

**NEW EARLIEST WASATCHIAN  
MAMMALIAN FAUNA FROM THE EOCENE  
OF NORTHWESTERN WYOMING:  
COMPOSITION AND DIVERSITY IN A  
RARELY SAMPLED HIGH-FLOODPLAIN  
ASSEMBLAGE**

**PHILIP D. GINGERICH**

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Frontispiece: Aerial photograph of badlands at the south end of Polecat Bench. Red beds in the right half of the photograph are University of Michigan locality SC-67, yielding most specimens described here. Locality SC-308 is in red beds in the left center of the photograph, and locality SC-121 is in red beds at the left margin of the photograph. Clarks Fork Basin and Beartooth Mountains lie in the left distance.

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Ann Arbor, Michigan 48109  
Philip D. Gingerich, Director

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Dedicated to the Memory of  
PROFESSOR JOHN A. DORR, JR.  
1922 - 1986

Jack's interest was an important stimulus in much of this work.

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## ABSTRACT

A new earliest Wasatchian mammalian fauna is described from twenty localities in the Bighorn and Clarks Fork basins of northwestern Wyoming. These localities are in greenish gray sandstones and brightly colored mudstones within the Clarkforkian-Wasatchian boundary sandstone complex, or in brightly colored mudstones correlative with and lateral to the boundary sandstone. The fauna represents a new basal zone of the Wasatchian, here called zone  $Wa_0$ . Thirty-five mammalian genera and 41 mammalian species are known from zone  $Wa_0$ . Three genera and ten species are new. The  $Wa_0$  fauna includes the earliest North American records of Artiodactyla, hyaenodontid Creodonta, Perissodactyla, and true Primates, but the  $Wa_0$  fauna is dominated by hyopsodontids and phenacodontids, and it is compositionally intermediate between those of the preceding Clarkforkian land-mammal age and succeeding Wasatchian land-mammal age. Indices of diversity are high, and the pattern of rank abundance of species fits a model of biotic dependence. High diversity and biotic dependence are characteristics of Wasatchian but not Clarkforkian faunas. The  $Wa_0$  fauna includes eleven small species with larger Clarkforkian and/or Wasatchian congeners. All of the small species appear in the  $Wa_0$  fauna without Clarkforkian precursors intermediate in size. The depositional setting of  $Wa_0$  mammals and associated fauna can be used to test the idea that a sudden appearance of small forms is due to rapid evolution *in situ*.

A model for interpretation of the  $Wa_0$  fauna is developed based on distinctive sedimentological characteristics of the stratigraphic interval yielding it. The Clarkforkian-Wasatchian boundary sandstone is an extensive multistory sheet sandstone deposited during an interval of relatively slow basin subsidence or regional uplift. Fossiliferous sediments within and lateral to the boundary sandstone include paleosols of unusual maturity for the Clarks Fork Basin. Development of an extensive sheet sandstone indicates that during  $Wa_0$  time rivers removed more fine-grained sediment than they deposited. Erosive rivers channel into the substrate more than aggrading rivers do, and lateral floodplain environments stand higher relative to the water table. High floodplains tend to be better drained and less often flooded, with more mature soil development.

Animals inhabiting most depositional basins can be divided into aquatic, low-floodplain, and high-floodplain assemblages. The  $Wa_0$  aquatic fauna includes aquatic mollusks; the fishes *Lepisosteus* (very common) and *Amia*; the

turtles *Plastomenus* and *Echmatemys* (earliest record of the genus); and the crocodilian *Leidyosuchus*. The  $Wa_0$  terrestrial fauna includes several specimens of the rare dry-substrate land snail *Holospira*, the hoofed crocodilian *Pristichampsus* (earliest record of the genus), and as many as 13 endemic species of mammals, most of which are smaller than other congeners, like the condylarth *Ectocion parvus*. The alligatorid *Allognathosuchus* sp. and the condylarth *Ectocion osbornianus*, both common in Clarkforkian and other early Wasatchian faunas, are very rare in the  $Wa_0$  fauna. Faunas in which *Allognathosuchus* sp. and *Ectocion osbornianus* predominate are interpreted as low-floodplain faunas, and faunas in which *Holospira* and *Pristichampsus* are found and *Ectocion parvus* predominates are interpreted as high-floodplain faunas. Cenogram analysis of  $Wa_0$  mammals indicates that they inhabited a humid forest environment: the high floodplain was not dry, but it was better drained.

Presence of numerous small species in the  $Wa_0$  fauna with larger congeners elsewhere can be explained by a change in sampling regime from low floodplains to high floodplains. Rapid *in situ* diminution in size is not required. The  $Wa_0$  high-floodplain fauna differs at the species level from that normally sampled on low floodplains in that more small congeners are present, but most genera in one environment are present in the other. Higher taxa that make their first North American appearance in the  $Wa_0$  fauna, like Artiodactyla, Perissodactyla, and true Primates, also appear in immediately succeeding low-floodplain assemblages.

The  $Wa_0$  fauna appears to correlate best with earliest Sparnacian faunas in Europe. Evidence favoring correlation of part of the Clarkforkian land-mammal age with the early Sparnacian has changed and been supplemented, and this correlation can no longer be sustained. The Clarkforkian is again regarded as entirely Paleocene in age. Mammalian groups that first appeared in North America at the beginning of the Wasatchian (Artiodactyla, hyaenodontid Creodonta, Perissodactyla, and Primates) appeared as a group with no known precursors in the late Paleocene. These earliest representatives are interpreted as an integrated cohort of species immigrating to North America from elsewhere. An African or South Asian origin with subsequent dispersal via Asia and/or Europe is plausible as a working hypothesis, but there is as yet little direct evidence to substantiate this.



# I INTRODUCTION

Most modern orders of mammals made their first appearance in the North American fossil record during the Paleocene-Eocene transition, a transition that spanned the late Tiffanian, Clarkforkian, and early Wasatchian land-mammal ages. This transition is best represented in a continental setting in the Bighorn Basin and contiguous Clarks Fork Basin of northwestern Wyoming, where fluvial sediments shed from the rising Rocky Mountains buried and preserved abundant remains of early Cenozoic vertebrates. Subsequent uplift and erosion have exposed Paleocene and early Eocene sedimentary rocks over a large area. The most complete stratigraphic section of continental Paleocene and early Eocene sediments known anywhere is exposed on the southeastern side of Polecat Bench and along the southern rim of Sand Coulee, north and west of the town of Powell, Wyoming. This section includes strata yielding latest Cretaceous, early through late Paleocene, and early Eocene faunas.

The lower part of the Polecat Bench–Sand Coulee section, representing latest Cretaceous through middle Paleocene time, is relatively thin (ca. 100 m in thickness) and fossil localities are rare. These yield faunas representing the Lancian land-mammal age (latest Cretaceous), a single biochron of the Puercan land-mammal age (early Paleocene), and a single biochron of the Torrejonian land-mammal age (middle Paleocene). The upper part of the Polecat Bench–Sand Coulee section is much thicker (ca. 2,100 m in thickness) and it is fossiliferous virtually everywhere that it has been examined. Fossil localities in the upper part of the section yield faunas representing the last four of five commonly recognized biochrons or zones of the Tiffanian land-mammal age (late Paleocene), all three biochrons or zones of the Clarkforkian land-mammal age (late Paleocene, see discussion below), and the first five of seven commonly recognized biochrons or zones of the Wasatchian land-mammal age (early Eocene). These twelve successive biochrons or zones in a stratigraphic section 2,100 m thick represent seven to eight million years of geological time, the interval from about 59 Ma to 51 Ma (Berggren et al., 1978; Gingerich, 1983) or, using revised decay constants, the interval from about 61 Ma to 54 Ma (Berggren et al., 1985), spanning the Paleocene-Eocene transition. Each biochron represents, on average, about 0.6–0.7 m.y. In the absence of evidence bearing on

the lengths of individual biochrons, each biochron is assumed to be of approximately equal duration.

North American Paleocene mammalian faunas were dominated by the primitive allotherian order Multituberculata and the archaic eutherian orders Condylarthra, Pantodonta, Proprimates, Proteutheria, and Taeniodonta. Metatherian Marsupialia and eutherian Carnivora, Dermoptera, and Insectivora were also present. Of these, only Marsupialia, Carnivora, and Insectivora survive today in North America. Oxyaenid Creodonta appeared in the middle Tiffanian (Gingerich, 1980a), and Dinocerata, Edentata (s.l.), and Notoungulata appeared in the late Tiffanian (Gingerich, 1985b). Of these, only Edentata (s.l.) survive today. Rodentia and Tillodontia appeared in the early Clarkforkian (Rose, 1981a), and Chiroptera were present by the late Clarkforkian (Gingerich, 1987b). Rodentia and Chiroptera survive today. Artiodactyla, hyaenodontid Creodonta, Primates, and Perissodactyla appeared in the early Wasatchian, and all except Creodonta survive today. Thus nine of the ten modern orders known in North America today were present here by early Eocene times. Three of these were present in the Torrejonian and early Tiffanian before the Paleocene-Eocene transition began (Marsupialia, Insectivora, and Carnivora), and six orders appeared as part of the Paleocene-Eocene transition. One order appeared in the late Tiffanian (Edentata s.l.), two appeared in the Clarkforkian (Chiroptera and Rodentia), and three appeared at the beginning of the Wasatchian (Artiodactyla, Perissodactyla, and Primates). The tenth order found today in North America (Lagomorpha) appeared later in the Eocene.

A new earliest Wasatchian vertebrate fauna and mammalian faunal zone is described here. The new fauna includes the oldest North American representatives of Artiodactyla, Perissodactyla, and Primates, and the earliest records of several other mammalian families that make first appearances in the early Wasatchian. Comparison of the new earliest Wasatchian fauna with those in subjacent and superjacent zones in the Clarks Fork and Bighorn basins casts new light on the origin of the Wasatchian fauna. Comparison of the whole sequence of North American late Paleocene and early Eocene faunas with those of similar age in Asia and in Europe provides a broader geographic context for understanding the origin of modern orders of mammals.

CLARKFORKIAN AND EARLY WASATCHIAN  
LAND-MAMMAL AGES

It has taken many years to achieve a detailed chronology of the Paleocene-Eocene faunal transition in North America, and we owe our present understanding to the work of many investigators. The evidence at hand comes entirely from field expeditions, carried out over the course of some sixty field seasons, with relevant maps, notes, and specimens now archived principally at the American Museum of Natural History, the University of Michigan, and Yale University. Our knowledge of the Paleocene-Eocene transition is still imperfect and incomplete in the areas where it has been most intensively studied, the Bighorn and Clarks Fork Basins of northwestern Wyoming, and very little is known about the Paleocene-Eocene transition elsewhere in North America or elsewhere in the world. What follows is based on detailed investigation of one area, and there is a great need for further exploration and documentation of this interval of mammalian history elsewhere.

Clarkforkian Land-Mammal Age

The first investigation of the Paleocene-Eocene transition in North American mammalian faunas was carried out in 1911 by Walter Granger and William J. Sinclair, assisted by George Olsen, collecting for the American Museum of Natural History. They discovered an important transitional Paleocene-Eocene mammalian fauna, more or less by accident, as they tried to extend their work on "Wasatch" mammalian faunas from the central part of the Bighorn Basin into the northern Bighorn Basin.

When Granger's field party left the central basin heading northward, they were fortunate to encounter a U.S. Geological Survey group working near the Graybull River. The geologist in charge, Donnel Hewett, showed Granger and Sinclair an important unconformity separating the Fort Union Formation and overlying "Wasatch" in this area (see Hewett, 1926). A few days later, on August 2, Granger wrote to W. D. Matthew at the American Museum that he and Sinclair were planning to examine the west end of the McCullough Peaks, expecting to find a "Wind River" Ly-sitean or Lostcabinian fauna in red beds [Granger's "Letter no. 4" in the American Museum archives, written from Cody, Wyoming]. Instead Granger and Sinclair found a fauna lacking perissodactyls in drab Fort Union mudstones some 245 feet (75 m) below the lowest red bed. Aided no doubt by their encounter with Hewett, Granger and Sinclair recognized that a fauna from the Fort Union of the Bighorn Basin was important, and they recognized that this fauna was more primitive than a typical "Wasatch" fauna.

The collection was mailed to Matthew for his examination [unfortunately Granger's "Letter no. 5," which presumably accompanied this shipment, is missing in the American Museum archives] and, surprisingly, the collection was mailed without entering any information about it

in the 1911 Bighorn Wasatch field catalogue. On August 24, Granger wrote to Matthew ["Letter no. 6" written from Garland, Wyoming] saying that he and Sinclair were convinced that the new collection came from a lower horizon than any collected in the Bighorn Basin previously, and that they were hoping Mr. Hewett would find time to work on the unconformity between the drab Fort Union and red-banded Wasatch in the McCullough Peaks.

Matthew's response on receiving the new collection is worth quoting in part:

This fauna has no special suggestions of Torrejon affinities, except in a negative way. But the absence of Perissodactyls, Rodents and Artiodactyls, of *Hyopsodus* and *Pelycodus*, can hardly be wholly accidental. Note that these are just the groups which expand into the principal faunal elements of the late Eocene fauna, and have no predecessors in the Torrejon, while the groups present are mostly those which have predecessors in the Torrejon. In this broad way it is an intermediate fauna just such as you ought to find on the principles of successive migrations from northern Holarctic dispersion centres.

Of course one would like to have these preliminary results confirmed by larger collections. But even if you can get nothing more I should say you had very strong and weighty evidence for a new and distinct faunal horizon below the true *Coryphodon* zone. [American Museum archive copy of letter from Matthew to Granger, dated August 29, 1911.]

Granger's Bighorn Wasatch field catalogue for 1911 indicates that August 12 and 13 were spent collecting "About 3 mi. N. of Ralston" (W. J. Sinclair) and at the "Head of Big Sand Coulee" (W. Granger and G. Olsen). Specimens collected here, together with those collected on the west side of the McCullough Peaks, were provisionally referred to "Ralston beds" or a new "Ralston formation" by Sinclair and Granger (1912, p. 60). Later, following two additional summers of field work, the term "Ralston" was replaced by "Clark Fork" by Granger (1914), who regarded this fauna as possibly representing the top of the Paleocene. Our modern Clarkforkian land-mammal age owes its origin to this early work on the Clark Fork fauna. Jepsen (1930b), Simpson (1937), and others added new taxa to the Clarkforkian fauna. Wood (1967) reviewed the Clarkforkian fauna known at the time, and concluded that it "consists of four specimens referable to four mammalian genera, each from a different locality. . . . Such evidence scarcely warrants recognition of the Clark Fork as a provincial age, faunal zone, or member of the Polecat Bench Formation [Fort Union Formation]" (see Gingerich, 1976b, p. 56, for discussion). Following thorough field investigation, the Clarkforkian land-mammal age is now known to be represented by several thousand specimens coming from three distinct superposed zones Cf<sub>1</sub>, Cf<sub>2</sub>, and Cf<sub>3</sub>, in the Clarks Fork Basin, and from isolated sites in other basins (Rose, 1981a).

### Wasatchian Land-Mammal Age

Wasatch (or "Wahsatch") was first used by Hayden (1869) for a group of formations in the vicinity of Evanston, Wyoming, just east of the Wasatch Mountains. Fossil mammals, including type specimens of *Hyracotherium vasacciense* (Cope, 1872), *H. index* (Cope, 1873), *Coryphodon radians* Cope, 1872, *Phenacodus primaevus* Cope, 1873, and other species, were found in the upper or "Knight" part of the sequence. The term "Wasatch" or Wasatchian was soon extended to describe the *Hyracotherium-Coryphodon-Phenacodus* association when found in other areas of the Western Interior.

Granger (1914) recognized four subdivisions of the Big-horn Basin Wasatchian: Sand Coulee, Graybull, Lysite, and Lost Cabin. The first two subdivisions, Sand Coulee and Graybull, were also found in the Clarks Fork Basin, indeed the Sand Coulee subdivision was named for beds exposed in the Clarks Fork Basin. As outlined by Granger (1914, p. 207), the Clark Fork fauna lacked perissodactyls, the overlying Sand Coulee fauna was marked by the first appearance of "*Eohippus*" (*Hyracotherium*), the Gray Bull fauna was marked by the first appearance of "*Systemodon*" (*Homogalax protapirinus*), the Lysite fauna was marked by the addition of *Heptodon*, and the Lost Cabin fauna was marked by the addition of *Lambdaotherium*.

Early Wasatchian is here employed to refer to the Sandcouleean land-mammal subage of Granger, including three biochrons or zones:  $Wa_0$  (described here),  $Wa_1$ , and  $Wa_2$  (Gingerich, 1983). Middle Wasatchian is equivalent to the Graybullian land-mammal subage of Granger, including three biochrons or zones:  $Wa_3$ ,  $Wa_4$ , and  $Wa_5$  (Gingerich, 1983; the latter being Schankler's, 1980, *Bunophorus* interval zone). Late Wasatchian includes the Lysitean and Lostcabinian land-mammal subages of Granger, including at least two biochrons or zones:  $Wa_6$  (Lysitean) and  $Wa_7$  (Lostcabinian; Gingerich, 1983). One or both of the latter may warrant subdivision.

### Clarkforkian-Wasatchian Boundary Sandstone

Wood (1967, p. 27) noted that relegation of most Clarkforkian specimens to lower Eocene beds might make it possible to redefine a Sandcouleean fauna, and suggested that this be reappraised to determine conclusively whether or not such an interval could be distinguished. The idea that the Clarkforkian and Sandcouleean might be the same appeared initially to have merit, and Gingerich (1976a) showed *Pelycodus* ranging into the Clarkforkian on the assumption that the two were equivalent (confusing specimen labelling, implying that Princeton Clarkforkian and Wasatchian specimens came from a single Paint Creek locality, contributed to this misunderstanding as well). Analysis of 1975 field results showed clearly that the Clarkforkian and Sandcouleean are distinct.

After the 1975 field season, new specimens collected from sixty-four localities in the Clarks Fork Basin were

plotted on distribution maps. These maps showed that *Hyracotherium*, *Diacodexis*, *Hyopsodus*, *Cantius*, and other Wasatchian taxa were found at localities in the southwestern corner of the Clarks Fork Basin, while *Plesiadapis*, *Probathyopsis*, and other Clarkforkian taxa came from the adjacent central part of the basin. During the summer of 1976, collecting was concentrated in the area between the two sets of localities, Clarkforkian or Wasatchian, to locate the geographic and stratigraphic boundary between the two faunas. Once the boundary was located in several places, it was evident that a single sandstone complex separates Clarkforkian faunas below from Wasatchian faunas above, and that the unit could be traced across much of the Clarks Fork Basin (Figure 1). The Clarkforkian-Wasatchian boundary sandstone averages about 20 m thick in the Clarks Fork Basin, and distinct upper and lower sandstone units can be recognized in some areas (Figure 2). The boundary sandstone complex forms a conspicuous dip slope over much of the Sand Coulee area (Figure 3).

M. J. Kraus initiated a detailed sedimentological investigation of the Clarkforkian-Wasatchian boundary sandstone during the summer of 1978. This work involved mapping the sandstone over an area of some sixteen square miles (40 sq. km) and measuring five stratigraphic sections (Kraus, 1979, 1980). Kraus (1979) described the boundary sandstone as a laterally extensive, multistory, sheet sandstone varying from 12 to 31 m in thickness. It includes numerous channel structures that coalesce laterally and often vertically. Large-scale trough cross-stratification indicates northward trending paleocurrents. The sandstone is primarily fine- to medium-grained feldspathic litharenite with some lithic wacke. Kraus (1980) noted that mudstone units occur within the sheet sandstone complex, comprising 3% of her measured sections.

Kraus (1980) interpreted the Clarkforkian-Wasatchian boundary sandstone as having been deposited by a meandering stream system in which the finer facies of most of the channel deposits were truncated and eroded during subsequent channel meander migration. She further inferred that the lateral continuity of the boundary sandstone complex, its multistory character, and the paucity of associated overbank sediments reflect decreased subsidence in the Clarks Fork Basin and relatively slow rates of net sediment accumulation. By comparison with underlying and overlying parts of the stratigraphic section, where overbank mudstones are commonly preserved, the interval of the boundary sandstone appears to represent a time of unusually slow subsidence in the Clarks Fork Basin.

### DISCOVERY OF EARLIEST WASATCHIAN FAUNA

The first  $Wa_0$  mammals were collected by W. J. Sinclair on August 12, 1911, the first day he collected "about 3 mi. N. of Ralston" or at the "bluff north of Ralston" (southern end of Polecat Bench). Sinclair found a partial skeleton of

a mammal initially identified as ?*Sinopa* in the field catalogue, listed as a new species of *Limnocyon* by Sinclair and Granger (1912, p. 59), and finally made the holotype of a new genus and species of Clarkforkian creodont *Dipsalidictis platypus* by Matthew (1915a, p. 65). As described in the systematic section dealing with *D. platypus* below, the trigonid of right  $M_2$  of this specimen, AMNH 15857, was found in 1986, seventy-five years after the original discovery, at the locality now designated SC-67, which is at the southern end of Polecat Bench.

Bones and teeth from zone  $Wa_0$  are almost always light in color like those of zones  $Wa_5$  through  $Wa_7$  of the central Bighorn Basin. These contrast sharply with the dark brown or black bone and teeth found in Clarkforkian and other Wasatchian intervals in the Bighorn and Clarks Fork Basins. The holotype of *Dipsalidictis platypus* is light in color like virtually all  $Wa_0$  specimens collected subsequently. Two other specimens, the holotypes of *Ectocion parvus* (AMNH 16080) and *Meniscotherium priscum* (AMNH 16145), are listed by Granger (1915) as having been collected in 1911. Both are light in color as well and probably came from zone  $Wa_0$  at SC-67 or nearby. Granger (1914) drew attention to the red color of beds yielding his Sand Coulee fauna, but *Dipsalidictis platypus*, *Ectocion parvus*, and *Meniscotherium priscum* were all regarded as being Clarkforkian in age and there is no indication that he (or anyone else) regarded the light color of the holotypes of these three species as important or correlated light-colored bone with deeply weathered red sediment like that found on the southern end of Polecat Bench.

The next specimens collected from zone  $Wa_0$  on Polecat Bench were picked up by Japanese-Americans interned for the duration of World War II at the Heart Mountain Relocation Center, some 10 miles (16 km) from the southern end of Polecat Bench. One specimen of *Ectoganus*, collected by Jukichi Sakata in 1944, found its way into the Princeton University collection (YPM-PU 14678) and was later made the holotype of a new subspecies, *Ectoganus copei bighornensis* Schoch, 1981 (here elevated to species rank as *E. bighornensis*). A few additional Princeton specimens were collected in 1946 and 1962, including the holotype of a new arctocyonid condylarth described here, and the second known specimen of *Ectocion parvus*. The latter was collected by R. Wood, presumably while he was reinvestigating Sinclair's locality "in the bluff north of Ralston" as background for his Clarkforkian paper (Wood, 1967).

The first University of Michigan specimens from  $Wa_0$  localities SC-67, SC-69, and SC-71 were collected in 1976 (when these localities were approached from the top of Polecat Bench). Specimens collected in the first year included a dentary of a small *Hyracotherium* and the holotype of *Mimoperadectes labrus* Bown and Rose, 1979. Gingerich (1982) listed the fauna known at the time from SC-67, however the distinctiveness and importance of these localities was not recognized until 1984.

None of the earliest Wasatchian localities studied here

can be described as being richly fossiliferous, and  $Wa_0$  localities were passed over rapidly by American Museum, Princeton, and University of Michigan field parties working in the northern Bighorn and Clarks Fork basins. These were not recollected for many years because of their low productivity.

When the distinctiveness of many species in the  $Wa_0$  fauna and the fauna's importance for understanding faunal evolution were recognized, a new effort was made to collect fossil mammals from this interval. Most of the specimens known to date were found by intensive surface prospecting: an experienced collector finds, on average, one fragmentary jaw per day spent collecting at a  $Wa_0$  locality. Many months of diligent effort have been invested to acquire the fauna described here. The most productive localities have been collected and recollected many times. Locality SC-67, for example, has now been collected twenty-three times over the course of eleven summers.

Repeated collecting has led to recovery and reassociation of some scattered remains. Discovery of a missing part of Matthew's holotype of *Dipsalidictis priscus* has been noted. Pieces of crocodylian specimen UM 83566 (left and right dentaries) were found at locality SC-139 in 1977 and 1984. Hyaenodontid specimen UM 83460 (left and right dentaries with the trigonid of left  $M_3$ ) was found at locality SC-121 in 1984: the talonid and root of  $M_3$ , connecting the crown to the dentary, were found in 1985.

#### SYSTEMATIC PROTOCOL

Systematic identification and analysis of fossils from a new or poorly known fauna is a complicated process, and the reliability of the results depends in large measure on repeated examination and comparison of each specimen in different contexts. The protocol followed in studying remains collected from  $Wa_0$  localities involved three steps:

- (1) The entire collection was organized by locality, and within each locality by specimen number. Each specimen was tentatively identified to anatomical position and to family or genus, and each specimen was measured (all identifications and measurements were made by the author). Specimens were examined locality-by-locality and specimen-by-specimen within localities. Locality, specimen number, taxonomic identification, a brief description, and all measurements were entered into a database as they were recorded. The database was constructed to permit separate entry of length and width measurements for upper or lower, and left or right teeth, including deciduous premolars and ambiguous  $M^1$  or  $M^2$  and  $M_1$  or  $M_2$  identifications (denoted in tables by  $M^1$  and  $M_1$ , respectively). Taxonomic identifications were edited for consistency, preliminary faunal lists including both the total number of specimens and the minimum number of specimens



present at each locality were computed from the database, and statistical tables of measurements were computed for each species. Computer programs were written in BASIC to facilitate this.

