Family Paramyidae
    *Paramys* sp.

Notes, Buckman Hollow:

[1] UM 68358, an isolated right lower incisor, see Krause (1980).

[2] Gazin (1942) described the species *Plesiadapis rubeyi* from Buckman Hollow. Gingerich (1976b) synonymized *P. rubeyi* with *P. fodinatus*, a late Tiffanian species. Larger collections now available suggest that both *P. rubeyi* and *P. pearcei* (Gazin, 1956b) are synonyms of *P. dubius*, not of *P. fodinatus* (Gingerich, personal communication, 1979). Only one small species of *Plesiadapis* appears to be present.

[3] UM 68355 (Gingerich, 1978).

[4] Known also from the late Tiffanian of the Bighorn Basin and possibly the Clarkforkian of the Purdy Basin.

[5] Two species of *Phenacodus* are present. Gazin (1956b) mentioned that, in addition to typical *P. primaevus*, somewhat smaller specimens are also present, which he referred to *P. primaevus intermedius*. He allocated the smallest specimens to a new species, *P. almiensis* (Gazin, 1942). These specimens closely resemble those referred here to *P. vortmani*, from the Clark's Fork Basin. West (1976) considered *P. almiensis* to be a synonym of *P. vortmani*, but it is possible that *P. almiensis* is valid and is the proper name for the small Clarkforkian species of *Phenacodus*.

[6] UM 71339, a lower molar from the Chappo-1 locality (=UM locality BH-5) at Buckman Hollow. *Titanoides* is otherwise unknown from the Clarkforkian.

[7] Gazin (1956b) reported two upper premolars of *Probathyopsis* which, he observed, are larger than those of *P. praecursor* of the Clark's Fork Basin. UM 71331, a left $M_2$, also appears to be larger than *P. praecursor*. Gazin indicated that the USNM specimens were closer in proportions to *Bathyopsoides harrisorum*, from the Plateau Valley fauna, and he suggested that the latter might be a male of *Probathyopsis*.

[8] Gazin (1956b) referred a single $M_1$ (USNM 23063) to ?*Didymictis* sp., noting that the tooth is much smaller than in *Didymictis protenus proteus* and slightly smaller than in *Protictis haydenianus*. I have not seen the specimen, but Gazin's description suggests that it represents *Viverravus politus*.

## BITTTER CREEK, WASHAKIE BASIN, WYOMING

A large and diverse assemblage of Clarkforkian mammals has been recovered at a single site in the Washakie Basin, the "Big Multi Locality" (UCMP locality V76134), by Dr. D. E. Savage and his colleagues at the University of California at Berkeley. They have graciously permitted me to study this unpublished collection and to include this summary of its fauna. The sample consists primarily of isolated teeth obtained through screen-washing and it appears to be size-sorted, with a strong bias toward specimens of small size. The Big Multi Locality is situated in the Fort Union Formation, about 75–100 m below the base of the Wasatch Formation. It is the lowest productive mammal-bearing level in the Bitter Creek early Tertiary sequence.

The fauna comprises more than 25 species and is thus one of the most diverse Clarkforkian assemblages from a single locality. Among its constituents is *Plesiadapis cookei*, and almost all of the taxa also occur in the *P. cookei* Zone of the Clark's Fork Basin. The Big Multi fauna is compositionally very similar to that of the two richest sites for small mammals in the type area of the Clarkforkian, SC–143 (Paint Creek locality) and SC–188. It contains only one species that is unlike any known from the Clark's Fork Basin: a *Navajovius*-like microsyopid. Conspicuously absent from the assemblage, however, are *Coryphodon* and *Haplomylus*, typically common elements of Clarkforkian faunas. The Big Multi local fauna may be confidently considered middle Clarkforkian in age (*Plesiadapis cookei* Zone).

The locality derives its name from the discovery of a large species of multituberculate (?*Neoliotomus*) during initial field work. Unfortunately, the specimen was lost soon after and has not been recovered; hence its identity remains a mystery.

The Big Multi local fauna includes the following taxa:

Order MULTITUBERCULATA
  Family Neoplagiaulacidae
    *Ectypodus* sp.[1]
  Family Eucosmodontidae
    cf. *Microcosmodon conus*
Order POLYPROTODONTA
  Family Didelphidae
    cf. *Peradectes* sp.[2]
Order LIPOTYPHLA
  Family Nyctitheriidae
    cf. *Pontifactor bestiola*
  Family Erinaceidae
    cf. *Leipsanolestes* sp.
  Family uncertain
    erinaceoids, several species, unident.[3]
Order DERMOPTERA
  Family Plagiomenidae
    plagiomenid, unident.[4]
Order PRIMATES
  Family Microsyopidae
    *Niptomomys* sp.
    *Tinimomys graybulliensis*[5]
    ?undescribed microsyopid, near *Navajovius*[6]

Family Plesiadapidae
*Plesiadapis cookei*
*Plesiadapis dubius*[7]
*Chiromyoides* cf. *major*
Family Carpolestidae
*Carpolestes nigridens*
Family Paromomyidae
*Phenacolemur* cf. *pagei*
*Phenacolemur* cf. *simonsi*[8]
Order CONDYLARTHRA
Family Phenacodontidae
*Phenacodus primaevus*[9]
*Phenacodus vortmani*[9]
*Ectocion osbornianus*
Family Hyopsodontidae
cf. *Aletodon gunnelli*[10]
cf. *Apheliscus nitidus*[11]
Order TILLODONTIA
Family Esthonychidae
*Esthonyx* sp.[12]
Order DINOCERATA
Family Uintatheriidae
*Probathyopsis* sp.
Order CARNIVORA
Family Miacidae
*Didymictis* sp.
?*Viverravus* sp., near *V. acutus*
Order RODENTIA
Family Paramyidae
cf. *Paramys atavus*
paramyid, very small, unident.

Notes, Big Multi Locality:

[1] Specimens referable to *Ectypodus* resemble both *E. powelli* and *E. tardus*. $P_4$ length=3.10–3.20 (n=2), which is closer to the mean for *E. powelli*.

[2] It is possible that *Peratherium* is present in addition to *Peradectes*. Isolated upper molars in this sample have prominent stylar cusps B and D.

[3] Erinaceoid insectivores are common and diversified in the fauna. As many as five different species may be included here. Most specimens are isolated teeth, making accurate identification very difficult. These specimens bear resemblances to *Mckennatherium*, *Talpavus*, *Leipsanolestes*, *Litolestes*, and "*Leptacodon*."

[4] A single upper molar clearly represents a plagiomenid (L=2.5, B=3.4). It resembles both *Planetetherium mirabile* and *Plagiomene accola* but is not exactly like either one and may belong to an undescribed species. Additional specimens will be required in order to assess its precise affinities.

[5] This is the first record of this diminutive rare primate from outside the Bighorn Basin, where it is known from both Clarkforkian and early Wasatchian sediments.

[6] Two upper molars seem to represent a *Navajovius*-like microsyopid (Savage, personal communication), but they are larger than *N. kohlhaasae* of the Tiffany beds. A small $M_1$ and a lower central incisor clearly belong to a microsyopid and may represent the same species; alternatively they may belong to a fourth microsyopid in the fauna, perhaps a species of *Microsyops*.

[7] *Plesiadapis dubius* is represented only by an incomplete crown of the upper central incisor.

[8] A lower molar (L=1.5, B=1.3), much smaller than those of *Phenacolemur pagei*, is closest in size to *P. simonsi*. *P. simonsi* is known from early Wasatchian sediments of the Bighorn Basin and from a single upper tooth from the Clarkforkian of the Clark's Fork Basin.

[9] Two sizes of *Phenacodus* are present, apparently the same two species that occur in the Clark's Fork Basin and in the Togwotee Pass area.

[10] A single fragmentary upper molar is tentatively identified as *Aletodon gunnelli*.

[11] Specimens in this sample are closest in morphology to *Apheliscus nitidus*, but some are as large as or larger than *Phenacodaptes sabulosus* from the Bighorn Basin. The sample may represent a population transitional between the two species, as in the Togwotee Pass area.

[12] A fragmentary upper molar belongs to a small species of *Esthonyx*, possibly *E. xenicus*.

## PLATEAU VALLEY, PICEANCE BASIN, COLORADO

Patterson described many of the mammalian taxa from the Plateau Valley beds in a series of papers, mostly in the 1930s (Patterson, 1933, 1936, 1937, 1939, 1949a; Patterson and Simons, 1958; Patterson and West, 1973). Additions to the fauna and pertinent discussions have been presented by Jepsen (1940), Simons (1960), Wood (1967), and Gingerich (1976b, 1977, 1978). With the exception of Gingerich (1976b) and Rose (1977), previous authors have regarded the Plateau Valley faunas to be late Paleocene (Tiffanian) in age. Fossils have been derived from several localities at different stratigraphic levels in the Atwell Gulch Member of the Wasatch Formation (Donnell, 1969; De Beque Formation of Patterson and others). Work in progress by Allen J. Kihm (University of Colorado) indicates that the Plateau Valley faunas are partly of late Tiffanian age and partly of Clarkforkian age. Most of the fossiliferous levels occur in an interval from 0 to 100 m above the base of the Atwell Gulch Member (Kihm, written communication, January 1979). Kihm's preliminary data on the stratigraphic occurrences of taxa in the Plateau Valley beds indicate that the Tiffanian-Clarkforkian boundary occurs within the Plateau Valley beds. Information generously provided by Kihm permits a tentative assessment of which taxa in the Plateau Valley assemblage are most likely to be of Clarkforkian age, and I have indicated this in the list below.

The Plateau Valley fauna is dominated by species of large mammals, most of which are probably of late Tiffanian rather than Clarkforkian age. Nonetheless, small mammals are relatively rare in the fauna. This situation is likely to change as Kihm intensifies efforts at a quarry situated near the Tiffanian-Clarkforkian boundary; it has already produced teeth of at least four small taxa.

The following faunal list has been compiled by Kihm (except where noted) and is included with his permission. The probable age of known specimens of each taxon (based on stratigraphic data) is indicated (T=Tiffanian, CF=Clarkforkian). Where no notation is given, stratigraphic data are unavailable.

- Order MULTITUBERCULATA
  - Family Eucosmodontidae
    - *Neoliotomus conventus*, CF[1]
- Order PRIMATES
  - Family Plesiadapidae
    - *Plesiadapis dubius*, T,CF
  - Family Paromomyidae
    - cf. *Phenacolemur* sp., CF[2]
- Order CONDYLARTHRA
  - Family Arctocyonidae
    - *Lambertocyon ischyrus*, CF[3]
  - Family Phenacodontidae
    - *Phenacodus primaevus*, T
    - *Ectocion osbornianus*[4]
    - *Prosthecion major*, CF[5]
  - Family Hyopsodontidae
    - *Aletodon* sp.[6]
    - cf. *Haplomylus* sp., CF
- Order TILLODONTIA
  - Family Esthonychidae
    - *Esthonyx* sp.[7]
- Order PANTODONTA
  - Family Titanoideidae
    - *Titanoides primaevus*, T
    - *Titanoides zeuxis*, T
    - *Titanoides*? sp.[8]
  - Family Barylambdidae
    - *Barylambda faberi*, T,CF
    - *Haplolambda quinni*, T
    - *Leptolambda schmidti*, T-CF[9]
  - Family Coryphodontidae
    - *Coryphodon* sp., CF
- Order DINOCERATA
  - Family Uintatheriidae
    - *Bathyopsoides harrisorum*, T?
    - *Probathyopsis newbilli*, T
- Order TAENIODONTA
  - Family Stylinodontidae
    - *Lampadophorus expectatus*, T
- Order CREODONTA
  - Family Oxyaenidae
    - cf. *Dipsalodon* sp.

Notes, Plateau Valley:

[1] First reported from the Plateau Valley fauna by Jepsen (1940).

[2] Tentative identification by Kihm of an incomplete $M^3$ from his quarry.

[3] Described by Gingerich (1978) as a new species of *Mimotricentes*, and transferred to a new genus, *Lambertocyon*, by Gingerich (1979).

[4] From Patterson's faunal list (1936). West (1976) identified FMNH P15536 as a specimen of *Ectocion parvus*. Neither *E. osbornianus* nor *E. parvus* is included in Kihm's faunal tabulation, and it is possible, as he suggests (personal communication) that *Prosthecion* was formerly listed as *Ectocion osbornianus*.

[5] *Prosthecion major* was first described by Patterson and West (1973). It closely resembles specimens allocated to *Phenacodus vortmani* from the Clark's Fork Basin and *Phenacodus almiensis* from Buckman Hollow, and it seems possible that all three are local variants of the same species. *Phenacodus* is highly variable and the features used by Patterson and West to separate *Prosthecion* appear to be within the range of variation of *P. vortmani* as now known from the Clark's Fork Basin. Further study of phenacodontids is necessary to resolve this problem.

[6] Gingerich (1977) assigned FMNH P14952 questionably to *Aletodon gunnelli*, but it is smaller than the Clark's Fork Basin specimens of this species (Gingerich, personal communication) and may belong to a new species.

[7] Reported by Patterson (1936), but specimens not relocated by Kihm (personal communication).

[8] FMNH P26080 may represent a titanoideid otherwise unknown in the assemblage (Simons, 1960: 39).

[9] Stratigraphic level of the specimen is approximately on the Tiffanian-Clarkforkian boundary as currently understood.

## BIG BEND NATIONAL PARK, TEXAS

Schiebout (1974) described fossil mammals from several successive levels of the Black Peaks Formation, a unit primarily of Paleocene age. In the Big Bend area, the formation is about 170 m thick, and fossils have been found in the interval from 23 to 137 m. Most are clearly of latest Torrejonian or Tiffanian aspect. Schiebout regards the highest level (137 m) as Clarkforkian. It has yielded fragmentary remains of only two taxa, ***Hyracotherium angustidens*** and ***Barylambda*** **sp.** ***Hyracotherium*** suggests an early Wasatchian age; it is not known from any undoubted Clarkforkian assemblage. *Barylambda* apparently occurs in late Tiffanian and Clarkforkian sediments at Plateau Valley, but is unknown from post-Clarkforkian sediments. Hence, it appears that Schiebout's level 137 m includes a range extension for one taxon or the other.

The next productive horizon beneath level 137 m is at 105 m, and it has yielded two taxa of latest Tiffanian or Clarkforkian age. They are *Lambertocyon eximius* (Gingerich, 1979; Schiebout's "undescribed arctocyonid") and a stylinodontine taeniodont, either *Lampadophorus* or *Psittacotherium* (probably the former). *Lambertocyon* and *Lampadophorus* occur together in late Tiffanian beds in the Bighorn Basin, and the former is known from the Clarkforkian at Plateau Valley, while the latter occurs also in the Clarkforkian of the Bighorn Basin. The evidence is, therefore, inconclusive, but it is possible that either level 105 m or level 137 m, or both, are Clarkforkian.

## BAJA CALIFORNIA

A small but potentially important collection of fossil mammals has been described from between Punta Prieta and Rancho Rosarito in Baja California (Morris, 1966, 1968; Ferrusquia-Villafranca, 1978). It is the only other sample from southern North America (besides the one from Big Bend) that is possibly Clarkforkian in age, and it would probably be the southernmost Clarkforkian fauna known. Geophysical evidence indicates that Baja California is part of the Pacific plate and was farther south in the early Tertiary than it is today (Hamilton, 1961; Atwater, 1970). Consequently, if the Baja assemblage proves to be of Clarkforkian age, it may have bearing on the directions of migration and sites of origin of members of its fauna.

The Baja fauna as now known includes *Hyracotherium seekinsi*, *Esthonyx* sp., a barylambdid (new genus and species, Ferrusquia-Villafranca, 1978), and an indeterminate creodont. In addition, it includes the gastropod *Turritella pachecoensis* and seeds of the hackberry *Celtis*. In this assemblage, the barylambdid suggests Tiffanian or Clarkforkian age, *Esthonyx* suggests Clarkforkian or Wasatchian age, and *Hyracotherium* suggests Wasatchian age. *Turritella pachecoensis* is usually considered a Paleocene taxon, whereas *Celtis* is strictly confined to the Wasatchian in the Bighorn Basin (Hickey, personal communication, 1977). The mammalian fauna is more similar to that of Schiebout's level 137 m (Big Bend area, Texas) than to any of the northern Clarkforkian faunas.

The age of the Punta Prieta local fauna is equivocal, but it is possibly Clarkforkian. Better collections will be required here and in the Black Peaks Formation of Texas in order to establish their ages accurately and, thereby, to determine whether *Hyracotherium* really was a member of southern Clarkforkian faunas.

## POSSIBLE CLARKFORKIAN FAUNAL CORRELATIVES OUTSIDE NORTH AMERICA

Reference has been made in previous chapters to mammalian fossils from Europe and Asia that appear to be closely related to North American Clarkforkian taxa. In particular, the similarity between the larger species of *Plesiadapis* in North America and the Paris Basin has been emphasized for its potential value in correlating faunas between the two continents. Although the late Paleocene and early Eocene mammalian faunas of Europe and Asia contain several endemic forms, the number of taxa in common with North America continues to increase as early Tertiary mammalian assemblages become better known. Thus evidence is growing that this was a period of considerable faunal interchange in Holarctica. Certain Asian and European faunas contain elements so similar to those of the Clarkforkian and early Wasatchian of the Western Interior that it seems probable that these faunas are approximately the same age as those in North America.

It is interesting to note that the two most common genera in the Clarkforkian, *Ectocion* and *Phenacodus*, are not known from Asian or European faunas that might be Clarkforkian equivalents. This suggests that the dispersal routes between the continents may have acted as filters during the Clarkforkian.

### Europe

A high degree of resemblance between early Eocene mammalian faunas of Europe and North America has been well documented (Simpson, 1947; Savage, 1971; McKenna, 1975b). Late Paleocene faunas of the two continents show considerably less taxonomic similarity (Russell, 1964), but the resemblance is still sufficient to indicate interchange.

Sparnacian (early Ypresian, early Eocene) faunas of Europe are widely regarded to be about the same age as Wasatchian faunas from North America. More than 30 genera are shared by faunas on both continents (Savage, 1971; McKenna, 1975b). Gingerich (1976b) and Gingerich and Rose (1977) suggested that the early Sparnacian locality Meudon, in the Paris Basin, is about the same age as the North American Clarkforkian, because of the mutual first appearance in both faunas of *Paramys*, *Coryphodon*, *Oxyaena*, and a large species of *Plesiadapis* (*P. russelli* at Meudon, *P. cookei* in North America). Evidence discussed above (Chapter III, Age of Clarkforkian, and Chapter IV, *Plesiadapis gingerichi*) suggests that the earliest Sparnacian may be penecontemporary with the later Clarkforkian, but that the early Clarkforkian is closer in age to late Paleocene (Thanetian) faunas from Berru (Figure 6).

If this correlation—based largely on plesiadapids—is correct, evidence available at present suggests that *Paramys*, *Oxyaena*, and *Coryphodon* first appeared in Europe slightly later than they did in North America. This in turn suggests that dispersal of these taxa was from North America to Europe. The direction of interchange of *Plesiadapis* was probably the same direction; however, this conclusion is largely based on a more complete Paleocene fossil record in North America than in Europe. Recent discoveries from Ellesmere Island (West et al., 1977) lend support to an early Tertiary North Atlantic land connection between North America and Europe where intercontinental dispersal took place (Figure 68; Kurten, 1966; McKenna, 1972b).

### Asia

Four localities in the Gobi Desert of Mongolia have produced mammalian faunas that appear to be, at least in part, approximately equivalent in age to the Clarkforkian. The best known of these is Gashato (=Khashaat), the fauna of which was first described by Matthew and Granger (1925). Several authors have since added to the faunal list and discussed the significance of Gashato (e.g., Matthew et al., 1929; Szalay and McKenna, 1971). The other three localities are situated

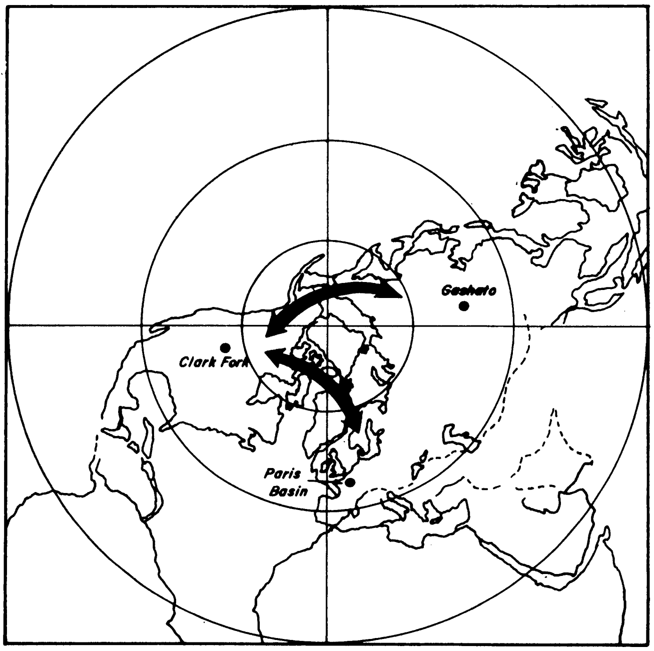

Figure 68. North Polar stereographic projection showing approximate positions of continents in the Clarkforkian (map adapted from Smith and Briden, 1977, map 18; modified after Szalay and McKenna, 1971, and McKenna, 1972b). Faunal evidence indicates that mammalian dispersal occurred between North America and Asia, and North America and Europe during the Clarkforkian.

in the Nemegt Basin, about 350 km west of Gashato. These localities, Naran Bulak, Ulan Bulak, and Tsagan Khushu, appear to be the same age as Gashato. Their mammalian faunas have been described by Flerov (1957), Gradzinski et al. (1968), Dashzeveg (1968, 1976, 1977), Shevyreva et al. (1975), Reshetov (1976), and Dashzeveg and McKenna (1977). Another site, Khaitchin Ula-II (outside the Nemegt Basin), may be about the same age as these four localities (Flerov and Dashzeveg, 1974). All references cited in this paragraph have been used to compile the faunal list in Table 37.

Most authors have considered the Gashato fauna to be of late Paleocene age, although its precise correlation with North American faunas has been nebulous. Van Valen and Sloan (1966) considered Gashato to be either late Paleocene or early Eocene in age, and they depicted this as Clarkforkian or "Graybullian" in their figures 1 and 4. Flerov (1957) believed that the upper Naran Bulak beds, as then known, were of early Eocene age, and he suggested that the fauna of this interval correlates with Wasatchian faunas of Wyoming. Preliminary faunal studies in the Clark's Fork Basin led us to conclude that the Gashato and Naran Bulak faunas "are not older than the beginning of the North American Clarkforkian" (Gingerich and Rose, 1977: 42). This opinion was supported by Dashzeveg and McKenna (1977: 126), who suggested that the Nemegt Basin localities "possibly coincide with part of the Sparnacian of Europe and the Clarkforkian and early Wasatchian of North America." Basalts from the mammal-bearing part of the Gashato Formation have been dated (using Soviet constants) at 51 ± 3 my B.P. (Shevyreva et al., 1975), an age that corresponds well with possible Clarkforkian or early Wasatchian correlation.

About half of the mammalian taxa now known from Gashato and the three Nemegt Basin localities have close relatives in the Clarkforkian or early Wasatchian of North America (Table 37). Four genera, *Hyopsodus*, *Coryphodon*, *Dissacus*, and *Pachyaena*, are known from Asia and North America (all are known also from the Sparnacian of Europe). *Hyopsodus*, *Coryphodon*, and *Dissacus*, are found in both Clarkforkian and early Wasatchian levels in the Bighorn Basin, whereas *Pachyaena* is not known from before the Wasatchian. The Mongolian uintathere genera *Prodinoceras* and *Mongolotherium* are very similar to *Probathyopsis*, so much so that they may be congeneric. Similarly, the distinctions between the Mongolian notoungulate *Palaeostylops iturus* and North American *Arctostylops steini* appear to be less significant than those separating *P. iturus* from sympatric *P. macrodon*, strongly suggesting that these also are congeners. The notoungulates and primitive uintatheres present in Mongolia suggest that these faunas are not younger than Clarkforkian. The omomyid primate *Altanius* may be related to early Wasatchian *Anemorhysis* (or *Tetonoides*). Omomyids are unknown before the Wasatchian in North America. Finally, the occurrence of a "*Sinopa*"-like hyaenodont at Tsagan Khushu is suggestive of Wasatchian age equivalence, since hyaenodontids are also unknown prior to the Wasatchian in North America. Hence, those elements in the Mongolian faunas that are similar to North American forms support the conclusions of Gingerich and Rose (1977) and Dashzeveg and McKenna (1977), that the Asian faunas are not older than Clarkforkian nor younger than Wasatchian.

Recent discoveries in China have revealed that a host of early Tertiary mammals found there are similar to North American forms. Faunas reported to be Paleocene or early Eocene in age include *Coryphodon* and *Hyopsodus*, as well as uintatheres, tillodonts, and arctostylopids similar to those from the Clarkforkian and Wasatchian of Wyoming (Zhai, 1978; Tong, 1978; Chow, 1960, 1963).

Table 37. Comparison of Gashato/Naran Bulak Mongolian mammalian fauna with Clarkforkian and Wasatchian North American faunas. (G=Gashato; NB=Naran Bulak; TK=Tsagan Khushu; UB=Ulan Bulak; KU=Khaitchin Ula-II; CF=Clarkforkian; W=Wasatchian)

| Mongolian Taxon | Close North American Relative |
|---|---|
| MULTITUBERCULATA | |
| *Prionessus lucifer*—G, ?NB | none |
| *Sphenopsalis nobilis*—G | none |
| PROTEUTHERIA | |
| *Hyracolestes ermineus*—G | none |
| *Sarcodon pygmaeus*—G, NB | none |
| ANAGALIDA | |
| *Praolestes nanus*—G | none |
| *Eurymylus laticeps*—G, NB | none |
| *Pseudictops lophiodon*—G, NB, TK | none |
| *Khashanagale zofiae*—G | none |
| *?Khashanagale* sp.—G | none |
| PRIMATES | |
| *Altanius orlovi*—TK | *Anemorhysis, Teilhardina*—W |
| CONDYLARTHRA | |
| *Hyopsodus orientalis*—TK | *Hyopsodus*—CF, W |
| MESONYCHIA | |
| *Dissacus indigenus*—NB, ?G | *Dissacus*—CF, W (also known before Clarkforkian) |
| *Pachyaena nemegetica*—NB | *Pachyaena*—W |
| EMBRITHOPODA | |
| *Phenacolophus fallax*—G | none |
| PANTODONTA | |
| *Archaeolambda planicanina*—NB, UB | *Haplolambda quinni, Barylambda faberi*—Tiffanian and CF |
| *Archaeolambda trofimovi*—KU | |
| *Coryphodon tsaganensis*—TK | *Coryphodon*—CF, W |
| DINOCERATA | |
| *Prodinoceras martyr*—G | *Probathyopsis praecursor, Bathyopsoides*—Tiffanian and CF |
| *Mongolotherium efremovi*—UB | |
| *Mongolotherium plantigradum*—NB, UB | |
| NOTOUNGULATA | |
| *Palaeostylops iturus*—G, NB | *Arctostylops steini*—Tiffanian and CF |
| *Palaeostylops macrodon*—G, NB | |
| ?RODENTIA | |
| *Gomphos elkema*—G (above main level) | ?paramyids—CF, W |
| CREODONTA | |
| "*Sinopa*"—like hyaenodont—TK | *?Arfia*—W |

It seems clear that faunal interchange occurred between Asia and North America at around Clarkforkian time. The presence of notoungulates and uintatheres, which are not known from Europe, indicates that at least some interchange occurred directly between Asia and North America. The mode and direction of dispersal is less obvious, however. Szalay and McKenna (1971) suggested that migration occurred from North America to Asia, before the Eocene, across a filter route through the Bering region. In the late Cretaceous, multituberculates and eutherians appear to have immigrated to North America from Asia (Kielan-Jaworowska, 1974). The configuration of Beringia in the Paleocene is unknown, but the mammalian evidence seems to me to indicate that dispersal was possible in either direction (Figure 68). This might account for the sudden appearance of certain immigrant taxa in North America, such as uintatheres, omomyids, and rodents, the origins of which are now obscure. There seems to be no compelling evidence at present of the direction of dispersal of mesonychids and notoungulates, partly because Paleocene faunas of Mongolia remain very poorly known.

# VI

# NON-MAMMALIAN BIOTA OF THE CLARKFORKIAN

IN THIS CHAPTER I present a brief summary of the flora, molluscs, and non-mammalian vertebrates of the type area of the Clarkforkian. My objective here is to place the mammalian fauna in its proper context as but one aspect of a diverse community of plants and animals. Very little is known concerning Clarkforkian representatives of many of the groups listed below and, for some of them, the short section included here is more complete than any other account now available. It is encouraging, however, that many of these groups are currently under intensive study in the Clarkforkian of the Clark's Fork Basin. Hence we may anticipate that work now in progress by Hickey (megaflora), Wing (megaflora and palynology), Hanley (mollusks), and Bartels (reptiles), will add substantially to our understanding of ecosystems during the Clarkforkian.

## FLORA OF THE CLARKFORKIAN

Like the mammalian fauna, the flora of the Clarkforkian is in many respects intermediate between those of the Tiffanian and the Wasatchian. Leaf-margin and species diversity data from fossil floras indicate a general decrease in mean annual temperature in western North America from late Cretaceous to late Paleocene time, with subsequent warming until the late Eocene (Wolfe and Hopkins, 1967; Wolfe, 1978; Hickey, 1980, and ms.). Paleocene floristic diversity was lower than that of the Cretaceous, with the nadir occurring in the Tiffanian (see Figure 75), a time characterized by small leaves of temperate aspect. An increase in mean annual temperature and probably equability took place in the Clarkforkian, and the Wasatchian was still warmer and more equable—conditions indicated partly by increased species richness and a higher proportion of species with entire-margined leaves (Hickey, personal communication, 1980). Subtropical forms appeared in greater numbers during the Clarkforkian and Wasatchian, while temperate forms declined. MacGinitie (1974: 1) noted that fossil floras of the Rocky Mountain region indicate "a trend from humid, warm temperate to dryer and more tropical conditions, from the Early Eocene to the Middle Eocene." Early Eocene floras of this region are perhaps better viewed as subtropical.

Hickey (1980) recently provided the first information on floras from the type area of the Clarkforkian. He reported 70 species in the Clarkforkian megaflora of the Clark's Fork Basin. Especially abundant is the laurel *Persites argutus*. Clarkforkian floras contain several elements common in older floras. The conifers *Glyptostrobus* and *Metasequoia* (the dawn redwood, today restricted to southeast Asia) continued from the Tiffanian into the Clarkforkian. *Cercidophyllum* and *Platanus* (the sycamore), both common angiosperms, persisted on levees and floodplains from Cretaceous into Eocene time. Clarkforkian swamps were dominated by conifers but also included horsetails and angiosperms such as water lilies. Teas and palms, present in late Cretaceous floras of the region but absent during most of the Paleocene, reappeared early in the Clarkforkian, indicating a warming trend. Broadleaf evergreens increased in variety in the Clarkforkian to comprise 35% of the species, whereas earlier in the Paleocene they accounted for less than 5% of the species. This, too, indicates warmer temperatures. In the Clark's Fork Basin, about 20 species in the megaflora make their first appearance in the Clarkforkian (Hickey, 1980). Pine pollen first appears in the late Clarkforkian (Hickey, personal communication).

In his analysis of the Clarkforkian flora of the Bear Den Member of the Golden Valley Formation, western North Dakota, Hickey (1977) recorded at least 41 species of plants (megaflora) belonging to 18 orders, principally angiosperms. About half of them do not persist above the Clarkforkian Bear Den Member, and eight are restricted to it. Of the 29 species that can be compared to living relatives, Hickey classified 28% as herbs, 10% as vines, 24% as shrubs or small trees, and 38% as trees. The Bear Den flora is most similar, among modern floras, to warm temperate to subtropical floras of China, Japan, and eastern North America.

Brown (1962), in an extensive review of Paleocene floras of the Rocky Mountain region, reported three species from the Clarkforkian Bear Creek locality (southern Montana): *Salix aquilina* (a willow), *Viburnum asperum*, and *V. cupanoides*. The latter species is also known from the Bear Den Member of the Golden Valley Formation (Hickey, 1977). Hickey (1980) has reported several additional species from the Bear Creek, Montana area.

Early Wasatchian floras display some important differences from Clarkforkian ones. Both Brown (1962) and Hickey (1977) regarded *Salvinia*, the floating fern, as an indicator of Wasatchian age. The hackberry, *Celtis*, is abundant in Wasatchian deposits of the Bighorn Basin (including the Clark's Fork Basin) and is another useful indicator of post-Clarkforkian beds. *Platycarya*, *Lygodium* (the climbing fern), and *Hemitelia* (the tree fern), also make their initial appearance in the early Wasatchian. Most of these are important indicators of warmer climates, and *Salvinia* is known to be intolerant to frost (Hickey, 1977).

European floras are known from the Paris Basin late Paleocene (Thanetian) at Rilly-la-Montagne and early Eocene (Sparnacian) at Sézanne. Russell (1975) listed the genera *Alnis*, *Laurus*, *Sassafras*, *Salix*, *Magnolia*, and *Vitis*, as common elements indicative of a warm temperate regime.

## MOLLUSCA

Nonmarine mollusks have been collected at more than 35 of the UM Clarkforkian localities in the Clark's Fork Basin, and they occur in all three zones. They are also abundant in the overlying Wasatchian strata. Dr. John Hanley (U.S. Geological Survey) has initiated a study of the mollusks of the Clark's Fork Basin and has kindly supplied a preliminary list of taxa identified so far. Most of them are terrestrial species, and all of the taxa identified to genus or species occur also in Wasatchian beds of the area. Hanley has recognized 19 additional unidentified morphotypes of terrestrial gastropods in the Clarkforkian that are not present in the Wasatchian, and 13 terrestrial morphotypes in the Wasatchian that do not occur in the Clarkforkian.

Hanley (personal communication, 1979) lists the following mollusks from the type Clarkforkian:

- GASTROPODA
  - *Protoboysia complicata*
  - *Discus ralstonensis*
  - *Gastrodonta coryphodontis*
  - *Oreohelix* spp.
  - *Grangerella megastoma*
  - *Grangerella sinclairi*
  - *Grangerella* sp. indet.
  - *Helicina evanstonensis*
  - Helicinidae: gen. and sp. indet.
  - *Microphysula* sp. indet.
  - Pupillidae: gen. and sp. indet.
  - Unidentified terrestrial gastropods (23 morphotypes)
  - *Physa* sp. indet.
  - *Pleurolimnaea* sp. indet.
  - *Biomphalaria* sp. indet.
  - Planorbidae: gen. and sp. indet.
  - ?Planorbidae: gen. and sp. indet., Form A
  - *Viviparus* sp. indet.
- PELECYPODA
  - Unionidae: gen. and sp. indet.

Conspicuously absent in the Clarkforkian are the terrestrial pulmonate *Polygyra* and the freshwater snails *Goniobasis* (*sensu lato*), *Lioplacodes*, and *Lymnaea*, all of which occur in the Wasatchian part of the section. *Polygyra* is common in the Wasatchian and *Goniobasis* is locally abundant. *Goniobasis* and *Lioplacodes* have been reported also from many Paleocene localities, e.g. the Flagstaff Formation of Utah (La Rocque, 1960) and the Paskapoo Formation of Alberta (Tozer, 1956). Their absence from the Clarkforkian is, therefore, probably a reflection of paleoecological differences, and it will not be surprising if they are eventually found in the Clarkforkian.

The presence of terrestrial gastropods in the Clarkforkian part of the Willwood Formation generally indicates the existence of moist habitats rich in calcium and organic matter (Hanley, 1976). However, the species diversity of these gastropods suggests that varied terrestrial habitats existed during Clarkforkian and Wasatchian time (Hanley, personal communication, 1979). Although most species prefer moist environments, many terrestrial snails can tolerate periods of desiccation lasting several years. Aquatic pulmonate snails of the Physidae and Planorbidae probably inhabited shallow, quiet, often ephemeral ponds (Hanley, 1976, personal communication, 1979). Like the terrestrial snails, some aquatic mollusks can also withstand periods of desiccation by estivating. Unionid clams have been found in the channel sandstones in the Clarkforkian, and one probable bivalve burrow has been identified (M. J. Kraus, personal communication).

As the distribution and composition of Clark's Fork Basin molluscan associations become better established, they should contribute to interpretations of the paleoecology and biostratigraphy of Clarkforkian and Wasatchian strata.

## OSTEICHTHYES

Except for a few local occurrences, remains of fishes are rare in Clarkforkian sediments of the Clark's Fork Basin. They are relatively common, however, at the Tiffanian Cedar Point Quarry. The contrast is not surprising, for fossils in the Clarkforkian come mainly from overbank mudstones, whereas Cedar Point Quarry is situated at the base of a channel sandstone (see Chapter VII). Estes (1975) noted that no fossil fishes are known from the late Tiffanian Princeton Quarry, but he attributed this to local paleoecology.

Very fragmentary specimens of the holosteans *Amia* sp. (bowfin) and *Lepisosteus* sp. (gar) are the only taxa identified thus far in the UM Clarkforkian collection, but it is likely that other forms are represented as well. Boreske (1974) reported an articulated skeleton of *Amia uintaensis*, including the skull and vertebral column, from the Clarkforkian Bear Creek local fauna.

The rarity of fishes in the Clarkforkian probably reflects restriction of permanent water at that time in the Clark's Fork Basin.

## AMPHIBIA

Amphibians are exceedingly rare in the type area of the Clarkforkian. Only a few specimens, referable to the Caudata, have been identified. The cryptobranchid salamander *Piceoerpeton willwoodense* Meszoely (1967) was described on the basis of a vertebra (PU 18021) from sec. 31, T.56 N., R.100 W., in the Clark's Fork Basin (vicinity of localities SC-50 and SC-55, late Clarkforkian, *Phenacodus-Ectocion* Zone). Naylor and Krause (1981) have reported a vertebra of *P. willwoodense* (UM 68429) from early Clarkforkian strata at locality SC-171 (*Plesiadapis gingerichi* Zone). A dentary fragment of *Cryptobranchus* sp. (UM 71316, Krause, personal communication, 1979) has been identified from the same zone at locality SC-227. No other amphibian specimens have been recognized in the colleciton.

## REPTILIA

The reptilian fauna of the Clarkforkian is moderately diverse, consisting of turtles, champsosaurs, crocodilians, lizards, and snakes. Gilmore (1942) reported indeterminate "allognathosuchids" and champsosaurs from the Clarkforkian of the type area and Estes (1975) discussed remains of the turtle, *Ptychogaster*, from the Ries ("Reiss") Locality (See Chapter V); but no adequate survey of Clarkforkian reptiles has yet appeared, although Cope, Gilmore, Mook, Estes, and others have described other Paleocene and Eocene herpetofaunas from the Bighorn Basin.

The Clarkforkian assemblage differs from that of Princeton Quarry (Gilmore, 1942; Estes, 1975) in having a much greater diversity of turtles, lizards, and crocodilians. However, this may well reflect the much greater area, stratigraphic thickness, and habitat diversity represented by the Clarkforkian collection.

The Clarkforkian "Big Multi" locality in the Washakie Basin contains a relatively low diversity of reptiles, only nine taxa so far identified: six turtles, two crocodilians, and a champsosaur (J. H. Hutchison, personal communication, December 1978). Hutchison has observed a dramatic increase in reptilian diversity in the Wasatchian of the Washakie Basin. While this is consistent with mammalian and floral evidence suggesting lower equability and mean annual temperatures during the Tiffanian and Clarkforkian, and an increase in both in the Wasatchian, diversity of reptiles is to some extent more dependent on water availability than on temperature (Hutchison, personal communication).

W. S. Bartels has identified more than 20 species of reptiles in the UM Clarkforkian collection and has compiled the preliminary faunal list presented below. I have added notes on certain taxa where pertinent.

- Order TESTUDINES
  - Family Baenidae
    - "*Baena*" sp.
  - Family Trionychidae
    - *Trionyx* sp.[1]
    - *Plastomenus* sp.[1]
    - unidentified trionychid
  - Family Emydidae
    - *Ptychogaster* sp.[2]
  - Family Testudinidae
    - unidentified testudinid
  - Family Cheloniidae
    - unidentified cheloniid
- Order EOSUCHIA
  - Family Champsosauridae
    - *Champsosaurus gigas*[1]
    - *Simoedosaurus* sp.[3]
- Order CROCODILIA
  - Family Crocodylidae
    - *Leidyosuchus* sp.
  - Family Alligatoridae
    - *Diplocynodon*, sp. nov.[4]
    - *Allognathosuchus* cf. *wartheni*[1,2,5]
    - *Ceratosuchus* cf. *burdoshi*[5,6]
- Order SQUAMATA
  - Suborder Lacertilia
    - Family Anguidae
      - *Odaxosaurus* cf. *piger*[1,2,7]
      - *Xestops* cf. *vagans*[1]
      - *Melanosaurus* cf. *maximus*[1,8]
      - cf. *Glyptosaurus* sp.
      - *Paraglyptosaurus* sp.

        cf. *Gerrhonotus* sp.
    Family Parasaniwidae
        cf. *Provaranosaurus* sp.[2]
    Family Xenosauridae
        *Exostinus* cf. *rugosus*[2]
Suborder Ophidia
    Family Boidae
        unidentified boid

Notes:

[1] Common to abundant in Clarkforkian of the Clark's Fork Basin.

[2] Genus reported from late Tiffanian Princeton Quarry; *Ptychogaster* known also from Clarkforkian Ries Locality (Estes, 1975).

[3] Sigogneau-Russell and Baird (1978) first reported this genus from the Clarkforkian of North America. Only two of their four specimens, PU nos. 22234 and 22199, from Bear Creek, are definitely of Clarkforkian age. The other two are from exposures in the Clark's Fork Basin near the Tiffanian-Clarkforkian boundary, but the precise age of these beds has not yet been determined.

[4] UM 69867, a dentary from the Clarkforkian-Wasatchian boundary sandstone.

[5] Genus also known from Clarkforkian of Bitter Creek section ("Big Multi" locality), Washakie Basin (Hutchison, personal communication, December 1978).

[6] First described from the Plateau Valley beds, Colorado (Schmidt, 1938), and hence either late Tiffanian or Clarkforkian. Only one specimen has been identified in the UM Clarkforkian collection.

[7] Formerly placed in either *Peltosaurus* or *Pancelosaurus*.

[8] Holotype of this species was described from the Clark's Fork Basin and is clearly of early Wasatchian age ("5 miles southeast of the mouth of Pat O'Hara Creek," Gilmore, 1928). A partial skull and lower jaws (UM 68365) from the Clarkforkian of Buckman Hollow also belong to this species.

## AVES

Avian fossils are very rare in the Clarkforkian of the Clark's Fork Basin. The UM collection includes fragments of unidentified bird eggshell from various Clarkforkian localities, and a distal tarsometatarsus of a medium-sized bird, also unidentified (UM 69343, from SC–53, upper *Plesiadapis cookei* Zone or lower *Phenacodus-Ectocion* Zone). I am unaware of any published records of birds of undoubted Clarkforkian age. Bartels (1980) indicates that two avian species, *Diatryma ajax* and *Eogeranoides campivagus*, are known from the Clarkforkian. However, Shufeldt's (1913) specimens of *D. ajax* are clearly from beds of early Wasatchian age in the Clark's Fork Basin, whereas the holotype of *E. campivagus* (PU 16179) is apparently from deposits of similar age south of Lovell. The latter specimen is from the Foster Gulch area, where exposures range from Tiffanian through Wasatchian in age. The precise locality (and hence, its age) is uncertain, but an early Wasatchian age is more likely.

# VII
# MAMMALIAN FAUNAL COMPOSITION

## INTRODUCTION

ASSESSMENT OF THE composition of fossil assemblages is necessary for understanding the evolution of mammalian faunas (particularly, here, the significance of Clarkforkian faunas), and it contributes to reconstruction of ancient mammalian communities. Ecological relationships are, of course, very complex, and the obvious limitations of the fossil record impose certain constraints on paleoecological interpretations. Ideally, such studies should include all aspects of a multifaceted ecosystem, but in practice it is often necessary to restrict consideration to only a small part, for instance the mammals. Nevertheless, considerable insight can be gained by investigation of the composition of fossil mammal assemblages.

One method of assessing the degree of resemblance between two faunas is by comparison of the number of taxa shared by both faunas to the total number of taxa in one or the other fauna or in both together (G. G. Simpson, 1960). Most previous considerations of taxonomic resemblance in successive mammalian faunas have been of this sort. It is desirable, however, to take investigations beyond the presence or absence of taxa, and to examine diversity in fossil mammal assemblages and patterns of change in diversity through time.

## ANALYSIS OF DIVERSITY

Definitions of diversity and approaches to its measurement and analysis vary considerably among authors (see Peet, 1974, and Whittaker, 1977, for excellent reviews of the subject). Diversity is a multiple concept, involving species number or richness, equitability or evenness in relative abundances of species, and heterogeneity, the combination of richness and evenness. In extant communities, relative abundance can be estimated directly from population counts or from biomass based on population counts. Fossil assemblages have several inherent differences from living populations, and several ways of estimating relative abundance have been proposed—some better than others, and some more applicable to certain fossil samples than to others (see Analysis of Diversity in Fossil Assemblages, below). A large number of indices have been proposed to measure the different aspects of diversity, but there is some disagreement over their applicability and interpretation. Most authors agree that the most basic component of diversity is species richness, a measure of the number of species in a sample (e.g. Peet, 1974; May, 1976; Whittaker, 1977). Comparisons of species richness are ideally made between samples of standard size, but this is more easily achieved in recent populations than in fossil assemblages.

Heterogeneity (or mixed or total diversity) indices have become a popular way to measure species diversity. E. H. Simpson (1949) first applied this concept to ecological situations and proposed an index of diversity

$$L = \sum_{i=1}^{s} [n_i(n_i-1)]/[N(N-1)] \qquad (1)$$

where $n_i$ is the number of individuals in species $i$, $s$ is the total number of species in the sample, and $N$ is total sample size. It may be regarded as the "weighted mean of the proportional abundances" (Peet, 1974) and is most sensitive to changes in relative abundance of the most common species. Simpson's index is larger for samples with less heterogeneity, hence several modifications have been suggested to circumvent this inverse relationship, most of them simply subtracting the value of this or a similar index from 1.0.

May (1976) suggested that the variance of the distribution of species abundances is a particularly useful measure of heterogeneity, and he advocated indices such as $\Sigma p_i^2$, $1-\Sigma p_i^2$, or $1/\Sigma p_i^2$, where $p_i$ is the frequency of the $i^{th}$ species. The second of these, known as the Gini index, may be considered as a form of the Simpson index, although it was introduced much earlier (Peet, 1974).

Probably the most widely used heterogeneity index is the Shannon index (variously called Shannon-Weaver or Shannon-Wiener index), which is derived from information theory. The Shannon index summarizes the information in a system (here, the diversity in a population) by the formula

$$H' = -\sum_{i=1}^{s} p_i \operatorname{Log} p_i \qquad (2)$$

(Shannon and Weaver, 1949; Peet, 1974), where $p_i$ again is the frequency of the $i^{th}$ species. Various authors substitute either the natural logarithm or $\log_2$ in this equation, and some use biomass per species rather than relative frequency as a measure of relative importance. In spite of widespread application of the Shannon index by ecologists and increasing use of the index by paleontologists (e.g. Lasker, 1976; Boucot, 1978), there is considerable debate over its proper use and meaning. For example, the value of $p_i$, like the total number of species in a community, cannot be exactly known; thus in practice it is estimated by $n_i/N$, an estimate that contributes a small error to the value of H′ (Peet, 1974). Failure to include all species (and $s$ always underestimates the total number of species) also results in a bias in $H'$, as Peet observed. Pielou (1966) suggested that the Shannon index is applicable only for average conditions in an indefinitely large population from which random samples can be drawn. Although this index is used as a measure of heterogeneity, i.e. species richness and evenness, it primarily reflects evenness (see also Whittaker, 1977). In contrast to the Simpson index, the Shannon index is highly sensitive to changes in abundance of the rarest species (Peet, 1974). Whittaker (1977) stated that the Shannon index is most responsive to changes in abundance of the common species, but this apparent discrepancy can be resolved by examination of the relationship of $p_i$ to $p_i ln\ p_i$ (Peet, 1974: figure 2). Rare species contribute relatively more to the Shannon index than to the Simpson index, but the contribution of common species does not decline until relative abundance of a taxon exceeds 37%. These and other problems with heterogeneity indices reflect the disagreement over how to combine species richness and evenness, and they prompted Whittaker (1977: 4) to remark "there is apparently no measure in use that successfully expresses mixed or total diversity." Despite their shortcomings, the Shannon and Simpson indices have proven to be informative measures of diversity in many cases, providing their limitations are realized.

Several authors have attempted to isolate the evenness component of heterogeneity and have proposed a number of indices of equitability or evenness. Lloyd and Ghelardi (1964) introduced the first of these indices into the ecological literature, but their measure of equitability is very difficult to calculate. Simpler measures have been suggested by Pielou (1966) and Whittaker (1972, 1977), among others. Pielou's index is written as

$$J = H'/\ln s \qquad (3)$$

where $H'$ is the Shannon index and $s$ is the number of species. It has been criticized because of its dependence on $H'$ and because $s$ should be the total number of species, not the observed number of species in a sample (Whittaker, 1977). Lasker (1976), however, asserted that $J$ is independent of species number and that it provides results often not obvious from values of the Shannon index alone. Although Whittaker preferred to measure diversity by species richness, he suggested an equitability index that he considers more appropriate than others (Whittaker, 1972, 1977):

$$E = s/(\log p_1 - \log p_s) \qquad (4)$$

where $s$ is species number, $p_1$ is the frequency of the most common species, and $p_s$ is the frequency of the rarest species. Like the heterogeneity indices, the equitability indices have limitations but can be highly informative.

Diversity may also be investigated using a model developed by MacArthur (1957, 1960), the so-called "broken-stick model." This model predicts that the abundance of the $r^{th}$ rarest species in a fauna is

$$p_r = \frac{N}{s} \sum_{i=1}^{r} \frac{1}{s-i+1} \qquad (5)$$

where *N* is total number of individuals and *s* is total number of species. From equation 5, it is possible to generate the theoretical distribution of abundances that would obtain if evenness is maximized (Lloyd and Ghelardi, 1964; Deevey, 1969); and the resulting curve, with relative abundance (frequency) plotted against the logarithm of the rank of abundance, is very nearly linear (see Figure 77). MacArthur (1960) found that this distribution, designated Type 1, closely approximates natural distributions of relative abundance in living bird populations. The closer that an observed distribution of abundances approaches that of MacArthur's Type 1 model, the greater the sample approaches maximum evenness. Thus comparisons of observed distributions to MacArthur's model provide important information about evenness in recent or fossil samples. An advantage to this method of examining diversity is that relative evenness can be evaluated independent of the number of species in the sample.

Not all natural populations have distributions of abundance that conform to MacArthur's Type 1 distribution. Hutchinson (1961) found that in many populations, such as some birds, diatoms, and arthropods, the most abundant species are more common and the rarest ones more rare than is predicted by MacArthur's Type 1 model. Hutchinson termed this a Type 4 distribution, and he suggested that it might result from temporary abundance of one species at the expense of others, before equilibrium is achieved. The Type 4 distribution contrasts with the Type 1 distribution and reflects low evenness.

## ANALYSIS OF DIVERSITY IN FOSSIL ASSEMBLAGES

Although the fossil record imposes biases on a sample that do not affect samples from extant communities, Deevey (1969: 224) observed that "some assemblages of fossils, including mammal bones in alluvium, show more ecological order than modern collections of species usually do." Indeed, in spite of these biases, considerable information can be derived from analysis of diversity of fossil assemblages. It is necessary, however, to be aware of the kinds of biases that affect fossil samples, and several authors have discussed them and suggested methods to correct for certain biases. Further study is essential to determine to what extent these corrections are necessary or applicable.

Numerous factors affect the sampling of a fossil assemblage and the degree to which it approximates the original living community; they have been discussed in detail by Shotwell (1955), Clark et al. (1967), Voorhies (1969), Behrensmeyer (1975), Behrensmeyer et al. (1979), and many others. Preservational biases, sorting by size and density, weathering, erosion, and other aspects of taphonomy all can affect the composition of a fossil assemblage. Corrections for these factors are not easily made, but their effects can often be readily recognized, and seriously biased samples can be identified. Differential preservability of different taxa can lead to error in taxonomic diversity indices (Lasker, 1976), but this problem does not appear to be serious for samples of fossil mammals, because of nearly universal use of teeth for identifying taxa and estimating relative abundance. Collecting techniques may also lead to biased samples, but rigor in collecting and careful locality and stratigraphic control will minimize error of this kind. One factor inherent in many fossil samples is the effect of time-averaging. Few fossil samples can be demonstrated to represent the fauna of a single time plane, as is the case in modern samples; rather, most fossil samples represent the fauna of a selected stratigraphic interval. Short-term variations in diversity are pooled in time-averaged fossil samples, usually resulting in greater diversity than occurred at any one time in the living sample (Peterson, 1977). However, such short-term variations are generally of less concern to paleontologists than are long-term changes in diversity; and for comparisons between comparable fossil samples this bias is probably insignificant. Finally, sample size itself must be considered. How large must a fossil sample be to adequately represent the diversity of the original community, or even of the total fossil assemblage? Wolff (1975) provided estimates of the numbers of specimens that might be needed to approximate species richness and relative abundances in the original population. As he observed, however, the estimates could vary for different fossil samples, and the ideal limits are much higher than are usually attained in fossil vertebrate samples. The analyses presented later in this chapter suggest that in many cases, a sample size of a few hundred specimens is sufficient to provide a relatively accurate estimate of species richness and evenness.

After a fossil sample has been collected, several additional factors will have an effect on diversity studies. The level and accuracy of taxonomic identification will certainly affect the analysis. For best results, it is necessary to study first-hand all fossils included in the estimates of diversity. This helps to insure consistency of identification and abundance estimates. The method of assessing relative abundance varies among authors, and it is clear that some methods result in greater potential error than others. Probably the most popular method of estimating relative abundance in vertebrate fossil assemblages is by the minimum number of individuals (MNI), usually determined by the frequency of the most common identifiable element (e.g. McKenna, 1960; Van Valen, 1964; West, 1973b). Although a bias is incurred when different species are represented by substantially different numbers of identifiable elements, this bias is probably much reduced if the number of identifiable elements is held relatively constant for different species, for example, by restricting the analysis to teeth in mammal assemblages (Van Valen, 1964). In estimating minimum numbers of individuals, some analysts attempt to take into account individual size and age (e.g. by comparing stages of wear in teeth), a procedure that is much easier for species represented by only a few individuals than for those known from a large number of specimens. This results in overestimation of rare constituents in the assemblage, which are already somewhat overestimated by the MNI method (see also Grayson, 1973, 1978; Holtzman, 1979); hence it is usually inadvisable to follow this practice. Grayson (1973) discussed other problems inherent in the MNI method especially as applied to archeological collections, but most of these are much less serious for fossil samples.

Because of these biases of the MNI determination, Holtzman (1979) advocated an alternative method of assessing relative abundance. His "weighted abundance of elements" (WAE) method may be preferable to the MNI method in some cases, but it involves certain arbitrary decisions (e.g. the number of identifiable elements) that can result in biases of its own.

Some paleontologists have estimated frequencies of taxa directly from the number of specimens of each taxon in the fossil sample (e.g. Clark et al., 1967); but in most vertebrate assemblages, where specimens tend to be fragmentary and disarticulated, this procedure greatly inflates the relative abundances of common taxa at the expense of the rarest ones. Shotwell (1955, 1958) proposed a formula for the "corrected number of specimens" that takes into account the number of different skeletal elements identified for each species. He also attempted to distinguish proximal and distal communities by the relative completeness of taxa as indicated by the "corrected number of specimens." Unfortunately, hydrodynamic sorting during burial injects a serious bias into this method (Voorhies, 1969; Behrensmeyer, 1975). Furthermore, the practical difficulty of assigning isolated postcranial bones to species in many fossil assemblages limits the utility of Shotwell's method.

Any of the estimates of relative abundance discussed here may be biased by variation in lifespan or generation time among different members of the assemblage. Thus a short-lived species might be expected to be relatively more common in a fossil assemblage than a species with much longer generation time. Van Valen (1964) attempted to reduce this error by multiplying the species frequency "by a constant corresponding to its estimated mean lifespan in years." Although longevity is generally correlated with body size, estimates of longevity must themselves be based on estimates of body size; hence this "correction" could potentially lead to additional error. For comparison of similar fossil assemblages, it seems probable that correction for differential longevity is unnecessary.

## PROCEDURE

The transition from archaic Paleocene faunas to more modern Eocene faunas is one of the most important episodes in mammalian history, marked by immigration of faunas that include the first representatives of several modern mammalian orders. To better understand this transitional period, it is particularly informative to examine the composition and diversity of mammalian assemblages through the interval. The Polecat Bench-Clark's Fork Basin sequence offers an exceptional opportunity to do this, for it contains the largest and best documented collections of fossil mammals available spanning the Paleocene and early Eocene. The data and analyses presented in this chapter are the result of first-hand study of all the collections involved. All counts of specimens are restricted to jaws and teeth, the most common and readily identifiable elements. Estimates of relative abundance have been made by the standard MNI method. In addition to successive samples from the northern Bighorn Basin, a few other assemblages were studied to determine if similar results obtained in faunas outside of this local sequence. Diversity has been measured by comparisons of species richness, the Simpson and Shannon heterogeneity indices, and the Whittaker equitability index. Because fluctuations in abundances of common taxa are more likely to be meaningful than are changes in frequency of rare species in comparisons of fossil assemblages, Simpson's index may be more appropriate than the Shannon index; but, as shown below, the three indices result in a similar pattern of changes in diversity through time (Figures 75 and 76). (The minor variations in diversity as measured by the different indices reflect slight differences in how the indices measure diversity, as discussed above.) The effects of biases outlined previously are likely to have been similar for comparable samples (i.e., those of similar size, collected by similar methods from deposits

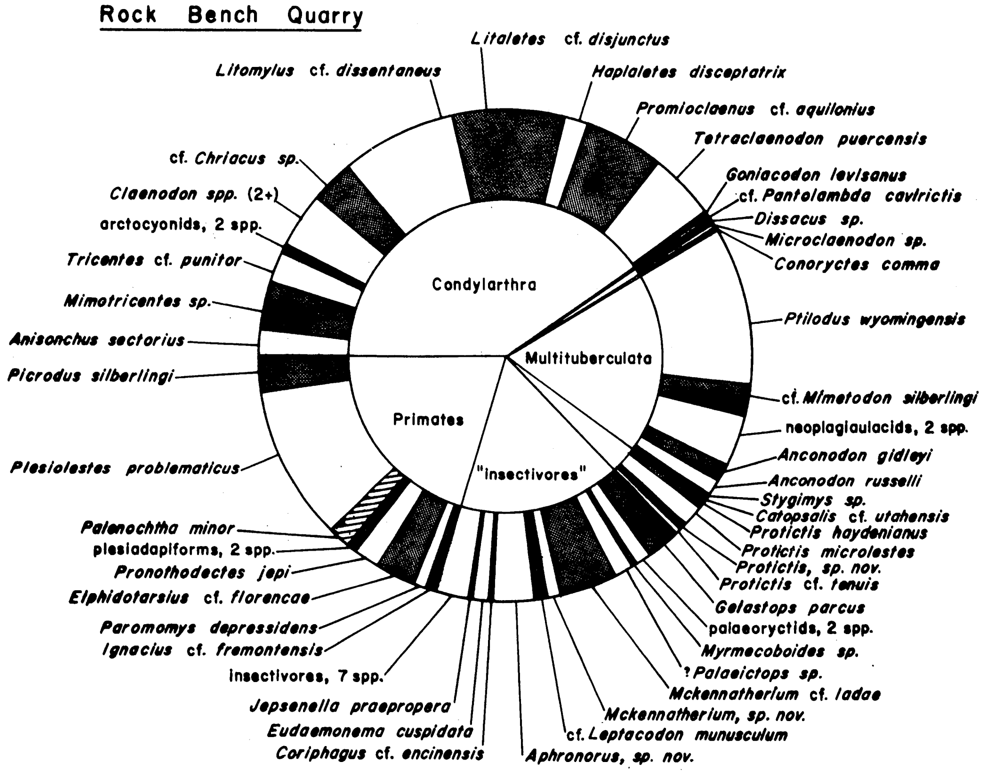

Figure 69. Relative abundances of mammalian taxa in the Rock Bench Quarry fossil assemblage, middle Paleocene (Torrejonian). Width of each sector reflects the percentage of the mammalian fauna represented by each taxon, as determined from the minimum number of individuals (see Table 38).

of the same kind), hence it is reasonable to compare these assemblages. They may not be directly comparable to living communities, however.