- (2) All specimens were examined a second time, grouping and comparing them taxon-by-taxon, one species at a time. Specimens were compared with each other, and they were compared with relevant casts and originals of type and reference specimens from localities earlier and later in time. This step required the greatest commitment of time. In the case of difficult groups, like the carnivorous mammals, considerable revision was required, both of taxonomic identifications and anatomical positions of teeth. Parts of what sometimes proved to be the same specimen collected at different times were reassociated at this stage. When study of a species was complete, the database was edited to correct identifications and the relevant systematic section of the paper was written (and previous sections were revised when necessary).
- (3) The corrected database was used to print new labels for all specimens, including all miscellaneous teeth sufficiently complete to permit identification. Specimens were relabeled, which constituted a third check on identifications of anatomical position and taxon. Corrections were made at every stage, demonstrating the importance of this structured protocol (even for experienced investigators). At the end, faunal lists were compiled for each locality showing total number of specimens and minimum number of individuals for each species, and revised tables of tooth measurements were computed for all species.

The presence of 14 mammalian orders, 20 families, 35 genera, and 41 species in the  $W_{a_0}$  fauna (334 mammalian specimens) conforms reasonably to the taxonomic richness observed in extant mammalian faunas (e.g., Fleming, 1973). It is possible that two or more biological species in the  $W_{a_0}$  fauna are erroneously confused in one or two instances because they cannot be distinguished by dental characteristics, but the final total of 41 species indicates that this is not likely to be a significant problem. Such error, if it exists, is in any case an error toward conservatism in terms of both taxonomy and diversity. More taxa will undoubtedly be added to the  $W_{a_0}$  fauna as more specimens are found in the future, but the sample available at present is sufficient to yield interesting generalizations regarding faunal composition, taxonomic and ecological diversity, and change across the Clarkforkian-Wasatchian boundary.

Virtually all vertebrate specimens from zone  $W_{a_0}$  are light in color, which is itself a valuable local biostratigraphic guide to the  $W_{a_0}$  fauna. Dark brown or black teeth at localities SC-51 and SC-182 (the greater part of the collection in each case) are, respectively,  $Cf_3$  and  $W_{a_1}$  in age. Dark specimens from SC-51 and SC-182 are not included

in the following analysis. Similarly, a small number of dark brown or black teeth from localities SC-67, SC-308, and SC-351 are regarded as contaminants from an overlying or underlying interval, and these too are omitted from the analysis. *Haplomylus speirianus* is the only taxon represented by a dark brown or black tooth that is not otherwise identified in the fauna (it is represented by a single isolated upper molar, part of UM 83876m, from SC-351).

Tooth measurements employed here are standard mesio-distal length (L) and buccolingual width (W). Mandibular depth was measured on the buccal side of the dentary beneath  $M_1$ . All measurements, unless otherwise noted, are in millimeters. Classification of gastropods generally follows Hubendick (1978), Solem (1978), and Burch (1982). Classification of lower vertebrates follows Carroll (1987).

Specimens collected by early expeditions are in the American Museum of Natural History, and the Princeton University collection (now at Yale University). Specimens collected in recent years, most of those available, are at the University of Michigan. University of Michigan specimen numbers followed by "m" are miscellaneous lots of seeds, snails, bones, and/or teeth not individually catalogued. These miscellaneous lots usually include a number of different taxa.

#### Institutional abbreviations

AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London
UM	University of Michigan Museum of Paleontology, Ann Arbor
YPM-PU	Princeton University collection, Yale University, Peabody Museum of Natural History, New Haven

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## II LITHOLOGY AND LOCALITIES

The earliest Wasatchian  $W_a_0$  fauna described in this report comes from a distinctively colored, deep red and bright orange mudstone sequence that lies within the Clarkforkian-Wasatchian boundary sandstone where this sandstone is exposed. In other areas there is little or no sandstone associated with the boundary unit (hence the general term "boundary unit" is often more appropriate than "boundary sandstone). Sandstone is the dominant lithology in the Clarks Fork Basin where the boundary unit was first recognized and studied. However, even here, distinct lower and upper sheet sandstones, separated by mudstones, can often be recognized (Figures 2 and 7).

At locality SC-67 (Figure 1), red mudstones predominate and the lower and upper parts of the boundary sandstone are thin or absent (Figure 4). The stratigraphic section at SC-67 includes a total of about 37 m of sediment of  $W_a_0$  age, with red beds predominating (Figures 4-6). Calcium carbonate nodules are abundant at SC-67, weathering out of mudstones of all colors. Examination of the sediment on a fresh surface indicates that much of it is deep red in color with gray mottles and gray halos around root traces, burrows, and concentrations of bone.

Detailed stratigraphic sections are not available over the whole study area, but on a regional scale it appears that the Clarkforkian-Wasatchian boundary unit yielding the  $W_a_0$  fauna is thickest (ca. 37 m) at locality SC-67 at the southern end of Polecat Bench, where mudstones and siltstones are the predominant lithologies of the unit. Sandstones are best developed in the area to the north and west of SC-67, between SC-67 and SC-345. East of SC-67 and west of SC-345 the boundary unit thins and sandstones disappear. Thus the area between SC-67 and SC-345 is likely to represent the depocenter of the Clarks Fork Basin during the Clarkforkian-Wasatchian transition. At locality FG-61 in Foster Gulch, 40 km southeast of SC-67, and at locality BR-2 near Worland, 110 km to the southeast of SC-67, the boundary unit is a deep red mudstone with little or no associated sandstone. At localities MP-38 and MP-40, 20 km south of SC-67, and at locality HG-3, 70 km south of SC-67, the boundary unit is bright orange in color with minor associated sandstone.

The Clarkforkian-Wasatchian boundary unit is distinctive by comparison with underlying and overlying intervals in the Clarks Fork and Bighorn basins. In some areas it is a complex, extensively reworked sheet sandstone and in other areas it is a sequence of mature paleosols with deep

red and purple B horizons, numerous calcium carbonate nodules, and prominent and abundant root mottling. The unit appears to represent unusually slow sediment accumulation and a long period of subaerial exposure (Kraus, 1979, 1980, 1985, 1987).

Earliest Wasatchian paleosols conform to Stage 4 in the Bown (1985) and Bown and Kraus (1987) paleosol maturation sequence for the Willwood Formation. Stage 4 paleosols normally form on "distal" (high) floodplains (Bown and Kraus, 1987). Less mature paleosols (Stages 1-3) representing "proximal" (low) floodplain environments predominate in underlying Clarkforkian and overlying Wasatchian strata of the Clarks Fork Basin.

### List of Localities

The distribution of earliest Wasatchian  $W_a_0$  localities in the Clarks Fork and Bighorn basins is shown in Figure 1. Each locality is described briefly below. All are in the Willwood Formation. Localities on the east side of the Bighorn Basin lie at the base of the Willwood, at the Fort Union-Willwood formational boundary. The most important locality is SC-67 at the southern end of Polecat Bench, and it receives the most extensive description. Topographic quadrangles are all U. S. Geological Survey 7.5 minute series unless otherwise noted.

#### *Bighorn River area near Worland*

**BR-2:** Horseshoe-shaped exposure of lowest red and orange mudstones in SE  $\frac{1}{4}$ , NE  $\frac{1}{4}$ , Section 11, Township 48 North, Range 92 West, Washakie County, Wyoming (McDermotts Butte Quadrangle). This locality is at the contact between the Willwood and Fort Union (= Polecat Bench) formations on the divide between the Bighorn River and Sand Creek, north and east of the town of Worland. It is on the northern edge of the Sand Creek-No Water Creek area, beyond any Willwood exposures studied by Bown (1979).

#### *Foster Gulch area between Lovell and Emblem*

**FG-61:** Exposure of bright red and purple mudstones, the lowest exposure of red in this area, in the NW  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , Section 28, Township 54 North, Range 96 West, Big Horn County, Wyoming (Jack Horner Reservoir Quadrangle). Viewed from the air, the red and purple beds

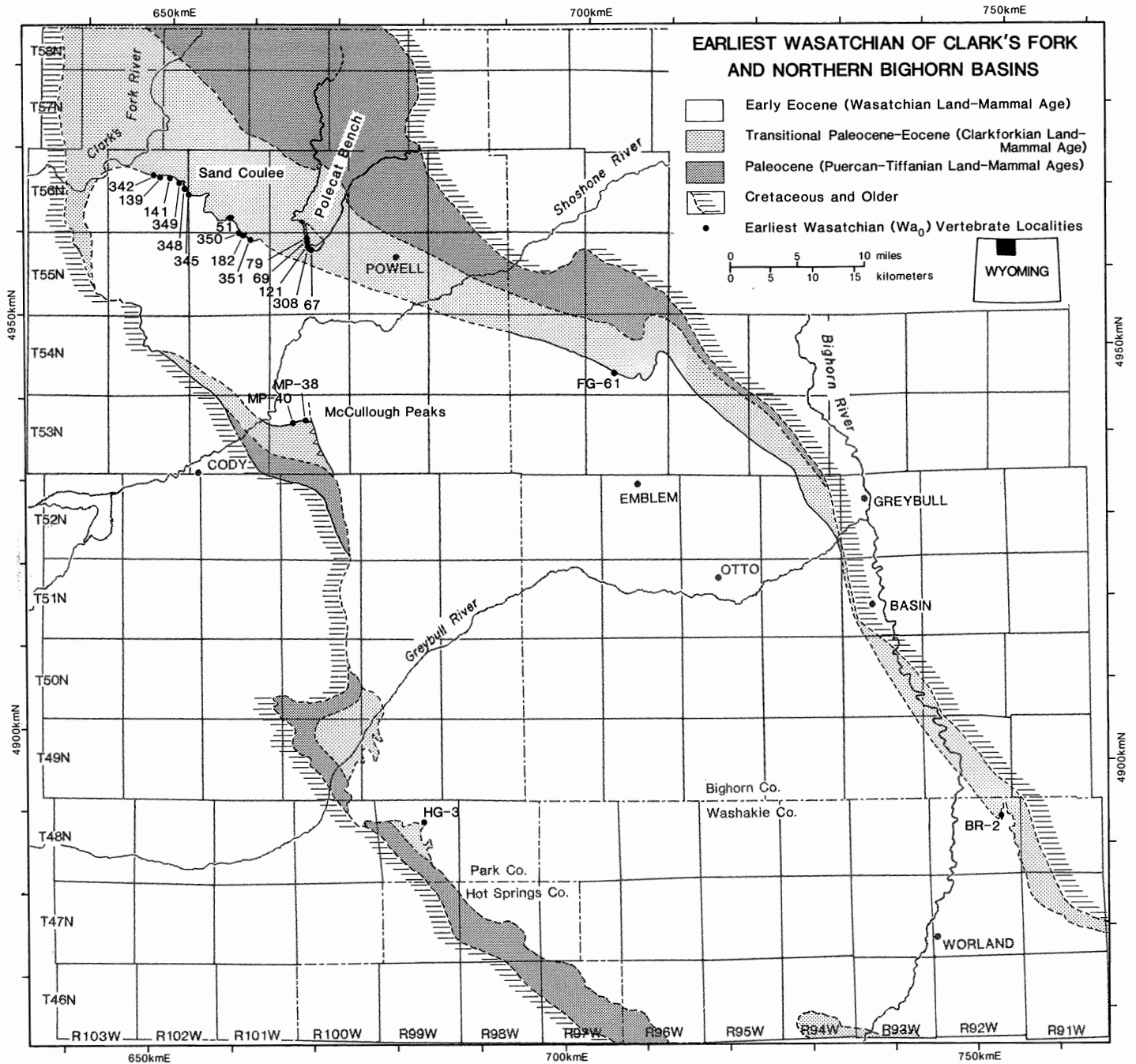


Figure 1. Distribution of earliest Wasatchian localities yielding a zone  $Wa_0$  mammalian fauna in the Bighorn and Clarks Fork basins of northwestern Wyoming. Most localities are at the southern tip of Polecat Bench or in Sand Coulee, but  $Wa_0$  faunas have also been found along the Bighorn River northeast of the town of Worland (locality BR-2), in Foster Gulch (FG-61), in the McCullough Peaks (MP-38 and MP-40), and southeast of the town of Cody (Hole-in-the-Ground locality HG-3, southeast of the town of Meeteetse).  $Wa_0$  faunas all occur in a narrow interval of distinctive deeply-weathered paleosols that forms a time line surrounding the Bighorn and Clarks Fork structural basins.

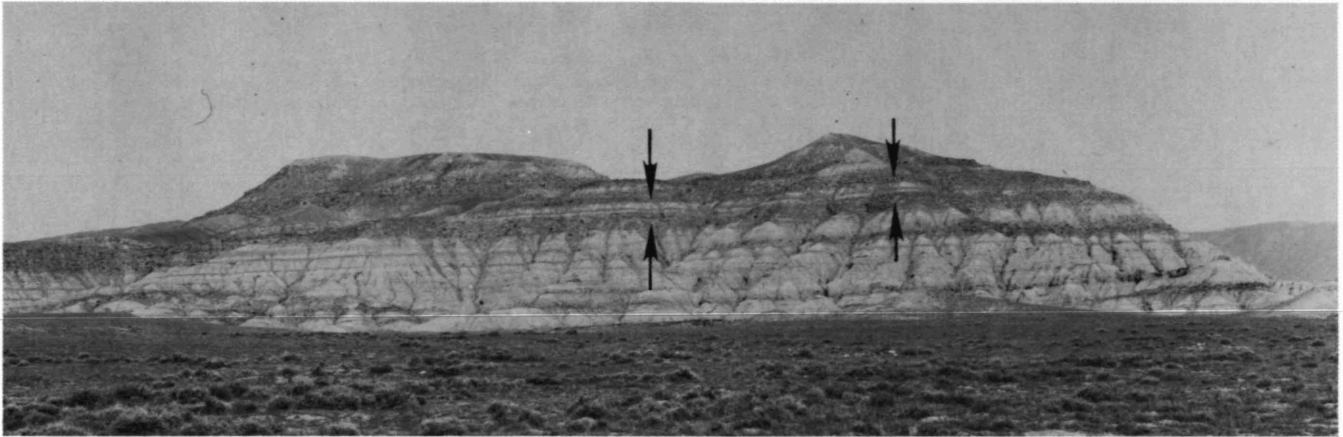


Figure 2. Clarkforkian-Wasatchian boundary sandstone cutting the middle of Saddle Mountain (Section 20, T56N, R101W) in the Sand Coulee area of the Clarks Fork Basin, northwestern Wyoming. View is to the northwest. Lower arrows identify lower part of boundary sandstone, and upper arrows identify upper part. A mudstone unit with a single bright red bed separates lower and upper parts of the boundary sandstone. Kraus (1979) gives the thickness of the lower sandstone unit here as 8 m, the thickness of the intervening mudstone unit as 2 m, and the thickness of the upper sandstone unit as 6 m.



Figure 3. Southwesterly dipping land surface formed by the Clarkforkian-Wasatchian boundary sandstone (Sections 28 and 29, T56N, R101W) in the Sand Coulee area of the Clarks Fork Basin, northwestern Wyoming. View is along strike toward the southeast. Dashed line (dotted in foreground) marks the upper limit of Clarkforkian strata. M. Kraus found a specimen of *Copecion davisi*, a species diagnostic of zone  $Wa_0$ , at locality SC-51 just over the far edge of this dip slope (arrow) in the course of thesis work on the boundary sandstone. Locality SC-27 at the base of escarpment in the upper right corner of photograph lies just above the boundary sandstone and yields a mammalian fauna of zone  $Wa_1$ .

exposed at FG-61 form a conspicuous broad red band across the surface of the earth. This red band, the base of the Willwood Formation, can be traced some 10 km to the northwest and about 20 km curving to the northeast and then southeast as shown in Figure 1. Much of this area is flat and grass covered. FG-61 is the only locality in the Foster Gulch area providing sufficient evidence to date the conspicuous band of lowest red exposures as  $Wa_0$  in age. One other area in the NE  $\frac{1}{4}$ , SE  $\frac{1}{4}$ , Section 33, Township 53 North, Range 94 West, Big

Horn County, Wyoming (Sheep Canyon Quadrangle) yielded a small concentration of *Lepisosteus* scales.

#### *Hole-in-the-Ground near Meeteetse*

**HG-3:** Exposure of bright red and orange mudstones and white sandstone in south center of SW  $\frac{1}{4}$ , Section 10, Township 48 North, Range 99 West, Park County, Wyoming (Wilson Spring Quadrangle). *Ectocion parvus* teeth came from steep-sided internally drained chimneys in

upper part of exposure. Locality is overlain by a coarse quartzite gravel conglomerate of late Wasatchian age (Lithosome F of Kraus, 1984), indicating that sediment representing much of early and all of middle Wasatchian time is missing here.

*McCullough Peaks area between Powell and Cody*

**MP-38:** Steeply dipping bright orange exposures south of Rough Gulch just east of the center of NE  $\frac{1}{4}$ , Section 16, Township 53 North, Range 100 West, Park County, Wyoming (Corbett Dam Quadrangle). Beds strike with a bearing of  $100^\circ$  and dip  $26^\circ$  NE.

**MP-40:** Steeply dipping bright orange exposures north of Rough Gulch in the SW  $\frac{1}{4}$ , NE  $\frac{1}{4}$ , Section 17, Township 53 North, Range 100 West, Park County, Wyoming (Corbett Dam Quadrangle). Beds strike with a bearing of  $90^\circ$  and dip  $21^\circ$  N.

*Sand Coulee area west and north of Powell*

**SC-51:** Head of valley in center of NW  $\frac{1}{4}$ , Section 34, Township 56 North, Range 101 West, Park County, Wyoming (Clark 15' Quadrangle). Most fossils from this locality are dark in color and latest Clarkforkian in age (Rose, 1981, p. 15), but one specimen, UM 69933, is light in color and represents a  $Wa_0$  species. This specimen was collected by M. J. Kraus in the course of her work on the Clarkforkian-Wasatchian boundary sandstone, and it was found in sandstone overlying the main locality.

**SC-67:** Good exposure of sharply weathering red and purple mudstones and white sandstones at the south end of Polecat Bench (Fig. 4), in the southwestern part of the NW  $\frac{1}{4}$ , NE  $\frac{1}{4}$ , Section 10, Township 55 North, Range 100 West, Park County, Wyoming (Elk Basin SW Quadrangle). Strike of beds here is  $303^\circ$  and dip is about  $1^\circ$  SW. This is the largest and by far the richest  $Wa_0$  locality. 255 out of a total of 334 earliest Wasatchian mammalian specimens known to date come from this locality. The fossiliferous interval is in a complex of red and gray mudstones about 15–20 m thick, with a lower purple bed near the base and several bright red beds near the top (see discussion of stratigraphy and sedimentation below, and stratigraphic section in Fig. 6). Most fossils were found on the surface, weathering out of red and gray mudstones along with abundant calcium carbonate soil nodules. Some specimens were also found weathering out of white sandstones (these sandstones appear white on weathered surfaces, but they are actually light gray or greenish gray when freshly broken). Screen washing of approximately one ton of a white sandstone (from a site shown in Fig. 5) yielded a few teeth of *Ectypodus* and *Arctodontomys*, taxa not otherwise known from the locality. Good sites for screen washing remain to be found. The lower part of the Clarkforkian-Wasatchian boundary sandstone is only about 1 m thick where it is

exposed along the eastern edge of the locality. Red beds in the upper part of the locality are generally too steep to be explored, and these are locally cut by thick channel sandstones (the upper part of the Clarkforkian-Wasatchian boundary sandstone at the east end of the locality, and also to the west of the locality).

**SC-69:** Exposure of variegated red beds at the southern end of Polecat Bench, in the SW  $\frac{1}{4}$ , SW  $\frac{1}{4}$  Section 3, Township 55 N, Range 100W, Park County, Wyoming (Elk Basin SW Quadrangle). Beds exposed here, including lower purple bed, can be traced laterally through localities SC-121 and SC-308 to locality SC-67. Minor faulting in the vicinity of locality SC-308 causes beds to be downdropped to the east, but they can still be traced continuously from SC-69 to SC-67. Apart from SC-67, this is the most productive basal Wasatchian locality, having yielded 28 specimens.

**SC-79:** Isolated west-facing horseshoe of red beds on the west side of Polecat Bench, in the NW  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , Section 3, Township 55 North, Range 100 West, Park County, Wyoming (Elk Basin SW Quadrangle).

**SC-121:** Red beds at the southern end of Polecat Bench, in the NW  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , Section 10, Township 55 North, Range 100 West, Park County, Wyoming (Elk Basin SW Quadrangle). SC-121 is between upper and lower parts of the Clarkforkian-Wasatchian boundary sandstone (Fig. 7). This is the third-most productive basal Wasatchian locality (after SC-67 and SC-69), yielding 23 specimens.

**SC-139:** Low isolated ridges of red beds near Little Sand Coulee, in the NW  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , Section 14, Township 56 North, Range 102 West, Park County, Wyoming (Clark 15' Quadrangle). The Clarkforkian-Wasatchian boundary sandstone includes upper and lower parts, with a prominent unit of red mudstones in between, throughout much of the Clarks Fork Basin. However, in the Little Sand Coulee area, these upper and lower sandstones often pass into thin beds that do not form prominent outcrops. Intervening red beds persist, and these can be traced across the Little Sand Coulee drainage basin to Chapman Bench on the west. SC-139 and SC-141 are in these red bed units.

**SC-141:** Isolated exposure of bright red beds in Little Sand Coulee drainage, in the SW  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , Section 13, Township 56 North, Range 102 West, Park County, Wyoming (Clark 15' Quadrangle). This locality is just north of a stock tank with the quarter-corner marker 14 + 13 at the south end of the dam. The lower part of the locality consists of orange and gray mudstones yielding black bones and teeth, including a partial skull of *Phenacodus*, that may be latest Clarkforkian in age. Scattered small *Gryphaea* are found on the surface here (included in UM 83883m), reworked from Mesozoic marine strata exposed during uplift of Beartooth Range 15 km to west.

**SC-182:** Early Wasatchian locality in the head of Big Sand Coulee, in the SW  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , Section 2, Township 55



Figure 4. Earliest Wasatchian locality SC-67 at the southern end of Polecat Bench, northwestern Wyoming. View is to the northeast, with the top of Polecat Bench, a Quaternary river terrace, in the background.  $W_0$  fauna comes from carbonate-nodule covered slopes in center and lower left of photograph, and in the valleys behind collectors (arrow). Photograph by George Junne.

North, Range 101 West, Park County, Wyoming (Elk Basin SW Quadrangle). Most fossils from this locality are dark in color and come from zone  $W_{a1}$ ; however one specimen of *Ectocion parvus* is light in color, suggesting that it came from the base of the Wasatchian exposed here.

**SC-308:** Exposure of red beds at south end of Polecat Bench, in SE  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , Section 10, Township 55 North, Range 100 West, Park County, Wyoming (Elk Basin SW Quadrangle). This locality lies between SC-67 and SC-121 at the same stratigraphic level.

**SC-342:** Exposure of white sandstone and mudstone, a thick red bed, and orange and gray mudstones just east of Little Sand Coulee, in the SE  $\frac{1}{4}$ , Section 10, Township 56 North, Range 102 West, Park County, Wyoming (Clark 15' Quadrangle). Underlying Clarkforkian-Wasatchian boundary sandstone separates this locality

from SC-138 to the north, yielding a Clarkforkian fauna. Thin overlying sandstone separates this locality from SC-89 across Little Sand Coulee to the southwest, which yields a  $W_{a1}$  fauna. Fossils here were found on the surface of the thick red bed.

**SC-345:** Locality at head of valley on Sand Coulee divide, just east of the center of Section 13, in SE  $\frac{1}{4}$ , Section 13, Township 56 North, Range 102 West, Park County, Wyoming (Clark 15' Quadrangle). *Ectocion parvus* and gar scales came from bright double red beds that run through the locality.

**SC-348:** East-facing exposures just above the level of SC-345, on Sand Coulee divide just east of the center of Section 13, in NE  $\frac{1}{4}$ , Section 13, Township 56 North, Range 102 West, Park County, Wyoming (Clark 15' Quadrangle). Locality includes red beds and a prominent purple bed. Most fossils, including *Pachyaena* and *Mia-*



Figure 5. Principal collecting interval of earliest Wasatchian locality SC-67 at the southern end of Polecat Bench, northwestern Wyoming. View is east, with the top of Polecat Bench up-slope to the left. Upper arrows point to part of the Clarkforkian-Wasatchian boundary sandstone overlying the locality. Arrow labelled "W" points to wash site in light gray or green sandstone. This sandstone, which weathers white, has yielded many surface finds as well. Holotype of *Cantius torresi* was found on the near slope of the hill at the point labelled "C." Ridge in right foreground has yielded many small specimens found on the surface among abundant carbonate soil nodules weathering out of red and gray mudstones. Town of Powell, Wyoming, is labelled "P" on the plain in the distance.

*cis* came from white sand exposed on a ridge above the purple bed.

**SC-349:** West-facing exposures of red beds at head of valley below SC-142 on Sand Coulee divide, in the SE  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , Section 13, Township 56 North, Range 102 West, Park County, Wyoming (Clark 15' Quadrangle). Locality has a prominent red bed through the middle. This locality is at the same level as SC-345, but overlying beds here are drab and not red and purple like those at SC-348.

**SC-350:** North-facing red beds at the head of Big Sand Coulee, in the NE  $\frac{1}{4}$ , NE  $\frac{1}{4}$ , Section 3, Township 55 North, Range 101 West, Park County, Wyoming (Elk Basin SW Quadrangle). Scattered small *Gryphaea* are found on the surface here (included in UM 83821m), as they are at SC-141.

**SC-351:** Steep red beds on both sides of a north-facing valley, in the east center of SE  $\frac{1}{4}$ , Section 2, Township 55 North, Range 101 West, Park County, Wyoming (Elk Basin SW Quadrangle). *Azygonyx* came from the slope high on the east side of the valley, and several other specimens came from a point of exposures on the west side of the valley.



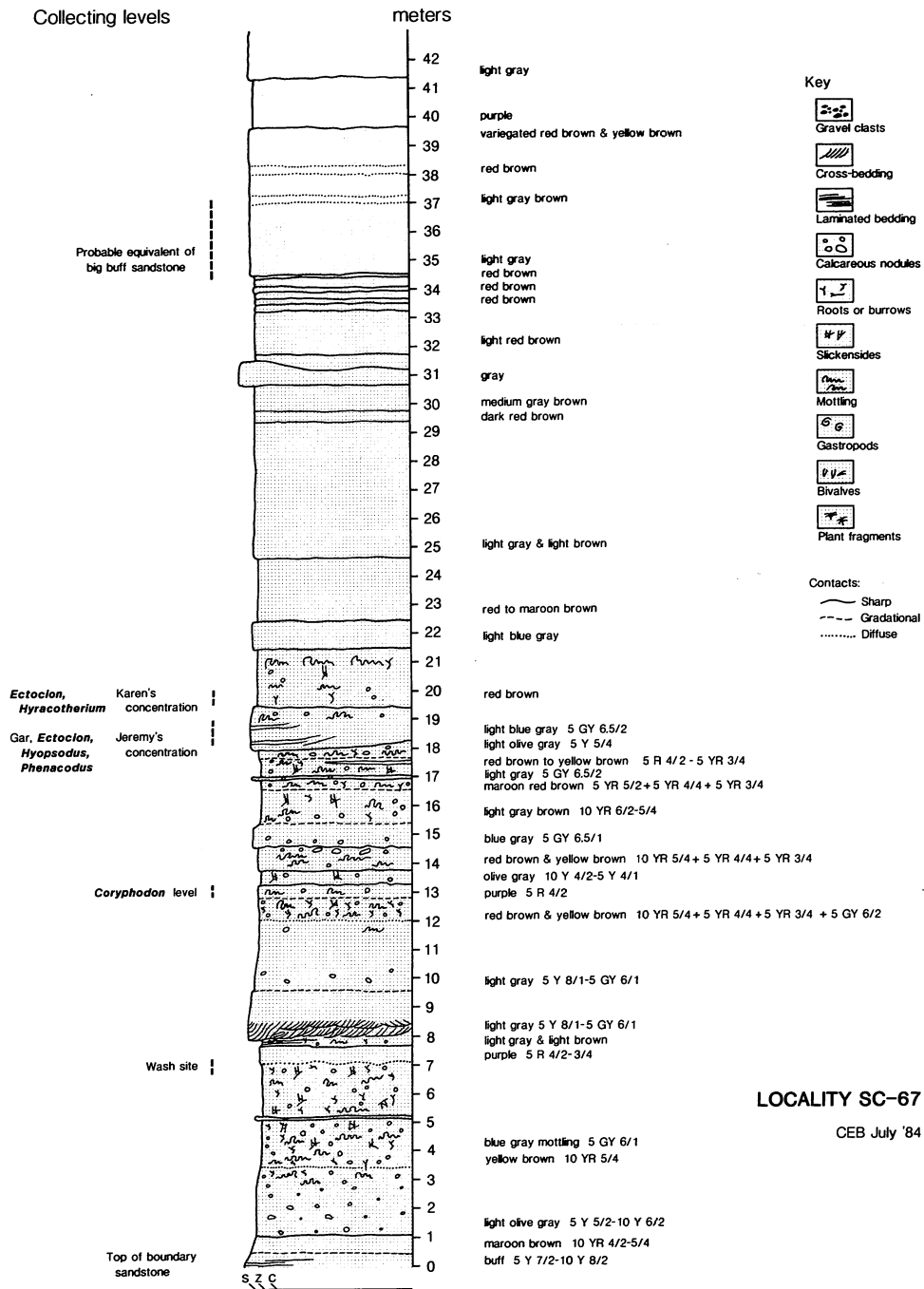


Figure 6. Stratigraphic section through locality SC-67 at the southern end of Polecat Bench, northwestern Wyoming. Section is measured from the top of the lower part of the boundary sandstone, which is itself less than 1 m thick here. Stratigraphic units project to the left in proportion to modal grain size; scale is given at bottom of diagram: S = sand, Z = silt, and C = clay. Virtually all fossils collected to date come from the lower 20 m of section (shown here in detail). An additional 15 m, to level of "big buff sandstone" (probable equivalent of upper boundary sandstone), is exposed on inaccessibly steep slopes. Jeremy's concentration refers to fossils found in 1984 by J. Hooker. Karen's concentration refers to fossils found in 1984 by K. Klitz. Stratigraphic section measured by Dr. Catherine Badgley.



Figure 7. Earliest Wasatchian locality SC-121 at the southern end of Polecat Bench, northwestern Wyoming. View is to the north, with the top of Polecat Bench in the right background. Lower arrows identify continuous sandstone that is the lower part of the Clarkforkian-Wasatchian boundary sandstone. Upper arrows identify upper part of Clarkforkian-Wasatchian boundary sandstone, which is less continuous here.  $Wa_0$  fauna is found in deeply weathered red and orange mudstones between these two sandstone units. Kraus (1987, fig. 6B) describes these intervening mudstones and gives their thickness here as ca. 18 m. Locality SC-308 is at the right edge of photograph, and locality SC-67 is at the same level 0.5 km farther to the right (east).

### III SYSTEMATIC PALEONTOLOGY

Fossils from Wasatchian zone  $W_{a_0}$  include stony endocarps of the elm-related tree *Celtis*, aquatic and terrestrial snails, fish, reptiles, birds, and forty-one species of mammals. A complete faunal list is given in Table 1.

Kingdom PLANTAE  
Division PTEROPSIDA  
Class ANGIOSPERMAE  
Subclass DICOTYLEDONEAE  
Order URTICALES  
Family ULMACEAE

*Celtis phenacodorum* (Cockerell, 1914)

*Referred specimens.* Locality HG-3: UM 92424m. Locality SC-67: UM 79890m, 83623m, 86003m, 87354m, and 87859m. Locality SC-69: UM 83825m and 86137m.

*Description.* *Celtis* endocarps from  $W_{a_0}$  localities are relatively small, averaging 5.0 mm in height, 4.1 mm in length across the meridional suture, and 3.8 mm in width across the main longitudinal crest of each hemisphere (measurements are maximum diameters, measured perpendicular to each other). A measure of volume of 19  $W_{a_0}$  endocarps is shown in Figure 8, illustrating both their variability in size and their small size relative to latest Clarkforkian endocarps.

*Discussion.* Stony endocarps of *Celtis* have long been known from sediments of Wasatchian age in the Clarks Fork Basin. Cockerell (1914) described one of these as the new species *Tithymalus phenacodorum*. Cockerell's specimen measured 4.75 mm in "length" (here called height) and 4.25 mm in "breadth" (corresponding to what is here called length or width, which are not very different in any case). The type locality of Cockerell's species—"five miles southeast of the mouth of Pat O'Hara Creek, Clarks Fork Basin, Wyoming"—is late early or early middle Wasatchian in age. Berry (1928) was the first to recognize that this species belongs in the genus *Celtis*. In recent years, *Celtis* endocarps have been collected from two  $W_{a_0}$  localities in the Clarks Fork Basin (SC-67 and SC-69) and from one  $W_{a_0}$  locality in the western Bighorn Basin (HG-3), demonstrating that their stratigraphic range extends to the base of the Wasatchian here.

Rose (1981, p. 138) stated that *Celtis* is a useful indicator of post-Clarkforkian beds in the Bighorn and Clarks Fork basins. Stony endocarps of *Celtis* are abundant in

Wasatchian strata, and the few endocarps of *Celtis* collected from latest Clarkforkian localities in the Clarks Fork Basin (e.g., from SC-10 and SC-343) have usually been isolated surface finds where there was some possibility that the endocarps washed down from a higher stratigraphic level. However, in recent years, endocarps of *Celtis* have been found in several latest Clarkforkian localities where there is no possibility of contamination from overlying sediments. The largest sample of these, UM 83742, is from orange and red flats in the SE 1/4, SW 1/4, Section 11, T 56 N, R 102 W, located just north of SC-139 in the Clarks Fork Basin. SC-139, with a  $W_{a_0}$  mammalian fauna, overlies the *Celtis* locality stratigraphically. *Celtis* endocarps are not known before the very latest Clarkforkian but, in light of new evidence, these can no longer be considered a wholly reliable indicator of the beginning of Wasatchian time.

*Celtis* endocarps from north of SC-139 are relatively large, averaging 6.0 mm in height, 4.6 mm in length, and 4.3 mm in width. The volumes of earliest Wasatchian and latest Clarkforkian *Celtis* endocarps are compared in Figure 8. Other latest Clarkforkian endocarps of *Celtis* are from localities HG-2 and MP-71.

Arnold (1947, p. 348) notes that Tertiary *Celtis* are often found in association with remains of grasses and grazing mammals, indicating that members of the genus have long been able to thrive where rainfall (or ground water) was below the optimum for many forest trees. *Celtis* endocarps are commonly preserved in calcium-rich environments, which may reflect favorable conditions for growth as well as preservation (Gingerich, 1987b).

Kingdom ANIMALIA  
Phylum MOLLUSCA  
Class GASTROPODA  
Subclass PROSOBRANCHIA  
Order TAENIOGLOSSA or MESOGASTROPODA  
Family PLEUROCERIDAE

*Elimia* or *Pleurocera* sp.  
Fig. 9A

*Referred specimens.* Locality SC-67: UM 79893m, 82387m, 83637m, 86003m, and 87859m. Locality SC-69: UM 66145m and 83825m. Locality SC-121: UM 83464m and 85671m. Locality SC-308: UM 76237m. Locality SC-348: UM 83817m.

Table 1. Faunal list, number of specimens, and minimum number of individual mammals at Wa<sub>0</sub> localities in the Bighorn and Clarks Fork Basins

Taxon	Locality											
	BR-2	FG-61	HG-3	MP-38	MP-40	SC-51	SC-67	SC-69	SC-79	SC-121	SC-139	SC-141
<b>GASTROPODA</b>												
<i>Elimia</i> or <i>Pleurocera</i> sp.	-	-	-	-	-	-	5	2	-	2	-	-
" <i>Hydrobia</i> " sp.	-	-	-	-	-	-	-	1	-	-	-	-
Cf. <i>Gyraulus</i> sp.	-	-	-	-	-	-	-	1	-	-	-	-
<i>Holospira</i> sp.	-	-	-	-	-	-	1	-	-	-	1	-
<b>OSTEICHTHYES</b>												
<i>Lepisosteus</i> sp.	1	-	-	1	1	-	24	3	1	4	2	-
<i>Amia</i> sp.	-	-	-	-	-	-	1	-	-	-	-	-
<b>REPTILIA</b>												
Cf. <i>Plastomenus</i> sp.	-	-	-	-	-	-	4	-	-	-	-	-
<i>Echmatemys</i> sp.	-	-	-	-	-	-	2	-	-	-	-	-
Cf. <i>Proxestops</i> sp.	-	-	-	-	1	-	-	-	-	-	-	-
<i>Melanosaurus maximus</i> Gilmore	-	-	-	1	-	-	8	4	1	1	1	-
<i>Allognathosuchus</i> sp.	-	-	-	-	-	-	1	-	-	-	-	-
<i>Leidyosuchus</i> sp.	-	-	-	-	-	-	7	-	2	-	2	-
<i>Pristichampsus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-
<b>AVES</b>												
Gen. and sp. indet.	-	-	-	-	-	-	1	-	-	1	-	-
<b>MAMMALIA</b>												
<i>Ectypodus tardus</i> (Jepsen)	-	-	-	-	-	-	3/2	-	-	-	-	-
<i>Mimoperadectes labrus</i> Bown and Rose	-	-	-	-	-	-	1/1	1/1	-	-	-	-
Cf. <i>Niptomomys</i> sp.	-	-	-	-	-	-	1/1	-	-	-	-	-
<i>Arctodontomys wilsoni</i> (Szalay)	-	-	-	-	-	-	1/1	-	-	-	-	-
<i>Phenacolemur praecox</i> Matthew	-	-	-	-	-	-	1/1	-	-	-	-	-
<i>Cantius torresi</i> Gingerich	-	-	-	-	-	-	5/4	2/2	-	-	-	-
<i>Esthonyx spatularius</i> Cope	-	-	-	-	-	-	1/1	-	-	-	-	-
<i>Azygonyx gunnelli</i> n. gen. and sp.	-	-	-	-	-	-	5/1	-	-	-	-	-
<i>Azygonyx</i> sp.	-	-	-	-	-	-	1/1	-	-	-	-	-
<i>Coryphodon</i> sp.	-	1/1	-	-	-	-	10/2	-	-	-	1/1	-
<i>Ectoganus bighornensis</i> Schoch	-	-	1/1	-	-	-	10/2	-	-	-	-	-
<i>Dipsalidictis platypus</i> Matthew	-	-	-	-	-	-	6/3	-	-	-	-	1/1
<i>Dipsalidictis transiens</i> (Matthew)	-	-	-	-	-	-	?	-	1/1	-	-	-
<i>Palaeonictis</i> sp.	-	-	-	-	-	-	1/1	-	-	-	-	-
<i>Acarictis ryani</i> Gingerich and Deutsch	-	-	-	-	-	-	2/1	-	-	-	-	-
<i>Prototomus deimos</i> Gingerich and Deutsch	-	-	-	-	-	-	3/1	-	-	-	-	-
<i>Arfia junnei</i> n. sp.	-	-	-	-	-	-	15/3	1/1	1/1	1/1	-	-
<i>Prolimnocyon eeri</i> n. sp.	-	-	-	-	-	-	1/1	-	-	-	?	-
<i>Viverravus bowni</i> Gingerich	-	-	-	-	-	-	1/1	-	-	-	-	-
<i>Viverravus politus</i> Matthew	-	-	-	-	-	-	1/1	-	-	-	-	-
<i>Didymictis leptomytus</i> Cope	-	-	-	-	1/1	-	12/5	-	-	-	-	-
<i>Miacis winkleri</i> Gingerich	-	-	-	-	-	-	1/1	-	-	-	-	-
Cf. <i>Acritoparamys atavus</i> (Jepsen)	-	-	-	-	-	-	1/1	-	-	-	-	-
<i>Acritoparamys atwateri</i> (Loomis)	-	-	-	-	-	-	6/3	-	-	-	-	-
<i>Paramys taurus</i> Wood	-	-	-	-	-	-	7/3	-	-	-	1/1	-
<i>Thryptacodon barae</i> n. sp.	-	-	-	1/1	-	-	-	-	-	1/1	-	-
<i>Chriacus badgleyi</i> n. sp.	-	-	-	-	-	-	2/1	-	2/2	2/1	-	-
<i>Princetonia yalensis</i> n. gen. and sp.	-	-	-	-	-	-	1/1	-	-	-	-	-
<i>Dissacus praenuntius</i> Matthew	-	-	-	-	-	-	4/1	-	-	-	-	-
<i>Pachyaena ossifraga</i> Cope	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hypsodus loomisi</i> McKenna	-	-	-	-	-	-	31/13	2/1	3/1	2/2	-	-
<i>Ectocion parvus</i> Granger	-	-	1/1	-	-	-	57/11	1/1	-	1/1	1/1	-
<i>Ectocion osbornianus</i> (Cope)	-	-	-	-	-	-	1/1	-	-	-	-	-
<i>Phenacodus</i> cf. <i>P. intermedius</i> Granger	-	-	-	-	-	-	7/1	-	-	-	-	?
<i>Copecion davisii</i> n. gen. et sp.	1/1	-	-	-	-	1/1	26/7	4/1	4/2	-	1/1	-
<i>Meniscotherium priscum</i> Granger	-	-	-	-	-	-	?	-	-	-	-	-
<i>Diacodexis ilicis</i> n. sp.	-	-	-	-	-	-	4/2	-	-	-	-	-
<i>Hyracotherium sandrae</i> n. sp.	-	1/1	-	-	-	-	20/4	1/1	2/1	4/1	2/2	-
<i>Hyracotherium grangeri</i> Kitts	-	-	-	-	-	-	3/2	-	-	-	-	-
<i>Palaeonodon nievelti</i> n. sp.	-	-	-	-	-	-	3/2	-	-	2/2	-	-
Cf. <i>Asiabradypus</i> sp.	-	-	-	-	-	-	1/1	-	-	-	-	-
Totals for Mammalia:	1/1	2/2	2/2	1/1	1/1	1/1	255/89	12/8	13/8	13/9	6/6	1/1

Entries for Mammalia are total number of specimens/minimum number of individuals [TNS/MNI]; other entries reflect number of samples from each locality that include each species.

Table 1. Faunal list, number of specimens, and minimum number of individual mammals at Wa<sub>0</sub> localities in the Bighorn and Clarks Fork Basins (continued)

Taxon	Locality								Totals	
	SC-182	SC-308	SC-342	SC-345	SC-348	SC-349	SC-350	SC-351	TNS/MNI	% (MNI)
<b>GASTROPODA</b>										
<i>Elimia</i> or <i>Pleurocera</i> sp.	-	1	-	-	1	-	-	-	11	-
" <i>Hydrobia</i> " sp.	-	-	-	-	-	-	-	-	1	-
Cf. <i>Gyraulus</i> sp.	-	-	-	-	-	-	-	-	1	-
<i>Holospira</i> sp.	-	-	-	2	-	1	-	-	5	-
<b>OSTEICHTHYES</b>										
<i>Lepisosteus</i> sp.	-	1	-	1	1	1	1	2	44	-
<i>Amia</i> sp.	-	-	1	-	-	-	-	-	2	-
<b>REPTILIA</b>										
Cf. <i>Plastomenus</i> sp.	-	-	-	-	-	-	1	-	5	-
<i>Echmatemys</i> sp.	-	-	-	-	-	-	-	-	2	-
Cf. <i>Proxestops</i> sp.	-	-	-	-	-	-	-	-	1	-
<i>Melanosaurus maximus</i> Gilmore	-	-	1	-	1	1	1	2	22	-
<i>Allognathosuchus</i> sp.	-	-	1	-	-	1	-	-	3	-
<i>Leidyosuchus</i> sp.	-	-	1	1	-	-	1	-	14	-
<i>Pristichampsus</i> sp.	-	-	-	-	1	-	-	-	1	-
<b>AVES</b>										
Gen. and sp. indet.	-	-	-	-	?	-	-	-	2	-
<b>MAMMALIA</b>										
<i>Ectypodus tardus</i> (Jepsen)	-	-	-	-	-	-	-	-	3/2	1.3
<i>Mimoperadectes labrus</i> Bown and Rose	-	-	-	-	-	-	-	-	2/2	1.3
Cf. <i>Niptomomys</i> sp.	-	-	-	-	-	-	-	-	1/1	0.7
<i>Arctodontomys wilsoni</i> (Szalay)	-	-	-	-	-	-	-	-	1/1	0.7
<i>Phenacolemur praecox</i> Matthew	-	-	-	-	1/1	-	-	-	2/2	1.3
<i>Cantius torresi</i> Gingerich	-	-	-	-	-	-	-	-	7/6	4.0
<i>Esthonyx spatularius</i> Cope	-	-	-	-	-	-	-	-	1/1	0.7
<i>Azygonyx gunnelli</i> n. gen. and sp.	-	?	-	-	-	-	-	1/1	6/2	1.3
<i>Azygonyx</i> sp.	-	-	-	-	-	-	-	-	1/1	0.7
<i>Coryphodon</i> sp.	-	-	-	-	-	-	-	-	11/4	2.6
<i>Ectoganus bighornensis</i> Schoch	-	-	-	-	-	-	-	-	11/3	2.0
<i>Dipsalidictis platypus</i> Matthew	-	-	-	-	-	-	-	-	7/4	2.6
<i>Dipsalidictis transiens</i> (Matthew)	-	-	-	-	-	-	-	-	1/1	0.7
<i>Palaeonictis</i> sp.	-	-	-	-	-	-	-	-	1/1	0.7
<i>Acarictis ryani</i> Gingerich and Deutsch	-	-	-	-	-	-	-	-	2/1	0.7
<i>Prototomus deimos</i> Gingerich and Deutsch	-	-	-	-	-	1/1	-	-	4/2	1.3
<i>Arfia junnei</i> n. sp.	-	1/1	-	-	1/1	-	-	-	20/8	5.3
<i>Prolimnocyon eerius</i> n. sp.	-	-	-	-	-	-	-	-	1/1	0.7
<i>Viverravus boweni</i> Gingerich	-	-	-	-	-	-	-	-	1/1	0.7
<i>Viverravus polius</i> Matthew	-	-	-	-	-	-	-	-	1/1	0.7
<i>Didymictis leptomytus</i> Cope	-	-	-	-	-	-	-	-	13/6	4.0
<i>Miacis winkleri</i> Gingerich	-	-	-	-	1/1	-	1/1	-	3/3	2.0
Cf. <i>Acritoparamys atavus</i> (Jepsen)	-	-	-	-	-	-	-	-	1/1	0.7
<i>Acritoparamys atwateri</i> (Loomis)	-	1/1	-	-	-	-	-	1/1	8/5	3.3
<i>Paramys taurus</i> Wood	-	-	-	-	-	-	1/1	-	9/5	3.3
<i>Thryptacodon barae</i> n. sp.	-	-	-	-	-	-	-	-	2/2	1.3
<i>Chriacus badgleyi</i> n. sp.	-	-	?	-	-	-	-	-	6/4	2.6
<i>Princetonia yalensis</i> n. gen. and sp.	-	-	-	-	-	-	-	-	1/1	0.7
<i>Dissacus praenuntius</i> Matthew	-	-	-	-	-	-	-	-	4/1	0.7
<i>Pachyaena ossifraga</i> Cope	-	-	-	-	1/1	-	-	-	1/1	0.7
<i>Hyopsodus loomisi</i> McKenna	-	1/1	1/1	-	-	-	-	-	40/19	12.5
<i>Ectocion parvus</i> Granger	1/1	1/1	-	-	-	-	-	2/1	66/18	11.8
<i>Ectocion osbornianus</i> (Cope)	-	-	-	-	-	-	-	1/1	2/2	1.3
<i>Phenacodus</i> cf. <i>P. intermedius</i> Granger	-	-	-	-	-	-	-	-	7/1	0.7
<i>Copecion davisii</i> n. gen. et sp.	-	1/1	-	1/1	1/1	1/1	-	2/1	42/18	11.8
<i>Meniscotherium priscum</i> Granger	-	-	-	-	-	-	-	-	-	-
<i>Diacodexis ilicis</i> n. sp.	-	2/1	-	-	-	-	-	-	6/3	2.0
<i>Hyracotherium sandrae</i> n. sp.	-	-	-	-	-	-	-	-	30/10	6.6
<i>Hyracotherium grangeri</i> Kitts	-	-	-	-	-	-	-	-	3/2	1.3
<i>Palaeanodon nievelti</i> n. sp.	-	-	-	-	-	-	-	-	5/4	1.3
Cf. <i>Asiabradypus</i> sp.	-	-	-	-	-	-	-	-	1/1	0.7
Totals for Mammalia:	1/1	7/6	1/1	1/1	5/5	2/2	2/2	7/5	334/152	99.3

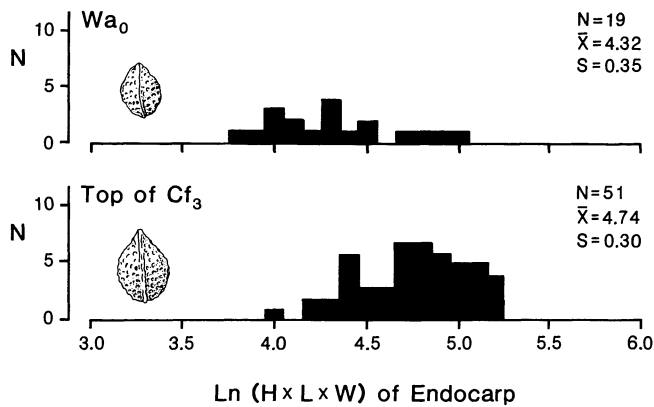


Figure 8. Distribution of sizes of stony endocarps of *Celtis phenacodorum* from the earliest Wasatchian (all specimens from zone  $Wa_0$ ) and from the latest Clarkforkian (UM 83742 from north of SC-139) of northwestern Wyoming. Measure of size plotted here is proportional to volume (apical height multiplied by meridional length multiplied by width across the main crests). Note broad distribution of sizes in both samples, and significantly smaller mean size in  $Wa_0$  sample (Student's  $t = 5.02$ , d.f. = 68,  $p < .001$ ). Inset figures of modal *Celtis* endocarps from each interval drawn to same scale for comparison.

**Description.** The  $Wa_0$  sample of *Elimia/Pleurocera* consists of some 25 specimens, many of which are internal molds without shell material. The best preserved, UM 76237m from SC-308, are broken, but these retain excellent shell material. These pleurocerids have a high-spired, dextrally coiled shell with many whorls. Shells measure 27–30 mm in height and 9–11 mm in width. The shell wall is thick and solid. Whorls are axially plicate, spirally striate, and faintly tuberculate. Viewed in polished section, the columella appears slightly twisted (Fig. 9A), but this characteristic alone does not distinguish *Elimia* from *Pleurocera*. Specimens with complete apertures will be required to determine which genus is represented.

**Discussion.** Burch (1982, p. 211) regards *Elimia* H. & A. Adams 1854 as a valid senior synonym of the much-used genus *Goniobasis* Lea 1862. *Elimia* and *Pleurocera* are aquatic species, living in lakes and streams on a variety of substrates. Several specimens from SC-67 are preserved as sand-filled internal molds, suggesting that they lived in or were washed into streams of moderate energy.