The faunas examined here are, from oldest to youngest, Rock Bench, Cedar Point, and Princeton Quarries (Torrejonian to Tiffanian), and several intervals of Clarkforkian and early Wasatchian age, all of these in the Polecat Bench-Clark's Fork Basin sequence. For comparison, the samples from Gidley and Scarritt Quarries (Torrejonian and Tiffanian of the Crazy Mountain Field, Montana), and from three levels of the early Wasatchian of the southern Bighorn Basin are also examined.

The objective of this chapter is twofold: to provide a summary of the data now available for the successive faunas considered here, and to provide analyses and interpretations of these data. The analyses are only a beginning; many more studies are needed to establish patterns of diversity through time. Thus the interpretations are intended as hypotheses to be tested by further studies of mammalian faunal composition.

## TORREJONIAN FAUNAS

### Rock Bench Quarry (Polecat Bench Sequence)

Rock Bench Quarry was discovered by Dr. G. L. Jepsen of Princeton University in the late 1920s, after he and co-workers "unexpectedly exposed a tooth of *Ptilodus* and a small insectivore jaw . . . [in] an extremely coarse, almost conglomeratic, sandstone" (Jepsen, 1930b: 475). In 1940, Jepsen proposed the name Rock Bench Quarry for this productive zone. Seven forms identified from the quarry beds by 1929 were included in Jepsen's (1930b) first monograph on the Polecat Bench faunas, and he expanded the list to 12 in 1940 by adding four more species of multituberculates and the plesiadapiform primate *Elphidotarsius*. Russell (1967) emended the faunal list and lengthened it by including two species of pantodonts identified by Simons (1960). Except for these accounts and a few studies of selected taxa (e.g. Bown and Gingerich, 1973; Rose, 1975a; Gingerich, 1976b; West, 1976), little has been

Table 38. Mammalian faunal composition of Rock Bench Quarry.
Asterisk (*) denotes species known also from Gidley Quarry.
Plus (+) denotes species closely related to one known from Gidley Quarry.

| Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|
| Order MULTITUBERCULATA | | |
| Family Eucosmodontidae | | |
| +*Stygimys* sp.[1] | 1/1 | .002 |
| Family Taeniolabididae | | |
| *Catopsalis* sp.[2] | 1/1 | .002 |
| Family Cimolodontidae | | |
| *Anconodon gidleyi* | 17/6 | .012 |
| *Anconodon russelli* | 10/5 | .010 |
| Family Ptilodontidae | | |
| +*Ptilodus wyomingensis*[3] | 180/51 | .103 |
| Family Neoplagiaulacidae | | |
| *cf. *Mimetodon silberlingi* | 19/10 | .020 |
| neoplagiaulacid, sp. 1[4] | 2/2 | .004 |
| +neoplagiaulacid, sp. 2[5] | 28/15 | .030 |
| Order PROTEUTHERIA | | |
| Family Palaeoryctidae | | |
| *Gelastops parcus* | 60/11 | .022 |
| +palaeoryctid, sp. F[6] | 5/3 | .006 |
| +palaeoryctid, sp. G[6] | 4/2 | .004 |
| Family Leptictidae | | |
| +*Myrmecoboides* sp. | 3/2 | .004 |
| +?*Palaeictops* sp. | 32/6 | .012 |
| "*Diacodon*" sp. A[7] | 8/3 | .006 |
| "*Diacodon*" sp. B[7] | 5/2 | .004 |
| leptictid, sp. nov.[8] | 5/2 | .004 |
| Family Pentacodontidae | | |
| +*Aphronorus*, sp. nov.[9] | 55/13 | .026 |
| +*Coriphagus* cf. *encinensis*[10] | 1/1 | .002 |
| Family Mixodectidae | | |
| *Eudaemonema cuspidata* | 23/5 | .010 |
| Family Apatemyidae | | |
| *Jepsenella praepropera*[11] | 5/4 | .008 |
| Family uncertain | | |
| species A[12] | 2/1 | .002 |
| species B[12] | 1/1 | .002 |
| species D[12] | 2/1 | .002 |
| species E[12] | 2/1 | .002 |
| Order LIPOTYPHLA | | |
| Family Nyctitheriidae | | |
| +cf. *Leptacodon munusculum*[13] | 5/4 | .008 |
| Family Adapisoricidae | | |
| *Mckennatherium* cf. *ladae*[14] | 32/18 | .036 |
| *Mckennatherium*, sp. nov.[15] | 7/4 | .008 |
| Order PRIMATES | | |
| Family Microsyopidae | | |
| +*Plesiolestes problematicus* | 142/50 | .101 |
| *Palenochtha minor* | 9/7 | .014 |
| Family Plesiadapidae | | |
| +*Pronothodectes jepi*[16] | 27/8 | .016 |
| cf. *Pronothodectes* sp.[17] | 3/2 | .004 |
| Family Carpolestidae | | |
| *Elphidotarsius* cf. *florencae*[18] | 26/13 | .026 |
| Family Paromomyidae | | |
| *Paromomys depressidens* | 12/4 | .008 |
| *Ignacius* cf. *fremontensis*[19] | 6/3 | .006 |
| Family Picrodontidae | | |
| *Picrodus silberlingi* | 26/12 | .024 |
| Family uncertain | | |
| plesiadapiform, new[20] | 1/1 | .002 |
| Order CONDYLARTHRA | | |
| Family Arctocyonidae[21] | | |
| *Goniacodon levisanus*[22] | 5/2 | .004 |
| *Tricentes* cf. *punitor*[23] | 88/10 | .020 |
| +*Mimotricentes* sp.[24] | 41/15 | .030 |
| cf. *Chriacus* sp.[25] | 91/14 | .028 |
| *Claenodon* spp.[25] | 105/20 | .040 |
| +arctocyonid, small[26] | 3/2 | .004 |
| arctocyonid, sp. nov.[27] | 1/1 | .002 |
| Family Phenacodontidae | | |
| *Tetraclaenodon puercensis*[28] | 148/21 | 042 |
| Family Hyopsodontidae | | |
| *Haplaletes disceptatrix* | 14/8 | .016 |
| *Litomylus* cf. *dissentaneus*[29] | 106/37 | .074 |
| *Litaletes* cf. *disjunctus*[30] | 148/37 | .074 |
| *Promioclaenus aquilonius* | 76/26 | .052 |
| Family Periptychidae | | |
| *Anisonchus sectorius* | 43/9 | .018 |
| Order MESONYCHIA | | |
| Family Mesonychidae | | |
| +*Dissacus* sp. | 6/2 | .004 |
| Microclaenodon sp.[31] | 3/1 | .002 |
| Order PANTODONTA | | |
| Family Pantolambdidae | | |
| +cf. *Pantolambda cavirictum*[32] | 3/1 | .002 |
| Order TAENIODONTA | | |
| Family Stylinodontidae | | |
| +*Conoryctes* sp. | 3/1 | .002 |
| Order CARNIVORA | | |
| Family Miacidae | | |
| *Protictis haydenianus* | 10/3 | .006 |
| *Protictis microlestes* | 17/7 | .014 |
| *Protictis* cf. *tenuis* | 3/2 | .004 |
| *Protictis*, sp. nov.[33] | 6/3 | .006 |
| Totals | 1687/497 | .996 |

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[1] PU 14471, edentulous dentary with incisor. Possible occurrence of this genus at Rock Bench was noted by Sloan and Van Valen (1965) and was confirmed by Sloan in 1978 (personal communication). This is the latest record of *Stygimys*.

[2] PU 19043, an isolated molar.

[3] *P. wyomingensis* is probably a junior synonym of *P. montanus* from Gidley Quarry.

[4] PU nos. 16584 and 16585, lower dentitions. $P_4$ length=3.25–3.40; $P_4$ serrations 11; $M_1$ cusp formula 6:4; incisor stout.

[5] Many specimens, including PU nos. 18216–18219, 20851, and 22217. $P_4$ length=4.4–5.3 ($\overline{X}$=4.84, n=14); $P_4$ serrations 11–12. Similar to *Neoplagiaulax grangeri* from Gidley Quarry, but slightly smaller.

[6] Small palaeoryctids, possibly related to *Stilpnodon*. Palaeoryctids F and G (designations of C. B. Wood, unpublished) differ mainly in size and are probably congeneric. Palaeoryctid F includes PU nos. 14747–14749, 17505, and 21136. Palaeoryctid G includes PU nos. 14440, 18465, and uncatalogued specimens.

[7] Closely related (possibly conspecific) forms of uncertain affinities, but probably leptictids. Designations are those of C. B. Wood. Species A includes PU nos. 14144, 14730, 14757, 19537, 21160, 21161, and two uncatalogued teeth. Species B includes PU nos. 14756, 14758, 21179, and uncatalogued specimens.

[8] PU nos. 14023, 14851, 17430, 19873, and 21164 represent an enigmatic form that resembles both leptictids and pentacodontids in various features (C. B. Wood, personal communication). $P_3$ and $P_4$ are large, and $P_4$ is molarized with a large paraconid and metaconid; both features suggest leptictid affinities (Wood, personal communication).

[9] These are the specimens referred to as *Palaeosinopa* sp. by Jepsen (1930b: 504) and subsequent authors. Mean size slightly larger than *Aphronorus fraudator* from Gidley Quarry. Probably a new species closely allied with or derived from *A. fraudator*.

[10] PU 19805, left dentary with $M_{1-3}$. Larger than *C. montanus* from Gidley Quarry but compares well with *C. encinensis* from the Torrejonian of the San Juan Basin.

[11] Rock Bench specimens discussed by West (1973a).

[12] Designations of C. B. Wood (unpublished). These are small insectivores that appear to represent different species from any listed so far. They may be palaeoryctids or pentacodontids (Wood, personal communication). Species A includes PU nos. 14850 and 21137; species B is PU 17409; species D includes PU nos. 19838 and 21138; species E includes PU nos. 14732 and 18461.

[13] Very small, $M_1$ length=1.3–1.4. These specimens also resemble *Mckennatherium ladae* but are about 20% smaller.

[14] Very similar to *Mckennatherium ladae*, but slightly larger than the type sample from Gidley Quarry ($M_1$ mean length=1.65, n=10).

[15] About 30% larger than *M. ladae* but morphologically similar. Includes PU nos. 14738, 14746, 18688, 19641, 19843, and uncatalogued specimens.

[16] First named and described from Rock Bench by Gingerich (1975, 1976b). *P. jepi* is descended from *P. matthewi* of Gidley Quarry.

[17] PU nos. 14224, 14793, and 17535 have molars much narrower than in *Pronothodectes jepi*. They probably represent a new species.

[18] Presence of *Elphidotarsius* at Rock Bench was first reported by Jepsen (1940: 234), and a detailed account of Rock Bench specimens was presented by Rose (1975a). They average slightly larger than the holotype from Rock Bench Quarry but are otherwise essentially identical.

[19] PU nos. 14280, 14790, 14842, 18479, 18481, and 18862 (PU 14790 was incorrectly identified as *Ignacius frugivorus*, and its locality erroneously given as Cedar Point Quarry by Bown and Rose, 1976: 113). These specimens are slightly smaller than *Paromomys depressidens*, with which isolated molars may be confused. Lower jaws clearly affirm their identity as *Ignacius* rather than *Paromomys*, however, for there are only two premolars ($P_3$ small and two-rooted, $P_4$ smaller than $M_1$). The diastema between the enlarged central incisor and $P_3$ is very short. To the extent that they can be compared with the fragmentary holotype of *I. fremontensis* (Gazin, 1971), they are identical. Gazin first described this species from the late Torrejonian Shotgun local fauna and placed it in the genus *Phenacolemur*; Bown and Rose (1976) transferred it to *Ignacius*.

[20] PU 19794, right dentary with $M_{1-3}$ ($M_1$ length=2.1, breadth=1.3; $M_2$ length=2.2, breadth=1.4) This unique specimen possesses a mosaic of features characteristic of plesiadapids, microsyopids, and paromomyids. It has squared trigonids with small, lingual paraconids. The enamel is moderately crenulated and there is a rugosity in the region where a mesoconid would develop.

[21] The arctocyonids from Rock Bench are a particularly confusing group, comprising at least five or six species, and perhaps as many as ten. Size and morphology are highly variable, and there is considerable intergradation, making consistent separation by size or structure exceedingly difficult. The tabulation presented here is based on my study of Rock Bench arctocyonids up to April 1978 (through the courtesy of Drs. D. Baird and L. Van Valen). Van Valen (1978) has recently identified seven species (one of them new) from Rock Bench: *Chriacus katrinae* (sp. nov.), *Chriacus orthogonius* (here called *Tricentes punitor*), *Prothryptacodon furens*, *Colpoclaenus ?silberlingi* and *Arctocyonides montanensis* (both here listed as *Claenodon* spp.), *Mimotricentes subtrigonus*, and *Goniacodon levisanus*.

[22] First reported from Rock Bench by Gingerich (1978).

[23] Most specimens included here are most similar to *Tricentes punitor* from Gidley Quarry, but some resemble the slightly older *T. provocator* (a synonym of *T. punitor*?) in having an unbasined talonid on $P_4$; hence it is possible that two closely allied species have been grouped here. *T. punitor* was initially described as a species of *Metachriacus* (Simpson, 1935), which was later placed in synonymy with *Tricentes* (Van Valen and Sloan, 1965). Recently, Van Valen (1978) has considered *T. punitor* to be a junior synonym of *Chriacus orthogonius* Russell.

[24] Slightly smaller than *Tricentes punitor* and with broader, lower, and flatter crowned teeth with bulbous cusps. $P_4$ is simple (no paraconid or metaconid) and relatively broad. PU 16613 (right dentary with $M_{2-3}$ and alveoli for $P_{3-4}$-$M_1$) differs from other specimens in this sample by lacking $P_{1-2}$ and having a long diastema as in *Spanoxyodon*: however, its tooth morphology is closer to that of *Mimotricentes*. It may be an abnormal individual or possibly represents a different species.

[25] Specimens similar to *Chriacus* and *Claenodon* are the most difficult to sort out. Some specimens seem clearly to belong to one genus or the other, but other specimens exhibit almost continuous intergradation between the two extremes. Cusps range from relatively high and acute to low and rounded or flattened, and the degree of crenulation is highly variable (but greater in the lower crowned specimens). As Van Valen (1978) indicated, some of these specimens probably belong to *Colpoclaenus*. I have included the acute-cusped specimens in cf. *Chriacus* sp. and the lower crowned specimens in *Claenodon*.

[26] PU nos. 14750 and 14751 and UM 66124. Similar to *Tricentes punitor* but molars narrower, cusps more acute, premolars somewhat smaller, simpler, more trenchant, and much narrower; $P_3$ much smaller than $P_4$ (in PU 14750).

[27] PU 19792, left dentary with $P_2$, $P_4$, and alveoli of $P_1$ and $P_3$. $P_2$ is separated from adjacent teeth by diastemata. $P_4$ is submolariform, with a minute paraconid and a large, high metaconid. This specimen appears to represent a different species of arctocyonid from all others in the collection.

[28] Rock Bench sample recently studied by West (1976).

[29] Mean size is slightly larger than that of the sample of *Litomylus dissentaneus* from Gidley Quarry.

[30] Placed in the new species *Litaletes ondolinde* by Van Valen (1978).

[31] PU 22226 and two uncatalogued teeth in the Princeton collection, identified by Van Valen (1978) as *Microclaenodon assurgens*.

[32] The suffix *-lambda*, a Greek letter, is (like all Greek letters) neuter (H. D. Cameron, personal communication); hence the endings of certain specific names of pantodonts have been modified accordingly in these lists. Simons (1960) listed also *Caenolambda jepseni* questionably from Rock Bench Quarry, but I could not locate any specimens at Princeton that confirm that record.

[33] PU nos. 14232, 17466, 17511, 17575, 17635, and 18682 are small specimens of *Protictis* intermediate in size between *P. tenuis* and *P. microlestes* ($P_4$ length=3.4–3.7, n=3, $M_1$ length=3.5–4.0, n=5).

published regarding this important middle Paleocene assemblage. In the intervening period since Jepsen's initial review of the fauna, however, considerable excavation and collecting has been undertaken at Rock Bench, resulting in an extensive collection which includes many times the number of taxa published so far.

The Rock Bench local fauna is now one of the largest collections of Paleocene mammals known from a single horizon. More than 1700 specimens of jaws and teeth representing almost 60 species of mammals have been found (Figure 69), and the site is still productive. Many of the taxa are similar or identical to those from other middle Paleocene sites of the Western Interior, particularly Gidley Quarry (Montana), but many are new and as yet undescribed, precluding precise identifications in the faunal list below.

Rock Bench Quarry occurs in a clay-gall sandstone at the base of a thick channel sand, about 200 feet above the base of the Polecat Bench Formation. Vertebrates are most numerous in the thin lens containing flattened clay galls, a mode of occurrence often associated with concentrations of bones and teeth in the Polecat Bench Formation. Although the collection is dominated by small mammal fossils, many jaws and teeth of larger-bodied forms have also been found, suggesting that hydraulic size-sorting, although probably a factor, has not imposed a serious bias on the Rock Bench Quarry sample.

In addition to the specimens summarized in Table 38, there are hundreds of isolated mammalian teeth not included in the total number. They are mostly incisors and premolars that cannot be confidently identified to species, as well as many upper teeth of condylarths for which the specific assignment is in doubt. Since most counts (for minimum numbers) are based on lower molars, which tend to be the most numerous identifiable elements, exclusion of these isolated teeth probably has not significantly affected the relative frequencies.

Nearly all of the specimens from Rock Bench Quarry are in the Princeton collection; a small number are housed at the University of Michigan Museum of Paleontology.

### Gidley Quarry (Crazy Mountain Field, Montana)

In 1905, Albert C. Silberling found remains of fossil vertebrates in a shale exposure on the edge of a coulee in the Crazy Mountain Field, Montana. Having recognized the potential of the site (his locality 4), Silberling showed it to Dr. James Gidley of the National Museum during Gidley's visit to Montana in 1909. Gidley initiated excavation at the site, which was named in his honor, and it became one of the richest and most important Paleocene mammal sites in the world. An account of the development of the quarry and a detailed survey of its fauna (based on the National Museum collection) was provided by Simpson (1937a). Little can be added to his thorough study, save for a few additions and minor emendations to the faunal list. Since his study, however, a large and very important additional collection was obtained at Gidley Quarry and now resides at the American Museum of Natural History—much of it still unpublished. Both collections were studied for the survey presented here.

Previous to Simpson's major monograph on the Crazy Mountain Field faunas, Gidley (1915, 1923) had described some of the primates and an insectivore from Gidley Quarry. Silberling Quarry, stratigraphically slightly below Gidley Quarry, yielded a smaller collection of essentially the same taxa (Douglass, 1908; Simpson, 1937a). I have restricted the present review to the fauna of Gidley Quarry only.

Simpson (1937a: 32) estimated that Gidley Quarry had produced "about 800 good identifiable mammal specimens and perhaps 1500 single teeth and other unimportant fragments," and he listed a total of 382 identified mammal jaws belonging to about 45 species. With the addition of the American Museum collection, the total exceeds 1000 identifiable specimens, about 75% of which are jaws (Table 39). In both the National Museum and American Museum collections there are large numbers of unprepared specimens, as well as many isolated teeth (mostly incisors and premolars) that cannot yet be confidently identified. As with comparable material in the Rock Bench Quarry collection, I have excluded these specimens from my survey. The probability that their omission has not significantly affected the composition of the assemblage is heightened by the close similarity of my results to those of Simpson (1937a: 61, table 4).

As at Rock Bench Quarry, the collection from Gidley Quarry is dominated by mammals of small size. Remains of larger mammals are rarer than at Rock Bench, but several large species are present and are represented by specimens of substantial size (e.g., a lower jaw of *Pantolambda*, USNM 8384; jaws of *Claenodon*, USNM nos. 8363 and 8388; and a partial skull and lower jaws of *Claenodon*, USNM 8362). Occurrence of these relatively large specimens suggests that hydraulic size-sorting did not seriously bias this sample.

Russell (1967) presented a revised faunal list for Gidley and Silberling Quarries, including all published records up to that time. His combined list showed at least 58 and perhaps as many as 62 species, but at least 6 of them are not from Gidley Quarry itself. In Table 39,

Table 39. Mammalian faunal composition of Gidley Quarry.
Asterisk (*) denotes species known also from Rock Bench Quarry.
Plus (+) denotes species closely related to one known from Rock Bench Quarry.

| Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|
| Order MULTITUBERCULATA | | |
| Family Eucosmodontidae | | |
| +*Stygimys jepseni*[1] | 4/2 | .005 |
| Family Cimolodontidae | | |
| **Anconodon gidleyi* | 4/2 | .005 |
| **Anconodon russelli* | 15/8 | .021 |
| Family Ptilodontidae | | |
| +*Ptilodus montanus* | 159/34 | .088 |
| *Ptilodus douglassi*[2] | 8/4 | .010 |
| Family Neoplagiaulacidae[3] | | |
| +*Neoplagiaulax grangeri* | 5/2 | .005 |
| **Mimetodon silberlingi*[4] | 14/8 | .021 |
| *Parectypodus sinclairi* | 14/9 | .023 |
| *Mesodma*, sp. nov.[5] | 1/1 | .003 |
| neoplagiaulacid, sp. nov. 1[6] | 5/4 | .010 |
| neoplagiaulacid, sp. nov. 2[7] | 6/4 | .010 |
| neoplagiaulacids, indet. | 4/2 | .005 |
| Order PROTEUTHERIA | | |
| Family Palaeoryctidae | | |
| **Gelastops parcus* | 10/5 | .013 |
| *Avunculus didelphodonti*[8] | 2/2 | .005 |
| +*Stilpnodon simplicidens*[9] | 6/3 | .008 |
| ?palaeoryctid, unident.[10] | 1/1 | .003 |
| Family Leptictidae | | |
| +*Myrmecoboides montanensis* | 3/1 | .003 |
| +*Prodiacodon concordiarcensis*[11] | 3/2 | .005 |
| +*Prodiacodon furor*[11] | 3/2 | .005 |
| Family Pentacodontidae | | |
| +*Aphronorus fraudator* | 55/23 | .060 |
| *cf. *Aphronorus*, sp. nov.[12] | 2/1 | .003 |
| +*Coriphagus montanus* | 18/9 | .023 |
| Family Pantolestidae | | |
| *Propalaeosinopa diluculi*[13] | 17/8 | .021 |
| *Leptonysson basiliscus*[14] | 1/1 | .003 |
| Family Mixodectidae | | |
| **Eudaemonema cuspidata* | 32/9 | .023 |
| Family Apatemyidae | | |
| **Jepsenella praepropera*[15] | 1/1 | .003 |
| Family uncertain | | |
| insectivore, unident.[16] | 3/3 | .008 |
| Order LIPOTYPHLA | | |
| Family Nyctitheriidae | | |
| +*Leptacodon munusculum* | 7/4 | .010 |
| Family Adapisoricidae | | |
| **Mckennatherium ladae*[17] | 25/12 | .031 |
| ?adapisoricid, unident.[18] | 1/1 | .003 |
| Order PRIMATES | | |
| Family Microsyopidae | | |
| +*Palaechthon alticuspis* | 35/15 | .039 |
| **Palenochtha minor* | 17/9 | .023 |
| Family Plesiadapidae | | |
| +*Pronothodectes matthewi* | 16/5 | .013 |
| Family Carpolestidae | | |
| **Elphidotarsius florencae* | 1/1 | .003 |
| Family Paromomyidae | | |
| *Paromomys maturus* | 106/39 | .101 |
| **Paromomys depressidens* | 21/10 | .026 |
| Family Picrodontidae | | |
| **Picrodus silberlingi* | 17/10 | .026 |
| Order CONDYLARTHRA | | |
| Family Arctocyonidae | | |
| **Tricentes punitor*[19] | 49/17 | .044 |
| *Spanoxyodon latrunculus*[20] | 1/1 | .003 |
| *Prothryptacodon furens*[21] | 8/3 | .008 |
| +*Mimotricentes latidens* | 5/3 | .008 |
| *Claenodon montanensis*[22] | 8/3 | .008 |
| *Claenodon* sp.[23] | 1/1 | .003 |
| Family Phenacodontidae | | |
| **Tetraclaenodon puercensis* | 6/2 | .005 |
| Family Hyopsodontidae | | |
| **Haplaletes disceptatrix* | 25/10 | .026 |
| **Litomylus dissentaneus* | 24/8 | .021 |
| **Litaletes disjunctus* | 32/10 | .026 |
| **Promioclaenus aquilonius* | 140/43 | .111 |
| Family Periptychidae | | |
| **Anisonchus sectorius* | 20/5 | .013 |
| Order MESONYCHIA | | |
| Family Mesonychidae | | |
| +*Dissacus* sp. | 2/1 | .003 |
| Order PANTODONTA | | |
| Family Pantolambdidae | | |
| +*Pantolambda intermedium*[24] | 4/1 | .003 |
| Family Titanoideidae | | |
| *Titanoides simpsoni*[25] | 1/1 | .003 |
| Order TAENIODONTA | | |
| Family Stylinodontidae | | |
| +*Conoryctes comma* | 1/1 | .003 |
| Order CARNIVORA | | |
| Family Miacidae | | |
| *Ictidopappus mustelinus*[26] | 2/1 | .003 |
| *Protictis haydenianus*[26] | 5/3 | .008 |
| *Protictis microlestes*[26] | 46/13 | .034 |
| *Protictis tenuis*[26] | 5/3 | .008 |
| Totals | 1027/387 | 1.008 |

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[1] Simpson's ?*Parectypodus jepseni*, a taeniolabidoid, not a ptilodontoid, placed in the new genus *Stygimys* by Sloan and Van Valen (1965). These authors consider *Eucosmodon sparsus* Simpson, 1937, to be a synonym of *Stygimys jepseni*.

[2] The proper generic assignment of this species, which Simpson placed questionably in *Ptilodus*, has been a matter of debate. Krause (1977) cogently defended its inclusion in *Ptilodus*, a view shared by Sloan (personal communication, April 1978).

[3] There is some doubt as to the proper specific identification of some specimens of neoplagiaulacids from Gidley Quarry. There is no question, however, that the Gidley neoplagiaulacids are diverse, and there appear to be undescribed species among them.

[4] This species has been assigned to various genera, including ?*Ectypodus* (Simpson, 1937a) and *Mesodma* (Van Valen and Sloan, 1966). Krause (1977), following Sloan (unpublished), allocates it to *Mimetodon*.

the faunal list for Gidley Quarry alone is presented, and I have made notes where entries differ from those of Russell, or where new information or comments are pertinent.

## TIFFANIAN FAUNAS

### Cedar Point Quarry (Polecat Bench Sequence)

Continuing field work in the northern Bighorn Basin, directed by G. L. Jepsen, led to the discovery of Cedar Point Quarry in the late 1940s. Prospecting in exposures of the Polecat Bench Formation, Robert Witter and Albert Silberling found the first indications of a concentration of fossil vertebrates. The site was worked periodically during the ensuing two decades, but it was not intensively quarried until 1967. Thereafter, Princeton parties devoted a major part of each field season through 1972 to excavations at Cedar Point Quarry, resulting in the discovery of thousands of specimens of fossil vertebrates. Parties from the University of Michigan and Yale briefly worked the site together in 1974, and University of Michigan parties led by P. D. Gingerich spent parts of the 1975 and 1978 seasons collecting at Cedar Point Quarry. Most of the Cedar Point specimens are in the Princeton collection, but a moderate-sized collection is at the University of Michigan, and a small collection of primates is at Yale.

The quarry is located about 9 miles south of Lovell (SW¼, sec. 23, T.55 N., R.96 W., Big Horn County, Wyoming), some 30 miles east of Polecat Bench. Hence its stratigraphic position relative to the localities on and around Polecat Bench is based mainly on the fauna. Close taxonomic similarity between the faunas of Cedar Point and Scarritt Quarry (as well as other faunas) indicate that Cedar Point is approximately middle Tiffanian in age, slightly younger than Scarritt Quarry and slightly older than Long Draw, Divide, and Croc Tooth Quarries in the Polecat Bench sequence (Gingerich, 1975; Rose, 1977).

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[5] AMNH 35298, left dentary with $P_4$-$M_{1-2}$. $P_4$ length=2.30, $M_1$ length=1.45; $P_4$ serrations about 9; $M_1$ cusps 6:4. Sloan considers this specimen to represent a new species of *Mesodma* (notation on label).

[6] AMNH nos. 35518, 35524, 35525, 35533, and 35536, represent a new species (Sloan, personal communication). $P_4$ length=2.60–2.85 ($\overline{X}$=2.73, n=6), $P_4$ serrations 9–11.