#### Family HYDROBIIDAE

##### "*Hydrobia*" sp. Fig. 9B

**Referred specimen.** Locality SC-69: UM 66145m.

**Description.** The only specimen of this species from the earliest Wasatchian is a very small, dextral, high-spired shell with nine whorls. The shell measures 5.7 mm high and 1.6 mm wide. Sutures are impressed. Surface ornamentation consists of fine closely-spaced axial striae. The aperture is not preserved.

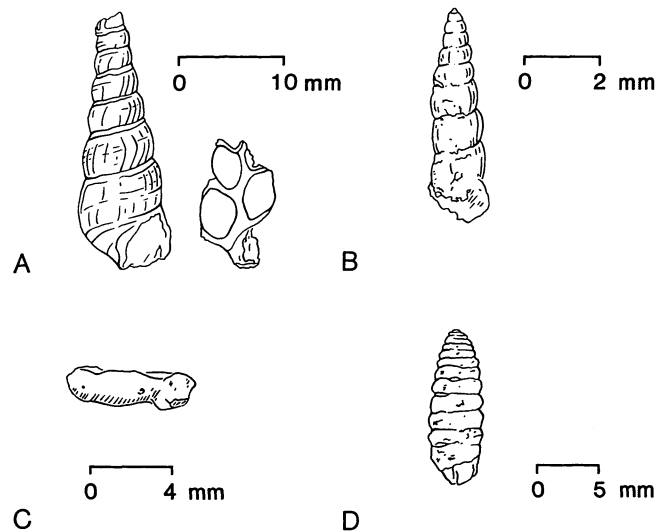


Figure 9. Freshwater and terrestrial mollusks from the earliest Wasatchian of northwestern Wyoming (all specimens from zone  $Wa_0$ ). A, aquatic pleurocerid *Elimia* or *Pleurocera* sp., UM 76237m, in lateral view; inset shows columella in polished section through axis of coiling. B, aquatic hydrobiid "*Hydrobia*" sp., UM 66145m, in lateral view. C, aquatic planorbid or ancycloplanorbid pulmonate cf. *Gyraulus* sp., UM 66145m, in lateral view. D, terrestrial urocoptid pulmonate *Holospira* sp., UM 83782m, in lateral view.

**Discussion.** This specimen resembles others referred to *Hydrobia* by La Rocque (1960); however, Burch (1982, p. 211) regards *Hydrobia* as a European genus that does not occur in North American waters. It is possible that *Hydrobia* inhabited both Europe and North America during the Eocene, but reference of North American specimens to this genus is questionable without better evidence. The name *Hydrobia* is used in quotation marks for lack of a better alternative at present. Hydrobiids are aquatic, but questionable identification precludes further environmental interpretation.

#### Subclass PULMONATA Order BASOMMATOPHORA or LIMNOPHILA Family PLANORBIDAE or ANCYCLOPLANORBIDAE

##### Cf. *Gyraulus* sp. Fig. 9C

**Referred specimen.** Locality SC-69: UM 66145m.

**Description.** The only specimen known from the earliest Wasatchian is a poorly preserved planispiral internal mold with no remaining shell material. The number of whorls and the direction of coiling cannot be ascertained. As preserved, the mold measures 1.7 mm in height and 5.8 mm in diameter.

**Discussion.** The specimen is referred to cf. *Gyraulus* sp. because this is a common early Eocene planorbid but better

material will be required to confirm the identification. Extant *Gyraulus* are found in shallow water and prefer environments with abundant vegetation.

Order STYLOMMATOPHORA  
Family UROCOPTIDAE

*Holospira* sp.  
Fig. 9D

*Referred specimens.* Locality SC-67: UM 87354m. Locality SC-139: UM 83569m. Locality SC-345: UM 83782m and 83812m. Locality SC-349: UM 83819m.

*Description.* A total of seven individuals are represented in the  $Wa_0$  collection. These are medium-sized cylindrical forms, tapering at both ends, with a large number of closely-spaced whorls. Fourteen whorls are present in the two most complete specimens. The specimen illustrated in Figure 9D is an internal mold, but other specimens retain shell material. This exhibits fine axial striae and slightly impressed sutures.

*Discussion.* These specimens are sufficiently well preserved that they can be referred with little question to the extant genus *Holospira*, a genus Pilsbry (1946, p. 111) characterized as living "always on limestone terrain, frequently in very hot and dry places." *Holospira* is the only terrestrial mollusk in the  $Wa_0$  fauna. It has not been found in the Clarks Fork Basin except at  $Wa_0$  localities, suggesting that the climate in the earliest Wasatchian may have been warmer and dryer than it was earlier in the Clarkforkian or later in the Wasatchian. Alternatively,  $Wa_0$  localities may just sample dryer and better drained paleoenvironments than those sampled in the Clarkforkian or later in the Wasatchian here. Terrestrial snails are abundant in many Clarkforkian and post- $Wa_0$  Wasatchian sites, and most of these are forms characteristic of wetter environments (e.g., Gingerich, 1987b, p. 316).

Phylum CHORDATA  
Class OSTEICHTHYES  
Order LEPISOSTEIFORMES  
Family LEPISOSTEIDAE

*Lepisosteus* sp.

*Referred specimens.* Locality BR-2: UM 87594m. Locality MP-38: UM 88160m. Locality MP-40: 88170m. Locality SC-67: UM 66140m, 66617m, 71768m, 74081m, 75423m, 79890m, 79893m, 80339m, 82387m, 83478m, 83617, 83618m, 83632, 83636m, 83637m, 83664m, 83741, 85595m, 86003m, 86233m, 86572m (large number of scales in wash concentrate), 87354m, 87859m, and 92356m. Locality SC-69: UM 83825m, 86134, and

86137m. Locality SC-79: UM 83647m. Locality SC-121: UM 66855, 66856m, 83464m, and 85671m. Locality SC139: UM 68033m and 83569m. Locality SC-308: UM 85596m. Locality SC-345: UM 83782m. Locality SC-348: UM 83817m. Locality SC-349: UM 83819m. Locality SC-350: UM 83821m. Locality SC-351: UM 83876m and 86565m.

*Description.* Most remains of *Lepisosteus* from  $Wa_0$  are isolated diamond-shaped ganoid scales, but some specimens (e.g., UM 66856m, 83464m, and 83664m) include distinctive opisthocoelous vertebrae, basioccipitals, and other cranial elements.

*Discussion.* Living *Lepisosteus* is a predatory fish inhabiting rivers and streams. *Lepisosteus* remains from  $Wa_0$  are all fragmentary, precluding specific identification. *Lepisosteus* is much more common here than it is in Clarkforkian or later Wasatchian localities in the Clarks Fork Basin. Smith et al. (1988) explain the poor representation of fish in floodplain deposits as a consequence of peak fish biomass lagging well behind peak sediment accumulation in each seasonal flood cycle. The Eocene locality studied by Smith et al., SC-213 in the early or middle Wasatchian of the Clarks Fork Basin, has a vertebrate fauna typical of most Clarkforkian and Wasatchian floodplain accumulations: *Lepisosteus* and other fish are relatively rare. One explanation for the unusual abundance of *Lepisosteus* in zone  $Wa_0$  might be that  $Wa_0$  localities sample the main and distributary channels of rivers more often than typical Clarkforkian and Wasatchian localities do. *Lepisosteus* is one of several aquatic taxa that are exceptionally well represented in earliest Wasatchian zone  $Wa_0$  (others are *Elimia* [or *Pleurocera*], *Amia*, and *Leidyosuchus*).

Order AMIIFORMES  
Family AMIIDAE

*Amia* sp.

*Referred specimens.* Locality SC-67: UM 66140m and, questionably, 92356m. Locality SC-342: UM 83574m.

*Description.* UM 66140m and 83574m are isolated amphicoelous cervical vertebrae of small *Amia*. The vertebrae measure 7.4 and 6.0 mm, respectively, in maximum diameter. UM 92356m includes a concretion full of broken bones, with one or two tooth-bearing bones that probably belong to *Amia* sp.

*Discussion.* These limited remains document the presence of a species of *Amia* in the  $Wa_0$  fauna. We can infer from the rarity of *Amia* vertebrae that this genus may have been less common than *Lepisosteus* in  $Wa_0$  localities, but it was still more common here than in most underlying Clarkforkian and overlying Wasatchian localities.

Class REPTILIA  
Subclass TESTUDINATA  
Order CHELONIA  
Family TRIONYCHIDAE

Cf. *Plastomenus* sp.

*Referred specimens.* Locality SC-67: UM 79893m, 80339m, 83618m, and 85595m. Locality SC-350: UM 83821m.

*Description.* These specimens are all fragmentary pieces of the carapace and plastron of relatively small soft-shell turtles.

*Discussion.* Trionychids are highly aquatic freshwater turtles commonly inhabiting rivers and streams. *Plastomenus* differs from *Trionyx* in being much smaller. Both are known from pre- and post-Wasatchian sediments (Hutchison, 1980).

Family EMYDIDAE

*Echmatemys* sp.  
Fig. 10

*Referred specimens.* Locality SC-67: UM 66617m and 83627.

*Description.* UM 83627 includes much of the plastron and several peripherals or pleurals from the carapace. UM 66617m includes a peripheral only. These correspond in size to a turtle of moderate size—in this case an *Echmatemys* with a carapace about 24 cm in length and 18 cm or so in width.

*Discussion.* Emydids are omnivorous pond and river turtles. *Echmatemys* is aquatic, but others are semiaquatic and even terrestrial. Hutchison (1980) states that *Echmatemys* is unknown in pre-Graybullian strata. He has since examined UM 83627 and confirmed that this is the earliest record of the genus (Hutchison, pers. comm., 1988).

CHELONIA indet.

*Referred specimens.* Locality SC-67: UM 79893m, 83636m, and 83637m. Locality SC-121: UM 83464m. Locality SC-348: UM 83817m.

*Description.* Several pieces of the carapace and plastron of indeterminate medium to large turtles are known. UM 79893m includes two phalanges of very large turtles (each phalanx measures 37 mm in length). These are similar in size to the phalanges of large *Trionyx*, but differ in shape and cannot be referred to that genus with any confidence.

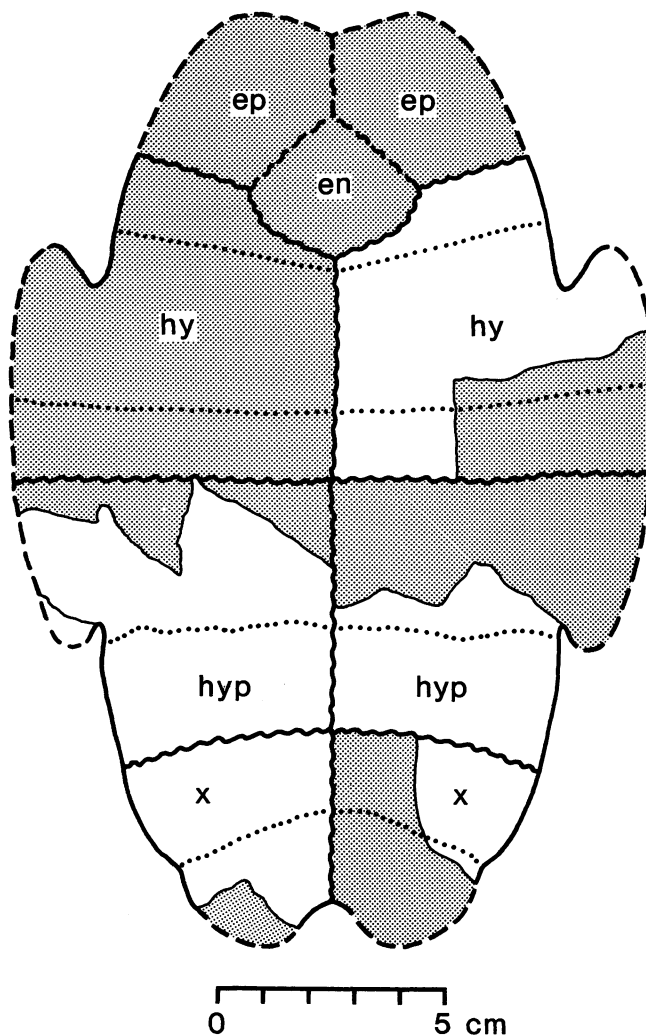


Figure 10. Reconstructed plastron of *Echmatemys* sp. from earliest Wasatchian locality SC-67, UM 83627, in ventral view. Dotted lines show impression of edges of horny scutes. Shaded elements are not preserved. Abbreviations: *en*, entoplastron; *ep*, epiplastron; *hy*, hyoplastron; *hyp*, hypoplastron; *x*, xiphiplastron.

Subclass DIAPSIDA  
Order SQUAMATA  
Suborder LACERTILIA  
Family ANGUIDAE  
Subfamily GLYPTOSAURINAE

Cf. *Proxestops* sp.

*Referred specimen.* Locality MP-40: UM 88170m.

*Description.* UM 88170m includes two osteoderms with the intermediate vermiculate-tuberculate surface sculpture characteristic of *Proxestops* (Gauthier, 1982).

*Discussion.* *Proxestops* is known from the early Paleo-



cene through early Eocene of North America (Gauthier, 1982, p. 21).

*Melanosaurus maximus* Gilmore, 1928

*Referred specimens.* Locality MP-38: UM 88160m. Locality SC-67: UM 74081m, 79890m, 82387m, 83478m, 83819m, 85595m, 86003m, 87354m, 92356m. Locality SC-69: UM 66145m, 83825m, 86136, 86137m. Locality SC-79: UM 83647m. Locality SC-121: UM 83464m. Locality SC-139: UM 68033m. Locality SC-342: UM 83574m. Locality SC-348: UM 83817m. Locality SC-350: UM 83821m. Locality SC-351: 83873 and 86565m.

*Description.* *Melanosaurus* material includes a frontal (UM 86003m), and numerous osteoderms and vertebrae. Dental remains are rare.

*Discussion.* Bartels (1983) notes that *Melanosaurus maximus* is by far the most common Clarkforkian lizard, especially in better-drained deposits of the Willwood Formation. *Melanosaurus* is also common in sediments of Wasatchian age (Sullivan, 1979).

LACERTILIA indet.

*Referred specimens.* Locality SC-67: UM 71768m, 79893m, 83623m, 86233m, and 87859m. Locality SC-308: UM 85596m.

*Description.* All of the indeterminate lacertilians in the  $W_a_0$  fauna are represented by vertebrae. Some of these may belong to the taxon described as Cf. *Proxestops* sp. above.

Subclass ARCHOSAURIFORMES

Order CROCODYLIA

Family ALLIGATORIDAE

*Allognathosuchus* sp.

*Referred specimens.* Locality SC-67: UM 83478m. Locality SC-139: UM 68033m is questionably from  $W_a_0$ . Locality SC-342: UM 87540. Locality SC-349: UM 83819m.

*Description.* UM 87540 includes dermal scutes, cranial fragments, and a small fragmentary dentary with two small postcanine teeth. These teeth have low crowns with vertically serrated enamel like those of anterior postcanines of *Allognathosuchus*. The other two specimens are collections of dermal scutes and a vertebral centrum.

*Discussion.* *Allognathosuchus* is a small, broad-snouted alligatorid that was a very common element in most Clarkforkian and Wasatchian faunas. Individuals typically were about one meter in total body length. Simpson (1930) interpreted *Allognathosuchus*, with its bulbous "molar" teeth, as a crocodylian of generalized dietary habits. *Allognathosuchus* is abundant in floodplain deposits of the preceding Clarkforkian and later Wasatchian, but it is represented by very few specimens in  $W_a_0$  localities—the only bulbous "molar" tooth of *Allognathosuchus* present in the entire  $W_a_0$  sample is a black tooth, UM 68033 from SC-

139, that is possibly a contaminant from a higher or lower level. *Lepisosteus* is an aquatic element indicating that the  $W_a_0$  fauna samples river channel taxa preferentially over the normal suite of low floodplain taxa (see discussion above). *Allognathosuchus* is a low floodplain element whose rarity indicates too that the common suite of low floodplain animals is not being sampled.

Family CROCODYLIDAE

*Leidyosuchus* sp.

*Referred specimens.* Locality SC-67: UM 77203m, 79890m, 83636m, 83638, 85595m, 87354m, and 87859m. Locality SC-79: UM 83643 and 83647m. Locality SC-139: UM 83566 and 83569m. Locality SC-342: UM 83574m. Locality SC-345: UM 83812m. Locality SC-350: UM 83821m.

*Description.* Most specimens are relatively large single teeth, dermal scutes, and/or vertebrae. UM 83566 includes long narrow left and right dentaries of a juvenile. UM 83638 is a proximal femur lacking only the distal articulation; intact this femur measured about 20 cm in length, indicating that it belonged to a crocodile 3–4 m in body length. UM 83643 includes a vertebral centrum, proximal femur, and complete astragalus of a crocodile similar in size to UM 83638.

*Discussion.* *Leidyosuchus* is the most common crocodylian in the earliest Wasatchian fauna described here. It is much larger than *Allognathosuchus*, and large individuals may have been as long as 5 m or more in total body length. *Leidyosuchus* is rare in most Clarkforkian and Wasatchian floodplain deposits, and it is considered to have been predominantly a channel and swamp-dwelling aquatic predator (Bartels, 1983).

*Pristichampsus* sp.

Fig. 11

*Referred specimen.* Locality SC-348: UM 83817m.

*Description.* UM 83817m is a single compressed recurved tooth with serrated anterior and posterior margins. The tooth measures 5.1 mm in maximum diameter at the base of the crown, 4.1 mm in least diameter at the base of the crown, and about 14.4 mm in crown height.

*Discussion.* This is the oldest record of *Pristichampsus* known anywhere, and the first from the Clarks Fork or Bighorn basins. The genus was originally described from Europe, and a single species, *P. vorax*, has been described from North America (see review by Langston, 1975). The specimen described here is too fragmentary for meaningful comparison with that species. The European ziphodont *Weigeltisuchus*, often synonymized with *Pristichampsus*, is notable in being more extensively armored than most crocodylians and in having hoof-like terminal phalanges (Kuhn, 1938). *Pristichampsus* was probably more terrestrial than most other crocodylians.

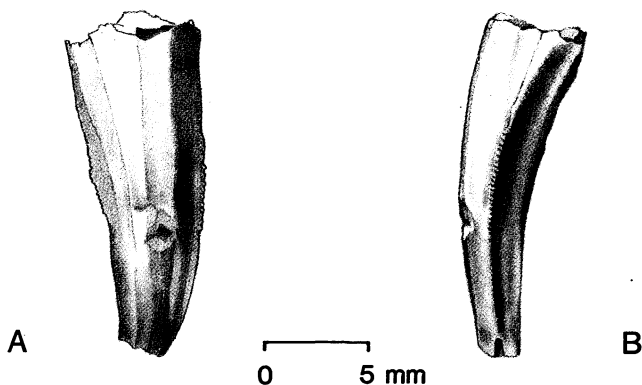


Figure 11. Isolated tooth of xiphodont crocodylian *Pristichampsus* sp., UM 83817m, from locality SC-348. A, lateral view. B, anterior view.

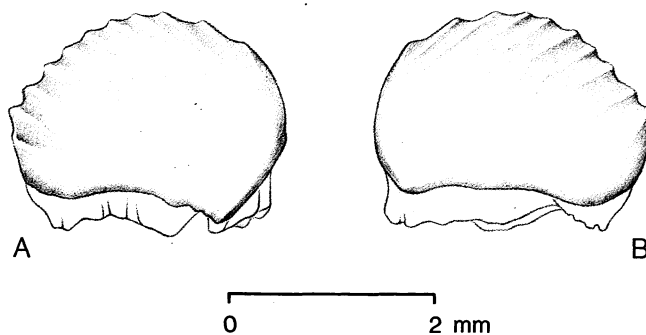


Figure 12. Premolar of *Ectypodus tardus*, UM 86572m. A and B, right P<sub>4</sub>, UM 86572m, in labial and lingual view.

CROCODYLIA indet.

*Referred specimens.* Locality SC-67: UM 82387m. Locality SC-69: UM 66145m and 83825m. Locality SC-121: UM 83464m.

*Description.* This material consists of dermal scutes and vertebral centra that may belong to either a large *Allognathosuchus* or a small *Leidyosuchus*.

Class AVES

AVES indet.

*Referred specimens.* Locality SC-67: UM 83478m. Locality SC-121: UM 85671m.

*Description.* UM 83478m is an avian cervical vertebra, and UM 85671m is the proximal part of an avian carpo-metacarpus. Neither of these is sufficiently complete for further identification. Fragmentary egg shell, presumably avian, has been found at several localities (e.g., SC-348: UM 83817m), but again this is not readily identifiable.

Class MAMMALIA

Order MULTITUBERCULATA  
Family NEOPLAGIAULACIDAE

*Ectypodus tardus* (Jepsen, 1940)  
Fig. 12

*Referred specimens.* Locality SC-67: UM 86572m (3 specimens).

*Description.* This sample, recovered by screen washing, includes the complete crown of a right P<sub>4</sub> and broken crowns of two others. The complete crown measures 2.8 mm in length and 0.9 mm in width. It has ten apical cusps and associated labial serrations.

*Discussion.* The complete crown described here matches Krause's (1982) revised diagnosis of *Ectypodus tardus* very closely. *E. tardus* does not occur in the Clarkforkian land-

mammal age (Krause, 1980), and it is known only from the Wasatchian (Krause, 1982).

Order MARSUPIALIA  
Family DIDELPHIDAE

*Mimoperadectes labrus* Bown and Rose, 1979

*Referred specimens.* Locality SC-67: UM 92347. Locality SC-69: UM 66144 (holotype).

*Description.* The new specimen is a left dentary with M<sub>3-4</sub> that adds little to Bown and Rose's (1979) original description of the holotype from Wa<sub>0</sub> locality SC-69. Measurements of Wa<sub>0</sub> *M. labrus* are summarized in Table 2.

*Discussion.* *Mimoperadectes labrus* is large for an Eocene didelphid, but it is still a small mammal. The small size and sharp teeth of *Mimoperadectes* identify it as one

Table 2. Measurements of *Mimoperadectes labrus* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
M <sup>1</sup> L	1	3.1	-	-	-
M <sup>1</sup> W	1	3.0	-	-	-
M <sup>2</sup> L	1	3.2	-	-	-
M <sup>2</sup> W	1	3.6	-	-	-
M <sup>3</sup> L	1	3.1	-	-	-
M <sup>3</sup> W	1	4.0	-	-	-
<i>Lower dentition</i>					
P <sub>4</sub> L	1	2.7	-	-	-
P <sub>4</sub> W	1	1.6	-	-	-
M <sub>1</sub> L	1	3.0	-	-	-
M <sub>1</sub> W	1	2.0	-	-	-
M <sub>2</sub> L	1	3.1	-	-	-
M <sub>2</sub> W	1	1.9	-	-	-
M <sub>3</sub> L	2	3.1 - 3.3	3.18	-	-
M <sub>3</sub> W	2	2.0 - 2.0	2.00	-	-
Mandibular depth:	1	6.6	-	-	-

Total number of specimens = 2

of the few insectivorous mammals discovered in the earliest Wasatchian to date.

#### Order PROPRIMATES

It is not possible to demonstrate a close phyletic connection between archaic plesiadapiform primates (Microsyopoidea and Plesiadapoidea) and primates of modern aspect (Tarsiioidea, Lemuroidea, Ceboidea, etc.). Archaic Microsyopoidea and Plesiadapoidea represent a much more primitive grade. The gap between Proprimates and true Primates is similar to that separating primates of prosimian grade from primates of simian or anthropoid grade. Recognition of Proprimates (including Plesiadapiformes) as a new archaic order with no living members parallels recognition of a separate archaic order Condylarthra distinct from Artiodactyla, Perissodactyla, etc.: both are likely to be paraphyletic in that they may have given rise to more advanced groups that are not classified within the same orders. The taxon Proprimates is compositionally equivalent to what I formerly called Praesimii (Gingerich, 1984a), but Proprimates is more appropriate as a name in contrasting included forms with all Primates of modern aspect (Prosimii plus Anthropoidea [or Simii]), not just Simii. Proprimates is appropriate too in that the name implies removal of the group from the order Primates. Proprimates includes Plesiadapiformes as a suborder or infraorder, with Plesiadapoidea and Microsyopoidea as superfamilies, and it may include Tupaiiformes and other quasi-primates as well (e.g., Apatemyidae, and possibly Plagiomenidae). Paromomyiformes of Szalay (1973) and Peneprimates of Hofstetter (1978) are equivalent in composition to the group here called Plesiadapoidea.

#### Superfamily MICROSYOPOIDEA Family MICROSYPIDAE

Cf. *Niptomomys* sp.

*Referred specimen.* Locality SC-67: UM 85591.

*Description.* UM 85591 is an edentulous right dentary with alveoli for four cheek teeth:  $P_4$ - $M_3$ . The anterior root of  $P_4$  remains in its alveolus, but all roots behind this are missing. Due to pathology, there is no alveolus for a central incisor or for any other teeth in front of  $P_4$ , and the anterior part of the dentary shows considerable bone remodeling where these teeth would have been. The dentary measures 2.7 mm in depth.

*Discussion.* This dentary is about the same size as that of *Niptomomys doreenae*, and the conformation of the jaw resembles that of a small uintasoricine. It is too large to belong to *Tinimomys graybullensis* and too small to belong to *Phenacolemur simonsi*.

UM 85591 was found on the surface of a greenish gray sandstone that weathers white at the east end of locality SC-67. Approximately one ton of this sandstone was subsequently washed, yielding several teeth catalogued as UM

86572m, but no teeth referable to the same taxon as this dentary were found.

#### *Arctodontomys wilsoni* (Szalay, 1969)

*Referred specimen.* Locality SC-67: UM 86572m.

*Description.* The small sample of teeth recovered from SC-67 by screen washing includes a right  $M_1$  of *Arctodontomys* that is identical to other later and more complete specimens referred to *A. wilsoni*.  $M_1$  measures 2.7 mm in length and 1.9 mm in width.

*Discussion.* UM 86572m is the earliest record of *A. wilsoni*, which is best known from the latter part of the early Wasatchian (Gunnell, 1985).

#### Superfamily PLESIADAPOIDEA Family PAROMOMYIDAE

#### *Phenacolemur praecox* Matthew, 1915

*Referred specimens.* Locality SC-67: UM 79890m. Locality SC-348: UM 83817m.

*Description.* UM 79890m is an edentulous right dentary preserving alveoli for  $M_3$ , including the anteroposteriorly-elongated posterior  $M_3$  alveolus characteristic of *Phenacolemur*. This matches *P. praecox* very closely in size. UM 83817m is a more complete left dentary, also edentulous, that preserves the root of  $I_1$  followed by roots and alveoli for  $P_4$ - $M_3$ . Tooth roots indicate that  $P_4$  was a large tooth; there is a mental foramen on the labial surface of the jaw below the anterior alveolus of  $M_1$ ; and the size and shape of the jaw conform to dentaries of *P. praecox*. This dentary measures 7.3 mm in depth.

*Discussion.* The holotype of *Phenacolemur praecox* is from the early Wasatchian of the Clarks Fork Basin (Matthew, 1915b, p. 479), and the species is reasonably common in collections from both the late Clarkforkian and the early Wasatchian (Rose, 1981, p. 66-67).

#### Order PRIMATES Family ADAPIDAE

#### *Cantius torresi* Gingerich, 1986 Fig. 13

*Referred specimens.* Locality SC-67: UM 83467, 83470 (holotype), 83475, 87341, and 87852. Locality SC-69: UM 66143 and 86132.

*Description.* *Cantius torresi* is a small adapid with relatively square upper molars and relatively short and broad lower premolars and molars (Gingerich, 1986). There is no trace of a hypocone on the posterolingual cingulum of  $M^1$  or  $M^2$  like that developed incipiently in European *C. eppi*. Three new specimens have been found since the species was described. The most complete of these is UM 87341, associated left dentary with  $P_2$ - $M_2$  and right dentary with  $M_{2-3}$  (Fig. 13). The left dentary evidently had two

Table 3. Measurements of *Cantius torresi* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
M <sup>1</sup> L	1	3.3	-	-	-
M <sup>1</sup> W	1	4.5	-	-	-
M <sup>2</sup> L	1	3.3	-	-	-
M <sup>2</sup> W	1	5.3	-	-	-
M <sup>3</sup> L	1	2.5	-	-	-
M <sup>3</sup> W	1	4.3	-	-	-
<i>Lower dentition</i>					
P <sub>2</sub> L	1	1.9	-	-	-
P <sub>2</sub> W	1	1.3	-	-	-
P <sub>3</sub> L	2	2.4 - 2.8	2.60	-	-
P <sub>3</sub> W	2	1.8 - 1.9	1.85	-	-
P <sub>4</sub> L	3	2.8 - 3.0	2.93	0.12	3.9
P <sub>4</sub> W	3	2.4 - 2.4	2.40	-	-
M <sub>1</sub> L	3	3.3 - 3.5	3.43	0.12	3.4
M <sub>1</sub> W	3	2.9 - 3.0	2.97	0.06	1.9
M <sub>2</sub> L	4	3.2 - 3.7	3.44	0.19	5.5
M <sub>2</sub> W	4	3.1 - 3.4	3.21	0.10	3.2
M <sub>3</sub> L	4	4.2 - 4.7	4.40	0.22	4.9
M <sub>3</sub> W	4	2.7 - 3.0	2.83	0.13	4.5
Mandibular depth:	5	6.6 - 7.8	7.18	0.55	7.7

Total number of specimens = 7

incisors like all other *Cantius*. There is no alveolus for I<sub>1</sub> preserved, but there is a small space for it in front of I<sub>2</sub>, which is represented by the base of a relatively large alveolus measuring approximately 0.5 mm in anteroposterior diameter and 0.1 mm in buccolingual diameter. The root of the lower canine is preserved in the jaw, and it measures 2.7 by 2.0 mm in diameter. The crown of P<sub>1</sub> is not preserved, but it is represented by a single root, circular in cross-section, measuring 1.0 mm in diameter. P<sub>2</sub> and P<sub>3</sub> have simple pointed crowns. P<sub>4</sub> has a large broad trigonid with distinct paraconid and metaconid cusps in addition to the protoconid. Molars in this dentary are similar to those described previously, but they are a little larger. The mandibular symphysis is well preserved on the medial side of the dentary. It was unfused, and the symphysis extends posteriorly as far as P<sub>3</sub>. The right dentary preserves intact crowns of M<sub>2,3</sub>, and the talonid of M<sub>3</sub> is narrow and rounded as it is in other early *Cantius*.

UM 87852 includes a left dentary with M<sub>1</sub> and M<sub>2</sub>, and a right dentary with P<sub>4</sub>, M<sub>1</sub>, and M<sub>3</sub>. UM 86132 from locality SC-69 is an isolated right M<sub>3</sub>. Measurements of Wa<sub>0</sub> *C. torresi* are summarized in Table 3.

*Discussion.* The new material indicates that *Cantius torresi* probably had a dental formula of 2.1.4.3, with I<sub>1</sub> smaller than I<sub>2</sub>. P<sub>1</sub> is single-rooted, and the mandibular symphysis is unfused as in all later *Cantius*. The new specimens are a little larger than those of *C. torresi* described previously, but they still fall well below the mean size of North American *C. ralstoni* (Fig. 14).

All *C. torresi* resemble *C. ralstoni* in having a crown

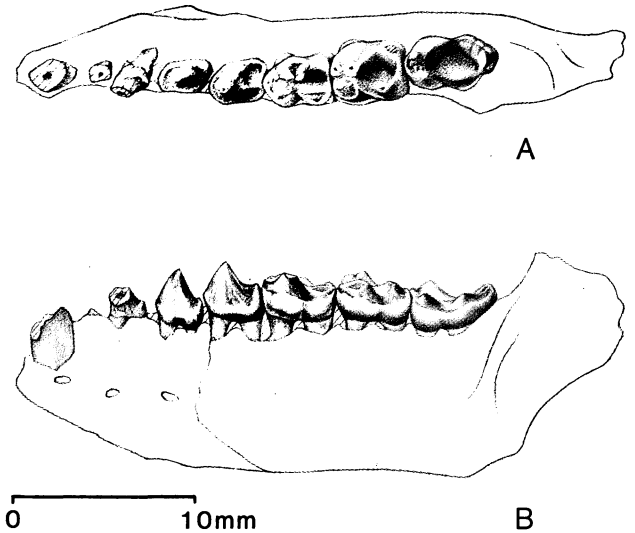


Figure 13. Lower dentition of *Cantius torresi*. A and B, left dentary with P<sub>2</sub>-M<sub>3</sub>, UM 87341, in occlusal and lateral view. Drawing is a composite based on both left and right sides of the jaw.

shape index (L/W) for P<sub>4</sub> of 1.17-1.25 and a crown shape index for M<sub>1</sub> of 1.14-1.17. Comparable values for *C. eppsi* are 1.33 for the P<sub>4</sub> index, and 1.25-1.31 for the M<sub>1</sub> index. *Cantius torresi* resembles its European counterpart *C. eppsi* in size, but differs in lacking any trace of a hypocone on the posterolingual cingulum of M<sup>1</sup> or M<sup>2</sup>. *C. torresi* resembles its North American descendant *C. ralstoni* in shape. I previously suggested (Gingerich, 1986) that European *C. eppsi* was equivalent to North American *C. ralstoni* in evolutionary grade, but considering the new slightly larger specimens described here, I now consider *C. eppsi* more nearly equivalent to *C. torresi* in grade.

Order TILLODONTIA  
Family ESTHONYCHIDAE

*Esthonyx spatularius* Cope, 1880

*Referred specimen.* Locality SC-67: UM 87354m.

*Description.* This specimen is a fragmentary left dentary with much of the crown of M<sub>3</sub> preserved. The trigonid is broken, but the talonid has the shape and wear characteristic of *Esthonyx* and it compares very well with AMNH 4809, the holotype of *E. spatularius*. M<sub>3</sub> measures 8.2 mm in length and 4.9 mm in width.

*Discussion.* *Esthonyx spatularius* is smaller than *Azygonyx gunnelli*, and it has a fused mandibular symphysis (not preserved in the specimen at hand). Transferring the known Clarkforkian esthonychids to *Azygonyx* (see below) makes this the earliest record of the genus *Esthonyx*. Two species of *Esthonyx* are present in the early and middle Wasatchian: *E. spatularius* Cope, 1880 and its larger de-

CLARK'S FORK BASIN CANTIUS

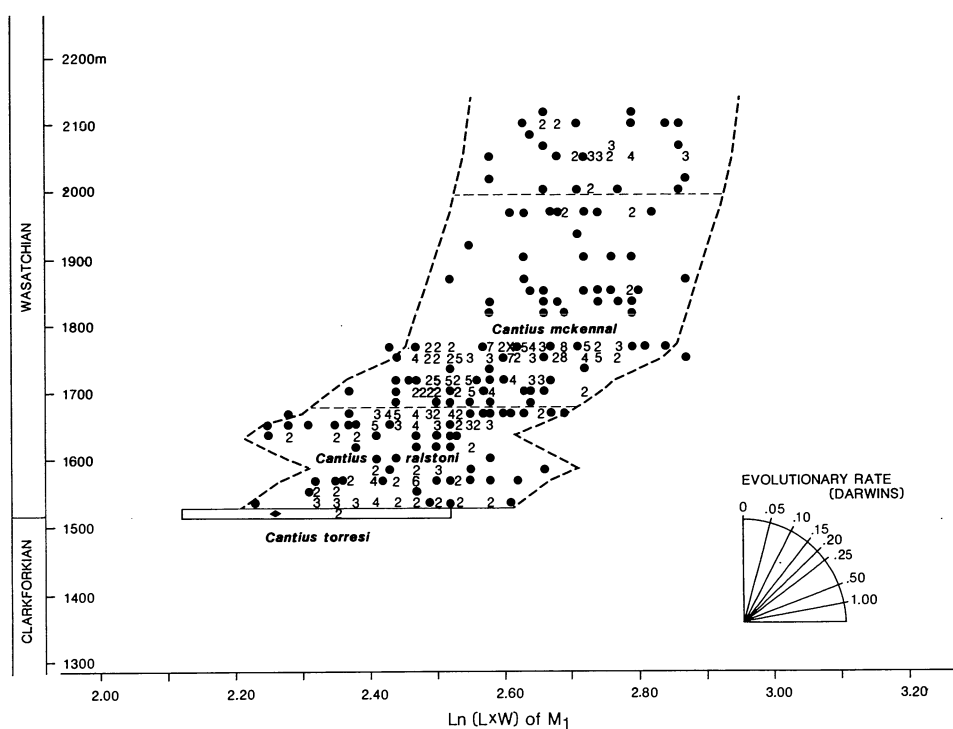


Figure 14. Stratigraphic distribution of early Wasatchian *Cantius* in the Clarks Fork Basin, Wyoming. Note abrupt appearance of *Cantius* in zone  $W_0$  (level 1520 m) and subsequent persistence of a single lineage here. Abscissa is natural logarithm of length multiplied by width of the first lower molar. Ordinate is measured level (meters) above Cretaceous-Tertiary boundary in Polecat Bench-Clarks Fork Basin stratigraphic section. Solid circles are individual specimens, integers represent multiple specimens, and  $x$  represents ten or more specimens falling at the same point. Solid diamonds are holotypes of known stratigraphic provenance; open diamonds are holotypes whose stratigraphic level is only approximately known. Heavy dashed lines are drawn 0.4 units apart, enclosing approximately two standard deviations on each side of mean, or 95% of total variation in a lineage (one out of 20 specimens might be expected to fall outside dashed lines). Light dashed lines are arbitrary boundaries separating named evolutionary stages within a lineage. Darwinometer is calibrated on the assumption that 100 m of section represents, on average, about 270,000 years and 10 m of section represents 27,000 years (Gingerich, 1982). In the interest of comparability, all plots of stratigraphic distribution in this paper are scaled to maintain a constant relationship between morphology on the abscissa and stratigraphic level (time) on the ordinate. Specimens plotted here are in the UM collection.

scendant *E. bisulcatus* Cope, 1874. These are usually interpreted as successional species in a single lineage, but there is some suggestion of a morphological break in tooth size separating them at the 1800 m level in the Clarks Fork Basin (Figure 17; this break appears to coincide with a condensed stratigraphic interval represented by a multistoried sheet sandstone at this level; Badgley and Gingerich, 1988).

**Azygonyx**, new genus

*Type species.* *Azygonyx gunnelli* new species.

*Included species.* Clarkforkian *Azygonyx grangeri* (Simpson, 1937), Clarkforkian *A. latidens* (Simpson, 1937), Clarkforkian *A. xenicus* (Gingerich and Gunnell, 1979), Clarkforkian *A. ancylion* (Gingerich and Gunnell,

1979), earliest Wasatchian *A. gunnelli* new species (type species), and early Wasatchian *A. sp.* (see below). *Azygonyx* is presently known only from North America.

*Diagnosis.* Species of *Azygonyx* differ from those of North American *Esthonyx*, *Megalesthonyx*, *Trogosus*, and *Tillodon* in having an unfused mandibular symphysis. Differs from European *Plesiasthonyx* (possible junior synonym of *Esthonyx*) in having smooth enamel on lower premolars. Differs from Asian *Basalina* in having an unfused mandibular symphysis. Differs from Asian *Adapidium* and *Kuan-chuanianus* in having less sharply crested lower molars. Differs from Asian *Lofochaius* and *Meiostylodon* in having a more separated paracone and metacone on upper molars (inclusion of these genera in *Esthonychidae* is questionable in any case).

**Etymology.** *a*, absence, *zygos*, yoke or joining, and *onyx* (Gr., masculine), talon or claw, in allusion to the unjoined claw-like anterior teeth in unfused left and right mandibular rami distinguishing species of this genus. Use of "*onyx*" to refer to claw-like incisors parallels Cope's use of this root in forming *Esthonyx*.

**Discussion.** *Azygonyx* is distinctive among esthonychids in having an unfused mandibular symphysis. The most specialized species, the type species (described below), is small and relatively deep-jawed, with crowded, nearly vertical anterior teeth. This specialization involves characteristics that distinguish late Wasatchian *Megalesthonyx* Rose, 1972, from contemporary species of *Esthonyx*, but the direction of specialization is opposite that observed in *Megalesthonyx*. The latter has a greatly elongated, fused mandibular symphysis, and well-spaced procumbent anterior teeth. The four named Clarkforkian esthonychids are transferred to *Azygonyx* because they resemble *Azygonyx gunnelli* more closely than they do contemporary *Esthonyx spatularius* or later *E. bisulcatus* (type species of *Esthonyx*).

***Azygonyx gunnelli*, new species**

Figs. 15-16

**Holotype and referred specimens.** Locality SC-67: UM 83664m, 87340, 87346, 87859m, and 92356m; UM 71768m, 83478m, 83618m, and 83636m may also belong to this species. Locality SC-308: UM 76237m may belong here. Locality SC-351: UM 83874 (holotype).

**Diagnosis.** *Azygonyx gunnelli* differs from members of the principal *Azygonyx* lineage (Clarkforkian *A. xenicus*, *A. ancylion*, *A. latidens*, and *A. grangeri*) in having a more vertical  $I_2$  tusk (the posterior edge of the root of  $I_2$  rises at an angle of about  $80^\circ$ , as compared with an angle of about  $45^\circ$  in other species of the genus). *A. gunnelli* also differs in having the mandibular symphysis relatively shorter anteroposteriorly and deeper vertically, in having the anterior teeth more crowded, and in having a single-rooted  $P_2$ . It is well outside the range of variation of these features observed within or among the Clarkforkian species.

**Etymology.** Named for Dr. Gregg F. Gunnell in recognition of his interest in Tillodontia and the leading role he has played in finding and collecting new Clarkforkian and early Wasatchian mammals.

**Description.** The holotype, UM 83874, is the most complete specimen known. It includes several upper teeth; a left dentary with  $C_1$ ,  $M_1$ , and  $M_3$ ; a nearly complete right dentary with  $I_2$  and  $C_1$ - $M_3$  (Fig. 15); cranial fragments; left proximal ulna and radius (Fig. 16); left astragalus and calcaneus (Fig. 16); and other carpal and tarsal elements, including several broken metapodials and disarticulated phalanges. Most referred and questionably referred specimens are isolated anterior teeth not associated with identifiable cheek teeth.

In the holotype,  $I^1$  is represented by the tip of the crown.

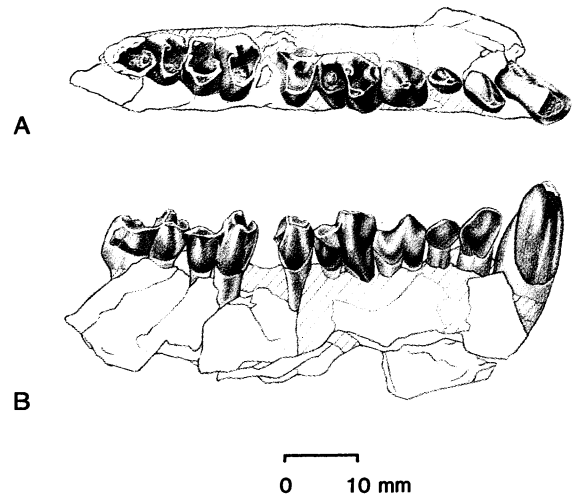


Figure 15. Lower dentition of *Azygonyx gunnelli* new species. A and B, right dentary with  $I_2$ ,  $C_1$ , and  $P_2$ - $M_3$ , UM 83874 (holotype), in occlusal and lateral view. Note vertical implantation of enlarged  $I_2$  characteristic of this species (lateral and posterior parts of  $I_2$  alveolus are preserved in pieces of jaw that fit together, precluding a more procumbent orientation of this tooth).

All enamel is worn off of the lingual occlusal surface, which is surrounded by a continuous surface of enamel on the medial, anterior (labial), and distal sides of the crown.  $I^2$  has a massive oval crown with anterior, posterior, and lingual ridges of enamel. The crown of  $C^1$  is broken, but it clearly resembled the larger  $I_2$  in form.  $I^2$  and  $C^1$  were clearly single-rooted.  $P^2$  is double-rooted. It has a simple crown with anterior and posterior ridges and a lingual fold of enamel.  $P^3$ ,  $P^4$ , and  $M^1$  are represented by fragmentary crowns that appear to differ little from these teeth in other *Azygonyx* and *Esthonyx*. Crowns of  $M^2$  and  $M^3$  are typically esthonychid in form. All of the crowns of upper teeth are isolated, and it is impossible to determine their spacing or orientation.

Left and right mandibular rami and their associated dentition have been reassembled from many pieces of bone and broken tooth crowns.  $I_1$  has not been found but there is ample room for a narrow high-crowned esthonychid incisor between the midline of the dentary and  $I_2$ , and  $I_1$  was certainly present in life.  $I_2$  itself is typically esthonychid in being high-crowned, with enamel covering only the anterior part of the medial surface and a broader anterior part of the labial surface of the crown. Exposed dentine is worn as if the tooth had been used to strip vegetation in some way.  $I_3$ , if present at all, must have been a very small tooth because there is little space for it between  $I_2$  and  $C_1$  ( $I_3$  was definitely lost in some Wasatchian *A. grangeri*).  $C_1$  is a little more high-crowned, but otherwise resembles  $I^3$  and  $C^1$  in form.  $P_2$  is single-rooted, with the smallest crown of all the cheek teeth: it resembles  $C_1$ , but differs in being much smaller and in being much lower in crown height. The crown of  $P_3$  is bulbous, with a large blunt protoconid,

Table 4. Measurements of *Azygonyx gunnelli* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
I <sup>2</sup> L	-	-	-	-	-
I <sup>2</sup> W	1	5.4	-	-	-
I <sup>3</sup> L	1	5.9	-	-	-
I <sup>3</sup> W	1	5.7	-	-	-
C <sup>1</sup> L	1	5.4	-	-	-
C <sup>1</sup> W	-	-	-	-	-
P <sup>2</sup> L	1	5.6	-	-	-
P <sup>2</sup> W	1	3.7	-	-	-
P <sup>3</sup> L	2	7.7 - 8.7	8.20	-	-
P <sup>3</sup> W	1	8.4	-	-	-
M <sup>2</sup> L	1	8.2	-	-	-
M <sup>2</sup> W	1	12.5	-	-	-
M <sup>3</sup> L	1	5.7	-	-	-
M <sup>3</sup> W	1	9.9	-	-	-
<i>Lower dentition</i>					
I <sub>1</sub> L	1	8.7	-	-	-
I <sub>1</sub> W	2	4.6 - 4.8	4.70	-	-
C <sub>1</sub> L	1	5.6	-	-	-
C <sub>1</sub> W	1	4.7	-	-	-
P <sub>2</sub> L	1	4.6	-	-	-
P <sub>2</sub> W	1	3.5	-	-	-
P <sub>3</sub> L	2	6.0 - 6.9	6.45	-	-
P <sub>3</sub> W	2	5.1 - 5.8	5.45	-	-
P <sub>4</sub> L	2	7.8 - 8.6	8.20	-	-
P <sub>4</sub> W	2	7.2 - 7.2	7.20	-	-
M <sub>1</sub> L	1	8.5	-	-	-
M <sub>1</sub> W	2	7.8 - 8.1	7.95	-	-
M <sub>2</sub> L	2	8.9 - 9.3	9.10	-	-
M <sub>2</sub> W	2	8.2 - 8.5	8.35	-	-
M <sub>3</sub> L	1	10.1	-	-	-
M <sub>3</sub> W	1	6.8	-	-	-

Total number of specimens = 6

distinct pre- and postprotocristids, and a basined talonid. P<sub>4</sub> resembles P<sub>3</sub>, but it is larger and has distinct paraconid, metaconid, and entoconid cusps in addition to the large protoconid. M<sub>1</sub>-M<sub>3</sub> are typically esthonychid in form. Measurements of upper and lower teeth of the type and principal referred specimens are listed in Table 4.

The mandibular symphysis is unfused. Its posterior margin rises almost vertically, and the symphysis here is 15-16 mm deep (the horizontal ramus is 18-19 mm deep beneath P<sub>2,3</sub>). The left mandibular condyle is preserved intact and it has a large posteriorly-facing articular surface on the medial part of the condyle for articulation with the postglenoid process of the squamosal. A fragment of the right squamosal is preserved. It has a small rounded postglenoid process and a small postglenoid foramen medial to this.

Postcranial remains associated with the holotype include the distal extremity of the right scapula, which measures 19 by 10.5 mm across the glenoid. It resembles the distal part of the scapula of *Trogosus* illustrated by Gazin (1953, fig. 28) in having the coracoid set off medially and separated from the glenoid surface by a distinct fossa. Part of the left radius and proximal ulna are preserved (Fig.

16A,B). The proximal end of the radius articulates with the lateral surface of the ulna, and the capitulum of the radius is rounded (measuring 12.7 by 10.8 mm), indicating that *Azygonyx* was capable of considerable pronation and supination of the manus. Middle Eocene *Trogosus*, on the other hand had a much less circular radial capitulum that articulated more medially with the ulna (Gazin, 1953).

The astragalus of *Azygonyx* (Fig. 16D,E) differs from that of *Trogosus* in having a longer neck. It has a broad capitulum that is strongly curved but shallow dorsoventrally, and the trochlea of the astragalus is broad and shallow. There is a distinct accessory articulation for the medial malleolus of the tibia extending from the dorsal surface of the capitulum along the medial side of the astragal body. This together with the high and anteriorly placed astragal foramen suggests very limited movement of the astragalus relative to the tibia. The astragalus measures 24.8 mm in length, 13.2 mm in width across the trochlea, 14.2 mm in width across the capitulum, and 7.7 mm in capitular depth. The calcaneus is large relative to the astragalus, measuring 36.9 mm in total length, with a large calcaneal tuberosity and broad sustentacular process. The calcaneal tuberosity alone measures 20.4 mm in length (measured from the back of the ectal astragal facet), and the body of the calcaneus is 26.0 mm wide measured at its widest point (across the sustentacular process). When articulated with the astragalus, the calcaneal tuberosity is directed sharply downward (Fig. 16E), indicating a habitually plantigrade foot posture. The left navicular is preserved intact (Fig. 16F). It is short anteroposteriorly, measuring only 5.6 mm in length. Only the proximal surface of the cuboid is preserved (Fig. 16F). All metapodials are broken, but there are several intact phalanges (see composite in Fig. 16C). Terminal phalanges are transversely compressed, markedly curved, unclawed claws, like those described by Gazin (1953) in *Trogosus hyracoides*. The position of phalangeal articulations, like the angulation of the calcaneus, suggests a habitually plantigrade foot.

*Discussion.* The holotype of *Azygonyx gunnelli*, UM 83874, is interesting because it was initially discovered as a scatter of broken pieces of bone and teeth on the surface at locality SC-351. Excavation revealed an association of cranial and postcranial elements in pieces, already broken in the rock. This indicates that breakage occurred before burial, or possibly by trampling during or just after burial. Taken together, these remains are among the most complete of any early esthonychid.

Gingerich and Gunnell (1979) interpreted *Azygonyx* (early "*Esthonyx*") as being rhizophagous, based on the pattern of wear on anterior teeth, and suggested that it may have been piglike in diet. The new postcranial material described here indicates that *Azygonyx* had considerable forearm flexibility and a plantigrade foot, suggesting that it was probably more bearlike than piglike in locomotor pattern.