[7] AMNH nos. 35520, 35522, 35523, 35528, 35534, and 35535, represent a second new species (Sloan, personal communication). $P_4$ length=2.85–3.25 ($\overline{X}$=3.02, n=6), $P_4$ serrations 11–12.

[8] Described by Van Valen (1966).

[9] USNM nos. 9643 and 9851 and AMNH 35952 may belong to a different species, closely related to *Stilpnodon simplicidens*.

[10] USNM 9821, probably a small palaeoryctine. Right dentary fragment with the talonid of $M_1$ and $M_2$; $M_2$ length=1.75.

[11] See Novacek (1977). *P. furor*, described by Novacek, is somewhat larger than *P. concordiarcensis* and also differs from it in details of premolar morphology.

[12] AMNH nos. 35293 and 35294. These specimens are very similar to the species of *Aphronorus* from Rock Bench Quarry; they are larger than *A. fraudator*. They also bear certain resemblances to PU 14023 and other specimens from Rock Bench Quarry that may represent a new leptictid (see Rock Bench note 8).

[13] This species, initially placed in the genus *Palaeosinopa* (Simpson, 1935), was subsequently transferred to *Bessoecetor* (Simpson, 1937a), the latter now regarded as a synonym of *Propalaeosinopa*. As Van Valen (1967: 226–227) has pointed out, *P. diluculi* includes *P. thomsoni* (from Scarritt Quarry), and both may be junior synonyms of *P. albertensis* Simpson. I believe the latter proposed synonymy requires further documentation, however; hence I use *P. diluculi* here.

[14] Described by Van Valen (1967) as a leptictid. C. B. Wood (personal communication, September 1977) has pointed out to me several features in common with pantolestids, and I follow his assessment that *Leptonysson* is better placed in the Pantolestidae.

[15] First described from Gidley Quarry by Simpson (1940); see also McKenna (1963) and West (1973a).

[16] USNM nos. 9339, 9498, and 9699 may represent a pantolestid different from other taxa listed here. These specimens have high, simple, pointed premolars. The affinities of these three specimens are unclear, and it is conceivable that they represent lipotyphlans rather than proteutherians.

[17] Originally placed in the genus *Leptacodon* by Simpson. Van Valen (1965) proposed the name *Mckennatherium libitum* for one specimen, AMNH 35437, but it is not specifically distinct from "*Leptacodon*" *ladae*. The latter species is now placed in the genus *Mckennatherium* (Krishtalka, 1976a).

[18] USNM 9510, right dentary with $M_{1-3}$. The specimen appears to belong to a distinctive adapisoricid related to *Mckennatherium*.

[19] Includes four specimens in the AMNH collection labelled as *Metachriacus provocator*. See Rock Bench note 23.

[20] Differs from *Tricentes punitor* primarily by lacking $P_{1-2}$ and having a long diastema anterior to $P_3$. The unique type specimen may be an abnormal specimen of *T. punitor*.

[21] Probably distinct from *Tricentes punitor* but very closely allied to it. Isolated teeth of these two taxa may be easily confused.

[22] I include here *Claenodon silberlingi* and *C. latidens*, but the latter is possibly a valid species.

[23] USNM 6158, left dentary with $M_2$, is slightly larger and has much broader teeth than *C. montanensis*. This may be the same as *C. latidens* (USNM 8388).

[24] See Rock Bench note 31.

[25] Described by Simons (1960).

[26] MacIntyre (1966) provided a detailed account of the Gidley Quarry miacids.

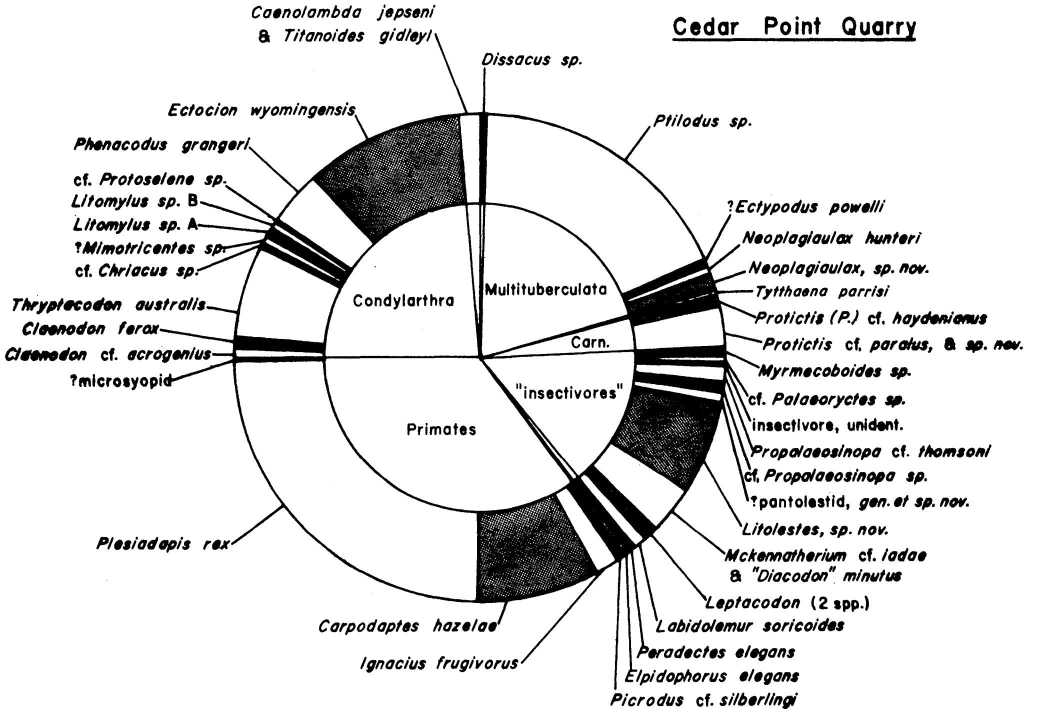

Figure 70. Relative abundances of mammalian taxa in the Cedar Point Quarry fossil assemblage, late Paleocene (middle Tiffanian). Width of sectors determined as in Figure 69 (see Table 40).

No faunal list for Cedar Point has been published previously and, although parts of the collection have been studied or are currently under study, little of it has yet been discussed in the literature (but see West, 1973a on apatemyids, and 1976 on phenacodontids; Rose, 1975a on carpolestids; and Gingerich, 1976b on plesiadapids). Cedar Point Quarry is the richest known Tiffanian vertebrate locality, with about 2000 identifiable mammalian specimens (nearly half jaws, the remainder isolated teeth). There are, in addition, many hundreds of unidentified incisors, premolars, and isolated mammalian skeletal elements, as well as considerable other vertebrate material, representing fishes, turtles, lizards, crocodilians, champsosaurs, salamanders, and birds. About 40 species of mammals are present in the collection (Table 40, Figure 70). Some of them are known also from Scarritt Quarry, but the number of species at Cedar Point is more than twice that at Scarritt. The mammalian fauna of the Brisbane and Judson localities in North Dakota (Holtzman, 1978) is larger and more diverse than that of Scarritt Quarry and is very similar to that of Cedar Point, differing from the latter primarily by its greater diversity and abundance of multituberculates.

Cedar Point Quarry, like Rock Bench Quarry, occurs in a clay-gall sandstone at the base of a thick channel sand. The productive layer is, in most places, only a few inches thick, and it lies immediately above a floodplain clay. Flattened clay galls, torn up from the clay, and plant debris (some of the considerable size), are abundant in the fossil-bearing layer. This bed appears to have been deposited very rapidly as a result of relocation of a channel during its meandering across the floodplain. Productive outcrops that are probably part of the same horizon as the quarry have been found over the ridge and about 100 m southwest of the quarry ("Cedar Point Quarry annex"), and about ¼ mile west of the quarry ("Wayne's Ridge"). Fossils from the "annex" have been included here as part of the sample from Cedar Point Quarry.

There is little evidence of size-sorting in the Cedar Point sample. Much of the material is small, but there is also a large number of jaws of medium-sized to relatively

Table 40. Mammalian faunal composition of Cedar Point Quarry.

| Taxon | Total/MNI | Freq.(MNI) | Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|---|---|---|
| Order MULTITUBERCULATA | | | Family Carpolestidae | | |
| Family Ptilodontidae | | | *Carpodaptes hazelae* | 77/40 | .080 |
| *Ptilodus* sp.[1] | 331/90 | .179 | Family Paromomyidae | | |
| Family Neoplagiaulacidae | | | *Ignacius frugivorus* | 20/8 | .016 |
| *Neoplagiaulax hunteri* | 3/2 | .004 | Family Picrodontidae | | |
| *Neoplagiaulax*, sp. nov.[2] | 17/6 | .012 | *Picrodus* cf. *silberlingi* | 4/3 | .006 |
| cf. *Ectypodus powelli*[3] | 4/3 | .006 | Order CONDYLARTHRA | | |
| Order POLYPROTODONTA | | | Family Arctocyonidae | | |
| Family Didelphidae | | | cf. *Chriacus* sp.[15] | 3/2 | .004 |
| *Peradectes elegans* | 5/3 | .006 | ?*Mimotricentes* sp.[16] | 2/2 | .004 |
| Order PROTEUTHERIA | | | *Thryptacodon australis* | 152/30 | .060 |
| Family Palaeoryctidae | | | *Claenodon ferox*[17] | 14/4 | .008 |
| cf. *Palaeoryctes* sp.[4] | 7/2 | .004 | *Claenodon* cf. *acrogenius*[18] | 6/3 | .006 |
| Family Leptictidae | | | Family Phenacodontidae | | |
| *Myrmecoboides* sp.[5] | 3/3 | .006 | *Phenacodus grangeri* | 99/18 | .036 |
| Family Pantolestidae | | | *Ectocion wyomingensis* | 181/52 | .103 |
| *Propalaeosinopa* cf. *diluculi*[6] | 12/5 | .010 | Family Hyopsodontidae | | |
| ?*Propalaeosinopa* sp.[7] | 7/4 | .008 | *Litomylus* sp. A[19] | 10/3 | .006 |
| ?pantolestid, new[8] | 7/3 | .006 | *Litomylus* sp. B[19] | 4/2 | .004 |
| Family Apatemyidae | | | cf. *Protoselene* sp.[20] | 1/1 | .002 |
| *Labidolemur soricoides* | 9/4 | .008 | Order MESONYCHIA | | |
| Family uncertain | | | Family Mesonychidae | | |
| insectivore, unident.[9] | 1/1 | .002 | *Dissacus* sp.[21] | 4/2 | .004 |
| Order LIPOTYPHLA | | | Order PANTODONTA | | |
| Family Nyctitheriidae | | | Family Pantolambdidae | | |
| cf. *Leptacodon tener*[10] | 8/4 | .008 | *Caenolambda jepseni* | 5/1 | .002 |
| cf. *Leptacodon munusculum*[10] | 1/1 | .002 | Family Titanoideidae | | |
| Family Adapisoricidae | | | *Titanoides gidleyi*[22] | 20/4 | .008 |
| *Mckennatherium cf. ladae*[11] | 35/16 | .032 | Family uncertain | | |
| Family Erinaceidae | | | pantodonts, indet. | 9/2 | .004 |
| *Litolestes*, sp. nov.[12] | 68/31 | .062 | Order CREODONTA | | |
| Order DERMOPTERA | | | Family Oxyaenidae | | |
| Family Plagiomenidae | | | *Tytthaena parrisi*[23] | 3/1 | .002 |
| *Elpidophorus elegans*[13] | 1/1 | .002 | Order CARNIVORA | | |
| Order PRIMATES | | | Family Miacidae | | |
| ?Family Microsyopidae | | | *Protictis* cf. *haydenianus*[24] | 11/4 | .008 |
| ?microsyopid, indet.[14] | 1/1 | .002 | *Protictis* cf. *paralus*[25] | 20/7 | .014 |
| Family Plesiadapidae | | | *Protictis* sp.[26] | 6/3 | .006 |
| *Plesiadapis rex* | 811/128 | .254 | *Protictis*, sp. ident.[27] | 6/3 | .006 |
| | | | Totals | 1988/503 | 1.002 |

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[1] Similar to *P. montanus* but $P_4$ averaging longer than in that species. An uncatalogued Princeton specimen is much smaller ($P_4$ length=6.0) and may belong to a different species, but it is tentatively included here.

[2] Many specimens, representing a new species (Sloan, personal communication, 1978), smaller than *N. hunteri* ($P_4$ length=4.40–5.10, X=4.73, n=12). Profile of $P_4$ differs from that of *N. hunteri*. $P_4$ serrations 11 or 12 (15 in *N. hunteri*).

[3] Uncatalogued Princeton specimens, $P_4$ length=2.60–3.00 (n=3). $P_4$ serrations variable, from 8 or 9 to 12 or more, suggesting there may be more than one species in this small sample. Sloan (personal communication, April 1978) suggests that these are nearest to *Ectypodus powelli*.

[4] Small palaeoryctid similar to but slightly larger than form from Princeton Quarry.

[5] Larger than Torrejonian *Myrmecoboides montanensis* ($M_1$ length=2.90–3.00, n=2). These specimens probably represent a new species.

[6] Similar to, but slightly larger than *P. diluculi* from Gidley and Scarritt Quarries; possibly an undescribed species.

[7] A pantolestid larger than *Propalaeosinopa diluculi*, and about the size of *Leptonysson basiliscus* from Gidley Quarry. $M_1$ length=3.4–3.5 (n=5). Probably a new species.

[8] PU nos. 20027, 21239, 21416, and UM nos. 64504, 66659, and two teeth in UM 64530. These specimens appear to represent large pantolestids (possibly more than one species), almost certainly new. Van Valen (1978) has proposed the name *Niphredil radagasti* for PU 21416 (see also Gingerich, 1980a,b). They are near the size of Wasatchian *Palaeosinopa veterrima* and larger than all other Paleocene pantolestids, including *Leptonysson* and *Palaeosinopa simpsoni* (see Dorr, 1977). The upper molars (PU 20027 and UM 66659) are transversely broad with a low but distinct hypocone shelf. They are distinctive in having a more reduced metacone than in most other pantolestids. $P_3$ and $P_4$ are large ($P_4$ length=6.4 in PU 21239, 5.5 in PU 21416) and $P_4$ is narrow and bladelike and has a basal paraconid and a small, high metaconid. $M_1$ length=5.25 (PU 21416).

[9] UM 63116, left dentary with one damaged molar, length about 2.0. The trigonid is large and high, the talonid small, basined, and with twinned hypoconid and hypoconulid. These features suggest that this is a palaeoryctid, and it may belong to the same species identified as cf. *Palaeoryctes* sp. above (see note 4).

[10] Identified by Krishtalka (1976b) and C. B. Wood (personal communication, 1977). *Leptacodon tener* and *L. munusculum* are very similar in size and structure and, although they may be distinct, it is possible that only one of them exists at Cedar Point.

[11] Most of the specimens referred here closely conform in size and morphology to *Mckennatherium* cf. *ladae* from Rock Bench Quarry, but some also resemble "*Diacodon*" *minutus* from Princeton Quarry. The two taxa are very difficult to separate and are grouped here, although two or three species may actually be present in this sample (Wood, personal communication).

[12] Larger than *Litolestes ignotus* (Princeton Quarry) and *L. notissimus* (Scarritt Quarry); slightly smaller than *L. lacunatus* (Bison Basin, see Gazin, 1956a).

[13] UM 64565, left dentary with $M_{1-3}$, first reported from Cedar Point by Rose and Simons (1977).

[14] An isolated upper incisor in UM 63118 displays morphology believed to belong to microsyopids (e.g., Gingerich, 1976b), but no other specimens referable to this family have been found at the quarry.

[15] PU 20782, 21214, and an uncatalogued lower molar, resemble *Chriacus*. The best preserved specimen, PU 20782, is a left dentary with $P_4$–$M_2$ and alveoli for all other teeth. Both $P_2$ and $P_3$ appear to be two-rooted, and there is a diastema between the alveoli for the canine and $P_2$; $P_1$ is absent. $P_4$ is submolariform, with a small basal paraconid and a large, high metaconid; the talonid is narrow and is not basined. This specimen closely resembles *Chriacus*, near *C. pelvidens*, from the Bison Basin Tiffanian (USNM 20983, Gazin, 1956a: plate 5, figure 1). Van Valen (1978) recently designated PU 20782 as the holotype of a new species, *Chriacus oconostotae*.

[16] PU 19570, left dentary with $M_{1-3}$ and part of $P_4$, and an uncatalogued $M_1$ in the Princeton collection, are most similar to *Mimotricentes*, and may represent *M. fremontensis* Gazin (Van Valen, 1978). The molars are low-crowned, very broad, and have rounded cusps. Aside from having a smaller $M_1$, the specimens also bear close resemblance to *Thryptacodon*.

[17] Possibly more than one species is represented here. $M_1$ length ranges from 8.85 (UM 64394) to 12.20 (PU 20814). Confusion may arise because large specimens of *Claenodon ferox* approach the size of *C.* cf. *acrogenius*. Although some of the size variability may be explained by sexual dimorphism, there are clearly at least two large arctocyonids in the fauna.

[18] Large species, close to *Claenodon acrogenius* Gazin (1956a) from the Bison Basin. Van Valen (1978) places this species in the genus *Mentoclaenodon*. UM 63100 is an exceptionally well preserved right dentary with $P_4$–$M_3$.

[19] There appear to be two closely allied species of *Litomylus* in the fauna. Species A is larger and has a relatively longer $P_4$ ($P_4$ length=4.50–4.65, n=2; $M_1$ length=4.05–4.25, n=4). In species B, $P_4$ length=4.05 (n=1) and $M_1$ length=3.70 (n=2). Species A includes PU nos. 19963, 21450, 22016, and several uncatalogued teeth. Species B includes PU nos. 20009, 21449, 22016, and UM 64638.

[20] PU 20795, left dentary with $M_{1-2}$ ($M_1$ length=3.15). It is distinctly smaller than specimens assigned above to *Litomylus* and may be related to *Protoselene* (D. C. Parris, personal communication).

[21] UM 64510 is a relatively large upper molar (length=18.0, breadth=20.3) that may belong to a species of *Dissacus*, near *D. saurognathus*, or to a primitive species of *Pachyaena*. A smaller mesonychid may also be present.

[22] First reported from Cedar Point by Simons (1960: 37, footnote).

[23] PU nos. 22352 (holotype), 22353, and 21454 (Gingerich, 1980a). This is the oldest known oxyaenid (and oldest known creodont), older than AMNH 55499 from the Tiffany beds above Mason Pocket (Van Valen, 1966).

[24] Closely comparable to *Protictis haydenianus* from Gidley and Rock Bench Quarries, but slightly smaller.

[25] *Protictis paralus* was described from the Tiffanian Judson local fauna of western North Dakota (Holtzman, 1978).

[26] Slightly smaller than *Protictis* cf. *paralus* ($P_4$ length=3.9–4.1, n=2; $M_1$ length=3.7–4.2, n=3; in *P.* cf. *paralus*, mean $P_4$ length=4.03, n=4; mean $M_1$ length=4.63, n=9). Cusps of $P_4$ somewhat less distinct than in *Protictis* cf. *paralus*. Includes PU nos. 19987, 21244, and some teeth included in PU nos. 22011 and 22012.

[27] Under this heading are placed several isolated molar trigonids of a small species of *Protictis*, either *Protictis* cf. *paralus* or the slightly smaller species.

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large mammals, such as *Ectocion*, *Phenacodus*, and *Claenodon*. One of the largest specimens from the quarry is a virtually complete skull of *Claenodon* (PU 20778), the only substantial part of a mammalian skull known from the quarry. There are several large sections of turtle carapace and plastron in the Princeton collection and a partial cranium of the crocodilian *Allognathosuchus* in the University of Michigan collection (UM 63119).

### Scarritt Quarry (Crazy Mountain Field, Montana)

The Scarritt Quarry was discovered by Albert Silberling and was collected extensively by the third Scarritt Expedition of the American Museum of Natural History in 1935. Simpson described most of the fauna in two papers shortly thereafter (1936, 1937b), and in each he presented a summary of faunal composition based on numbers of specimens. Even these rough estimates of relative abundance are not very different from those calculated below (Table 41) using the minimum number of individuals estimate, with a slightly larger sample than was available to Simpson. The Scarritt Quarry sample is much smaller than those of the other Paleocene quarries discussed here, a factor that is probably partly responsible for its low species richness. Nevertheless, Scarritt Quarry is an important site because it is tied to a measured stratigraphic section (it is about 2150 feet above Gidley Quarry).

Simpson (1937b) listed 10 identified species and three

Table 41. Mammalian faunal composition of Scarritt Quarry.
Asterisk (*) denotes species known also from Cedar Point Quarry.
Plus (+) denotes species closely related to one known from Cedar Point Quarry.

| Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|
| Order MULTITUBERCULATA | | |
| Family Ptilodontidae | | |
| +*Ptilodus* sp.[1] | 3/1 | .010 |
| Family Neoplagiaulacidae | | |
| **Neoplagiaulax hunteri*[2] | 64/24 | .247 |
| Order PROTEUTHERIA | | |
| Family Palaeoryctidae | | |
| +palaeoryctid, unident.[3] | 1/1 | .010 |
| +*Paleotomus senior*[4] | 1/1 | .010 |
| Family Pantolestidae | | |
| +*Propalaeosinopa diluculi*[5] | 31/13 | .134 |
| +*Palaeosinopa simpsoni*[6] | 2/1 | .010 |
| Family Apatemyidae | | |
| *Unuchinia asaphes*[7] | 1/1 | .010 |
| Order LIPOTYPHLA | | |
| Family Nyctitheriidae | | |
| +*Leptacodon* cf. *tener* | 7/4 | .041 |
| Family Erinaceidae | | |
| +*Litolestes notissimus* | 68/32 | .330 |
| Order DERMOPTERA | | |
| Family Plagiomenidae | | |
| **Elpidophorus elegans*[8] | 14/4 | .041 |
| Order PRIMATES | | |
| Family Plesiadapidae | | |
| +*Plesiadapis anceps*[9] | 10/2 | .021 |
| Family Carpolestidae | | |
| **Carpodaptes hazelae*[10] | 11/6 | .062 |
| Family Paromomyidae | | |
| **Ignacius frugivorus*[11] | 3/2 | .021 |
| Order CONDYLARTHRA | | |
| Family Arctocyonidae | | |
| **Thryptacodon* cf. *australis* | 8/2 | .021 |
| cf. *Tricentes* sp.[12] | 1/1 | .010 |
| Order MESONYCHIA | | |
| Family Mesonychidae | | |
| +*Dissacus* sp.[13] | 1/1 | .010 |
| Order PANTODONTA | | |
| Family Titanoideidae | | |
| +*Titanoides zeuxis* | 1/1 | .010 |
| Totals | 227/97 | .998 |

[1] Three isolated teeth, AMNH nos. 33826 and 33989 and PU 14540. Simpson (1936, 1937b) identified them as ptilodontid.

[2] MNI estimated, in this case, from half the total number of $P_4$s, as listed in the AMNH catalogue. Specimens were not available for study.

[3] First record of a small palaeoryctine from Scarritt Quarry. AMNH 35221, left dentary with $P_4$–$M_2$ ($M_1$ length=1.50, breadth=1.35).

[4] AMNH 33990, a lower molar, holotype of *Palaeosinopa senior* Simpson, was placed in the new genus *Paleotomus* by Van Valen (1967). Two upper teeth that Simpson referred to *Palaeosinopa senior* were described as a new species of *Palaeosinopa* by Van Valen (1967). Van Valen regarded *Paleotomus* as a didelphodontine palaeoryctid, but Gingerich (1980) recently suggested that Simpson was correct in assigning all three specimens to the Pantolestidae.

[5] *Propalaeosinopa thomsoni* Simpson, 1936, is a junior synonym of *P. diluculi* (see Gidley Quarry note 13).

[6] AMNH nos. 33828 and 33991, Simpson's (1937b) referred upper teeth of *Palaeosinopa senior*. Description of a new genus, *Paleotomus*, for the holotype of this species (Van Valen, 1967), necessitated a new species name for the referred specimens. Dorr (1977) described a partial skull of *P. simpsoni* from the late Tiffanian Dell Creek Quarry, Hoback Basin, Wyoming.

[7] McKenna (1963) redescribed this taxon and argued for its inclusion in the Apatemyidae.

[8] See detailed description by Szalay (1969a). *Elpidophorus* was transferred from the Mixodectidae to the Plagiomenidae by Rose (1975b).

[9] Discussed by Gingerich (1976b)

[10] Discussed by Rose (1975a).

[11] This is the type species of *Ignacius*, considered by some authors to be a synonym of *Phenacolemur*. For distinctions between the two genera, see Chapter 4 and Bown and Rose (1976), Rose and Gingerich (1976).

[12] E. Manning (personal communication) has identified AMNH 33827 as a specimen of an arctocyonid similar to *Tricentes*.

[13] AMNH 35969, an upper tooth.

more indeterminant forms from Scarritt Quarry. A few additional taxa have been identified since then, bringing the total to 17 species (Table 41). This relatively low number would almost surely be increased if additional collecting yielded a sample size comparable to that of the other quarries. Scarritt Quarry is developed in a shell bed and in clay just above and below the mollusks (Simpson, 1937a), and the sample appears to be biased by size-sorting. Only one large specimen, a jaw of *Titanoides zeuxis*, has come from the site, and it was found on the surface in many fragments.

The fauna of Scarritt Quarry is similar in many respects to that of Cedar Point Quarry but seems to be slightly older (based on smaller size or more primitive grade of species present). Taxa similar or identical to those known also from Cedar Point are indicated in Table 41.

Nearly all of the Scarritt Quarry specimens are in the American Museum of Natural History, but a few specimens are in the Princeton collection.

## Princeton Quarry (Polecat Bench Sequence)

Princeton Quarry, like Rock Bench Quarry, was discovered by G. L. Jepsen, during initial field work in the Bighorn Basin in the late 1920s. The quarry is situated on the western side of Polecat Bench (eastern edge of the Clark's Fork Basin: SE¼, sec. 21, T.57 N., R.100 W., Park County), northeast of the UM Clarkforkian localities (see Figure 2). It is about 2200 feet above Rock Bench Quarry, in the upper part of the interval designated as the "Silver Coulee beds" by Jepsen (1940). In contrast to Rock Bench and Cedar Point Quarries, Princeton Quarry is not developed in a coarse, light-colored sandstone; rather, the fossils come from a very fine-grained gray-green sandstone, almost a siltstone. Beneath the productive layer is a coarser sand, and above it is shale (Jepsen, 1940).

Jepsen (1930b, 1940) referred to the "Silver Coulee beds" (and specifically Princeton Quarry, in 1930) as a "Tiffany-Bear Creek faunal equivalent." We now know that the quarry is intermediate in age between the Tiffany beds (Mason Pocket, Ignacio, Colorado) and Bear Creek. The measured sections presented in Chapter II (Figure 3) start at Princeton Quarry and show that it lies in the upper part of the Polecat Bench Formation, about 400 m below the base of the Clarkforkian. Faunal evidence indicates that Princeton Quarry is younger than Cedar Point Quarry and slightly younger than Long Draw, Croc Tooth, and Divide Quarries. Thus the age of Princeton Quarry is later, but not latest, Tiffanian. (This assessment differs from my earlier view that Princeton Quarry lies approximately on the Tiffanian-Clarkforkian boundary [Rose, 1977] and may be considered earliest Clarkforkian [Rose, 1975a], opinions reached prior to our biostratigraphic investigations in the Clark's Fork Basin.) Schaff Quarry, Fritz Quarry, and Jepsen Valley Quarry, all near Princeton Quarry, have produced smaller collections of about the same age.

Jepsen (1930b) listed 13 mammalian species from Princeton Quarry. In his 1940 study of the multituberculates, Jepsen noted that at least 28 genera of mammals had by then been discovered at Princeton Quarry but, except for the multituberculates, he did not enumerate them until nearly 30 years later (Jepsen and Woodburne, 1969). Jepsen and Woodburne's list, however, includes taxa from the quarry as well as those found in nearby strata of about the same level. The faunal compilation presented in Table 42 is restricted to Princeton Quarry alone and is followed by a list of additional taxa found in close proximity to the quarry. The distinction allows us to infer that the Princeton Quarry assemblage is biased by size-sorting (most of the large species being rare or absent in the quarry assemblage) or by its depositional environment, or perhaps a combination of both factors. For example, Jepsen and Woodburne included five species of pantodonts and two of uintatheres in their Princeton Quarry faunal list, but as far as I have been able to determine, none of them has been found at the quarry itself. A bias in the quarry sample is further suggested by the relative rarity of phenacodontid condylarths, which are common as surface finds in the vicinity of the quarry. (Here relative abundance proves to be more informative than presence or absence data. However, the relative abundance of phenacodontids at surface localities in the interval from Princeton Quarry through the Clarkforkian is probably exaggerated by various biases—preservational, sorting, or collecting—that have limited the microfauna at these sites.)

The mammalian assemblage of Princeton Quarry and its environs provides us with our best picture of very later Paleocene faunas. Many of the taxa represented appear to be derivatives of the earlier Tiffanian fauna known from the Bighorn Basin, but some forms (e.g. *Probathyopsis* and *Arctostylops*) appear to be new immigrants. Unfortunately, biases in the Princeton Quarry assemblage suggest that this sample does not provide an accurate example of faunal diversity at this level.

Most of the collection from Princeton Quarry and the immediate vicinity is at Princeton University. Smaller samples are housed at the University of Michigan and the Museum of Comparative Zoology at Harvard.

## DISCUSSION OF PALEOCENE QUARRY ASSEMBLAGES

Examination of Tables 38–42 reveals that the mammalian assemblages preserved at the middle Paleocene Rock Bench and Gidley Quarries are very diverse in terms of both species richness and evenness (the most common species at the Torrejonian quarries are much less abundant compared to the most common species at Cedar Point Quarry). High evenness in the Torrejonian assemblages is also indicated by Whittaker's index (Table 55 and Figure 75). The late Paleocene quarry samples surveyed here are considerably less diverse in both characteristics. This is particularly evident in a comparison between Rock Bench and Cedar Point Quarries, both of which have produced very large samples of similar size from the same kind of channel lag deposit.

The species richness of the five quarry samples studied

Table 42. Mammalian faunal composition of Princeton Quarry.

| Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|
| Order MULTITUBERCULATA | | |
| Family Eucosmodontidae | | |
| *Neoliotomus conventus* | 4/1 | .005 |
| *Microcosmodon conus*[1] | 7/4 | .022 |
| *Pentacosmodon pronus* | 2/1 | .005 |
| Family Ptilodontidae | | |
| *Prochetodon cavus*[1] | 12/3 | .016 |
| Family Neoplagiaulacidae | | |
| *Neoplagiaulax hazeni*[1] | 4/1 | .005 |
| *Mimetodon churchilli* | 2/1 | .005 |
| *Parectypodus laytoni* | 9/5 | .027 |
| *Ectypodus powelli* | 10/8 | .043 |
| neoplagiaulacids, indet.[2] | 5/– | — |
| Order POLYPROTODONTA | | |
| Family Didelphidae | | |
| *Peradectes elegans* | 4/3 | .016 |
| ?*Peratherium* sp.[3] | 1/1 | .005 |
| Order PROTEUTHERIA | | |
| Family Palaeoryctidae | | |
| cf. *Palaeoryctes* sp.[4] | 11/4 | .022 |
| Family Leptictidae | | |
| *Prodiacodon* cf. *concordiarcensis*[5] | 2/1 | .005 |
| ?*Palaeictops* sp.[6] | 3/3 | .016 |
| Family Apatemyidae | | |
| *Unuchinia* sp. | 3/2 | .011 |
| Order LIPOTYPHLA | | |
| Family Nyctitheriidae | | |
| *Leptacodon packi* | 8/5 | .027 |
| Family Erinaceidae | | |
| *Litolestes ignotus* | 25/14 | .076 |
| Family uncertain | | |
| "*Diacodon*" *minutus*[7] | 43/17 | .092 |
| adapisoricid or nyctithere, unident.[8] | 11/6 | .032 |
| Order PROTEUTHERIA or LIPOTYPHLA | | |
| Family uncertain | | |
| *Apternodus*-like species A[9] | 1/1 | .005 |
| *Apternodus*-like species B[9] | 1/1 | .005 |
| Order PRIMATES | | |
| Family Microsyopidae | | |
| *Micromomys silvercouleei*[10] | 1/1 | .005 |
| Family Plesiadapidae | | |
| *Plesiadapis fodinatus*[11] | 112/19 | .103 |
| Family Carpolestidae | | |
| *Carpolestes dubius*[12] | 48/13 | .070 |
| Family Paromomyidae | | |
| *Phenacolemur pagei* | 51/17 | .092 |
| Order CONDYLARTHRA | | |
| Family Arctocyonidae | | |
| cf. *Tricentes* sp.[13] | 14/5 | .027 |
| *Thryptacodon* sp. | 3/2 | .011 |
| *Claenodon* sp.[14] | 1/1 | .005 |
| Family Phenacodontidae | | |
| *Phenacodus* sp.[15] | 3/1 | .005 |
| *Ectocion osbornianus*[16] | 15/5 | .027 |
| Family Hyopsodontidae | | |
| *Phenacodaptes sabulosus*[17] | 103/27 | .146 |
| Order MESONYCHIA | | |
| Family Mesonychidae | | |
| *Dissacus* cf. *navajovius*[18] | 5/2 | .011 |
| Order CARNIVORA | | |
| Family Miacidae | | |
| *Didymictis*, ?sp. nov.[19] | 5/1 | .005 |
| cf. *Viverravus*, sp. nov.[20] | 12/4 | .022 |
| viverravine, sp. A[21] | 2/2 | .011 |
| viverravine, sp. B[22] | 1/1 | .005 |
| Order uncertain | | |
| Suborder PALAEANODONTA | | |
| Family Metacheiromyidae | | |
| *Propalaeanodon schaffi*[23] | 2/2 | .011 |
| Totals | 546/185 | .996 |

The following additional taxa have been found in close proximity to Princeton Quarry:

Order CONDYLARTHRA
  Family Arctocyonidae
    *Anacodon? nexus*
  Family Phenacodontidae
    *Phenacodus* cf. *vortmani*

Order PANTODONTA
  Family Barylambdidae
    *Haplolambda quinni*[24]
    *Leptolambda schmidti*[24]
  Family Titanoideidae
    *Titanoides primaevus*[24]
  Family Cyriacotheriidae[25]
    *Cyriacotherium argyreum*[25]

Order DINOCERATA
  Family Uintatheriidae
    *Probathyopsis* sp.[26]
Order TAENIODONTA
  Family Stylinodontidae
    cf. *Lampadophorus* sp.[27]
Order NOTOUNGULATA
  Family Arctostylopidae
    *Arctostylops* cf. *steini*[28]
Order CREODONTA
  Family Oxyaenidae
    cf. *Oxyaena* sp.[29]
    ?*Dipsalodon matthewi*[30]
    *Dipsalodon churchillorum*, sp. nov.[31]

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[1] Krause (1977) recently discussed Princeton Quarry specimens of these species in comparison to multituberculates from the Ravenscrag Formation of Saskatchewan.

[2] A few teeth and fragments of teeth. They are not included in the MNI estimate because they are probably referable to one of the four identified species and would not increase the MNI for those taxa.

[3] PU 17810, left dentary with $P_{1-3}M_{1-4}$. The molars have high, acute entoconids and posteriorly projecting hypoconulids, both characteristic of *Peratherium*. The specimen almost surely represents a second species of marsupial at Princeton Quarry.

[4] Several well preserved upper and lower jaws, larger than Torrejonian *Palaeoryctes puercensis* and very near the size of Clarkforkian *P. punctatus.*

[5] PU nos. 14137 and 21162. Very close in size and structure to holotype of *Diacodon pearcei* Gazin (1956a), USNM 20970, from the Tiffanian of the Bison Basin, and to *Prodiacodon concordiarcensis* from Gidley Quarry. Novacek (1977) considers these two species to be conspecific.

[6] PU nos. 14157, 14526, and 21163. PU 14526 is a skull and associated skeleton, the only nearly complete specimen from the quarry. These three specimens appear to have the characteristics of *Palaeictops* (see Novacek, 1977), but further study is necessary to verify that two different leptictids are present in the fauna.

[7] Princeton Quarry specimens discussed by Krishtalka (1976a).

[8] A number of small jaws similar to *Leptacodon packi* are included here. According to C. B. Wood (personal communication, 1977), these unidentified specimens include at least two different species. Some of the specimens here may be referable to *L. packi.*

[9] Jepsen and Woodburne (1969) included ?*Apternodus* in their faunal list of Princeton Quarry mammals, almost certainly a reference to the specimens listed here as species A and B. PU 16521 (species A) is the back of a skull including the basicranium, with flaring squamosals (?), thus resembling the skull of *Apternodus.* Notes on its label by M. C. McKenna and C. B. Wood identify this specimen as an *Apternodus*-like form. PU 14116 (species B), a left dentary with $P_4$-$M_2$ ($M_1$ length=1.0a), has greatly reduced molar talonids, as in *Apternodus.* It appears to be much too small to belong to the same species as PU 16521.

[10] Described by Szalay (1974) as a paromomyid; transferred to Microsyopidae by Bown and Rose (1976).

[11] Discussed by Gingerich (1976b).

[12] Redescribed and figured by Rose (1975a)

[13] Probably closely allied to or derived from *Tricentes punitor.* There may be two similar species included under this heading.

[14] A single uncatalogued upper molar in the Princeton collection.

[15] PU 17834, two isolated teeth about the size of *Phenacodus primaevus.* An incomplete upper premolar is included in UM 68860.

[16] Princeton Quarry specimens were placed in this species by West (1976)

[17] See additional discussion and figures in Gazin (1959).

[18] PU nos. 13924, 16135, and three isolated teeth, uncatalogued. PU 16135 includes relatively complete dentaries and associated maxilla with one tooth; it is the most complete large specimen from the quarry. Length of $M_{1-3}$=36.0, near the size of *D. navajovius* and distinctly smaller than *D. praenuntius* and *D. saurognathus.*

[19] PU nos. 13937, 13961, 14317, 14319, 14320. Probably a new species, smaller than *D. protenus* and Clarkforkian *D. protenus proteus* ($P_4$ length=8.0; $M_1$ length=8.4; $M_2$ length=5.9; in PU 13937). Specimens of *Didymictis* from the early Clarkforkian probably belong to the same species as these Princeton Quarry specimens.

[20] Slightly smaller than *Viverravus politus* and slightly more primitive. Probably the immediate predecessor of *V. politus.* PU 16495, a crushed but relatively complete skull with partial dentition, contains the oldest known carnivoran endocranial cast (Radinsky, 1977).

[21] PU nos. 16523 and 17844, $M_1$ length=3.5. Probably a new species closely related to small species of *Viverravus.*

[22] An uncatalogued Princeton specimen, right $M_1$ (length=4.4, breadth of trigonid=2.2). This appears to represent a small viverravine larger than species A but smaller than cf. *Viverravus*, sp. nov.

[23] Two left humeri, PU nos. 13928 and 13929, probably belong to this species. The holotype (MCZ 20122) is from Jepsen Valley Quarry, about a mile southeast of Princeton Quarry and at about the same stratigraphic level (Rose, 1979).

[24] Jepsen and Woodburne (1969) listed five species of pantodonts among the Princeton Quarry fauna. Simons (1960) listed all five as coming from the "Silver Coulee beds," but he specified that *Titanoides gidleyi* and *T. majus* came from stratigraphically below Princeton Quarry. The four species in my list seem to be from strata closer to the level of Princeton Quarry, but I have found no records that indicate that any of them have been found at the quarry itself.

[25] New taxa, Rose and Krause (in press).

[26] Several specimens in the Princeton and MCZ collections.

[27] Several specimens at Princeton, including PU 21499, about 16 associated teeth including canines.

[28] MCZ 20004, partial skull and lower jaws with nearly complete dentition, found by C. R. Schaff (MCZ). Possibly a new species, but clearly very closely related to *Arctostylops steini.*

[29] PU 18961, associated teeth, appears to belong to a species of *Oxyaena*, near *O. transiens.* It is possible, however, that it represents *Dipsalodon churchillorum.*

[30] PU 17948 consists of tooth fragments of a large oxyaenid, possibly *Dipsalodon matthewi.* UM 67177 (SC-86), tooth fragments of an oxyaenid from the southern exposures along Polecat Bench, probably at about the level of Princeton Quarry, may belong to *D. matthewi.* All other known specimens of this rare palaeonictine are of Clarkforkian age.

[31] PU 17846, the holotype, is from Storm locality, very near Princeton Quarry (see description in Chapter 4).

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here, together with a few other pertinent samples, may be summarized as follows:

| | |
|---|---|
| Tiffanian | |
| Princeton Quarry | 36 species |
| Mason Pocket, Colorado (E. Manning, personal communication) | 16 species |
| Judson-Brisbane, North Dakota (Holtzman, 1978) | 37 species |
| Cedar Point Quarry | 38 species |
| Scarritt Quarry | 17 species |
| Torrejonian | |
| Rock Bench Quarry | 57 species |
| Gidley Quarry | 55 species |
| Swain Quarry, south-central Wyoming (Rigby, 1980) | 50 species |

Each of the samples listed above, except for the combined Judson and Brisbane faunas (which are from the same stratigraphic level and depositional environment), is derived from a single fossil-bearing level, and they probably represent the closest approximation to sampling the fauna of a single time plane that is known in the early Cenozoic mammalian record. The close similarity in species richness and the large sample sizes at the three Torrejonian quarries suggest that these samples provide a relatively good estimate of species number, and that only very rare species remain to be discovered. These features also apply to two of the Tiffanian samples, those from Cedar Point and the penecontemporary Judson-Brisbane faunas, which show remarkable conformity in species richness. The samples from Scarritt Quarry and Mason Pocket are much smaller (but still among the best known Tiffanian faunas), and this is reflected in their much lower species richness. The Princeton Quarry sample, of late Tiffanian age, appears to agree closely in species richness with Cedar Point and Judson-Brisbane but, as previously noted, its sample is clearly biased (by size-sorting and possibly local paleoecology). Therefore, measures of diversity at Princeton Quarry may not be comparable to those for the other quarry samples. I have included it in the analyses, however, since it is the only large sample of late Tiffanian age. From Table 42, it can be seen that at least 12 species of larger mammals, not found at Princeton Quarry itself, occur in adjacent strata at about the same level. Had sorting not been a factor at Princeton Quarry, its species richness would probably have been higher, although the effects on equitability cannot at present be evaluated.

Modern mammalian faunas obviously differ considerably from those of the Paleocene, but it is of some interest to compare the species richness at the Paleocene quarries to that observed in some modern faunas. Evidence suggests that Paleocene climates were, in general, warmer and more equable than the present-day climate of Wyoming; hence the most comparable faunas to those of the Paleocene are probably those of the subtropical and tropical regions today. Davis (1962) listed 77 species of mammals, exclusive of bats, inhabiting the North Borneo rain-forest. For comparison, he noted that 79 nonvolant species of mammals had been reported in a study of the Lower Tropical Zone of Panama. By contrast, only 40 species (excluding bats) inhabit the temperate forests of Virginia. Fleming (1973), examining more localized habitats, found 35 mammalian species (including bats) in each of two Michigan forests and 70 mammalian species (including bats) in each of two forests in the Panama Canal Zone. If comparisons to Paleocene faunas are valid to any extent, these figures suggest that the quarry samples provide a relatively good estimate of species richness in living assemblages of Paleocene mammals. They further conform to evidence that it was warmer and more equable in the middle Paleocene than in the late Paleocene (Wolfe, 1978), since species richness declined from middle to late Paleocene. As in modern faunas, carnivorous mammals comprise a relatively small proportion of the Paleocene assemblages (roughly 5%).

Relative abundances of the most important higher taxa at the five Paleocene quarries studied here are summarized in Table 43. The dominance of archaic forms, particularly multituberculates and plesiadapiform primates, is obvious. Plesiadapids were especially abundant in the Tiffanian. These features appear to be characteristic of many large assemblages of middle and late Paleocene age (e.g. Holtzman, 1978). Condylarths are another important constituent of Paleocene faunas. A dramatic decline in hyopsodontids apparently occurred from the Torrejonian into the Tiffanian; however, the one specialized hyopsodontid that occurs at Princeton Quarry is the most abundant species in that sample. The explanation for this change is unclear but may reflect paleoecology, immigration of faunas, or other factors. The fauna of Scarritt Quarry, although composed almost entirely of species identical or similar to those at Cedar Point, shows strikingly different frequencies of several important taxa. This might be due to sorting, local ecological factors, or its smaller sample size; and it is probable that the Scarritt Quarry assemblage does not provide an accurate picture of diversity in the Tiffanian. Comparisons with other faunas (such as Judson and Brisbane, see Holtzman, 1978) suggest that the Cedar Point assemblage is a much more accurate sample of the middle Tiffanian fauna, and that it better reflects diversity in the middle Tiffanian.

The faunas from Rock Bench and Gidley Quarries are very similar in diversity and in taxa represented. More than one-third of the species represented in these assemblages are identical, and nearly another third appear to be very closely related (Tables 38 and 39). These are the most common species present in all but one case (two primate species, see Table 43), and about 60% of the individuals in each sample belong to species common to both samples.

Clark et al. (1967) contended that "obviously-transported quarry assemblages" do not accurately provide information on ancient populations. There is little evidence of abrasion among jaws and teeth in the Paleocene quarry samples analyzed here, suggesting that, although some were clearly water-laid, they have

Table 43. Relative abundances of some important taxa in the Paleocene quarry assemblages.
Sample sizes are indicated by a fraction; the numerator is the total number of specimens, the denominator is MNI.
Numbers in parentheses following percentages give the number of species of the higher taxon that are present in the quarry sample.

| Taxon | *Gidley*<br>1027/387 | *RBQ*<br>1683/494 | *CPQ*<br>1988/503 | *Scarritt*<br>227/97 | *PQ*<br>546/185 |
|---|---|---|---|---|---|
| Multituberculates | 21% (11) | 18% (8) | 20% (4) | 26% (2) | 13% (8) |
| *Ptilodus, Prochetodon* | 9% | 10% | 18% | 1% | 2% |
| Primates | 23% (7) | 20% (8) | 36% (4) | 10% (3) | 26% (4) |
| plesiadapids | 1% (1) | 2% (1) | 25% (1) | 2% (1) | 11% (1) |
| *Palaechthon, Plesiolestes* | 4% | 10% | | | |
| *Paromomys maturus* | 10% | | | | |
| Arctocyonids | 8% (5+) | 13% (8) | 8% (5) | 3% (2) | 5% (3) |
| Phenacodontids | 1% (1) | 4% (1) | 14% (2) | | 4% (2) |
| Hyopsodontids | 18% (4) | 22% (4) | 1% (3) | | 15% (1) |

not been transported far. Moreover, the close comparison between the Gidley and Rock Bench assemblages (which are geographically separated and occur in different lithologies) suggests that what transport may have occurred has not seriously altered their composition. The general similarity between the Tiffanian Cedar Point and Judson-Brisbane assemblages, and the contrast in diversity of the Cedar Point assemblage compared to that from Rock Bench (despite their close proximity and similar geologic occurrence), offer further support that these samples do provide relatively accurate representations of middle and late Paleocene mammalian faunal composition in the northern Western Interior.

Several diversity indices were computed for the Paleocene quarry samples (Table 55) and three are depicted in Figures 75 and 76. As would be expected from Tables 38–42, the indices show a diversity high in the Torrejonian, followed by a sharp drop in diversity (both evenness and species richness) in the middle Tiffanian. Less apparent from the tables is the close correspondence in the indices for Rock Bench and Gidley Quarries. The decline in mammalian diversity in the Tiffanian apears to match a decline in the species richness of megafloras and in the number of species with entire-margined leaves in the late Paleocene (Figure 75), a phenomenon interpreted to indicate a cooling trend and lower equability from early to late Paleocene (Wolfe and Hopkins, 1967; Wolfe, 1978). Paleobotanical evidence indicates that temperatures and equability increased again from late Paleocene to early Eocene time (Hickey, 1977; Wolfe, 1978). Oxygen isotope data indicates a similar amelioration in paleotemperatures from the late Paleocene to the early Eocene in northwestern Europe (Buchardt, 1978).

The higher species richness and evenness in the Rock Bench assemblage as compared to that at Cedar Point is immediately obvious in a plot of the frequencies of species against their rank of abundance in the assemblages (Figure 77). The Rock Bench sample has a distribution approaching that predicted from MacArthur's Type 1 model, thus indicating high equitability; whereas the Cedar Point sample has the type 4 distribution described by Hutchinson (1961)—with two species very abundant—which he associated with instability. The relatively low diversity at Cedar Point may be a reflection of cooler climate and lower equability in the middle Tiffanian than in the Torrejonian.

## CLARKFORKIAN AND WASATCHIAN FAUNAS

Nearly all the Clarkforkian samples from the type area are surface lag accumulations collected by prospecting overbank deposits. They are time-averaged (each sample pooled from a specified stratigraphic interval), and sorting and/or sampling biases have restricted the number and relative abundance of very small mammals. For these reasons, the samples from the eight successive Clarkforkian levels analyzed here (Tables 44–51) are not directly comparable to the Paleocene quarry assemblages discussed above; however, the major differences in diversity from the Paleocene assemblages are probably valid. Only one Clarkforkian locality in the study area (SC–188) has produced a concentration of micromammalian fossils. Its faunal composition is compared to that of the Bear Creek Quarry, north of the study area, in Table 52, to provide some indication of the small-mammal fauna that is apparently not preserved at most Clarkforkian sites. It is immediately clear that the faunal compositions at these quarries differ substantially from the compositions of the intervals analyzed from surface collections. However, it must be emphasized that the Bear Creek and SC–188 samples themselves are obviously biased by sorting and, in any case, are

*text continued on p. 164*

Table 44. Mammalian Faunal Composition, *Plesiadapis gingerichi* zone, 370–470 m below boundary sandstone.*

| Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|
| Order MULTITUBERCULATA | | |
| Family Eucosmodontidae | | |
| *Neoliotomus conventus* | 2/2 | .015 |
| *Microcosmodon rosei* | 1/1 | .008 |
| Family Ptilodontidae | | |
| *Prochetodon* cf. *cavus* | 1/1 | .008 |
| Order PROTEUTHERIA | | |
| Family Pantolestidae | | |
| *Palaeosinopa* sp. | 2/2 | .015 |
| ?Order LIPOTYPHLA, incertae sedis | | |
| cf. "*Diacodon*" *minutus* | 1/1 | .008 |
| Order PRIMATES | | |
| Family Plesiadapidae | | |
| *Plesiadapis dubius* | 18/10 | .076 |
| *Plesiadapis gingerichi* | 8/5 | .038 |
| Family Carpolestidae | | |
| *Carpolestes nigridens* | 3/2 | .015 |
| Family Paromomyidae | | |
| *Phenacolemur pagei* | 3/2 | .015 |
| Order CONDYLARTHRA | | |
| Family Arctocyonidae | | |
| *Thryptacodon* cf. *antiquus* | 3/2 | .015 |
| Family Phenacodontidae | | |
| *Phenacodus primaevus* | 39/19 | .144 |
| *Phenacodus vortmani* | 1/1 | .008 |
| *Phenacodus* sp. | 9/8 | .061 |
| *Ectocion osbornianus* | 110/42 | .318 |
| Family Hyopsodontidae | | |
| *Haplomylus simpsoni* | 1/1 | .008 |
| *Phenacodaptes/Apheliscus* intermediate | 2/1 | .008 |
| *Apheliscus nitidus* | 1/1 | .008 |
| Order MESONYCHIA | | |
| Family Mesonychidae | | |
| *Dissacus* cf. *praenuntius* | 3/3 | .023 |
| Order TAENIODONTA | | |
| Family Stylinodontidae | | |
| cf. *Lampadophorus* sp. | 1/1 | .008 |
| Order PANTODONTA | | |
| Family Coryphodontidae | | |
| *Coryphodon* sp. | 2/2 | .015 |
| Order TILLODONTIA | | |
| Family Esthonychidae | | |
| *Esthonyx xenicus* | 2/2 | .015 |
| Order DINOCERATA | | |
| Family Uintatheriidae | | |
| *Probathyopsis praecursor* | 6/5 | .038 |
| Order CARNIVORA | | |
| Family Miacidae | | |
| *Didymictis* sp. | 10/8 | .061 |
| *Viverravus acutus* | 1/1 | .008 |
| *Viverravus politus* | 1/1 | .008 |
| Order CREODONTA | | |
| Family Oxyaenidae | | |
| cf. *Oxyaena transiens* | 2/2 | .015 |
| *Oxyaena? lichna* | 1/1 | .008 |
| Order RODENTIA | | |
| Family Paramyidae | | |
| *Paramys* cf. *atavus* and *Paramys* sp. | 10/4 | .030 |
| Totals | 244/131 | .997 |

*Includes combined samples from UM localities SC–82, 83, 156, 157, 169, 170, 171, 172, 173, 174, 177, 179, 215, 216, 217, 226, 227, 250, 251.

Table 45. Mammalian Faunal Composition, *Plesiadapis cookei* zone, 260–320 m below boundary sandstone.*

| Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|
| Order PROTEUTHERIA | | |
| Family Palaeoryctidae | | |
| *Palaeoryctes punctatus* | 1/1 | .011 |
| Family Leptictidae | | |
| cf. *Prodiacodon tauricinerei* | 1/1 | .011 |
| Family Pantolestidae | | |
| *Palaeosinopa* sp. | 3/1 | .011 |
| Order PRIMATES | | |
| Family Microsyopidae | | |
| *Microsyops simplicidens* | 1/1 | .011 |
| Family Plesiadapidae | | |
| *Plesiadapis dubius* | 1/1 | .011 |
| *Plesiadapis cookei* | 7/3 | .032 |
| *Chiromyoides potior* | 1/1 | .011 |
| Family Paromomyidae | | |
| *Phenacolemur pagei* | 4/3 | .032 |
| Family Arctocyonidae | | |
| cf. *Tricentes* sp. | 1/1 | .011 |
| Order CONDYLARTHRA | | |
| ?"*Chriacus*" sp. | 1/1 | .011 |
| Family Phenacodontidae | | |
| *Phenacodus primaevus* | 26/10 | .108 |
| *Ectocion osbornianus* | 129/35 | .376 |
| Family Hyopsodontidae | | |
| *Aletodon gunnelli* | 2/1 | .011 |
| *Haplomylus simpsoni* | 5/3 | .032 |
| *Apheliscus nitidus* | 7/4 | .043 |
| Order MESONYCHIA | | |
| Family Mesonychidae | | |
| *Dissacus praenuntius* | 3/3 | .032 |

Table 45. Continued.

| Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|
| Order TAENIODONTA | | |
| Family Stylinodontidae | | |
| cf. *Lampadophorus* sp. | 1/1 | .011 |
| Order PANTODONTA | | |
| Family Coryphodontidae | | |
| *Coryphodon* sp. | 2/2 | .022 |
| Order TILLODONTIA | | |
| Family Esthonychidae | | |
| *Esthonyx ancylion* | 3/2 | .022 |
| Order DINOCERATA | | |
| Family Uintatheriidae | | |
| *Probathyopsis praecursor* | 2/2 | .022 |
| Order CARNIVORA | | |
| Family Miacidae | | |
| *Didymictis protenus proteus* | 14/7 | .075 |
| *Viverravus acutus* | 1/1 | .011 |
| Order CREODONTA | | |
| Family Oxyaenidae | | |
| *Oxyaena* sp. | 3/2 | .022 |
| Order RODENTIA | | |
| Family Paramyidae | | |
| *Paramys* spp. (2 species?) | 9/6 | .065 |
| Totals | 228/93 | .994 |

*Includes combined samples from UM localities SC-92, 93, 136, 137, 197.

Table 46. Mammalian Faunal Composition, *Plesiadapis cookei* zone, 240–250 m below boundary sandstone.*

| Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|
| Order MULTITUBERCULATA | | |
| Family Neoplagiaulacidae | | |
| *Ectypodus powelli* | 1/1 | .014 |
| Order PROTEUTHERIA | | |
| Family Pantolestidae | | |
| *Palaeosinopa* sp. | 1/1 | .014 |
| Family Apatemyidae | | |
| *Apatemys* sp. | 1/1 | .014 |
| Order PRIMATES | | |
| Family Plesiadapidae | | |
| *Plesiadapis cookei* | 3/3 | .042 |
| Family Paromomyidae | | |
| *Phenacolemur pagei* | 3/2 | .028 |
| Order CONDYLARTHRA | | |
| Family Arctocyonidae | | |
| *Thryptacodon* cf. *antiquus* | 3/3 | .042 |
| Family Phenacodontidae | | |
| *Phenacodus primaevus* | 15/8 | .111 |
| *Phenacodus vortmani* | 1/1 | .014 |
| *Ectocion osbornianus* | 76/21 | .292 |
| Family Hyopsodontidae | | |
| *Aletodon gunnelli* | 1/1 | .014 |
| *Haplomylus simpsoni* | 4/2 | .028 |
| *Apheliscus nitidus* | 3/3 | .042 |
| Order MESONYCHIA | | |
| Family Mesonychidae | | |
| *Dissacus praenuntius* | 4/4 | .056 |
| Order TAENIODONTA | | |
| Family Stylinodontidae | | |
| cf. *Lampadophorus* sp. | 1/1 | .014 |
| Order PANTODONTA | | |
| Family Coryphodontidae | | |
| *Coryphodon* sp. | 10/4 | .056 |
| Order TILLODONTIA | | |
| Family Esthonychidae | | |
| *Esthonyx ancylion* | 5/3 | .042 |
| Order CARNIVORA | | |
| Family Miacidae | | |
| *Didymictis protenus proteus* | 5/3 | .042 |
| *Viverravus acutus* | 1/1 | .014 |
| ?*Uintacyon rudis* | 1/1 | .014 |
| Order CREODONTA | | |
| Family Oxyaenidae | | |
| *Oxyaena aequidens* | 5/3 | .042 |
| *Oxyaena transiens* | 1/1 | .014 |
| oxyaenid, indet. | 3/2 | .028 |
| Order RODENTIA | | |
| Family Paramyidae | | |
| *Paramys* sp. | 3/2 | .028 |
| Totals | 151/72 | 1.005 |

*Includes combined samples from UM localities SC-108, 109, 110, 189, 190, 195. Quarry sample from SC-188 is not included (see table 52).