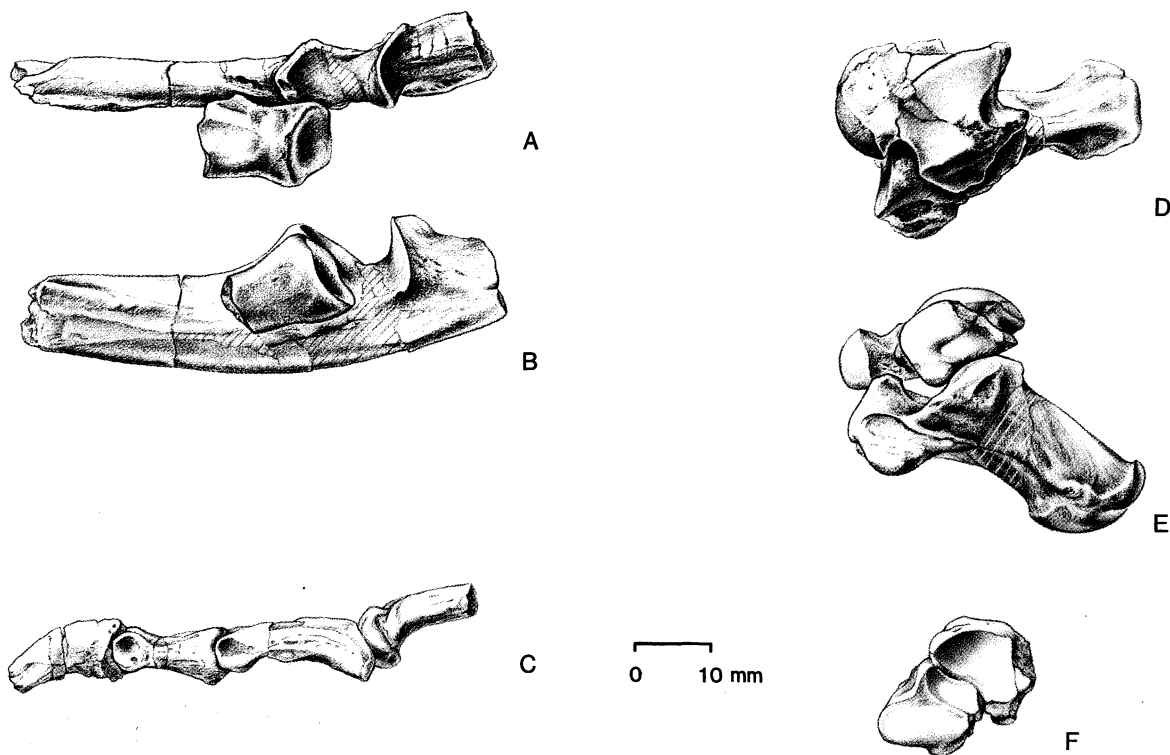


Figure 16. Postcranial remains of *Azygonyx gunnelli*, new species, UM 83874 (holotype). A and B, left ulna and proximal end of radius in dorsal and lateral view. C, metapodial and phalanges in medial or lateral view. D and E, left astragalus and calcaneus in dorsal and lateral view. F, proximal surfaces of left navicular and cuboid. Note rounded capitulum of radius, indicating pronation-supination capability. Claws are large and laterally compressed. Astragalus has relatively long neck and a distinct articular facet for the medial malleolus of the tibia. Tuberosity of calcaneus is directed sharply downward, indicating habitually plantigrade foot posture.

#### *Azygonyx* sp.

*Referred specimens.* Locality SC-67: UM 83740; UM 66616 and 66617m probably represent a second, larger species of *Azygonyx*.

*Description.* UM 83740 is an esthonychid P<sup>4</sup> that measures 10.3 mm in length and 13.9 mm in width. It is too large to belong to either *Esthonyx spatularius* or *Azygonyx gunnelli*. It matches the size and form of late Clarkforkian and early Wasatchian specimens referred to *A. latidens* and *A. grangeri* very closely, indicating that a third esthonychid species was present in zone Wa<sub>0</sub>. UM 66617m is an isolated I<sub>2</sub>, measuring 9.9 mm in length and 5.8 mm in width, that also appears to be too large to belong to *A. gunnelli*.

UM 66616 includes associated postcranial remains of a large *Azygonyx*. These include part of a right astragalus with a distinct facet on the dorsal surface of the medial part of the neck contacting the medial malleolus of the tibia. The capitulum of the astragalus measures 16.9 mm in width and 8.7 mm in depth. The right calcaneus measures 45.7 mm in total length, with a calcaneal tuberosity measuring 19.2 mm in length from the posterior edge of the ectal

astragalar facet. The navicular measures 7.4 mm in length anteroposteriorly. Several phalanges are preserved intact. All terminal phalanges are broken and they are missing the distal part critical for determining curvature. Proximal parts of terminal phalanges indicate that these were laterally compressed, deep, and probably unfissured.

*Discussion.* The stratigraphic distribution and systematics of latest Paleocene and early Eocene Esthonychidae were last reviewed by Gingerich and Gunnell (1979). An updated chart of the stratigraphic distribution of Clarks Fork Basin esthonychids is shown in Figure 17. *Azygonyx*, here separated from *Esthonyx*, is represented by four species in a single lineage, *A. xenicus* (Gingerich and Gunnell, 1979), *A. ancylion* (Gingerich and Gunnell, 1979), *A. latidens* (Simpson, 1937), and *A. grangeri* (Simpson, 1937), a fifth species *A. gunnelli* n.sp., interpreted as a specialized offshoot of the principal *Azygonyx* lineage, and a sixth group of specimens referred to *Azygonyx* that may represent the reappearance of *A. latidens* or the diminution of *A. grangeri*. More specimens will be required to distinguish between these alternatives. *Azygonyx latidens* is usually considered to be a synonym of *A. grangeri*—*A. latidens* is recognized as a distinct stage of evolution here because it



## CLARK'S FORK BASIN ESTHONYCHIDAE

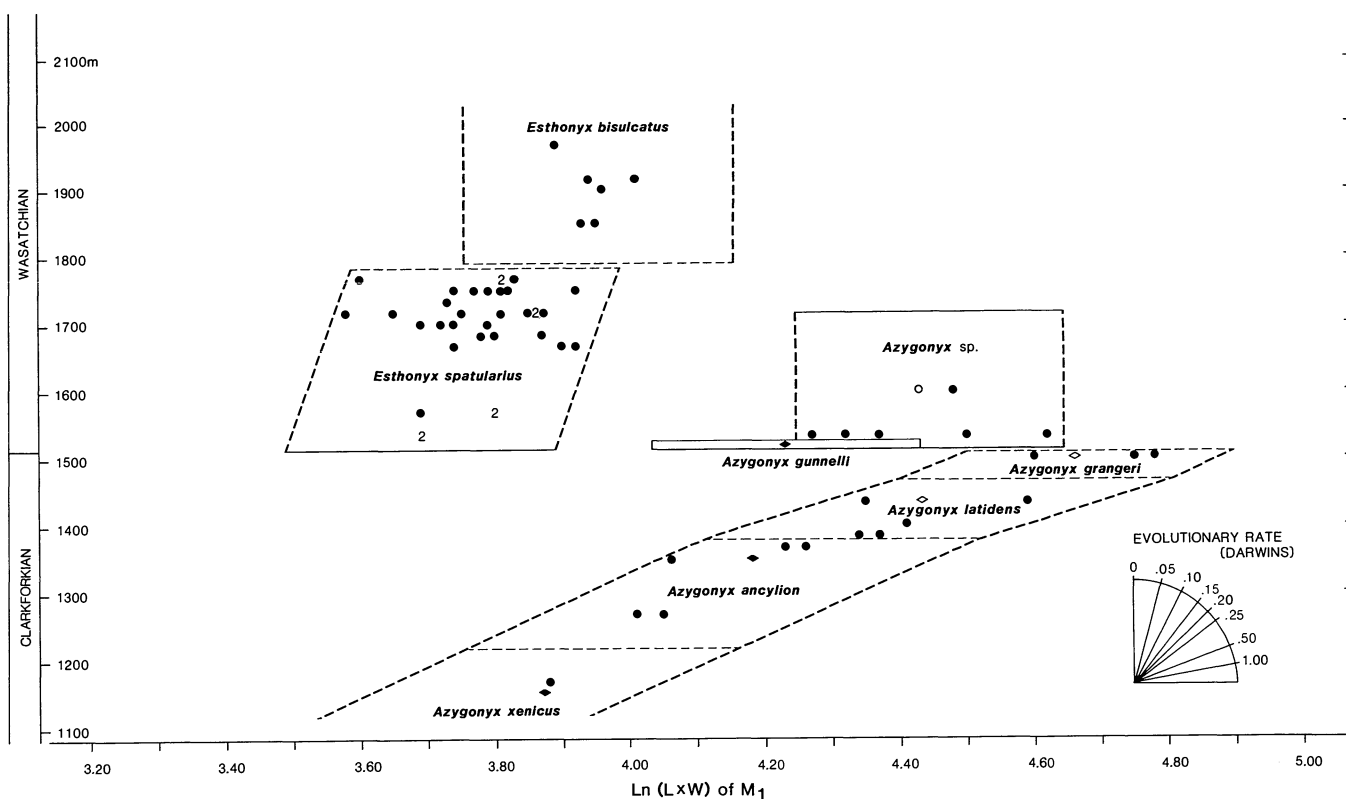


Figure 17. Stratigraphic distribution of early Wasatchian Esthonychidae in the Clarks Fork Basin, Wyoming. *Esthonyx* made its first appearance in zone  $Wa_0$  (level 1520 m) and subsequently persisted as a single lineage offset sharply in the stratigraphic interval between 1760 and 1800 m. *Azygonyx* made its first appearance in the early Clarkforkian and appears to have evolved rapidly toward larger tooth size and body size. This trend was interrupted in zone  $Wa_0$  (level 1520 m) when smaller *A. gunnelli* replaced *A. grangeri* abruptly. Later *Azygonyx* sp. may be derived from *A. gunnelli* or from *A. grangeri*. Symbols as in Figure 14. Specimens plotted here are in the UM collection.

is the same size as later Wasatchian *Azygonyx* and it may contribute to understanding evolutionary complexity evident in the Clarkforkian-Wasatchian transition.

*Esthonyx* is not known before the beginning of the Wasatchian, and *Azygonyx* is not known after early Wasatchian zone  $Wa_2$ . Three species, *Esthonyx spatularius*, *Azygonyx gunnelli*, and *Azygonyx* sp., are present in zone  $Wa_0$ .

Order PANTODONTA  
Family CORYPHODONTIDAE

*Coryphodon* sp.

**Referred specimens.** Locality FG-61: UM 85290. Locality SC-67: UM 79890m, 79892, 80339m, 82387m, 82624, 83613, 83618m, 83628, 83659, and 85595m. Locality SC-139: UM 68033m.

**Description.** Most specimens are postcranial remains or

fragmentary teeth. The only specimens with complete teeth are UM 82387m, an isolated  $P^1$ ; UM 83613, associated incisors, canine, and premolars with a part of the crown of an upper or lower canine measuring about 28 mm in diameter,  $P_1$ ,  $P_3$ , and  $P_4$ ; and UM 83628, an associated upper canine and  $P_3$ . Measurements of  $Wa_0$  *Coryphodon* sp. are summarized in Table 5.

**Discussion.** These teeth are a little smaller than those of most Clarkforkian *Coryphodon proterus* and they compare well with specimens of *Coryphodon* from early Wasatchian zone  $Wa_1$ . The latter, like *C. proterus*, retain a distinct entoconid and a posteriorly placed hypoconulid, characteristics seen also in European *Coryphodon eoacaenus*. Simons (1972, p. 35–36) and Lucas (1984, p. 247–256) refer some early Wasatchian *Coryphodon* from North America to *C. eoacaenus*. Earliest Wasatchian teeth are similar in size to those of *C. eoacaenus* but specimens described here are inadequate to permit confident allocation to that species.

Table 5. Measurements of *Coryphodon* sp. from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
I <sup>1</sup> L	1	17.2	-	-	-
I <sup>1</sup> W	1	12.5	-	-	-
I <sup>2</sup> L	1	19.6	-	-	-
I <sup>2</sup> W	1	15.7	-	-	-
C <sup>1</sup> L	1	21.6	-	-	-
C <sup>1</sup> W	1	21.3	-	-	-
P <sup>1</sup> L	1	12.5	-	-	-
P <sup>1</sup> W	1	9.0	-	-	-
<i>Lower dentition</i>					
I <sub>3</sub> L	1	19.3	-	-	-
I <sub>3</sub> W	1	11.0	-	-	-
P <sub>1</sub> L	1	11.9	-	-	-
P <sub>1</sub> W	1	7.3	-	-	-
P <sub>3</sub> L	2	16.6 - 21.8	19.20	-	-
P <sub>3</sub> W	2	15.3 - 15.8	15.55	-	-
P <sub>4</sub> L	1	22.0	-	-	-
P <sub>4</sub> W	1	17.9	-	-	-

Total number of specimens = 11

Table 6. Measurements of *Ectoganus bighornensis* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
P <sup>3</sup> L	2	10.7 - 10.7	10.70	-	-
P <sup>3</sup> W	2	13.3 - 14.0	13.65	-	-
M <sup>1</sup> L	2	9.9 - 10.5	10.20	-	-
M <sup>1</sup> W	2	12.2 - 12.6	12.40	-	-
M <sup>2</sup> L	1	10.2	-	-	-
M <sup>2</sup> W	1	11.7	-	-	-
M <sup>3</sup> L	1	8.7	-	-	-
M <sup>3</sup> W	1	9.8	-	-	-
<i>Lower dentition</i>					
M <sub>1</sub> L	2	11.5 - 11.5	11.50	-	-
M <sub>1</sub> W	2	11.1 - 11.3	11.20	-	-
M <sub>1/2</sub> L	1	11.5	-	-	-
M <sub>1/2</sub> W	1	11.2	-	-	-
M <sub>2</sub> L	1	11.7	-	-	-
M <sub>2</sub> W	1	11.3	-	-	-
M <sub>3</sub> L	1	10.8	-	-	-
M <sub>3</sub> W	1	10.6	-	-	-

Total number of specimens = 11

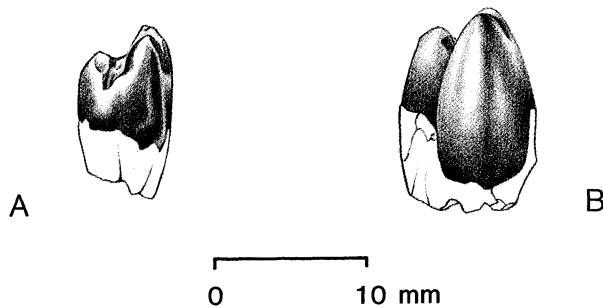


Figure 18. Comparison of size, hypsodonty, and stylinodonty in contemporary lineages of *Ectoganus*. Stylinodonty refers to the development of enamel pillars or ribbons confined to labial and lingual surfaces of the cheek teeth like those in the genus *Stylinodon*. A, right M<sub>3</sub> of *Ectoganus bighornensis*, UM 83629, from earliest Wasatchian locality SC-67, in labial view. B, right M<sub>3</sub> (reversed, original is left M<sub>3</sub>) of *Ectoganus lobdelli*, UM 71330, from middle Clarkforkian Buckman Hollow locality, in labial view. Note greater development of stylinodonty at an earlier stage in the larger *E. lobdelli* - *E. gliriformis* lineage.

Order TAENIODONTA  
Family STYLINODONTIDAE

*Ectoganus bighornensis* Schoch, 1981

Fig. 18A

*Referred specimens.* Locality HG-3: UM 92222. Locality SC-67: YPM-PU 14678 (holotype) and 18052 (not seen); UM 66617m, 77203m, 79885, 79890m, 83471, 83479, 83629, and 86003m.

*Description.* The holotype described by Schoch (1981, 1986), comprising seven associated teeth, is still the most complete specimen of *Ectoganus bighornensis* known. This species is distinguished from contemporary *E. lobdelli*

(Fig. 18B) by its smaller size and less developed stylinodonty (compare Figs. 18A and B). Most specimens listed here are fragmentary pieces of canines or cheek teeth. UM 83471 includes a complete M<sup>1</sup> or M<sup>2</sup>, and UM 83629 is a complete M<sub>3</sub>. UM 83479 is an isolated middle phalanx that almost certainly belongs to this species. Measurements of Wa<sub>0</sub> *E. bighornensis* are summarized in Table 6.

*Discussion.* Schoch (1986) considered *Ectoganus copei bighornensis* to be an early stage in the evolution of a lineage leading to *Ectoganus copei copei*. He attempted to convey this information in formal nomenclature by naming both stages as subspecies of *E. copei*, a species he described from the middle or late Wasatchian of the Bighorn Basin. Schoch (1986) also recognized two other subspecies of *Ectoganus*, *Ectoganus gliriformis lobdelli* and *Ectoganus gliriformis gliriformis* as stages in the evolution of a second lineage of larger individuals. I agree with Schoch that specimens of *Ectoganus* are appropriately divided into four groups, but I disagree that these should be called subspecies and doubt relationships he postulates between the groups. The subspecies category was first used for geographic variants, and use of subspecies in a chronological sense confuses geographic and temporal concepts. Binomials identify Schoch's four *Ectoganus* groups as readily as trinomials do, more economically.

After comparing all UM taeniodont specimens from the late Tiffanian, the Clarkforkian, and the Wasatchian of the Bighorn and Clarks Fork basins, it appears that all Tiffanian and Clarkforkian specimens and those from early Wasatchian zones Wa<sub>1</sub> and Wa<sub>2</sub> are appropriately placed in *Ectoganus lobdelli*, while middle and late Wasatchian specimens from zone Wa<sub>3</sub> and higher are appropriately referred to *E. gliriformis*. Specimens in both species groups

are relatively large, but members of the latter have higher crowned, more stylinodont cheek teeth. Specimens of *Ectoganus bighornensis* are smaller than those of both *E. lobdelli* and *E. gliriformes*, and they have less high crowned and less stylinodont cheek teeth than either.

According to Schoch (1986, p. 77), *Ectoganus copei* is the size of *E. bighornensis* but it differs from *E. bighornensis* in having "all teeth extremely hypsodont; incisors and  $P^1_{1-2}$  approach the totally rootless condition of the canine[s]." This is exactly the wording Schoch used to diagnose *E. gliriformis* from *E. lobdelli* (Schoch, 1986, p. 75). Extreme hypsodonty is a characteristic that is usually given more weight than small size in grouping closely related species. Hence *E. copei* is likely to be more closely related to the *E. lobdelli*-*E. gliriformis* lineage than it is to *E. bighornensis* (which is another reason to recognize *E. bighornensis* as a full species).

Schoch (1986, fig. 58) showed the stratigraphic range of *Ectoganus bighornensis* to extend through much of the Clarkforkian and early Wasatchian, but all known specimens are, in fact, restricted to  $W_{a_0}$ .

Order CREODONTA  
Family OXYAENIDAE  
Subfamily OXYAENINAE

*Dipsalidictis platypus* Matthew, 1915

Fig. 19

**Referred specimens.** From locality SC-67: AMNH 15857 (holotype), UM 66137 (now including 86231), 83616, 83623m, 87354m, and questionably 66617m and 74080. Locality SC-141: UM 67255.

**Description.** The holotype includes parts of both maxillae and both dentaries, and well preserved postcranial remains, all described by Matthew (1915). The most complete new specimen is UM 66137, including a right dentary with  $M_{1-2}$ , part of right  $P^4$ , right  $M^{1-2}$ , and associated tarsal elements (including several fissured claw-bearing terminal phalanges) collected in 1976. More of this specimen, including right  $P_3$  and part of  $P^4$ , was collected in 1985 and catalogued as UM 86231. Reassociated, this is now the best maxilla of the species known (Fig. 19A,B).  $P^3$  is three-rooted with a small but distinct protocone cusp on the lingual side of the crown.  $P^4$ - $M^2$  in this specimen are typically oxyaenid in form. UM 87354m includes a well preserved right  $P^3$  that is very similar but lacks any trace of a medial root or protocone cusp found in UM 66137. New lower teeth duplicate those in the holotype and add no further information. Dental measurements are given in Table 7.

UM 66137 includes nearly complete left and right astragali and calcanei (Fig. 19D), and UM 83616 includes the body of a left astragalus and calcaneus. The first two astragali measure 20.8 and 20.4 mm in length (same individual), and the latter two measure 13.2 and 12.7 mm in width across the body of the astragalus. The bodies of the latter

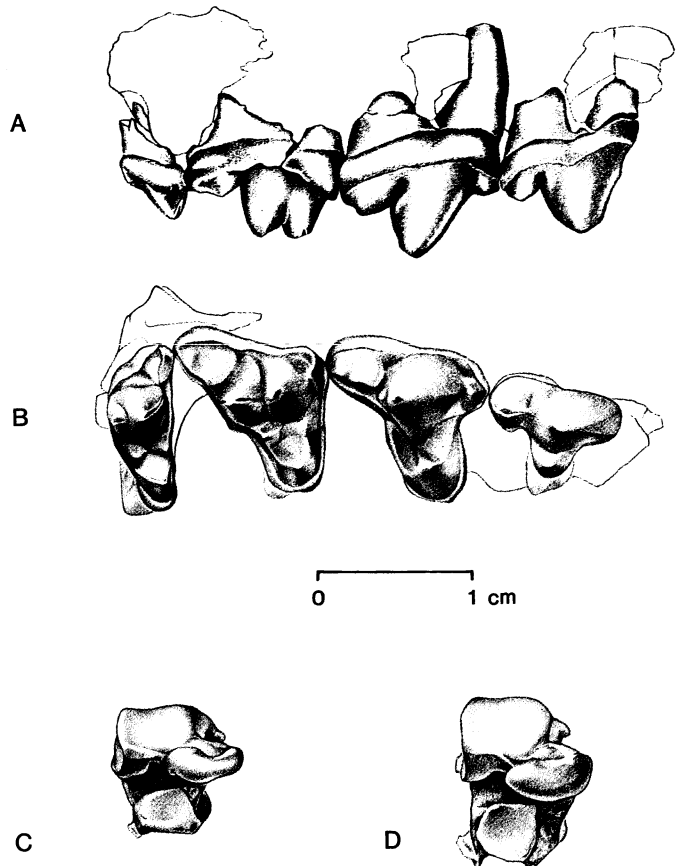


Figure 19. Dentition and tarsus of *Dipsalidictis platypus*. A and B, right maxilla, UM 66137, in lateral and occlusal view. Note distinct protocone cusp on  $P^3$  in this specimen. C, right astragalus and calcaneus, AMNH 15857 (holotype) in anterior view. D, right astragalus and calcaneus, UM 66137, in anterior view. Note shallow astragalar body and shallow cuboid facet of calcaneus in AMNH 15857, and deeper development of these features in UM 66137.

two astragali measure 9.1 and 10.5 mm in height. The three calcanei measure 30.8, 30.5, and 30.2 mm in length, and the first and third measure 17.7 and 17.5 mm in total width measured across the sustentacular process. The cuboid facets on the three measure  $9.0 \times 7.9$ ,  $9.2 \times 7.9$ , and  $9.1 \times 7.2$  (width  $\times$  height), respectively. For comparison, the holotype astragalus measures 18.0 mm in total length, 14.1 mm in width across the body, and 8.0 mm in height. The holotype calcaneus measures 27.7 mm in total length and 15.1 mm in width across the sustentacular process, with a cuboid facet measuring  $8.9 \times 6.4$  mm.

Specimens questionably referred to this species are UM 66617m, the anterior part of a left dentary preserving the mandibular symphysis but lacking tooth crowns, and UM 74080, a left  $dP_4$  and associated protocone of  $M_1$ . These specimens are slightly larger than others referred to *D.*

Table 7. Measurements of *Dipsalidictis platypus* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
C <sup>1</sup> L	1	6.6	-	-	-
C <sup>1</sup> W	1	5.0	-	-	-
P <sup>3</sup> L	2	8.0 - 8.4	8.20	-	-
P <sup>3</sup> W	2	4.3 - 6.0	5.15	-	-
P <sup>4</sup> L	2	10.1 - 10.2	10.15	-	-
P <sup>4</sup> W	2	8.8 - 9.6	9.20	-	-
M <sup>1</sup> L	2	8.6 - 9.5	9.05	-	-
M <sup>1</sup> W	1	9.8	-	-	-
M <sup>2</sup> L	2	4.7 - 5.1	4.90	-	-
M <sup>2</sup> W	1	11.2	-	-	-
<i>Lower dentition</i>					
C <sub>1</sub> L	1	6.7	-	-	-
C <sub>1</sub> W	1	5.2	-	-	-
P <sub>1</sub> L	1	2.6	-	-	-
P <sub>1</sub> W	1	2.8	-	-	-
P <sub>3</sub> L	1	6.4	-	-	-
P <sub>3</sub> W	1	3.6	-	-	-
P <sub>4</sub> L	1	8.7	-	-	-
P <sub>4</sub> W	1	4.3	-	-	-
M <sub>1</sub> L	4	8.0 - 8.4	8.25	0.17	2.1
M <sub>1</sub> W	4	5.4 - 5.4	5.39	0.03	0.5
M <sub>2</sub> L	2	8.4 - 9.3	8.83	-	-
M <sub>2</sub> W	2	6.0 - 6.3	6.15	-	-
Mandibular depth:	3	14.7 - 17.1	16.12	1.26	7.8

Total number of specimens = 7

*platypus*, but they do not preserve parts that are easily comparable and identifiable.