Table 47. Mammalian Faunal Composition, *Plesiadapis cookei* zone, 180 m level below boundary sandstone.*

| Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|
| Order MULTITUBERCULATA | | |
| Family Eucosmodontidae | | |
| *Microcosmodon rosei* | 1/1 | .006 |
| Family Neoplagiaulacidae | | |
| *Ectypodus powelli* | 1/1 | .006 |
| Order POLYPROTODONTA | | |
| Family Didelphidae | | |
| *Peradectes* cf. *chesteri* | 4/4 | .023 |
| Order PROTEUTHERIA | | |
| Family Pantolestidae | | |
| *Palaeosinopa* sp. | 2/2 | .012 |
| ?Order LIPOTYPHLA, incertae sedis | | |
| cf. "*Diacodon*" *minutus* | 1/1 | .006 |
| Order PRIMATES | | |
| Family Microsyopidae | | |
| ?*Niptomomys* sp. | 1/1 | .006 |
| Family Plesiadapidae | | |
| *Plesiadapis cookei* | 61/19 | .110 |
| Family Carpolestidae | | |
| *Carpolestes nigridens* | 2/2 | .012 |
| Family Paromomyidae | | |
| *Phenacolemur pagei* | 7/6 | .035 |
| *Ignacius graybullianus* | 1/1 | .006 |
| Order CONDYLARTHRA | | |
| Family Arctocyonidae | | |
| *Thryptacodon* cf. *antiquus* | 1/1 | .006 |
| Family Phenacodontidae | | |
| *Phenacodus primaevus* | 36/15 | .087 |
| *Phenacodus vortmani* | 7/4 | .023 |
| *Ectocion osbornianus* | 171/48 | .277 |
| Family Hyopsodontidae | | |
| *Haplomylus simpsoni* | 3/3 | .017 |
| Order MESONYCHIA | | |
| Family Mesonychidae | | |
| ?*Dissacus* sp. | 2/1 | .006 |
| Order PANTODONTA | | |
| Family Coryphodontidae | | |
| *Coryphodon* sp. | 24/13 | .075 |
| Family Cyriacotheriidae | | |
| *Cyriacotherium psamminum* | 1/1 | .006 |
| Order TILLODONTIA | | |
| Family Esthonychidae | | |
| *Esthonyx ancylion* | 17/7 | .040 |
| Order DINOCERATA | | |
| Family Uintatheriidae | | |
| *Probathyopsis praecursor* | 7/3 | .017 |
| Order NOTOUNGULATA | | |
| Family Arctostylopidae | | |
| *Arctostylops steini* | 2/2 | .012 |
| Order CARNIVORA | | |
| Family Miacidae | | |
| *Didymictis protenus proteus* | 21/13 | .075 |
| *Viverravus acutus* | 1/1 | .006 |
| *Viverravus politus* | 2/2 | .012 |
| *Uintacyon rudis* | 1/1 | .006 |
| Order CREODONTA | | |
| Family Oxyaenidae | | |
| *Oxyaena* cf. *aequidens* | 10/6 | .035 |
| Order RODENTIA | | |
| Family Paramyidae | | |
| *Paramys* spp. (2 or 3 species) | 27/14 | .081 |
| Totals | 414/173 | 1.003 |

*Includes combined samples from UM localities SC–19, 20, 62, 115, 116, 117, 127, 201, 238.

Table 48. Mammalian Faunal Composition, *Phenacodus-Ectocion* zone, 140–150 m below boundary sandstone.*

| Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|
| Order MULTITUBERCULATA | | |
| Family Neoplagiaulacidae | | |
| *Ectypodus powelli* | 1/1 | .007 |
| Order POLYPROTODONTA | | |
| Family Didelphidae | | |
| *Peradectes* cf. *chesteri* | 1/1 | .007 |
| Order PROTEUTHERIA | | |
| Family Pantolestidae | | |
| *Palaeosinopa* sp. | 3/3 | .020 |
| Order LIPOTYPHLA | | |
| Family Erinaceidae | | |
| cf. *Leipsanolestes siegfriedti* | 1/1 | .007 |
| Order DERMOPTERA | | |
| Family Plagiomenidae | | |
| *Plagiomene accola* | 3/2 | .013 |
| Order PRIMATES | | |
| Family Carpolestidae | | |
| *Carpolestes nigridens* | 1/1 | .007 |
| Family Paromomyidae | | |
| *Phenacolemur pagei* | 3/3 | .020 |
| Order CONDYLARTHRA | | |
| Family Arctocyonidae | | |
| *Thryptacodon* cf. *antiquus* | 1/1 | .007 |
| cf. *Tricentes* sp. | 1/1 | .007 |
| Family Phenacodontidae | | |
| *Phenacodus primaevus* | 42/19 | .125 |
| *Phenacodus vortmani* | 4/2 | .013 |
| *Ectocion osbornianus* | 152/51 | .336 |
| Family Hyopsodontidae | | |
| *Aletodon gunnelli* | 2/1 | .007 |
| *Haplomylus simpsoni* | 5/4 | .026 |
| *Apheliscus nitidus* | 2/2 | .013 |
| Order PANTODONTA | | |
| Family Coryphodontidae | | |
| *Coryphodon* sp. | 8/7 | .046 |
| Family Cyriacotheriidae | | |
| *Cyriacotherium psamminum* | 2/2 | .013 |

Table 48. Continued.

| Taxon | Total/MNI | Freq.(MNI) | Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|---|---|---|
| Order TILLODONTIA | | | *?Viverravus politus* | 1/1 | .007 |
| Family Esthonychidae | | | *Uintacyon rudis* | 1/1 | .007 |
| *Esthonyx ancylion* | 8/6 | .039 | Order CREODONTA | | |
| *Esthonyx grangeri* | 1/1 | .007 | Family Oxyaenidae | | |
| Order DINOCERATA | | | *Oxyaena aequidens* | 1/1 | .007 |
| Family Uintatheriidae | | | oxyaenid, indet. | 2/2 | .013 |
| *Probathyopsis praecursor* | 6/5 | .033 | Order RODENTIA | | |
| Order CARNIVORA | | | Family Paramyidae | | |
| Family Miacidae | | | *Paramys* cf. *atavus* | 9/5 | .033 |
| *Didymictis protenus proteus* | 29/18 | .118 | *Paramys* cf. *excavatus* | 6/3 | .020 |
| | | | *Paramys* sp. | 11/7 | .046 |
| | | | Totals | 307/152 | 1.004 |

*Includes combined samples from UM localities SC-28, 29, 49, 56, 163, 164, 175, 176, 202, 234, 235.

Table 49. Mammalian Faunal Composition, *Phenacodus-Ectocion* zone, 90–110 m below boundary sandstone.*

| Taxon | Total/MNI | Freq.(MNI) | Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|---|---|---|
| Order PROTEUTHERIA | | | Order MESONYCHIA | | |
| Family Leptictidae | | | Family Mesonychidae | | |
| cf. *Prodiacodon tauricinerei* | 1/1 | .007 | *Dissacus* sp. | 3/3 | .021 |
| Family Pantolestidae | | | Order TAENIODONTA | | |
| *Palaeosinopa* sp. | 1/1 | .007 | Family Stylinodontidae | | |
| ?Order LIPOTYPHLA, | | | cf. *Lampadophorus* sp. | 1/1 | .007 |
| incertae sedis | | | Order PANTODONTA | | |
| cf. "*Diacodon*" *minutus* | 1/1 | .007 | Family Coryphodontidae | | |
| Order DERMOPTERA | | | *Coryphodon* sp. | 9/9 | .064 |
| Family Plagiomenidae | | | Family Cyriacotheriidae | | |
| *Plagiomene accola* | 3/3 | .021 | *Cyriacotherium psamminum* | 1/1 | .007 |
| Order PRIMATES | | | Order TILLODONTIA | | |
| Family Plesiadapidae | | | Family Esthonychidae | | |
| *Plesiadapis dubius* | 3/3 | .021 | *Esthonyx grangeri* | 9/6 | .043 |
| Family Paromomyidae | | | Order DINOCERATA | | |
| *Phenacolemur praecox* | 2/2 | .014 | Family Uintatheriidae | | |
| Order CONDYLARTHRA | | | *Probathyopsis praecursor* | 5/4 | .029 |
| Family Arctocyonidae | | | Order CARNIVORA | | |
| *Thryptacodon* cf. *antiquus* | 1/1 | .007 | Family Miacidae | | |
| Family Phenacodontidae | | | *Didymictis protenus proteus* | 9/7 | .050 |
| *Phenacodus primaevus* | 53/23 | .164 | *Viverravus politus* | 2/2 | .014 |
| *Phenacodus vortmani* | 9/5 | .036 | *Uintacyon rudis* | 3/3 | .021 |
| *Ectocion osbornianus* | 123/36 | .257 | Order CREODONTA | | |
| Family Hyopsodontidae | | | Family Oxyaenidae | | |
| *Aletodon gunnelli* | 6/4 | .029 | *Oxyaena* cf. *transiens* | 6/4 | .029 |
| *Hyopsodus* sp. | 1/1 | .007 | cf. *Dipsalodon matthewi* | 1/1 | .007 |
| *Haplomylus simpsoni* | 7/3 | .021 | *Palaeonictis peloria* | 1/1 | .007 |
| *Apheliscus nitidus* | 2/2 | .014 | Order RODENTIA | | |
| | | | Family Paramyidae | | |
| | | | *Paramys* spp. (2 or 3 species) | 23/12 | .086 |
| | | | Totals | 286/140 | .997 |

*Includes combined samples from UM localities SC-21, 48, 50, 57, 72, 101, 102, 105, 106, 149, 150, 183, 204.

Table 50. Mammalian Faunal Composition, *Phenacodus-Ectocion* zone, 50–60 m below boundary sandstone.*

| Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|
| Order PROTEUTHERIA | | |
| Family Apatemyidae | | |
| *Apatemys* sp. | 1/1 | .009 |
| Order LIPOTYPHLA | | |
| Family Erinaceidae | | |
| cf. *Leipsanolestes siegfriedti* | 1/1 | .009 |
| Order DERMOPTERA | | |
| Family Plagiomenidae | | |
| *Plagiomene accola* | 2/2 | .019 |
| Order PRIMATES | | |
| Family Microsyopidae | | |
| *Microsyops* sp. | 1/1 | .009 |
| Family Paromomyidae | | |
| *Phenacolemur praecox* | 7/4 | .037 |
| Order CONDYLARTHRA | | |
| Family Arctocyonidae | | |
| *Thryptacodon* cf. *antiquus* | 5/3 | .028 |
| Family Phenacodontidae | | |
| *Phenacodus primaevus* | 28/12 | .111 |
| *Phenacodus vortmani* | 8/6 | .056 |
| *Ectocion osbornianus* | 102/28 | .259 |
| Family Hyopsodontidae | | |
| *Aletodon gunnelli* | 4/4 | .037 |
| *Haplomylus simpsoni* | 7/5 | .046 |
| *Apheliscus nitidus* | 2/2 | .019 |
| Order MESONYCHIA | | |
| Family Mesonychidae | | |
| *Dissacus praenuntius* | 1/1 | .009 |
| Order PANTODONTA | | |
| Family Coryphodontidae | | |
| *Coryphodon* sp. | 5/4 | .037 |
| Family Cyriacotheriidae | | |
| *Cyriacotherium psamminum* | 4/2 | .019 |
| Order TILLODONTIA | | |
| Family Esthonychidae | | |
| *Esthonyx grangeri* | 9/5 | .046 |
| Order DINOCERATA | | |
| Family Uintatheriidae | | |
| *Probathyopsis praecursor* | 5/4 | .037 |
| Order NOTOUNGULATA | | |
| Family Arctostylopidae | | |
| *Arctostylops steini* | 1/1 | .009 |
| Order CARNIVORA | | |
| Family Miacidae | | |
| *Didymictis protenus proteus* | 12/7 | .065 |
| *Viverravus politus* | 2/2 | .019 |
| *Uintacyon rudis* | 5/2 | .019 |
| miacid, indet. | 1/1 | .009 |
| Order CREODONTA | | |
| Family Oxyaenidae | | |
| *Oxyaena transiens* | 1/1 | .009 |
| oxyaenid, indet. | 1/1 | .009 |
| Order RODENTIA | | |
| Family Paramyidae | | |
| *Paramys* cf. *atavus* | 2/1 | .009 |
| *Paramys* sp. | 7/6 | .056 |
| Order Uncertain | | |
| Suborder PALAEANODONTA | | |
| Family Metacheiromyidae | | |
| *Palaeanodon ?parvulus* | 1/1 | .009 |
| Totals | 225/108 | 1.000 |

*Includes combined samples from UM localities SC-22, 25, 60, 73, 76, 90, 159, 162, 203, 233.

probably too small to offer a very accurate representation of diversity, even among the small mammals.

Even if the Paleocene quarry assemblages are not directly comparable to the Clarkforkian surface samples, the latter *are* comparable to the Wasatchian samples from the Clark's Fork Basin, which have been collected by the same methods from essentially identical deposits. Some sort of preservational bias (or change in rate of sedimentation?) has resulted in a lower yield of specimens per unit volume in Clarkforkian strata, but it is assumed that any such bias would have been essentially random with respect to all but the smallest mammalian fossils in both the Clarkforkian and the Wasatchian. Because of smaller sample sizes at Clarkforkian sites, it has been necessary to combine samples from several sites within a specified interval to arrive at a larger sample that more accurately reflects the composition of that interval. Some of the resulting sample sizes may yet be inadequate to portray the diversity accurately (as suggested by variations in the diversity indices for the Clarkforkian samples, Figure 75), but they should offer a good approximation; and the relative consistency of the compositions (Tables 44–51) and the diversity indices (Table 55) of most of the intervals supports this. Small species, however, are probably under-represented in these samples.

Four levels in the early Wasatchian of the Clark's Fork Basin have been examined, the lower two each represented by a sample from a single site and the upper two by pooled samples from thicker stratigraphic intervals (Table 53). All four are surface samples, affected by the same biases as the Clarkforkian samples. For

Table 51. Mammalian Faunal Composition, *Phenacodus-Ectocion* zone, 10–30 m below boundary sandstone.*

| Taxon | Total/MNI | Freq.(MNI) |
|---|---|---|
| Order LIPOTYPHLA | | |
| Family Nyctitheriidae | | |
| cf. *Leptacodon packi* | 1/1 | .005 |
| Order DERMOPTERA | | |
| Family Plagiomenidae | | |
| *Worlandia inusitata* | 1/1 | .005 |
| Order PRIMATES | | |
| Family Microsyopidae | | |
| *Microsyops* sp. | 1/1 | .005 |
| *Niptomomys doreenae* | 2/2 | .011 |
| Family Plesiadapidae | | |
| *Plesiadapis dubius* | 1/1 | .005 |
| Family Paromomyidae | | |
| *Phenacolemur praecox* | 8/4 | .021 |
| Order CONDYLARTHRA | | |
| Family Arctocyonidae | | |
| *Thryptacodon* cf. *antiquus* | 5/4 | .021 |
| ?"*Chriacus*" sp. | 1/1 | .005 |
| Family Phenacodontidae | | |
| *Phenacodus primaevus* | 29/14 | .075 |
| *Phenacodus vortmani* | 6/6 | .032 |
| *Ectocion osbornianus* | 276/62 | .332 |
| Family Hyopsodontidae | | |
| *Aletodon gunnelli* | 4/2 | .011 |
| *Hyopsodus* sp. | 1/1 | .005 |
| *Haplomylus simpsoni* | 17/11 | .059 |
| *Apheliscus nitidus* | 3/3 | .016 |
| Order MESONYCHIA | | |
| Family Mesonychidae | | |
| *Dissacus praenuntius* | 6/5 | .027 |
| Order PANTODONTA | | |
| Family Coryphodontidae | | |
| *Coryphodon* sp. | 4/4 | .021 |
| Order TILLODONTIA | | |
| Family Esthonychidae | | |
| *Esthonyx grangeri* | 11/9 | .048 |
| Order CREODONTA | | |
| Family Oxyaenidae | | |
| *Oxyaena transiens* | 1/1 | .005 |
| *Palaeonictis peloria* | 1/1 | .005 |
| oxyaenid, indet. | 1/1 | .005 |
| Order RODENTIA | | |
| Family Paramyidae | | |
| *Paramys* cf. *atavus* | 18/9 | .048 |
| *Paramys* sp. | 40/16 | .086 |
| Order DINOCERATA | | |
| Family Uintatheriidae | | |
| *Probathyopsis praecursor* | 2/2 | .011 |
| Order CARNIVORA | | |
| Family Miacidae | | |
| *Didymictis protenus proteus* | 25/13 | .070 |
| *Viverravus acutus* | 1/1 | .005 |
| *Viverravus* sp. nov. | 1/1 | .005 |
| *Viverravus politus* | 10/9 | .048 |
| miacid, indet. | 1/1 | .005 |
| Totals | 478/187 | .997 |

*Includes combined samples from UM localities SC–10, 23, 24, 75, 77, 81, 103, 107, 138, 140, 152, 153, 154, 155, 184, 230.

comparison, three successive levels in the early Wasatchian of the southern Bighorn Basin (Bown, 1979) have also been analyzed (Table 54). Bown's samples include a larger proportion of small mammals, partly as a result of his use of quarrying and washing techniques in addition to surface prospecting, but also apparently because small mammals are preserved in greater numbers in the sediments of his sequence than in the Clark's Fork Basin. (The proportion of small mammals is approximately the same in all three levels, although Bown employed screen-washing and quarrying only in the lowest of the three levels examined here. Winkler [1979], on the other hand, found a sharp increase in frequency of small mammals, particularly multituberculates and insectivores, by screen at an early Wasatchian site [SC–210] in the Clark's Fork Basin.)

## DISCUSSION OF CLARKFORKIAN AND WASATCHIAN FAUNAS

The data in Tables 44–51 have been summarized in three diagrams that depict the composition of the mammalian fauna of each zone in the Clarkforkian (Figures 71–73). Although there are minor differences between successive levels, the fauna of these samples remains relatively stable throughout the Clarkforkian. Species richness is low (22 to 28 species per interval), but these samples are probably too small to indicate the total species richness during each zone. The *Plesiadapis gingerichi* Zone is still poorly known. It was necessary to combine all samples from this zone in order to compile Table 44, and only 26 species have been discovered from this zone to date. When the three intervals from the

*text continued on p. 171*

Table 52. Mammalian Faunal Composition at two Clarkforkian sites with a predominance of small mammals.

| Taxon | BEAR CREEK | | SC–188 | |
|---|---|---|---|---|
| | Total/MNI | Freq.(MNI) | Total/MNI | Freq.(MNI) |
| Order MULTITUBERCULATA | | | | |
| Family Eucosmodontidae | | | | |
| *Microcosmodon rosei* | | | 3/1 | .014 |
| Family Neoplagiaulacidae | | | | |
| *Ectypodus powelli* | | | 10/6 | .086 |
| Order POLYPROTODONTA | | | | |
| Family Didelphidae | | | | |
| *Peradectes* cf. *chesteri* | | | 11/3 | .043 |
| cf. *Peradectes* sp. | 1/1 | .013 | | |
| Order PROTEUTHERIA | | | | |
| Family Leptictidae | | | | |
| cf. *Prodiacodon tauricinerei* | | | 3/1 | .014 |
| Family Pantolestidae | | | | |
| cf. *Palaeosinopa* sp. | 6/3 | .040 | | |
| Family Pentacodontidae | | | | |
| *Protentomodon ursirivalis* | 6/5 | .067 | | |
| ?*Aphronorus* sp. | 2/1 | .013 | | |
| Family Apatemyidae | | | | |
| *Apatemys kayi* | 8/4 | .053 | | |
| *Apatemys* sp. | | | 1/1 | .014 |
| Order LIPOTYPHLA | | | | |
| Family Nyctitheriidae | | | | |
| cf. *Leptacodon packi* | | | 11/4 | .057 |
| cf. *Plagioctenodon krausae* | | | 2/1 | .014 |
| Family Erinaceidae | | | | |
| *Leipsanolestes siegfriedti* | 22/12 | .160 | 1/1 | .014 |
| ?Order LIPOTYPHLA | | | | |
| cf. "*Diacodon*" *minutus* | | | 4/2 | .029 |
| Order DERMOPTERA | | | | |
| Family Plagiomenidae | | | | |
| *Planetetherium mirabile* | 59/20 | .270 | | |
| *Worlandia inusitata* | | | 32/6 | .086 |
| Order PRIMATES | | | | |
| Family Microsyopidae | | | | |
| *Niptomomys doreenae* | | | 3/1 | .014 |
| *Tinimomys graybulliensis* | | | 2/1 | .014 |
| ?microsyopid, indet. | 2/1 | .013 | | |
| Family Plesiadapidae | | | | |
| *Plesiadapis dubius* | 4/2 | .027 | | |
| *Plesiadapis cookei* | | | 15/3 | .043 |
| *Chiromyoides potior* | 1/1 | .013 | | |
| Family Carpolestidae | | | | |
| *Carpolestes nigridens* | 15/7 | .093 | 15/4 | .057 |

Table 52. Continued.

| Taxon | BEAR CREEK | | SC-188 | |
|---|---|---|---|---|
| | Total/MNI | Freq.(MNI) | Total/MNI | Freq.(MNI) |
| Family Paromomyidae | | | | |
| *Phenacolemur pagei* | 6/3 | .040 | 12/2 | .029 |
| *Ignacius graybullianus* | | | 3/1 | .014 |
| Order CONDYLARTHRA | | | | |
| Family Arctocyonidae | | | | |
| *Thryptacodon* cf. *antiquus* | | | 1/1 | .014 |
| *Thryptacodon pseudarctos* | 10/2 | .027 | | |
| Family Phenacodontidae | | | | |
| *Phenacodus primaevus* | 2/1 | .013 | 2/1 | .014 |
| *Ectocion osbornianus* | | | 16/3 | .043 |
| Family Hyopsodontidae | | | | |
| *Haplomylus simpsoni* | 5/2 | .027 | 1/1 | .014 |
| cf. *Phenacodaptes sabulosus* | 4/2 | .027 | | |
| Order MESONYCHIA | | | | |
| Family Mesonychidae | | | | |
| *Dissacus* sp. | 4/1 | .013 | 1/1 | .014 |
| Order TAENIODONTA | | | | |
| Family Stylinodontidae | | | | |
| *Lampadophorus lobdelli* | 4/1 | .013 | | |
| Order PANTODONTA | | | | |
| Family Coryphodontidae | | | | |
| *Coryphodon* sp. | | | 1/1 | .014 |
| Order TILLODONTIA | | | | |
| Family Esthonychidae | | | | |
| *Esthonyx ancylion* | | | 1/1 | .014 |
| Order NOTOUNGULATA | | | | |
| Family Arctostylopidae | | | | |
| *Arctostylops steini* | | | 1/1 | .014 |
| Order CARNIVORA | | | | |
| Family Miacidae | | | | |
| *Didymictis protenus proteus* | | | 9/2 | .029 |
| *Viverravus* sp. nov. | | | 3/1 | .014 |
| ?*Viverravus* sp. | 2/2 | .027 | | |
| *Uintacyon rudis* | | | 1/1 | .014 |
| Order CREODONTA | | | | |
| Family Oxyaenidae | | | | |
| *Oxyaena aequidens* | | | 1/1 | .014 |
| Order RODENTIA | | | | |
| Family Paramyidae | | | | |
| *Paramys atavus* | 15/4 | .053 | 56/13 | .186 |
| *Paramys* sp. | | | 17/4 | .057 |
| Totals | 178/75 | 1.002 | 239/70 | .997 |

Table 53. Mammalian Faunal Composition at Four Levels of the early Wasatchian (Graybullian).*

| Taxon | 50 m level: SC-4 | | 180–200 m: SC-54 | | 250–350 m interval | | 400–500 m interval | |
|---|---|---|---|---|---|---|---|---|
| | Total/MNI | Freq.(MNI) | Total/MNI | Freq.(MNI) | Total/MNI | Freq.(MNI) | Total/MNI | Freq.(MNI) |
| Order MULTITUBERCULATA | | | | | | | | |
| Family Eucosmodontidae | | | | | | | | |
| *Neoliotomus ultimus* | 1/1 | .008 | | | | | | |
| Family Neoplagiaulacidae | | | | | | | | |
| cf. *Ectypodus tardus* | | | | | | | 1/1 | .005 |
| Order POLYPROTODONTA | | | | | | | | |
| Family Didelphidae | | | | | | | | |
| *Mimoperadectes labrus* | | | | | | | 1/1 | .005 |
| Order PROTEUTHERIA | | | | | | | | |
| Family Palaeoryctidae | | | | | | | | |
| *Didelphodus absarokae* | | | 3/2 | .013 | | | | |
| Family Leptictidae | | | | | | | | |
| cf. *Prodiacodon* sp. | 1/1 | .008 | | | 2/2 | .017 | 1/1 | .005 |
| Family Pantolestidae | | | | | | | | |
| *Palaeosinopa* sp. | | | | | 1/1 | .008 | | |
| Family Apatemyidae | | | | | | | | |
| *Apatemys* sp. | 2/1 | .005 | 1/1 | .006 | 1/1 | .008 | 1/1 | .005 |
| Order DERMOPTERA | | | | | | | | |
| Family Plagiomenidae | | | | | | | | |
| *Plagiomene multicuspis* | 1/1 | .008 | | | 4/4 | .034 | 6/3 | .015 |
| Order PRIMATES | | | | | | | | |
| Family Microsyopidae | | | | | | | | |
| *Microsyops wilsoni/angustidens* | 1/1 | .008 | 4/2 | .013 | | | 12/6 | .030 |
| ?small microsyopid, indet. | | | | | 1/1 | .008 | | |
| Family Paromomyidae | | | | | | | | |
| *Phenacolemur praecox* | 8/4 | .031 | 19/5 | .031 | | | 14/5 | .025 |
| *Ignacius graybullianus* | | | 5/3 | .019 | | | 1/1 | .005 |
| Family Adapidae | | | | | | | | |
| *Pelycodus ralstoni/mckennai/trigonodus* | 37/14 | .109 | 49/14 | .088 | 13/7 | .059 | 39/12 | .059 |
| Family Omomyidae | | | | | | | | |
| *Tetonius homunculus* and *Pseudotetonius ambiguus* | | | | | 1/1 | .008 | 14/8 | .040 |
| *Tetonoides* sp. or *Teilhardina americana* | 1/1 | .008 | | | | | | |
| Order CONDYLARTHRA | | | | | | | | |
| Family Arctocyonidae | | | | | | | | |
| *Thryptacodon antiquus* | 8/2 | .016 | 3/2 | .013 | 1/1 | .008 | 5/1 | .005 |
| arctocyonid, indet. | | | | | | | 1/1 | .005 |
| Family Phenacodontidae | | | | | | | | |
| *Phenacodus primaevus* | 6/2 | .016 | 4/2 | .013 | 8/6 | .050 | 24/6 | .030 |
| *Phenacodus vortmani* | 11/4 | .031 | | | | | | |
| *Phenacodus* cf. *brachypternus* | 1/1 | .008 | | | | | | |
| *Ectocion osbornianus* | 47/12 | .093 | 49/12 | .075 | 8/6 | .050 | 3/2 | .010 |
| Family Hyopsodontidae | | | | | | | | |
| *Hyopsodus* spp. | 41/15 | .116 | 111/31 | .195 | 49/19 | .160 | 132/32 | .158 |
| *Haplomylus speirianus* | 27/8 | .062 | 60/16 | .101 | 8/6 | .050 | 65/21 | .103 |
| *Apheliscus* sp. | 2/1 | .008 | 2/1 | .006 | | | 2/2 | .010 |
| Order MESONYCHIA | | | | | | | | |
| Family Mesonychidae | | | | | | | | |

Table 53. Continued.

| Taxon | 50 m level: SC-4 | | 180–200 m: SC-54 | | 250–350 m interval | | 400–500 m interval | |
|---|---|---|---|---|---|---|---|---|
| | Total/MNI | Freq.(MNI) | Total/MNI | Freq.(MNI) | Total/MNI | Freq.(MNI) | Total/MNI | Freq.(MNI) |
| *Dissacus* sp. | 1/1 | .008 | | | | | | |
| *Pachyaena* sp. | | | 1/1 | .006 | 3/3 | .025 | 3/2 | .010 |
| Order TAENIODONTA | | | | | | | | |
| Family Stylinodontidae | | | | | | | | |
| *Ectoganus* sp. | | | | | 1/1 | .008 | | |
| Order PANTODONTA | | | | | | | | |
| Family Coryphodontidae | | | | | | | | |
| *Coryphodon* sp. | 2/1 | .008 | 4/2 | .013 | 20/9 | .076 | 8/5 | .025 |
| Order TILLODONTIA | | | | | | | | |
| Family Esthonychidae | | | | | | | | |
| *Esthonyx grangeri* | 2/1 | .008 | | | | | | |
| *Esthonyx spatularius* | 9/3 | .023 | 9/3 | .019 | 5/4 | .034 | 17/7 | .034 |
| Order PERISSODACTYLA | | | | | | | | |
| Family Equidae | | | | | | | | |
| *Hyracotherium* spp. | 100/20 | .155 | 177/24 | .151 | 81/19 | .160 | 100/25 | .123 |
| Family Isectolophidae | | | | | | | | |
| *Homogalax* sp. | 6/2 | .016 | 7/3 | .019 | 5/4 | .034 | 8/7 | .034 |
| Order ARTIODACTYLA | | | | | | | | |
| Family Dichobunidae | | | | | | | | |
| *Diacodexis metsiacus* | 40/11 | .085 | 64/13 | .082 | 6/4 | .034 | 50/15 | .074 |
| Order CARNIVORA | | | | | | | | |
| Family Miacidae | | | | | | | | |
| *Didymictis protenus* | 7/2 | .016 | 4/2 | .013 | | | 8/6 | .030 |
| *Viverravus acutus* | 1/1 | .008 | 4/2 | .013 | 1/1 | .008 | 3/2 | .010 |
| *Viverravus politus* | 2/1 | .005 | | | | | | |
| *Uintacyon* cf. *massetericus* | 3/2 | .016 | 1/1 | .006 | | | | |
| *Miacis exiguus* | | | 1/1 | .006 | 5/5 | .042 | | |
| *Vulpavus* sp. | | | | | | | 1/1 | .005 |
| miacid, indet. | | | | | 1/1 | .008 | 2/2 | .010 |
| Order CREODONTA | | | | | | | | |
| Family Oxyaenidae | | | | | | | | |
| *Oxyaena* spp. | 6/2 | .016 | 5/2 | .013 | 10/5 | .042 | 5/3 | .015 |
| Family Hyaenodontidae | | | | | | | | |
| *Arfia* sp. | 2/1 | .008 | 14/5 | .031 | 7/4 | .034 | 4/1 | .005 |
| *Prolimnocyon* cf. *atavus* | | | 3/2 | .013 | | | | |
| small hyaenodontids, unident. | | | 1/1 | .006 | 1/1 | .008 | 7/5 | .025 |
| Order RODENTIA | | | | | | | | |
| Family Paramyidae | | | | | | | | |
| *Paramys* spp. | 21/11 | .085 | 13/4 | .025 | 4/1 | .008 | 49/17 | .083 |
| cf. *Microparamys* sp. | 1/1 | .008 | | | 1/1 | .008 | | |
| Order Uncertain | | | | | | | | |
| Suborder PALAEANODONTA | | | | | | | | |
| Family Metacheiromyidae | | | | | | | | |
| *Palaeanodon ignavus* | | | | | 1/1 | .008 | 1/1 | .005 |
| Unidentified carnivore or insectivore (2 or 3 spp.) | | | 7/2 | .013 | | | | |
| Totals | 398/129 | 1.000 | 625/159 | 1.002 | 249/119 | .997 | 588/203 | 1.003 |

*Levels are measured above the Clarkforkian-Wasatchian boundary sandstone. SC-4 is in *Pelycodus ralstoni* zone; SC-54 is in *Pelycodus mckennai* zone; 250–350 m interval is upper *Pelycodus mckennai* zone or lower *Pelycodus trigonodus* zone; 400–500 m interval is in *Pelycodus trigonodus* zone. 250–350 m interval includes combined samples from UM localities SC-32, 33, 34, 35, 36, 63, 114. 400–500 m interval includes combined samples from UM localities SC-64, 111, 112, 113, 148.

Table 54. Mammalian faunal composition at three levels of the early Wasatchian (Graybullian) in the No Water Creek area, southeastern Bighorn Basin (based on collections of Bown, 1979).

| Taxon | 150 ft level | | 288 ft level | | 590 ft level | |
|---|---|---|---|---|---|---|
| | Total/MNI | Freq.(MNI) | Total/MNI | Freq.(MNI) | Total/MNI | Freq.(MNI) |
| Order MULTITUBERCULATA | | | | | | |
| Family Eucosmodontidae | | | | | | |
| *Neoliotomus ultimus* | 1/1 | .004 | | | | |
| Family Neoplagiaulacidae | | | | | | |
| *Parectypodus* sp. "A" | 8/2 | .008 | | | | |
| Order POLYPROTODONTA | | | | | | |
| Family Didelphidae | | | | | | |
| *Peratherium mcgrewi* | 2/2 | .008 | | | | |
| *Peradectes chesteri* | 6/4 | .016 | 1/1 | .011 | | |
| *Mimoperadectes* sp. | | | | | 1/1 | .011 |
| Order PROTEUTHERIA | | | | | | |
| Family Palaeoryctidae | | | | | | |
| *Didelphodus absarokae* | 3/2 | .008 | 1/1 | .011 | | |
| Family Leptictidae | | | | | | |
| *Prodiacodon tauricinerei* | 10/3 | .012 | 6/4 | .044 | 2/2 | .022 |
| Family Pantolestidae | | | | | | |
| ?*Palaeosinopa* cf. *lutreola* | 1/1 | .004 | | | | |
| Family Apatemyidae | | | | | | |
| *Apatemys* sp. | 2/1 | .004 | | | | |
| Order LIPOTYPHLA | | | | | | |
| Family Adapisoricidae | | | | | | |
| cf. *Scenopagus* sp. | 2/2 | .008 | | | | |
| Family Nyctitheriidae | | | | | | |
| *Pontifactor* cf. *bestiola* | 9/3 | .012 | | | | |
| *Plagioctenodon krausae* | 17/5 | .021 | 2/1 | .011 | 1/1 | .011 |
| ?*Plagioctenoides microlestes* | 1/1 | .004 | | | | |
| Family Erinaceidae | | | | | | |
| *Leipsanolestes* cf. *siegfriedti* | | | 1/1 | .011 | | |
| ?*Leipsanolestes simpsoni* | | | | | 1/1 | .011 |
| ?Order LIPOTYPHLA, unident. | | | | | | |
| small insectivore, indet. | 13/6 | .025 | 3/2 | .022 | | |
| Order PRIMATES | | | | | | |
| Family Microsyopidae | | | | | | |
| *Microsyops wilsoni* | 19/6 | .025 | 2/2 | .022 | | |
| *Niptomomys doreenae* | 54/10 | .041 | 1/1 | .011 | 1/1 | .011 |
| *Tinimomys graybulliensis* | 3/1 | .004 | | | 1/1 | .011 |
| Family Paromomyidae | | | | | | |
| *Ignacius graybullianus* | 1/1 | .004 | | | | |
| *Phenacolemur praecox* | 9/3 | .012 | 3/2 | .022 | 1/1 | .011 |
| *Phenacolemur simonsi* | 4/3 | .012 | 1/1 | .011 | | |
| Family Adapidae | | | | | | |
| *Pelycodus ralstoni/trigonodus* | 66/17 | .070 | 12/5 | .056 | 2/2 | .022 |
| *Pelycodus*, ?sp. nov. | | | | | 21/8 | .089 |
| Family Omomyidae | | | | | | |
| *Tetonoides* sp. | 6/2 | .008 | 1/1 | .011 | 1/1 | .011 |
| *Teilhardina americana* | 2/1 | .004 | | | | |
| *Tetonius homunculus* | 2/2 | .008 | 1/1 | .011 | 9/5 | .056 |
| Order CONDYLARTHRA | | | | | | |
| Family Arctocyonidae | | | | | | |
| *Thryptacodon antiquus* | 3/3 | .012 | | | | |
| Family Phenacodontidae | | | | | | |
| *Phenacodus primaevus* | 1/1 | .004 | 3/3 | .033 | 2/2 | .022 |
| *Ectocion osbornianus* | 47/14 | .058 | 3/3 | .033 | 2/1 | .011 |
| Family Hyopsodontidae | | | | | | |
| *Hyopsodus* sp. | 71/13 | .053 | 1/1 | .011 | 55/15 | .167 |
| *Haplomylus speirianus* | 159/27 | .111 | 58/14 | .156 | 36/10 | .111 |
| *Apheliscus* sp. | 7/3 | .012 | 7/3 | .033 | | |

Table 54. Continued.

| Taxon | 150 ft level | | 288 ft level | | 590 ft level | |
|---|---|---|---|---|---|---|
| | Total/MNI | Freq.(MNI) | Total/MNI | Freq.(MNI) | Total/MNI | Freq.(MNI) |
| Order PANTODONTA | | | | | | |
| Family Coryphodontidae | | | | | | |
| *Coryphodon* sp. | 1/1 | .004 | 3/3 | .033 | 6/3 | .033 |
| Order TILLODONTIA | | | | | | |
| Family Esthonychidae | | | | | | |
| *Esthonyx spatularius* | 4/3 | .012 | 4/3 | .033 | 1/1 | .011 |
| Order PERISSODACTYLA | | | | | | |
| Family Equidae | | | | | | |
| *Hyracotherium angustidens* | 281/35 | .144 | 70/9 | .100 | 32/13 | .144 |
| Order ARTIODACTYLA | | | | | | |
| Family Dichobunidae | | | | | | |
| *Diacodexis metsiacus* | 95/18 | .074 | 21/6 | .067 | 10/3 | .033 |
| Order CARNIVORA | | | | | | |
| Family Miacidae | | | | | | |
| *Didymictis protenus* | 2/2 | .008 | 1/1 | .011 | | |
| *Viverravus acutus* | 9/4 | .016 | 2/2 | .022 | 4/3 | .033 |
| *Uintacyon masseterius* | 4/3 | .012 | | | 1/1 | .011 |
| cf. *Uintacyon* sp. | 1/1 | .004 | 2/2 | .022 | | |
| miacid, unident. | 1/1 | .004 | | | 1/1 | .011 |
| Order CREODONTA | | | | | | |
| Family Oxyaenidae | | | | | | |
| *Oxyaena* sp. | 6/2 | .008 | 3/3 | .033 | 1/1 | .011 |
| Family Hyaenodontidae | | | | | | |
| *Arfia opisthotoma* | 3/2 | .008 | 2/1 | .011 | 4/3 | .033 |
| *Prototomus* sp. | 2/1 | .004 | 3/1 | .011 | | |
| *Tritemnodon* sp. | 2/1 | .004 | | | 2/2 | .022 |
| *Prolimnocyon atavus* | 3/2 | .008 | | | 1/1 | .011 |
| Order RODENTIA | | | | | | |
| Family Paramyidae | | | | | | |
| *Paramys excavatus* | 4/2 | .008 | 7/3 | .033 | 3/2 | .022 |
| *Paramys* sp., near *francesi* | 2/1 | .004 | | | 1/1 | .011 |
| *Reithroparamys* sp. | | | 2/2 | .022 | | |
| *Franimys* sp. | 7/3 | .012 | | | | |
| *Microparamys* sp. or gen. nov. | 41/4 | .016 | 1/1 | .011 | | |
| paramyids, indet. | 60/17 | .070 | 20/6 | .067 | 9/3 | .033 |
| Totals | 1057/243 | .992 | 248/90 | .996 | 212/90 | .996 |

*Plesiadapis cookei* Zone are combined, a much larger sample is available: 39 species are included in the samples analyzed from this zone. When all sites in the *P. cookei* Zone are examined (Figure 4), it may be seen that at least 60 species are known from this zone. The largest sample now available is from the *Phenacodus-Ectocion* Zone. Combining the four intervals analyzed here, there are 45 species represented, but only two more are added by including all known sites in the zone. Thus it appears that species richness declined from the middle to the late Clarkforkian, although this is not immediately obvious from comparison of species richness in the smaller samples of the intervals examined (Figure 76).

Most of the elements of the Clarkforkian fauna are holdovers or descendants from earlier Paleocene faunas. The most prevalent species are the same throughout the Clarkforkian, except for the large plesiadapids (*Plesiadapis gingerichi* and *P. cookei*, both used to characterize zones) and for evolutionary change within the lineages of *Phenacolemur* and *Esthonyx*. Faunal differences between intervals are otherwise mainly in rare species. Phenacodontids are overwhelmingly the most abundant constituents of the fauna, accounting for about 40–50% of the fauna in every interval. *Ectocion* itself is never less than 25% of the sample in any interval or in the combined samples for each zone. Several taxa

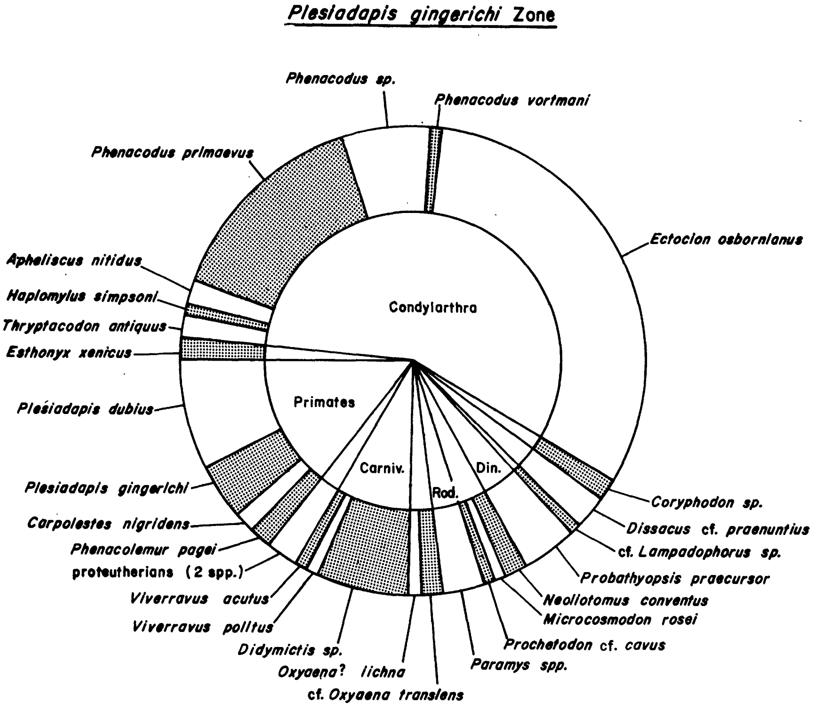

Figure 71. Relative abundances of mammalian taxa in the *Plesiadapis gingerichi* Zone, early Clarkforkian, based on pooled samples from 370–470 m below the Clarkforkian-Wasatchian boundary sandstone (see Table 44). Width of sectors determined as in Figure 69. Note overwhelming abundance of phenacodontid condylarths, especially *Ectocion osbornianus*, and first appearance of Clarkforkian immigrants *Paramys*, *Esthonyx*, *Coryphodon*, and *Haplomylus*.

appear for the first time in the Clarkforkian—rodents, tillodonts, *Haplomylus*, and *Coryphodon*—and all are relatively common.

As indicated by the abundance of *Ectocion*, evenness is very low throughout the Clarkforkian, more closely approaching that of the Cedar Point assemblage than of the Rock Bench assemblage (Figures 71–73; Table 55: Whittaker index). Even if small species had been more commonly preserved (thus increasing species richness) in the Clarkforkian samples, it seems unlikely that evenness would increase appreciably. In fact, evenness has been maximized in the Clarkforkian samples by combining collections for analysis. At individual Clarkforkian sites, *Ectocion* and *Phenacodus* often form a much larger proportion of the fauna, especially in the *Phenacodus-Ectocion* Zone. (If a correction factor for longevity of species were introduced in the analysis, the phenacodontids, relatively large mammals of the Clarkforkian, would become relatively more abundant than is indicated in the present analysis.)

Diversity indices for each of the sampled intervals are summarized in Table 55 and depicted in Figures 75 and 76. The minor variations in the indices for different levels are probably artifacts of the small sample sizes rather than reflections of real differences between samples. Values for the combined samples from each zone (as depicted in Figures 71–73) are relatively constant (value for Simpson index is 1.0–L, see equation 1, above):

| | Simpson (1-L) | Shannon (H') | Whittaker (E) |
|---|---|---|---|
| *Phenacodus-Ectocion* Zone | .873 | 2.75 | 20.7 |
| *Plesiadapis cookei* Zone | .875 | 2.76 | 19.4 |
| *Ples. gingerichi* Zone | .865 | 2.59 | 17.5 |

The slightly lower values for the *Plesiadapis gingerichi* Zone probably result from its much smaller combined sample size (resulting in lower apparent diversity) than from the other two zones. Estimates of diversity from individual Clarkforkian sites or from pooled samples representing thicker stratigraphic intervals demonstrate that diversity, particularly equitability, was low in the

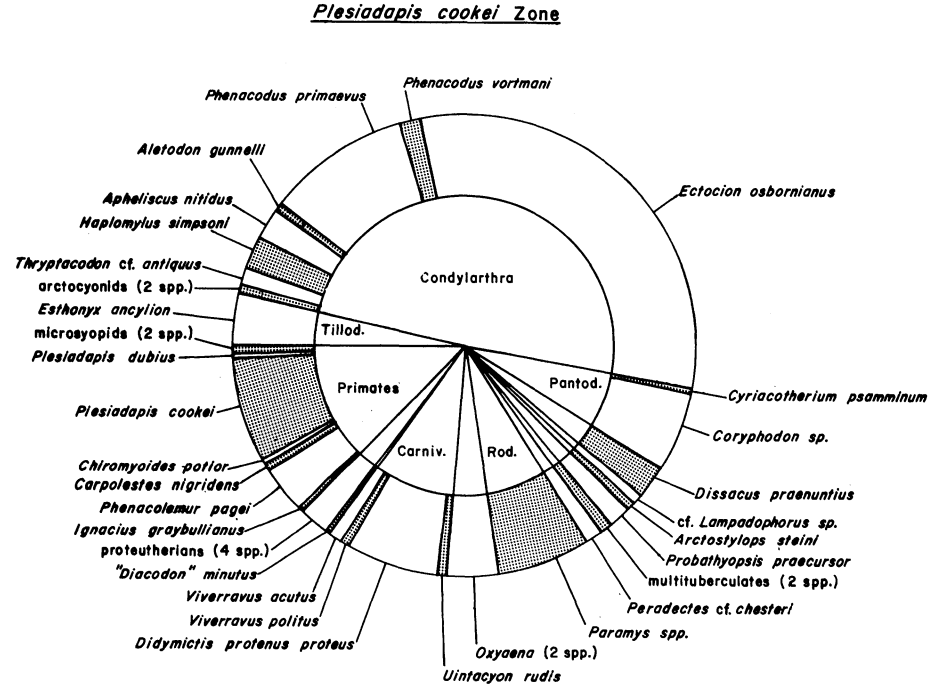

Figure 72. Relative abundances of mammalian taxa in the *Plesiadapis cookei* Zone, middle Clarkforkian, based on pooled samples from 180–320 m below the Clarkforkian-Wasatchian boundary sandstone (Tables 45, 46, and 47). Width of sectors determined as in Figure 69. Note continued abundance of phenacodontid condylarths and increasing relative numbers of the Clarkforkian immigrants *Paramys*, *Esthonyx*, *Coryphodon*, and *Haplomylus*.

Clarkforkian relative to the Torrejonian or the Wasatchian.

In Figure 77 the frequencies of Clarkforkian species are plotted against their rank of abundance for samples from the *Plesiadapis cookei* Zone (from Table 47) and the *Phenacodus-Ectocion* Zone (from Table 51). Both frequency distributions show similar patterns, and it is clear that they more closely resemble the distribution of the Cedar Point assemblage than that of the Rock Bench sample. Thus the Clarkforkian assemblages have Hutchinson's Type 4 distribution of abundances, with *Ectocion* much more abundant than predicted by MacArthur's Type 1 model. This is another way to illustrate that evenness was low in the Clarkforkian.

In a study of crustacean diversity in newly-formed lakes, Goulden (1969) found that immature or disturbed ecosystems display Type 4 abundance distribution, characteristic of low diversity. He suggested that "the species found as the early dominants are 'generalists,' physiologically and ecologically well adapted to fluctuating and unpredictable environments . . .If the 'generalist' had broad niche requirements, few species could coexist and therefore be established in the environment, and diversity would be low" (Goulden, 1969: 100). Mammalian diversity in the Clarkforkian may be analogous to Goulden's example, with phenacodontids as the generalists. Paleobotanical evidence indicates that a warming trend took place from late Paleocene to early Eocene time in the northern Western Interior, with a shift from warm temperate to subtropical regimes (Hickey, 1977), and that this followed a decline in mean annual temperature and equability from the late Cretaceous to the late Paleocene—the nadir occurring in the Tiffanian (Wolfe and Hopkins, 1967; Hickey, 1980). This may have been a source of "unpredictability" in the Tiffanian and Clarkforkian.

Species richness in megafloras and the frequency of species with entire-margined leaves increased from Tiffanian to Clarkforkian time (Figure 75). At first glance, this appears to conflict with the persistently low diversity in mammalian assemblages in the Clarkforkian. However, if the surface collections of mammals

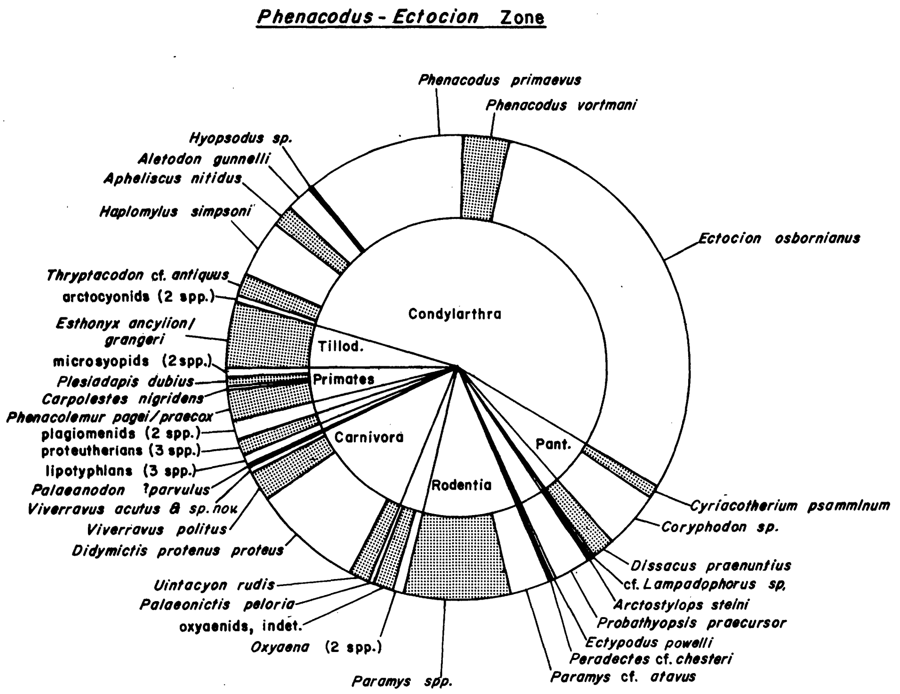

Figure 73. Relative abundances of mammalian taxa in the *Phenacodus-Ectocion* Zone, late Clarkforkian, based on pooled samples from 10–150 m below the Clarkforkian-Wasatchian boundary sandstone (Tables 48, 49, 50, 51). With of sectors determined as in Figure 69. Note continued abundance of phenacodontid condylarths and absence of *Plesiadapis cookei.*

from the Clarkforkian and Wasatchian were as rich in small mammals as the Paleocene quarry samples, species richness would probably be higher, resulting in somewhat higher diversity indices. Evenness in mammalian assemblages clearly remained low from the Tiffanian to the Clarkforkian, however, and this appears to have been true in megafloras as well (Hickey, 1980). Although the total number of plant species rose appreciably from the Tiffanian to the Clarkforkian, the average number of species per locality remained low, which is also in accord with the relatively low mammalian diversity at this time.

The compositions of four intervals in the early Wasatchian section in the Clark's Fork Basin are presented in Table 53, and one of them is depicted in Figure 74. Comparison to the Clarkforkian samples reveals a strikingly different fauna. Not only are several entirely new taxa present (perissodactyls, artiodactyls, adapid and omomyid primates), but some of them are very common. Many prevalent Clarkforkian forms are gone (e.g. plesiadapids) and others (such as phenacodontids and *Didymictis*) are drastically reduced in relative abundance. As far as can be determined, these changes occurred relatively suddenly.

Compared to the Clarkforkian samples, the Wasatchian samples are only slightly higher in species richness (28–32 species per interval, see Figure 76), and this may be a result of somewhat larger sample sizes in the Wasatchian. Evenness, however, shows a marked increase over that in the Clarkforkian (Figures 75 and 76, Table 55: Whittaker index). No single species comprises more than 20% of the fauna in any interval, and this high figure is achieved only in one sample (SC–54, for *Hyopsodus*; this abundance is probably the cause of the lower diversity indices for this site than for any other early Wasatchian sample). In the other samples, the most abundant species represents 15–16% of the fauna. (This applies also to locality SC–133, at the same level as SC–54.) The relatively high equitability of the early Wasatchian assemblages is illustrated by the close conformance of their rank abundance curves to MacArthur's Type 1 distribution (Figure 77). This is especially evident by comparison to the Clarkforkian rank abundance curves, for which species numbers are very similar, but a Type 4 distribution obtains.

Early Wasatchian mammal assemblages from the No Water Creek area in the southeastern Bighorn Basin

Table 55. Diversity indices of Paleocene and early Eocene mammalian assemblages. Values of the Simpson, Shannon, and Whittaker indices are shown for Torrejonian, Tiffanian, Clarkforkian, and early Wasatchian samples analyzed in this study. For the Simpson index, values shown are 1.0-*L* (see Equation 1, above).

| Faunal Sample | Simpson (1-*L*) | Shannon (H′) | Whittaker (E) |
|---|---|---|---|
| Wasatchian: No Water Creek fauna (southeastern Bighorn Basin) | | | |
| Level 590 | .929 | 2.83 | 22.1 |
| Level 288 | .950 | 3.07 | 25.1 |
| Level 150 | .943 | 3.22 | 28.7 |
| Wasatchian, Clark's Fork Basin | | | |
| 400-500 m | .928 | 2.92 | 21.3 |
| 250-350 m | .927 | 2.86 | 21.5 |
| 180-200 m: SC-133 | .932 | 3.06 | 24.6 |
| 180-200 m: SC-54 | .909 | 2.74 | 18.5 |
| 50 m: SC-4 | .925 | 2.85 | 24.1 |
| Clarkforkian, Clark's Fork Basin | | | |
| *Phenacodus-Ectocion* Zone: 10-30 m | .863 | 2.56 | 15.4 |
| *Phenacodus-Ectocion* Zone: 50-60 m | .906 | 2.78 | 18.5 |
| *Phenacodus-Ectocion* Zone: 90-110 m | .891 | 2.66 | 17.9 |
| *Phenacodus-Ectocion* Zone: 140-150 m | .852 | 2.49 | 16.7 |
| *Plesiadapis cookei* Zone: 180 m | .886 | 2.64 | 16.8 |
| *Plesiadapis cookei* Zone: 250-260 m | .894 | 2.66 | 17.4 |
| *Plesiadapis cookei* Zone: 320-360 m | .839 | 2.57 | 15.7 |
| *Plesiadapis gingerichi* Zone | .865 | 2.59 | 17.5 |
| Tiffanian | | | |
| Princeton Quarry | .937 | 2.97 | 24.6 |
| Cedar Point Quarry | .877 | 2.64 | 18.1 |
| Scarritt Quarry | .811 | 2.03 | 11.2 |
| Torrejonian | | | |
| Rock Bench Quarry | .954 | 3.40 | 33.3 |
| Gidley Quarry | .955 | 3.76 | 35.1 |

about 100 miles from the Clark's Fork Basin, have similar characteristics to those discussed above (see Table 54). Species richness is somewhat higher in the lowest sample (level 150), owing to quarrying and washing that yielded a greater number of small mammal fossils. For this reason, the Shannon heterogeneity index and Whittaker's equitability index are higher for this level than for levels 288 and 590 (Table 55). The Simpson index for level 150 is comparable to that of the other levels, suggesting that relative abundances of the commonest species are relatively stable in this sequence. Most of the indices of diversity for the No Water Creek assemblages are similar or only slightly higher than those of the Clark's Fork Basin early Wasatchian samples.

The constituents of the No Water Creek faunas are very similar to those in the Clark's Fork Basin early Wasatchian. Except for some of the very small mammal species and *Homogalax*, nearly all taxa are shared by both regions. Local ecological differences probably account for minor but very interesting differences in faunal composition between the two areas. For example, whereas *Hyopsodus* ranks first or second in abundance in all Clark's Fork Basin Wasatchian faunas, it is abundant only in the highest level of the No Water Creek sequence. *Haplomylus* is considerably more abundant than *Hyopsodus* in the two lower levels, but the reverse is true in the Clark's Fork Basin. Paleoecological studies may help elucidate these and other variations in composition between the two areas.

The fact that faunal composition and diversity are similar in the three levels of the No Water Creek section suggests that the biases inherent in surface samples may be less than expected, and not so great as to preclude their comparison to quarry assemblages.

## CONCLUSIONS FROM DIVERSITY ANALYSIS

Analysis of the composition and diversity of mammalian assemblages from Torrejonian through early Wasatchian in the northern Bighorn Basin indicates that diversity was high in the Torrejonian, much lower in the Tiffanian and Clarkforkian, and relatively high again in the early Wasatchian (chiefly due to increased equitability). Differences in sorting and sampling biases between the Paleocene quarry assemblages and the Clarkforkian and Wasatchian surface samples suggest that caution should be exercised when comparing their

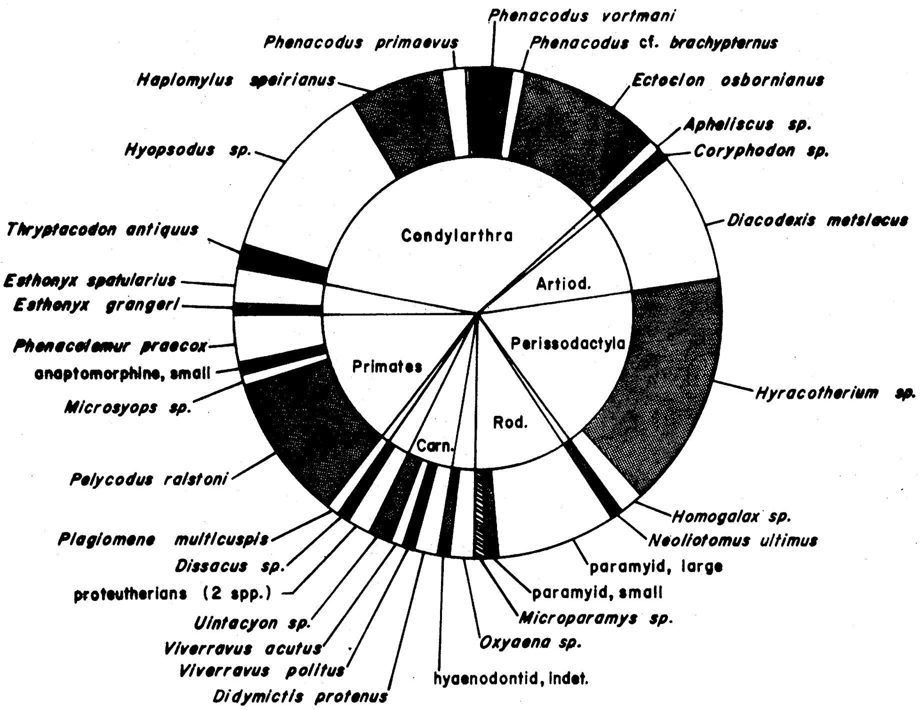

Figure 74. Relative abundances of mammalian taxa of the earliest Wasatchian at locality SC–4, 50 m above the Clarkforkian-Wasatchian boundary sandstone (Table 53). Width of sectors determined as in Figure 69. Note abundance of new immigrants *Hyracotherium*, *Diacodexis*, and *Pelycodus*, and dramatic decline of phenacodontid condylarths.

diversities. However, the similarity between the indices for the Wasatchian samples from No Water Creek—which include surface, quarry, and wash collections—indicates that surface samples can provide a reasonably good estimate of diversity that is at least roughly comparable to that derived from quarry samples. The general pattern of changes in mammalian diversity through time closely parallels curves based on paleobotanical evidence (species richness and leaf-margin data) that reflect a decline in temperature and equability from late Cretaceous to late Paleocene time and a subsequent increase in both from the late Paleocene to the early Eocene (Figure 75).