*Discussion.* New material includes the heavily worn trigonid of a right M<sub>2</sub> belonging to the holotype of the species, AMNH 15857, collected in 1911 by W. J. Sinclair from "blue beds" located "about 3 mi. N. of Ralston [Wyoming]" (the specimen was assigned field number 83 in the 1911 American Museum of Natural History field catalogue for the Bighorn Wasatch). The new trigonid, which fits perfectly onto the talonid and root of M<sub>2</sub> in AMNH 15857, is one of numerous miscellaneous teeth collected from SC-67 in 1986, seventy-five years later, and catalogued as UM 87354m. The new trigonid, now glued onto AMNH 15857, adds little to the morphology of this specimen, but the find is important in confirming that the holotype came from the locality now known as SC-67. Wa<sub>0</sub> strata are strikingly red at this locality, making the entry "blue beds" in the American Museum field catalogue difficult to explain. It is possible that catalogue information was recorded by someone other than Sinclair after the partial skeleton was discovered. Sinclair, Granger, and Olsen's collecting on subsequent days was concentrated in "blue beds" at the head of Big Sand Coulee, and they may have written "blue beds" opposite 1911-83 by mistake, intending to begin with the subsequent entry. Alternatively, the notation "blue beds" may have been recorded later, in Sinclair's absence, after the field party returned to the American Museum. The

new find indicates, in any case, that "blue beds" was almost certainly recorded in error.

New material includes two specimens preserving P<sup>3</sup>: one with a medial root and small but well developed protocone ("deuterocone"), and the other lacking both of these. Presence of a "deuterocone" on P<sup>4</sup> only (not on P<sup>3</sup>) figured prominently in the original diagnosis of *Dipsalidictis* (Matthew, 1915), and discovery that this characteristic is variable in the type species makes it likely that it is variable in other species of *Dipsalidictis* as well.

Matthew (1915a) emphasized the shallow body, flattened trochlea, and flat capitulum of the astragalus in describing and naming the type species of *Dipsalidictis*, and Matthew's holotype of *D. platypus* does exhibit this flattening of foot bones (Fig. 19C). However, the astragali and calcanei of new specimens described here are more normally proportioned (Fig. 19D), and neither shows the shallowness and flattening exhibited by the holotype.

*Dipsalidictis* is often synonymized with *Oxyaena* (e.g., Denison, 1938; Gingerich, 1980a; Rose, 1981). The type species of the former is *D. platypus* Matthew, 1915, discussed here, and the type species of the latter is *O. lupina* Cope, 1874, from the middle or late Wasatchian of New Mexico. The two genera are similar and undoubtedly closely related, but Clarkforkian and early Wasatchian species differ from middle and late Wasatchian species in having less open trigonids on the lower carnassials (trigonid shorter than broad, especially on M<sub>2</sub>; Matthew, 1915a, p. 46) and in having a more mobile, subdigitigrade foot (Gunnell, 1988).

#### *Dipsalidictis transiens* (Matthew, 1915)

*Referred specimens.* Locality SC-79: UM 83647m. Locality SC-67: UM 82387m is an additional but questionable Wa<sub>0</sub> record of this species.

*Description.* UM 83647m is an upper left canine that is too large to belong to *Dipsalidictis platypus*. It measures 9.6 mm in anteroposterior crown length and 6.6 mm in crown width, and it resembles upper canines of early Wasatchian *D. transiens* (e.g., UM 65322 from locality SC-4) very closely in both size and form. UM 82387m is the trigonid of a left M<sub>1</sub> or M<sub>2</sub> measuring 6.8 mm in width, making it too large to belong to *Dipsalidictis platypus* but the right size to represent *D. transiens*. The specimen is considered a questionable Wa<sub>0</sub> record of the species because it is dark in color, unlike UM 83647m and unlike virtually all other Wa<sub>0</sub> specimens from SC-67.

*Discussion.* UM 83647m indicates the presence of a second oxyaenid lineage in zone Wa<sub>0</sub>, comprising specimens about 20-30% larger than those of *Dipsalidictis platypus* in zone Wa<sub>0</sub>. Two names have been applied to early Wasatchian members of this lineage: *Oxyaena transiens* Matthew, 1915, and *Dipsalidictis amplus* Jepsen, 1930, both based on early Wasatchian type specimens (Denison, 1938, placed the latter in a separate genus *Dipsalidictides*).

Matthew's specific name has priority, but I follow Jepsen in referring the species in question to *Dipsalidictis* (see discussion above regarding *D. platypus*).

#### Subfamily PALAEOICTINAE

##### *Palaeonictis* sp.

*Referred specimen.* Locality SC-67: UM 92889.

*Description.* This specimen is the trigonid of a right  $M_2$ . The protoconid is relatively low, and the paraconid and metaconid are well separated. The trigonid measures 6.7 mm in width, which is much smaller than that observed in North American Clarkforkian *P. peloria* and at the small end of the range of variation observed in North American Wasatchian *P. occidentalis*. Known specimens of European *P. gigantea* are similar to this specimen in size.

*Discussion.* A large species of *Palaeonictis*, *P. peloria*, is present in Clarkforkian strata of the Clarks Fork Basin, and all previously known Wasatchian specimens are referred to *P. occidentalis* (Rose, 1981). The  $Wa_0$  species is much smaller than *P. peloria*. It is more similar to *P. occidentalis* in size and may possibly represent this species, *P. gigantea*, or a new small species. Identification to species clearly requires a more complete specimen.

#### Family HYAENODONTIDAE Subfamily PROVIVERRINAE

##### *Acarictis ryani* Gingerich and Deutsch, 1989

*Referred specimens.* Locality SC-67: UM 86572m and 87354m.

*Description.* UM 87354m is a broken right  $M_1$  set in a fragment of jaw. This tooth measured about 4.1 mm in length when complete. The trigonid is missing, precluding a width measurement. UM 86572m is a left  $M_3$  measuring about 4.2 mm in length and 2.4 mm in width, with a long narrow talonid resembling that seen in *Prototomus*.

*Discussion.* These remains are sufficient to indicate the presence of the very small hyaenodontid *Acarictis* in zone  $Wa_0$ , but they contribute little to our knowledge of its morphology.

##### *Prototomus deimos* Gingerich and Deutsch, 1989

*Referred specimens.* Locality SC-67: UM 66140m, 83662 and 87354m. Locality SC-349: UM 83819m.

*Description.* All four specimens of this species are fragmentary and can only be identified by comparison with more complete specimens from slightly younger localities in overlying strata. UM 66140m is a right  $P^4$  with a prominent labial cusp (metacone), short metastylid crest, and small protocone. UM 83819m is a right dentary with partial crowns of two very narrow premolars and the anterior part of  $M_1$ . UM 83662 is a fragmentary right dentary of a juvenile with the crown of  $M_3$  erupting. It has the closed

trigonid (paraconid relatively close to the metaconid) and long narrow talonid found in *Prototomus*, and matches *P. deimos* closely in size. UM 87354m is the trigonid of a left  $M_2$  that has the paraconid too close to the metaconid for a miacid, and it probably represents *P. deimos*. Measurements of  $Wa_0$  *P. deimos* are listed in Table 8.

*Discussion.* These specimens indicate the presence of a second small hyaenodontid in zone  $Wa_0$ .  $M_3$  in UM 83662 is very similar to that in BMNH M20212, a fragmentary dentary of Sparnacian age from Abbey Wood in England identified by Van Valen (1965, p. 659) as cf. *Prototomus* sp.

##### *Arfia junnei*, new species

Fig. 20

*Holotype and referred specimens.* Locality SC-67: UM 67664, 71767, 79890m (two specimens), 83618m, 83623m (two specimens), 83636m, 86003m, 86571, 87344 (holotype), 87349, 87859m (two specimens), and 92356m. Locality SC-69: UM 86135. Locality SC-79: UM 83646. Locality SC121: UM 83640. Locality SC-308: UM 85596m. Locality SC-348: UM 83814.

*Diagnosis.* Smallest species of *Arfia*, differing from early Wasatchian *A. zeke* in being about 13% smaller in linear dimensions (*A. zeke* is, in turn, about 13% smaller than *A. shoshoniensis* and *A. opisthotoma*).

*Etymology.* Named for George H. Junne, who found the holotype, in recognition of his many important discoveries of  $Wa_0$  mammals.

*Description.* The holotype, UM 87344, a left dentary with newly erupted  $M_1$ , is one of twenty specimens of this species known from zone  $Wa_0$ . Most are isolated teeth, but several associated teeth and jaws are known as well. UM 87859m includes a right  $P^2$  with a simple narrow crown, very weak labial cingulum, stronger lingual cingulum, but no lingual cusp. UM 83618m includes a left  $P^3$  with the lingual cingulum expanded as a distinct swelling, but again no lingual cusp (Fig. 20A,B). The most complete  $P^4$  is part of UM 83623m (Fig. 20C,D). This tooth has a high sharp paracone with a sectorial postparacrista and a distinct protocone. Two specimens, UM 71767 (Fig. 20G,H) and 79890m, preserve the crown of  $M^1$  intact.  $M^1$  has a prominent protocone, paracone, and metacone, and a shearing postmetacrista. These teeth resemble deciduous  $dP^4$  in having thin enamel that is perforated along the postmetacrista with very little wear (cf. UM 71767, Fig. 20E,F). Fragments of  $M^2$  are preserved with UM 71767, showing that this tooth had the enlarged postmetacrista seen in later species of *Arfia*.

The only lower premolar known to date is the posterior part of  $P_3$  (UM 79890m) preserved in a left dentary. UM 87344 (holotype) is a very shallow left dentary with a newly erupted  $M_1$  (Fig. 20I,J) measuring 5.6 mm in length and 3.2 mm in width. This tooth has a relatively low trigonid for a carnivorous mammal, with distinct protocon-

Table 8. Measurements of *Prototomus deimos* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
P <sup>4</sup> L	1	5.6	-	-	-
P <sup>4</sup> W	1	4.3	-	-	-
<i>Lower dentition</i>					
P <sub>3</sub> L	1	4.1	-	-	-
P <sub>3</sub> W	-	-	-	-	-
P <sub>4</sub> L	1	4.5	-	-	-
P <sub>4</sub> W	1	1.7	-	-	-
M <sub>2</sub> L	-	-	-	-	-
M <sub>2</sub> W	1	3.2	-	-	-
M <sub>3</sub> L	1	4.8	-	-	-
M <sub>3</sub> W	1	2.9	-	-	-
Mandibular depth:	1	7.9	-	-	-

Total number of specimens = 4

mid, paraconid, and metaconid cusps. The talonid is broadly basined with distinct hypoconid, hypoconulid, and entoconid cusps. Like M<sup>1</sup>, it might easily be mistaken for a deciduous premolar; however it articulates well with M<sup>1</sup> in UM 71767 where dP<sup>4</sup> is preserved in association. Two specimens preserve intact or nearly intact crowns of M<sub>2</sub>: UM 86135 (Fig. 20K,L) and UM 87349. These have a blocky shape, with the moderately high trigonids and the broad, squared talonid characteristic of M<sub>2</sub> in later species of *Arfia*. Two specimens preserve intact crowns of M<sub>3</sub>: UM 83460 (Fig. 20M,N) [trigonid length = 4.0 mm, trigonid width = 4.4 mm, and trigonid height = 6.8 mm], and UM 83623m [trigonid length = 4.0 mm, trigonid width = 4.3 mm, and trigonid height = 7.4 mm]. These teeth resemble M<sub>3</sub> in any generalized hyaenodontid in that they have a short and broad trigonid with a prominent metaconid (this is smaller and lower than the protoconid and paraconid), and a relatively narrow basined talonid.

UM 83460 preserves much of a left dentary (Fig. 20M,N) with alveoli for the canine, a single-rooted P<sub>1</sub>, and double-rooted P<sub>2-4</sub> and M<sub>1-3</sub>. The premolars (not preserved) were all fully erupted, but M<sub>3</sub> in this specimen is little worn and the mandibular ramus is shallow (measuring only 10.0 mm in depth beneath M<sub>1</sub>), suggesting that the individual involved was a young adult. Other specimens have deeper mandibular rami but only one, UM 85596m, extends as far forward as M<sub>1</sub>: it measures 13.3 mm in depth at this point. Measurements of the teeth of *A. junnei* are summarized in Table 9.

*Discussion.* *Arfia* is one of the most common carnivorous mammals in early Wasatchian faunas of North America. The stratigraphic distribution of species and changes in tooth size through time are shown in Figure 21. *Arfia* is interesting in developing a more open trigonid on M<sub>3</sub> through time, indicating progressive carnassial development. This trend is illustrated in Figure 22.

The first two specimens of *Arfia* to be found at SC-67, UM 67664 and 71767, were collected in 1976. Deutsch (1979) included these in the hypodigm of a new but then unpublished North American species (*Arfia zeke* Gingerich and Deutsch, 1989). At about the same time, I was shown several isolated teeth of a small creodont from the early Eocene locality of Dormaal in Europe, and I suggested to M. Godinot that these should be compared with North American *Arfia*. B. Lange-Badré independently identified *Arfia* in the Dormaal fauna, and Lange-Badré and Godinot (1982) subsequently described a new species, *Arfia woutersi*, based on five isolated molars from Dormaal. Specimens described here from SC-67 and other Wa<sub>0</sub> localities are important in confirming that some of the European teeth represent a primitive species of the otherwise North American genus *Arfia*, and they are important in clarifying some confusion in the original description of *Arfia woutersi*.

Lange-Badré and Godinot (1982) did not designate a holotype for *Arfia woutersi*, but rather designated two different specimens as syntypes: WL1147 (which they identified as M<sup>1</sup>) and WL169 (which they identified as M<sub>2</sub>). Lange-Badré and Godinot's figures are uncaptioned. Their text identifies WL1147 as the upper molar shown in figure 1a (and presumably 1b). I infer, based on a comparison of measurements given in Lange-Badré and Godinot's table with measurements of their figures, that WL169 is probably the lower molar shown in their figures 3a, 3d, and 3g. The ratio of M<sub>2</sub> length/M<sup>1</sup> length in Lange-Badré and Godinot's table ranges from 0.89–0.94, while M<sub>2</sub> length/M<sup>1</sup> length in a sample of Clarks Fork Basin *Arfia* ranges from 1.15 to 1.31. M<sub>2</sub> is always 15–31% longer than M<sup>1</sup> in *Arfia*, not shorter as reported by Lange-Badré and Godinot.

New material at hand from SC-67 and other Wa<sub>0</sub> localities indicates that only one of Lange-Badré and Godinot's syntypes represents a species of *Arfia*, and this specimen is incorrectly identified to tooth position. The upper molar described by Lange-Badré and Godinot (1982), WL1147, which could be either an M<sup>1</sup> or M<sup>2</sup>, has a short metastyle separated from the metacone by a profound fosse. This is very different from M<sup>1</sup> or M<sup>2</sup> in *Arfia*, where there is no distinct metastylar cusp separated from the metacone, but rather a curved shearing postmetacrista that is continuous with the metacone. WL1147 and the species it represents cannot be placed in *Arfia*. Comparison of good casts of two of the Dormaal lower molars, probably CL14 and CL22 (casts provided by M. Godinot), with UM 87344 indicates that the three Dormaal teeth identified as M<sub>2</sub> are all virtually identical to the holotype M<sub>1</sub> of *Arfia junnei*. They do not have the high trigonid and squared talonid characteristic of M<sub>2</sub> and thus they cannot be M<sub>2</sub>s. The fifth Dormaal specimen, CL13 identified as an M<sub>3</sub> by Lange-Badré and Godinot, is much smaller than M<sub>3</sub> in *Arfia junnei* and it may represent a third taxon.

Given that Lange-Badré and Godinot's syntypes of "*Arfia*" *woutersi* represent two different taxa, it is neces-

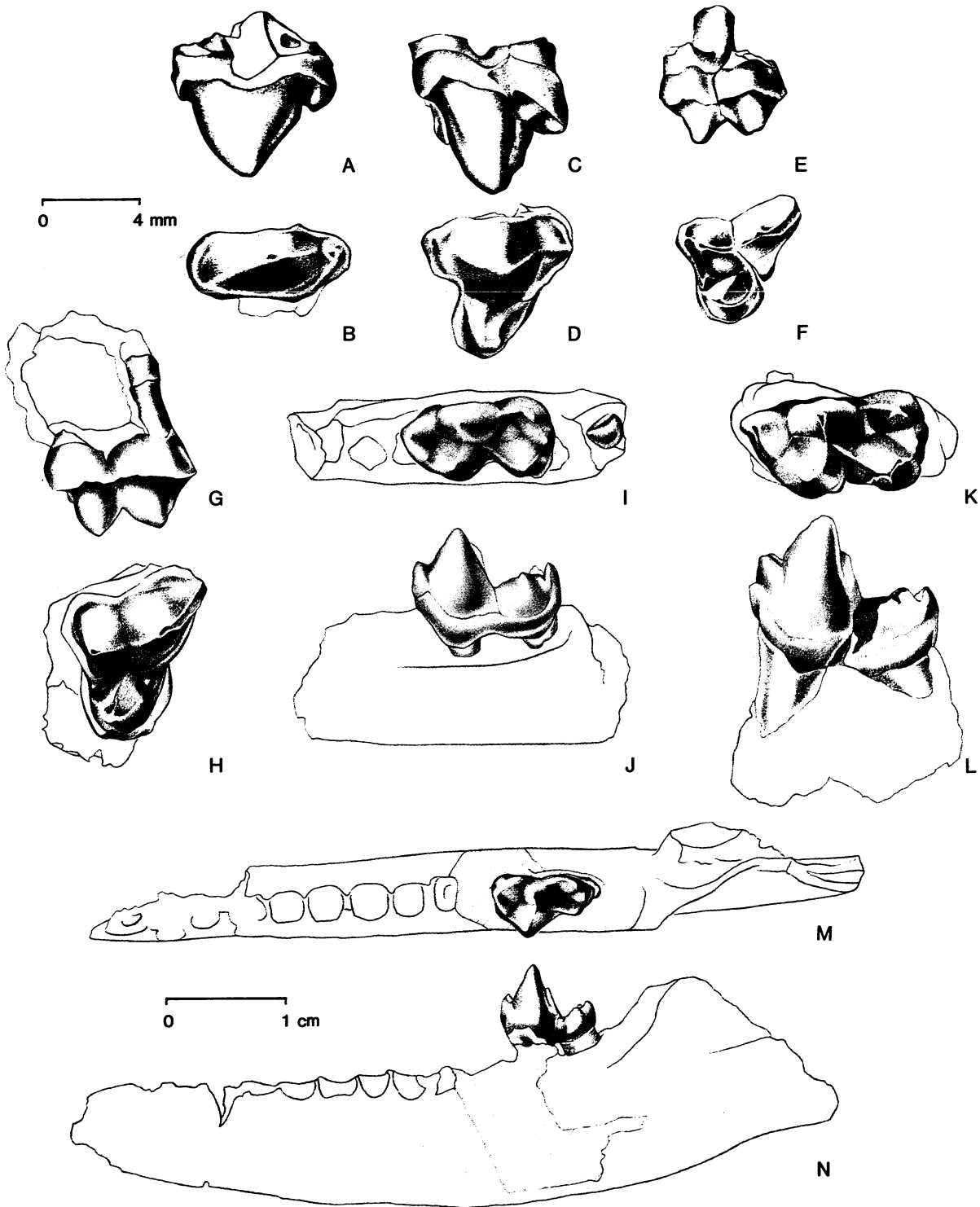


Figure 20. Dentition of *Arfia junnei*, new species. All specimens are shown in lateral and occlusal view. A and B, left P<sup>3</sup>, UM 83618m. C and D, left P<sup>4</sup>, UM 83623m. E and F, left dP<sup>4</sup>, UM 71767. G and H, left M<sup>1</sup>, UM 71767. I and J, left dentary of juvenile with freshly erupted M<sup>1</sup>, UM 87344 (holotype). K and L, left M<sup>2</sup>, UM 86135. M and N, left dentary of young adult with alveoli for C<sub>1</sub>-M<sub>2</sub> and the intact crown of M<sub>3</sub>, UM 83460.

CLARK'S FORK BASIN ARFIA

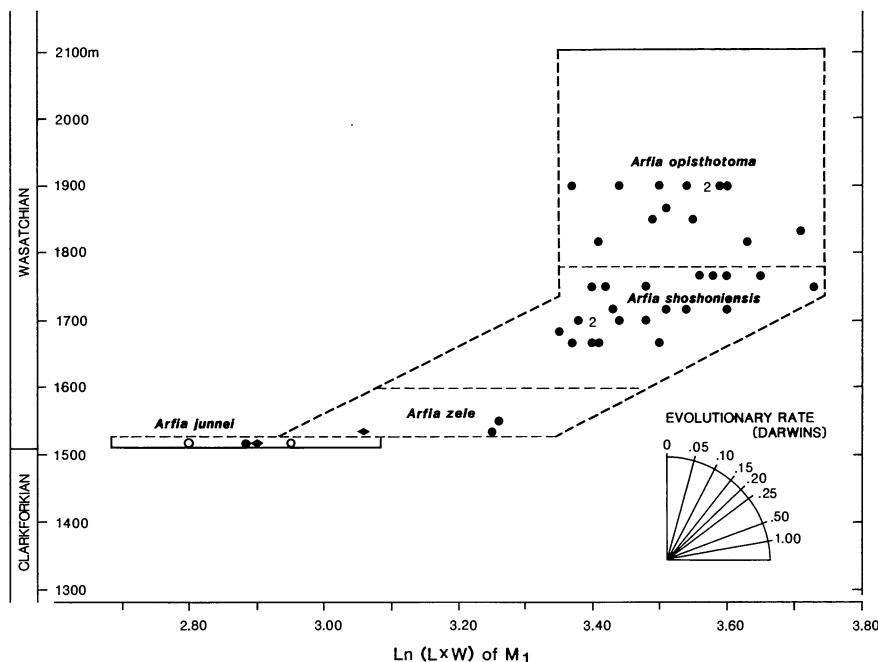


Figure 21. Stratigraphic distribution of early Wasatchian species of *Arfia*. Note the rapid increase in tooth size early in this lineage, followed by an interval of size stability (compare with trend in Figure 22). Symbols as in Figure 14. Specimens plotted here are in the UM collection.

Table 9. Measurements of *Arfia junnei* from  $W_{a_0}$

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
dP <sup>4</sup> L	1	5.0	-	-	-
dP <sup>4</sup> W	1	4.3	-	-	-
P <sup>2</sup> L	1	6.9	-	-	-
P <sup>2</sup> W	1	2.8	-	-	-
P <sup>3</sup> L	1	6.3	-	-	-
P <sup>3</sup> W	1	3.0	-	-	-
P <sup>4</sup> L	2	6.4 - 6.4	6.40	-	-
P <sup>4</sup> W	1	5.6	-	-	-
M <sup>1</sup> L	4	5.8 - 6.0	5.88	0.10	1.6
M <sup>1</sup> W	3	6.0 - 6.4	6.17	0.21	3.4
<i>Lower dentition</i>					
P <sub>3</sub> L	-	-	-	-	-
P <sub>3</sub> W	1	2.6	-	-	-
M <sub>1</sub> L	1	5.6	-	-	-
M <sub>1</sub> W	1	3.2 - 3.2	3.20	-	-
M <sub>2</sub> L	2	6.8 - 7.5	7.15	-	-
M <sub>2</sub> W	2	4.0 - 4.5	4.25	-	-
M <sub>3</sub> L	2	7.3 - 7.5	7.40	-	-
M <sub>3</sub> W	5	4.0 - 4.6	4.34	0.22	5.0
Mandibular depth:	2	10.1 - 13.3	11.73	-	-

Total number of specimens = 20

sary to designate a lectotype. Standard practice dictates that the lectotype be a syntype for which there is an unambiguously published illustration, and I here designate WL1147 as the lectotype of "*Arfia*" *woutersi*. This has the disadvantage of dissociating the species name *woutersi* from the genus to which it was first assigned (*woutersi* is whatever WL1147 is), but the general effect is positive in making the earliest species of *Arfia*, *A. junnei*, a species based on much more complete material than that originally described from Dormaal. Dormaal specimens CL-14, CL-22, and WL-169 are here referred to *A. junnei*; this is one of very few early Eocene species identified from both Europe and North America.

*Arfia junnei* brings to three the total number of proviverrine hyaenodontid creodonts known from zone  $W_{a_0}$ . This is the time of their first appearance in North America, and their morphological diversity on first appearance suggests that the group underwent its initial diversification elsewhere.

Subfamily LIMNOCYONINAE

***Prolimnocyon eerius*, new species**

Fig. 23

*Holotype and referred specimen.* Locality SC-67: UM 87353 (holotype). Locality SC-139: UM 83882 may possibly represent this species as well.



## CLARK'S FORK BASIN ARFIA

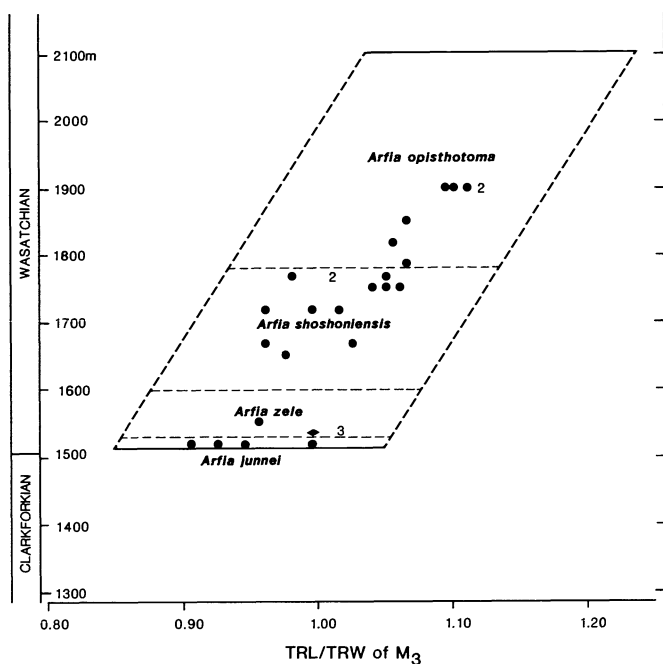


Figure 22. Trend toward more open trigonid on  $M_3$  in successive early and middle Wasatchian species of *Arfia*. Abscissa is ratio of trigonid length to trigonid width on  $M_3$ . Ordinate is stratigraphic level. Compare with trend in Figure 21. Symbols as in Figure 14. Specimens plotted here are in the UM collection.