Important faunal differences between successive levels have been discussed above, and they are variously attributed to local ecological factors, immigrations, and in some cases, sampling biases. Further studies are needed in many cases to clarify the explanations for faunal differences. Aside from a marked drop in species richness and evenness from the Torrejonian to the Tiffanian, the most significant faunal change occurs at the Clarkforkian-Wasatchian boundary, where immigrations resulted in the influx of several new and highly successful taxa that comprise a large proportion of the mammalian population (Figure 78). Accompanying this immigration is a return to high diversity, mainly characterized by high equitability, in the Wasatchian. The distributions of relative abundances in the Cedar Point sample (Tiffanian) and in the Clarkforkian samples, both low in evenness, fit the Type 4 distribution described by Hutchinson (1961) and Goulden (1969); whereas the more evenly distributed samples from Rock Bench (Torrejonian) and the Wasatchian intervals conform more closely to MacArthur's (1960) Type 1 model.

A plausible general explanation for these changes in diversity has been suggested by May (1976: 160–161):

> . . . as a system becomes more complex, in the sense of more species and a more rich structure of interdependence, it becomes more dynamically fragile. . . . In a

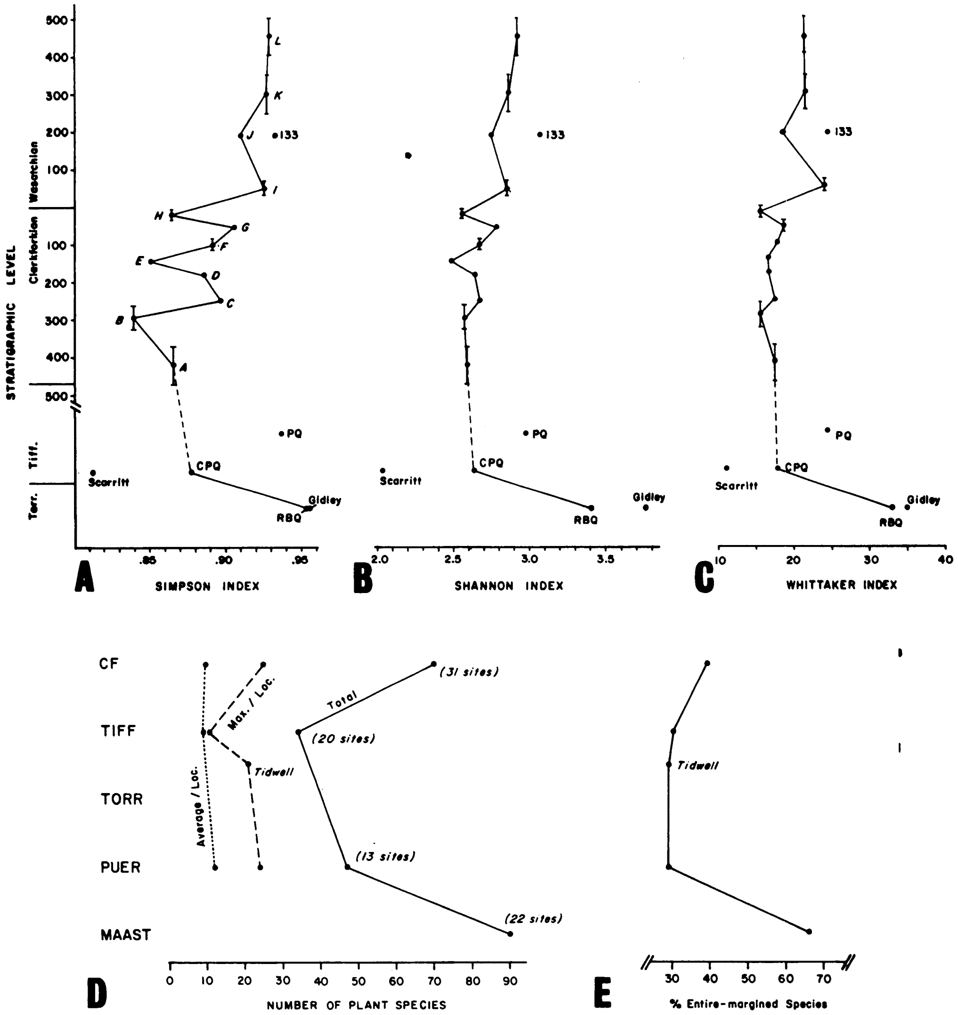

Figure 75. Change in mammalian faunal diversity across the Paleocene-Eocene boundary. Change in diversity indices for mammalian assemblages (A–C) is compared with species richness and leaf-margin data for fossil megafloras (D, E). In A, B, and C, three different indices for each mammalian sample are plotted against the stratigraphic level of the sample. The five Torrejonian and Tiffanian quarry assemblages are shown in approximate stratigraphic position, but their vertical scale is compressed with respect to that of the Clarkforkian and Wasatchian assemblages. The quarry samples (RBQ = Rock Bench Quarry, CPQ = Cedar Point Quarry, PQ = Princeton Quarry) may not be directly comparable to younger surface samples, hence they are connected to them by a dashed line. The graphs based on megaflora indicate warmer, more equable conditions in the Clarkforkian than in the Tiffanian, suggesting that diversity values for the Clarkforkian and Wasatchian mammalian faunas would be higher if sampling of these surface accumulations were comparable to that of the quarry assemblages. Diversity indices for Scarritt Quarry and Princeton Quarry may be misleading (see text), hence they are excluded from the diversity curves. Indices are plotted for eight levels or intervals in the Clarkforkian and four in the Wasatchian (A–H correspond to assemblages in Tables 44–51, respectively, and I–L correspond to successive levels analyzed in Table 53); vertical bars indicate the stratigraphic interval from which pooled samples were derived. Note sharp drop in diversity from Torrejonian to Tiffanian, and slight increase from Clarkforkian to Wasatchian, as indicated by all three indices. The increase in diversity in the Wasatchian reflects greater evenness (demonstrated by the Whittaker index) but no substantial increase in species richness. Species richness in megafloras (D) declines from a maximum in the Maastrichtian (based on samples from Lance, Fox Hills, and lower Medicine Bow Formations of Montana and Wyoming: Hickey, ms.) to a low in the Tiffanian. Total species known and maximum number of species/locality increased markedly in the Clarkforkian (Hickey, 1980). The number of localities contributing to the total number of species is shown in parentheses. The proportion of dicot species with entire-margined leaves (E) also decreases dramatically across the Cretaceous-Tertiary boundary and does not recover at all until the Clarkforkian (Hickey, 1980, and ms.). Data for Tidwell Quarry, southern Wyoming, from Roth (in Rigby, 1980); Puercan, Tiffanian, and Clarkforkian data based on sites in the northern Bighorn Basin, from Hickey (1980). Information on Wasatchian floras from the northern Bighorn Basin is not yet available.

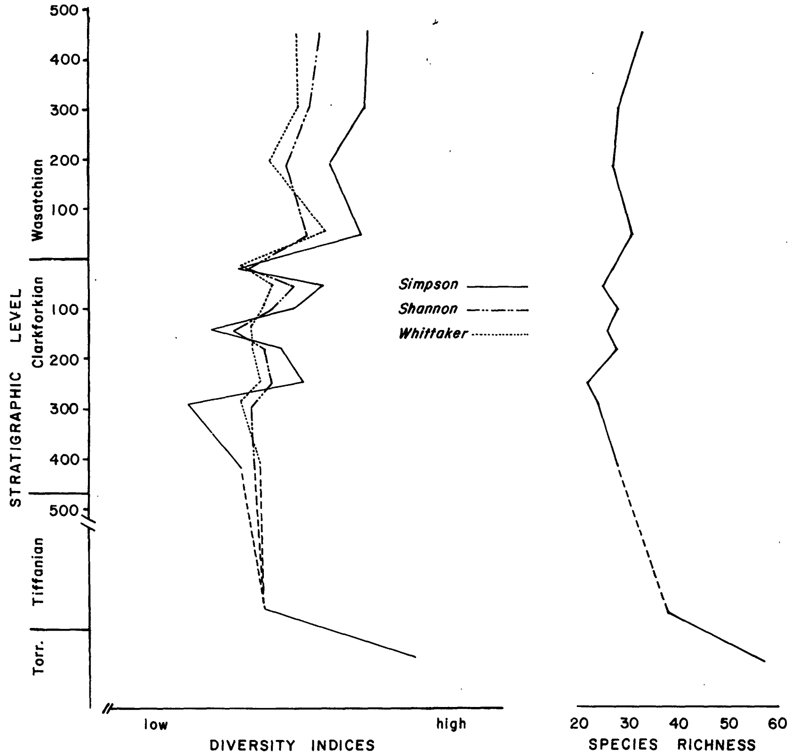

Figure 76. Diversity indices compared to species richness through time (same samples as in Figure 75). The three indices of Figure 75 are superimposed on the left to demonstrate their basic similarity. Species richness is highest in the Torrejonian, low in the Tiffanian, and appears lowest in the Clarkforkian; but it shows no dramatic changes thereafter, suggesting that higher diversity in the Wasatchian (graph at left) reflects an increase in evenness. Relatively low values for species richness in Clarkforkian and Wasatchian samples may be an artifact of the scarcity of very small mammals in surface samples. Paleobotanical evidence indicates that climatic conditions improved in the Clarkforkian, relative to the Tiffanian, suggesting that if mammalian sampling were more complete, the Clarkforkian-Wasatchian part of the graph might be shifted to the right.

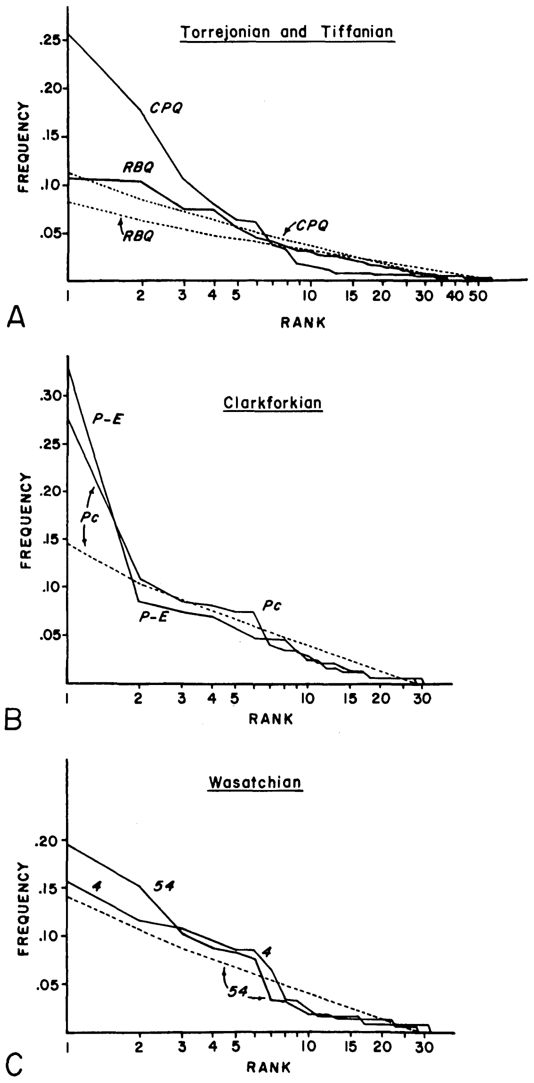

Figure 77. Rank abundance curves for successive Paleocene and early Eocene mammalian assemblages. The relative abundance (frequency) of each taxon is plotted against the logarithm of its rank of abundance in the fauna. Dotted lines indicate the theoretical distribution of abundances predicted from MacArthur's model (Type 1 distribution). Only one theoretical line is shown for the Clarkforkian and Wasatchian samples; the predicted distributions for the *Phenacodus-Ectocion* Zone and for SC–4 are almost the same as the lines shown, but lie very slightly below them. Samples compared are Rock Bench Quarry (RBQ), Cedar Point Quarry (CPQ), *Plesiadapis cookei* Zone (Pc, 180 m below boundary sandstone; Table 47), *Phenacodus-Ectocion* Zone (P-E, 10–30 m below boundary sandstone; Table 51), and early Wasatchian localities SC–4 and SC–54 (Table 53). Cedar Point Quarry and the Clarkforkian assemblages are low in equitability and approximate Hutchinson's Type 4 distribution; Rock Bench Quarry and the Wasatchian assemblages are much higher in evenness and more closely approach MacArthur's model distribution.

> predictable environment, the system need only cope with relatively small perturbations, and can therefore achieve this fragile complexity, yet persist. . . . In brief, a predictable ("stable") environment may permit a relatively complex and delicately balanced ecosystem to exist; an unpredictable ("unstable") environment is more likely to demand a structurally simple, robust ecosystem.

Thus the Torrejonian and Wasatchian may be envisioned as times of general ecological stability, while the Tiffanian and Clarkforkian were evidently times of unpredictability. This corresponds generally to evidence from fossil floras (Hickey, 1977, 1980; Wolfe 1978). It also conforms to Goulden's (1969) view that "generalists" are well adapted to such periods of unpredictability. The generalists of the Tiffanian were *Plesiadapis* and *Ptilodus*, while those of the Clarkforkian were the phenacodontid condylarths.

This study demonstrates that the fossil record can contribute considerable information on fluctuations in diversity through time. Results presented here document changes in mammalian diversity from the middle Paleocene into the early Eocene in the northern Bighorn Basin. A similar approach, applied to other faunas, should greatly improve our understanding of mammalian evolution; and it is hoped that this investigation will inspire further research in this direction.

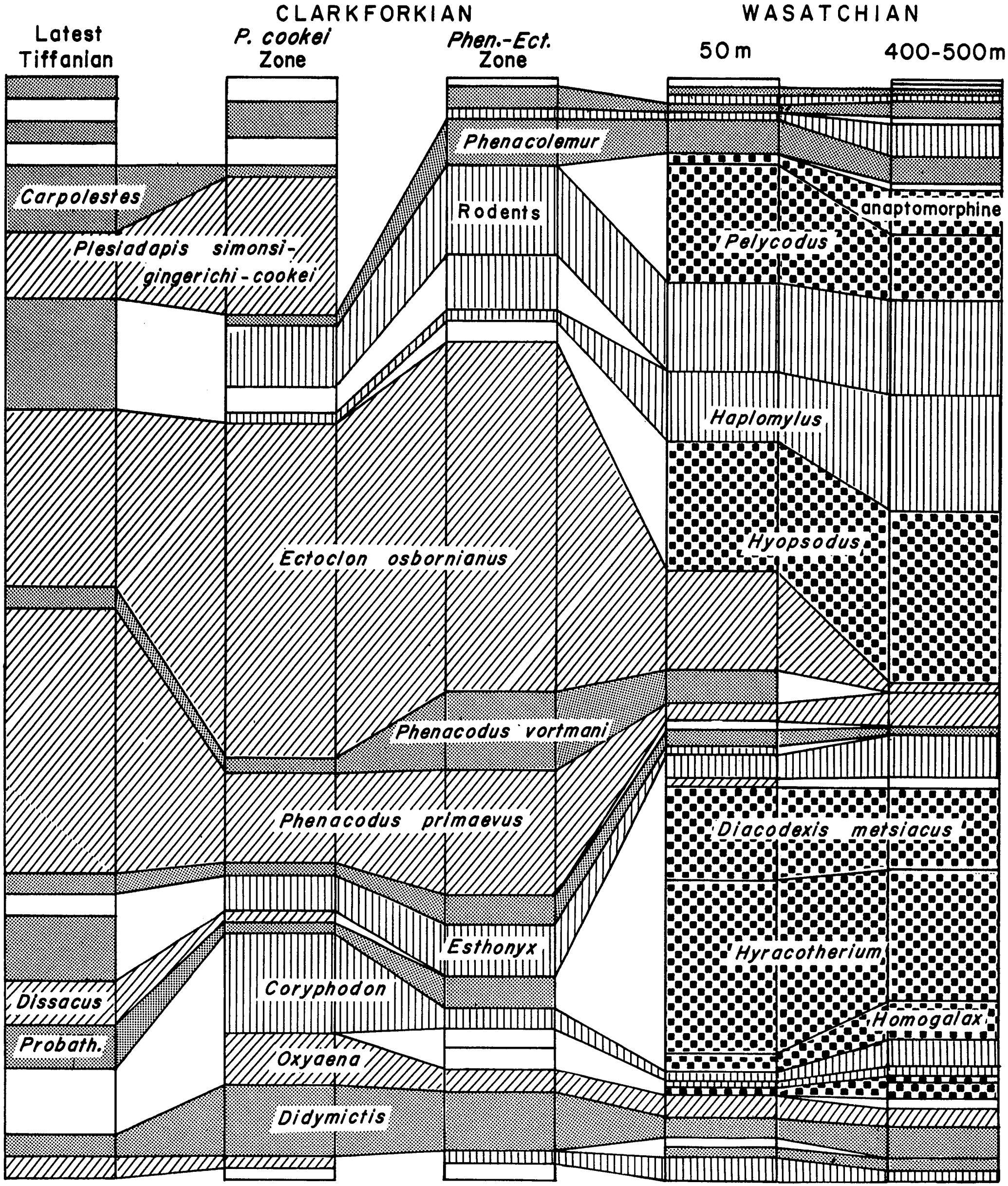

Figure 78. Mammalian faunal composition of surface localities at five intervals from latest Tiffanian into early Wasatchian of the Clark's Fork Basin. Width of each taxon in a column is proportional to its relative abundance (for simplicity, only the most important taxa are identified). Taxa marked by vertical lines are immigrants that first appear during the Clarkforkian. Those marked by a checkered pattern are immigrants that first appear at the beginning of the Wasatchian. (Two isolated teeth of *Hyopsodus* have been found in the *Phenacodus-Ectocion* Zone that are not indicated in the diagram.)

# VIII
# SUMMARY

THIS STUDY OF the Clarkforkian Land-Mammal Age has covered a number of subjects, including redefinition and characterization of the Clarkforkian, and a systematic revision of Clarkforkian mammals. Conclusions relating to specific aspects of the study have been presented in the appropriate sections of this report; hence they will not be repeated here. The major conclusions may be summarized as follows:

1. The Clarkforkian is a valid North American Land-Mammal Age, following the late Paleocene Tiffanian and preceding the early Eocene Wasatchian. Tentative correlations of parts of the later Tiffanian and Clarkforkian with late Thanetian and early Ypresian (early Sparnacian) faunas of the Paris Basin suggest that the Clarkforkian straddles the Paleocene-Eocene boundary, and that in North America this boundary occurs approximately between the early Clarkforkian (*Plesiadapis gingerichi* Zone) and middle Clarkforkian (*Plesiadapis cookei* Zone). Large samples of mammalian fossils have been collected from more than 100 sites of Clarkforkian age in the Clark's Fork Basin (northern Wyoming), which have been tied to measured stratigraphic sections that span late Tiffanian, Clarkforkian, and early Wasatchian age strata. Stratigraphic ranges and occurrences of all species have been recorded. All other known Clarkforkian mammalian assemblages from outside the type area are also reviewed. These data provide documentation of the Clarkforkian as a North American Land-Mammal Age, and may also be used to define the Clarkforkian as a local Stage.

2. The beginning of the Clarkforkian is defined by the initial occurrence of rodents (specifically *Paramys*), as well as the tillodont *Esthonyx*, the condylarth *Haplomylus*, and the pantodont *Coryphodon*, all of which appear to have immigrated into the Western Interior at about the same time. The end of the Clarkforkian (and the inception of the Wasatchian) is signaled by the first appearance of Artiodactyla (specifically *Diacodexis*), Perissodactyla (*Hyracotherium* and *Homogalax*), Primates of the families Adapidae (specifically *Pelycodus*) and Omomyidae, and probably hyaenodontid creodonts. The Clarkforkian fauna is otherwise dominated by mammals of Paleocene aspect. In addition to the taxa used to define the lower boundary of the Clarkforkian, numerous other mammalian species and genera make their first or last appearance during the Clarkforkian. It is therefore an intermediate fauna compositionally, as would be expected from its intermediate stratigraphic and temporal position. The Clarkforkian is further characterized by several index fossils (among them, *Plesiadapis cookei*, *Carpolestes nigridens*, *Apheliscus nitidus*, *Haplomylus simpsoni*, and *Esthonyx ancylion*), and by the abundant occurrence of the phenacodontids *Ectocion* and *Phenacodus*, the miacid *Didymictis*, the uintathere *Probathyopsis*, and several other taxa. Seventy mammalian species are recorded from the Clarkforkian in the type area, and at least 10 more are known from Clarkforkian deposits outside the type area. Eight new species are described herein (*Plagiomene accola*, *Microsyops simplicidens*, *Plesiadapis gingerichi*, *Haplomylus simpsoni*, *Oxyaena*? *lichna*, *Dipsalodon churchillorum*, *Palaeonictis peloria*, and *Paramys annectens*), and other new taxa, including five new genera, have been described elsewhere.

3. Three zones are recognized in the Clarkforkian of the type area. They are defined by the stratigraphic ranges of large plesiadapids and are designated the *Plesiadapis gingerichi* Zone (beginning in the late Tiffanian), the *Plesiadapis cookei* Zone, and the *Phenacodus-Ectocion* Zone. Certain other taxa, such as species of *Phenacolemur* and *Esthonyx*, are helpful in recognizing the zones. The three zones correspond approximately to early, middle, and late Clarkforkian, respectively.

4. Clarkforkian faunas have been recognized in several other sections in western and southern Wyoming and in Colorado. Questionable Clarkforkian assemblages are known from Texas and Baja California. Faunas of similar age are also known from the Nemegt Basin and elsewhere in Mongolia, as well as from the Paris Basin in Europe. These faunas indicate that considerable mammalian dispersal took place between North America and both Asia and Europe in the early Cenozoic.

5. Faunal composition has been analyzed at several stratigraphic levels from middle Paleocene (Torrejonian) through early Eocene (early Wasatchian) in the Polecat Bench-Clark's Fork Basin sequence. A general pattern

has emerged of high diversity (in both species richness and evenness) in the Torrejonian, a profound drop in diversity in the Tiffanian, continued relatively low diversity in the Clarkforkian, and a return to higher diversity (mainly evenness) in the early Wasatchian. This pattern is reinforced by comparison with other samples of the same age, and it appears to mirror a paleoclimatic curve (based on paleobotanical evidence) that indicates warm conditions in the Torrejonian, a drop in mean annual temperatures in the late Paleocene, and a general warming in the early Eocene. This suggests that high diversity (complexity) in the Torrejonian and Wasatchian may correlate with a "predictable" environment, whereas low diversity in the Tiffanian and Clarkforkian may be related to unpredictability. The latter situation often permits one or two "generalist" taxa to predominate, and this appears to be the case in Tiffanian and Clarkforkian assemblages. In addition to changes in diversity across the Clarkforkian-Wasatchian boundary, there were dramatic changes in faunal composition. Immigrant taxa (perissodactyls, artiodactyls, and adapid and omomyid primates) account for a large proportion of the Wasatchian fauna, whereas formerly dominant groups (e.g. phenacodontids and plesiadapiform primates) show a marked decline in abundance, almost surely due in part to competition with the immigrant taxa. The striking faunal turnover at the beginning of the Wasatchian may be related to climatic changes or other factors affecting the predictability of the environment, but the precise explanation remains unknown.

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# PLATE I

## CLARKFORKIAN EXPOSURES IN THE CLARK'S FORK BASIN

Figure 1.—Clarkforkian age exposures in the Willwood Formation at locality SC–62. Lowest outcrops are in the *Plesiadapis cookei* Zone. *P. cookei* has not been found above the prominent red-banded bed (arrows) in the lower part of the outcrop; strata above this bed are probably in the *Phenacodus-Ectocion* Zone. Photograph taken looking toward the northwest.

Figure 2.—Highest beds of Clarkforkian age in the Willwood Formation at localities SC–23 and SC–25 (*Phenacodus-Ectocion* Zone). Prominent sandstone (arrows) capping the lower exposures is the Clarkforkian-Wasatchian boundary sandstone. Photograph taken looking toward the northwest.

1

2

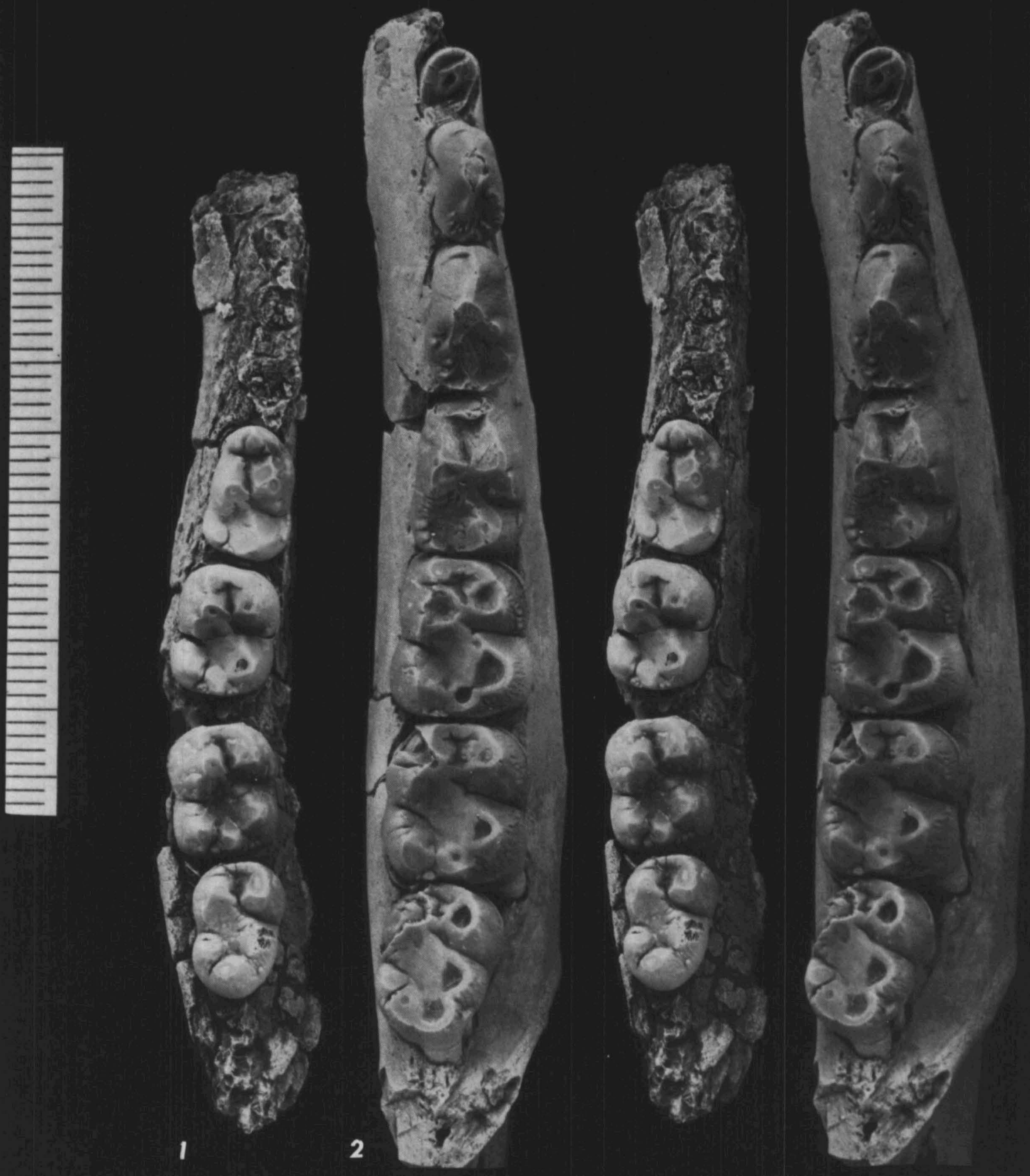
## PLATE 2

### CLARKFORKIAN *PHENACODUS* FROM THE CLARK'S FORK BASIN

All figures twice natural size, scale in mm.

Figure 1.—*Phenacodus vortmani*, right dentary with $P_4$-$M_3$ in occlusal view. Stereophotograph of UM 66922 from locality SC–127 (*Plesiadapis cookei* Zone).

Figure 2.—*Phenacodus primaevus*, right dentary with $P_2$-$M_3$. Stereophotograph of UM 65239 from locality SC–29 (*Phenacodus-Ectocion* Zone).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# PLATE 3

## CLARKFORKIAN *PHENACODUS* FROM THE CLARK'S FORK BASIN

All figures twice natural size, scale in mm.

Figure 1.—*Phenacodus* sp., left dentary with $M_{1-2}$ intermediate in size between *P. vortmani* and *P. primaevus*, in occlusal view. Stereophotograph of UM 71300 from locality SC–226 (*Plesiadapis gingerichi* Zone).

Figure 2.—*Phenacodus vortmani*, left maxilla with $P^4$-$M^3$ in occlusal view. Stereophotograph of UM 65668 from locality SC–59 (*Phenacodus-Ectocion* Zone).

Figure 3.—*Phenacodus primaevus*, left maxilla with $M^{1-3}$ in occlusal view. Stereophotograph of UM 66595 from locality SC–105 (*Phenacodus-Ectocion* Zone).


1
2
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# PLATE 4

## CLARKFORKIAN *PROBATHYOPSIS* AND *CORYPHODON* FROM THE CLARK'S FORK BASIN

Figures 1 and 2 natural size, scale in mm.

Figure 1.—*Probathyopsis praecursor*, left upper canine of female in lateral view. UM 69696 from locality SC–19 (*Plesiadapis cookei* Zone).

Figure 2.—*Probathyopsis praecursor*, right maxilla with $P^2$-$M^3$ of female (see fig. 1) in occlusal view. Stereophotograph of UM 69696 from locality SC–19 (*Plesiadapis cookei* Zone).

Figure 3 one half natural size, scale in mm.

Figure 3.—*Coryphodon* sp., mandible with left and right $I_2$ and C, right $P_1$-$M_3$, in occlusal view. UM 66162 from locality SC–73 (*Phenacodus-Ectocion* Zone).


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METRIC 1 2 3 4 5

## PAPERS ON PALEONTOLOGY NO. 26

# CLARKFORKIAN LAND-MAMMAL AGE