**Diagnosis.** Differs from other species of *Prolimnocyon* in being significantly smaller and in having a broader stylar shelf on  $M^2$ . Differs from *P. haematus* in being about 12–16% smaller in linear dimensions, and from *P. atavus* in being about 24–32% smaller. The presence of a large stylar cusp on the labial margin of left and right  $M^2$  may be an additional species-level characteristic.

**Etymology.** *eerios*, Gr., early; this is the earliest known species of *Prolimnocyon*.

**Description.** The holotype is a crushed skull with  $P^4$ - $M^3$  preserved on the left side (Fig. 23A,B) and  $M^1$ - $M^3$  preserved on the right side. This skull includes the right squamosal, petrosal, and occipital condyle (Fig. 23C,D).  $P^4$  is typically hyaenodontid in having a large pointed labial cusp (metacone) and a strong postmetacrista separated from the metastylar continuation of this crest by a constricted carnassial fossette. There is a small but distinct protocone located lingually and a little anteriorly relative to the metacone.  $M^1$ - $M^2$  have the paracone and metacone positioned close together, and  $M^1$  has a strong postmetacrista-metastylar crest like that on  $P^4$ . There is a broad stylar shelf on the labial side of  $M^2$ , but the postmetacrista-metastylar crest is less strongly developed. There is a large accessory stylar cusp on both left and right  $M^2$  that may be either a

species-level characteristic or a unique development in this one individual.  $M^3$  is reduced in size, with a single labial cusp (paracone?) and a distinct protocone.  $M^3$  has a single labial root and one lingual root. Measurements of the upper cheek teeth are listed in Table 10.

The basicranium is well preserved on the right side of the skull (Fig. 23D). There is a prominent postglenoid process with associated postglenoid foramen. The petrosal has a moderately large fenestra rotunda opening posteroventrally and a fenestra ovale opening laterally. As in *Limnocyon* (see Matthew, 1909, p. 436), the ventral surface of the petrosal has faint but distinct grooves for both stapelial and promontory branches of the internal carotid artery. These divide from the internal carotid just in front of the fenestra rotunda. The groove for the stapelial branch extends to the cochlear window (fenestra ovale), and the groove for the promontory branch passes forward across the ventral surface of the promontorium toward the foramen lacerum medium. Wible (1986) considers the laterally placed transpromontorial position of the internal carotid observed here in *Prolimnocyon* to be the primitive condition in mammals.

The skull measures 47 mm in length, as preserved, from the front of  $P^4$  to the back of the remaining occipital condyle, and it measures about 30 mm in width across the zygomatic arches. For comparison, the holotype skull of *P. haematus* measures about 54 mm in length from the front of  $P^4$  to the back of the occipital condyles. The latter has a total skull length of 75 mm, and thus the total skull length in *P. eerios* is estimated to have been about 65 mm.

UM 83882 is a partial upper molar that resembles  $M^1$  and  $M^2$  in *P. eerios*, but is too fragmentary to be identified with certainty.

**Discussion.** *Prolimnocyon eerios* is distinctive in being the smallest species of the genus.  $M^3$  is greatly reduced, even in this early species, indicating that reduction of the last upper and lower molars was acquired early in the evolution of the genus. Rigby (1980) described a species of "*Prolimnocyon*" from the middle Paleocene of southern Wyoming based on six isolated teeth. The type of Rigby's species is an upper molar that looks much more like a pantolestid than a limnocyonine. Evidence presented by Rigby is inadequate to justify extending the history of *Prolimnocyon* into the North American Paleocene. On the contrary, it appears that *Prolimnocyon* is part of a hyaenodontid radiation that did not reach North America until  $Wa_0$  time.

Order CARNIVORA  
Family VIVERRAVIDAE

*Viverravus boweni* Gingerich, 1987

**Referred specimen.** Locality SC-67: UM 87339.

**Description.** This specimen includes a fragmentary left dentary fragment preserving the talonid of  $M_1$ . The whole tooth is estimated to have measured ca. 3.5 mm in length

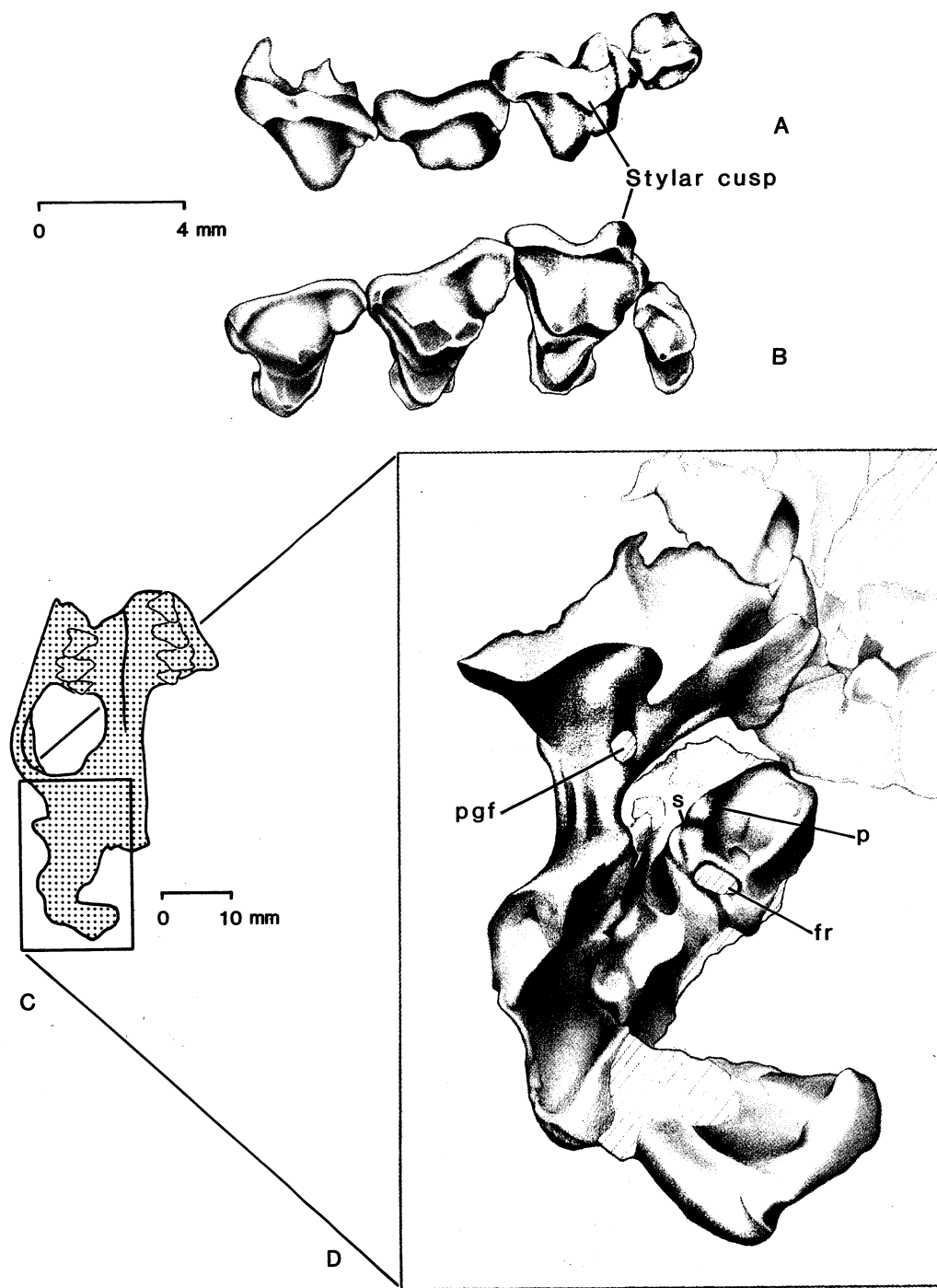


Figure 23. Dentition and partial cranium of *Prolimnocyon eerijs*, new species, UM 87353 (holotype). A and B, left P<sup>4</sup>-M<sup>3</sup> in lateral and occlusal view. Note large stylar cusp on labial cingulum of M<sup>2</sup>. C, outline of cranium, as preserved, in ventral view. D, right basicranium in ventral view. Abbreviations are as follows: *fr*, fenestra rotunda; *p*, promontory branch of internal carotid artery; *pgf*, postglenoid foramen; *s*, stapedial branch of internal carotid artery.

Table 10. Measurements of *Prolimnocyon eereus* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
P <sup>4</sup> L	1	4.1	-	-	-
P <sup>4</sup> W	1	3.5	-	-	-
M <sup>1</sup> L	1	4.1	-	-	-
M <sup>1</sup> W	1	4.1	-	-	-
M <sup>2</sup> L	1	4.1	-	-	-
M <sup>2</sup> W	1	5.1	-	-	-
M <sup>3</sup> L	1	1.7	-	-	-
M <sup>3</sup> W	1	3.3	-	-	-

Total number of specimens = 1

Table 11. Measurements of *Viverravus politus* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
M <sup>1</sup> L	1	4.6	-	-	-
M <sup>1</sup> W	1	5.9	-	-	-
M <sup>2</sup> L	1	2.2	-	-	-
M <sup>2</sup> W	1	4.6	-	-	-

Total number of specimens = 1

Table 12. Measurements of *Didymictis leptomytus* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
C <sup>1</sup> L	1	4.1	-	-	-
C <sup>1</sup> W	1	3.3	-	-	-
P <sup>2</sup> L	1	5.9	-	-	-
P <sup>2</sup> W	1	2.7	-	-	-
P <sup>3</sup> L	1	6.8	-	-	-
P <sup>3</sup> W	1	3.5	-	-	-
P <sup>4</sup> L	2	7.8 - 8.7	8.25	-	-
P <sup>4</sup> W	1	6.3	-	-	-
M <sup>1</sup> L	2	5.6 - 6.5	6.05	-	-
M <sup>1</sup> W	-	-	-	-	-
M <sup>2</sup> L	1	3.6	-	-	-
M <sup>2</sup> W	-	-	-	-	-
<i>Lower dentition</i>					
C <sub>1</sub> L	1	3.7	-	-	-
C <sub>1</sub> W	1	3.0	-	-	-
P <sub>1</sub> L	2	5.6 - 6.1	5.85	-	-
P <sub>1</sub> W	2	2.2 - 2.6	2.40	-	-
P <sub>2</sub> L	3	6.6 - 8.0	7.23	0.71	9.8
P <sub>2</sub> W	3	2.7 - 3.5	3.07	0.40	13.2
P <sub>3</sub> L	2	7.9 - 8.7	8.30	-	-
P <sub>3</sub> W	2	4.0 - 4.0	4.00	-	-
M <sub>1</sub> L	3	6.6 - 7.6	7.27	0.58	7.9
M <sub>1</sub> W	5	4.6 - 5.0	4.86	0.17	3.4
M <sub>2</sub> L	4	6.0 - 6.8	6.48	0.36	5.6
M <sub>2</sub> W	4	3.3 - 4.2	3.78	0.38	10.0
Mandibular depth:	2	9.6 - 11.7	10.65	-	-

Total number of specimens = 13

and 2.0 mm in width. The specimen also includes a fragmentary right dentary with the crown of P<sub>4</sub> (measuring ca. 3.2 mm in length).

*Discussion.* This small viverravid matches the type and referred specimens of *V. boweni* closely in size and form. The species is present at underlying Clarkforkian and overlying Wasatchian localities.

*Viverravus politus* Matthew, 1915

*Referred specimen.* Locality SC-67: UM 87857.

*Description.* UM 87857 is a left maxilla with M<sup>1-2</sup>. M<sup>1</sup> has the symmetrical stylar shelf, broad flat trigon, strong preprotocrista, and weak postprotocrista characteristic of *Viverravus*. M<sup>2</sup> is not well preserved, but it too clearly had a broad flat trigon. Measurements of *V. politus* are listed in Table 11.

*Discussion.* This specimen compares well with other early Wasatchian specimens of *Viverravus politus*, differing only in being a little smaller. The holotype of this species, AMNH 16113, was collected from "Point of Bluff N. of Ralston, upper strata" (according to American Museum field catalogue for Eocene Expedition, Wyoming, 1912, field no. 213). The specimen is dark in color, with black teeth, which might indicate that it came from a level above Wa<sub>0</sub>.

*Didymictis leptomytus* Cope, 1880

*Referred specimens.* Locality MP-40: UM 88170m. Locality SC-67: UM 71765, 71766, 83623m, 83630, 83635, 83636m, 83661, 83664m, 85590, 86003m, 87859m, and 92356m. Locality SC-79: 65623m.

*Description.* The most complete specimen of *Didymictis leptomytus* from zone Wa<sub>0</sub> is UM 83661, which includes good parts of both maxillae with both lower jaws in occlusion, and associated cranial fragments. The dentition of *D. leptomytus* is well known and need not be described here. Dental measurements of Wa<sub>0</sub> *D. leptomytus* are summarized in Table 12.

*Discussion.* *Didymictis leptomytus* is a small species of

the genus known from underlying Clarkforkian and overlying Wasatchian strata.

Family MIACIDAE

*Miacis winkleri* Gingerich, 1983

*Referred specimens.* Locality SC-67: UM 77203m. Locality SC-348: UM 83815. Locality SC-350: UM 83820.

*Description.* All three specimens are fragmentary dentaries preserving the talonid of M<sub>1</sub>. One specimen, UM 83820, includes the complete crown of M<sub>2</sub>. The crown measures 3.6 mm in length and 2.6 mm in width, and the trigonid measures 3.3 mm in height (height of the protocone above the base of the crown). The ratio of M<sub>2</sub> trigonid

height to crown width is 1.27, which lies within the range 1.27–1.44 observed in four specimens of *Miacis winkleri* and well above the range 1.07–1.18 observed in six specimens of *M. deuschi*. The talonid of  $M_2$  is narrow and a little less basined than is observed in most early *Miacis*. Mandibular depth ranges from 6.5 mm to 7.2 mm in the three specimens.

**Discussion.** Early *Miacis* from Europe, Asia, and North America are all very similar. *Miacis latouri* Quinet, 1968 from the early Sparnacian, at Dormaal in Belgium and *Miacis tenuis* (Zhen et al., 1975) from the early Eocene at Ningjiashan (Xinyu Formation, Jiangxi Province) in China each preserve  $P^4$  and  $M^1$ , and these are virtually identical to each other in size and form. The only difference of note is that the anterior and posterior cingula on  $M^1$  in *M. latouri* are a little more strongly developed than those of *M. tenuis*. Both are similar in size to *M. winkleri*. *M. latouri* and *M. winkleri* cannot be compared in detail because the former is based on upper cheek teeth and the latter on lowers. *M. tenuis* differs from  $Wa_0$  *M. winkleri* in having a lower trigonid on  $M_2$  (the trigonid height to crown width ratio here is about 1.18). Meaningful comparison of these three species will require more complete specimens.

Order RODENTIA  
Family PARAMYIDAE

Clarkforkian and early Wasatchian paramyid rodents are very generalized in dental morphology and they are usually known from small samples of fragmentary remains. Consequently paramyids are difficult to identify. Three species appear to be represented in the sample from  $Wa_0$  localities described here (Fig. 24). These differ in size, and they differ to a limited extent in cheek tooth morphology. Each has been identified using recent reviews of latest Paleocene and early Eocene rodents by Rose (1981), Korth (1984), and Ivy (1989).

Cf. *Acritoparamys atavus* (Jepsen, 1937)

**Referred specimen.** Locality SC-67: UM 86003m.

**Description.** This specimen is a small isolated lower incisor [measuring  $2.1 \times 1.1$ ].

**Discussion.** Cf. *Acritoparamys atavus* is the smallest paramyid from  $Wa_0$ . The tooth on which this record is based is dark in color, with black enamel, and it is added questionably to the  $Wa_0$  faunal list because it may possibly be a contaminant from a higher stratigraphic level. The species is, in any case, present in both Clarkforkian and later Wasatchian strata.

*Acritoparamys atwateri* (Loomis, 1907)

**Referred specimens.** Locality SC-67: UM 79890m, 82383, 83468, 86572m, 87354m, and 92351. Locality SC-308: UM 76237m. Locality SC-351: UM 86564.

**Description.** This species is represented by several den-

aries with one or two teeth, and by several isolated incisors and cheek teeth. UM 86572m includes an isolated right  $M^1$  or  $M^2$ . The most complete dentary is UM 83468, a right dentary with  $I_1$ , and intact crowns of  $P_4$  and  $M_3$ . This specimen preserves an accessory mental foramen below the posterior part of  $P_4$ , and the jaw measures 6.9 mm in depth beneath  $M_1$ . UM 82383 is a left dentary fragment with  $M_1$ , and UM 86564 is a left dentary with  $I_1$ ,  $M_2$ , and a jaw measuring about 7.5 mm in depth beneath  $M_1$ . UM 92351 is a left dentary fragment with  $M_3$ . Measurements of  $Wa_0$  *A. atwateri* are summarized in Table 13.

**Discussion.** Specimens described here have an accessory mental foramen and an elongated hypoconulid connected to the hypoconid and separated from the entoconid, characteristics listed by Korth (1984) as diagnostic of *Acritoparamys*. They match *A. atwateri* closely in size and form. Korth (1984) and Ivy (1989) consider this species to be present in strata of both Clarkforkian and early Wasatchian age.

*Paramys taurus* Wood, 1962

**Referred specimens.** Locality SC-67: UM 66617m, 75422, 79890m, 83478m (two specimens), 83636m, and 86572m. Locality SC-139: UM 83568. Locality SC-350: UM 83821m.

**Description.** Most specimens are jaw fragments and/or incisors. One dentary fragment, UM 75422, measures 6.9 in depth below  $M_1$ , and another, UM 83636m, measures 7.5 in depth. The latter has the small accessory mental foramen said to be diagnostic of *Acritoparamys*. The only cheek teeth are UM 66617m, a right  $M^1$  or  $M^2$ ; UM 86572m, a left  $M^3$ ; and UM 79890m, a right  $M_3$ . Measurements of  $Wa_0$  *P. taurus* are summarized in Table 14.

**Discussion.** These remains are very fragmentary, but they conform closely to the taxon identified as *Paramys taurus* by Korth (1984) and Ivy (1989). This species too is present in Clarkforkian and later Wasatchian strata.

Order CONDYLARTHRA  
Family ARCTOCYONIDAE

*Thryptacodon barae*, new species

Fig. 25

**Holotype and referred specimen.** Locality MP-38: UM 88160. Locality SC-121: UM 85669 (holotype).

**Diagnosis.** Smallest species of *Thryptacodon*. Differs from Tiffanian *Thryptacodon australis* in being 11–14% smaller in linear dimensions, from Clarkforkian *Thryptacodon* cf. *T. antiquus* and most early Wasatchian *T. antiquus* in being 15–25% smaller in most linear dimensions. Differs from late Wasatchian *T. loisi* in being 3–11% smaller, in having the same sized protoconid and metacoconid size on  $M_2$ , and retaining a distinct hypoconulid on  $M_2$ .

**Etymology.** Named for Ms. Bara Badgley who found the holotype and a number of other important  $Wa_0$  specimens.

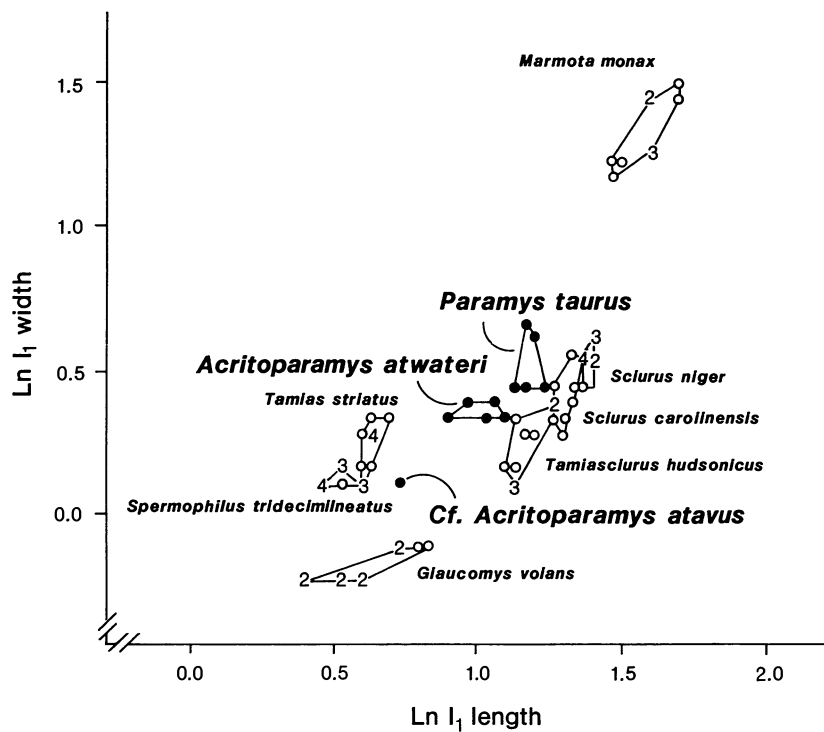


Figure 24. Size and shape of paramyid rodent incisors from earliest Wasatchian zone  $Wa_0$  in relation to those of seven species of living Sciuridae. Diagram indicates that a minimum of three species of Paramyidae are present in zone  $Wa_0$ . Abscissa is natural logarithm of maximum diameter of lower incisor measured in cross-section (crown length, not incisor length). Ordinate is natural logarithm of transverse diameter of lower incisor (crown width). Living specimens are all from Washtenaw County, Michigan (UM Museum of Zoology collection). Note that incisors of extant *Spermophilus*, *Tamias*, and *Marmota* are wider relative to their length than incisors of extant *Glaucomys*, *Tamiasciurus*, and *Sciurus* (falling on a line of similar slope but a higher intercept on the width axis). Incisors of *Acritoparamys* and *Paramys* are intermediate in shape. *Cf. Acritoparamys atavus* was probably about the size of living *Tamias striatus*, *Acritoparamys atwateri* was probably about the size of living *Tamiasciurus hudsonicus*, and *Paramys taurus* was probably about the size of living *Sciurus carolinensis*. Cheek teeth of Paramyidae and Sciuridae are similar functionally, and extant sciurids may be good living models for extinct paramyids.

**Description.** UM 88160 is a right  $M_1$  with a broken trigonid and complete talonid (Fig. 25C,D). The trigonid is more massive than that on  $M_1$  of *Chriacus*, but the position of cusps cannot be determined because of breakage. The talonid is broader than the trigonid, and it has the intermediate basin depth, moderately angled crests, small cusped hypoconulid, and moderately-sized sloping posterior cingulum typical of *Thryptacodon*. The holotype, UM 85669, is a right dentary fragment with intact crowns of  $M_2$  and  $M_3$  (Fig. 25A,B). Paraconids on these molars are located in the center of the anterior margin of the trigonid, a distinctive characteristic of *Thryptacodon*. The protoconid and metaconid are very nearly equal in size on both teeth. Talonids on  $M_2$  and  $M_3$  resemble that on  $M_1$ .  $M_3$  has a more anteroposteriorly elongated hypoconulid than is

typical of most *Thryptacodon*. Measurements of  $Wa_0$  *T. barae* are listed in Table 15.

**Discussion.** The limited material at hand is sufficient to document the presence of a distinctively small species of *Thryptacodon* in zone  $Wa_0$  (Fig. 26). This species differs sharply in size from Clarkforkian specimens identified as *Thryptacodon* cf. *T. antiquus* by Rose (1981). Intermediate specimens from the base of zone  $Wa_1$  suggest that later Wasatchian *T. antiquus* may be derived directly from *T. barae*.

***Chriacus badgleyi*, new species**

Fig. 27

**Holotype and referred specimens.** Locality SC-67: UM 79887 (holotype), 87348, and questionably 82387. Local-

Table 13. Measurements of *Acritoparamys atwateri* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
M <sup>1/2</sup> L	1	2.0	-	-	-
M <sup>1/2</sup> W	1	2.5	-	-	-
<i>Lower dentition</i>					
I <sub>1</sub> L	5	2.5 - 3.0	2.76	0.21	7.5
I <sub>1</sub> W	5	1.4 - 1.5	1.44	0.05	3.8
P <sub>4</sub> L	1	2.1	-	-	-
P <sub>4</sub> W	1	1.7	-	-	-
M <sub>1</sub> L	1	2.3	-	-	-
M <sub>1</sub> W	1	2.2	-	-	-
M <sub>2</sub> L	1	2.4	-	-	-
M <sub>2</sub> W	1	2.3	-	-	-
M <sub>3</sub> L	2	2.7 - 2.8	2.75	-	-
M <sub>3</sub> W	2	2.1 - 2.1	2.10	-	-
Mandibular depth:	3	6.9 - 7.5	7.27	0.32	4.4
Total number of specimens = 8					

Table 14. Measurements of *Paramys taurus* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
M <sup>1/2</sup> L	1	2.7	-	-	-
M <sup>1/2</sup> W	1	3.2	-	-	-
M <sup>3</sup> L	1	2.7	-	-	-
M <sup>3</sup> W	1	2.4	-	-	-
<i>Lower dentition</i>					
I <sub>1</sub> L	5	3.1 - 3.4	3.24	0.11	3.5
I <sub>1</sub> W	6	1.6 - 1.9	1.72	0.13	7.7
M <sub>3</sub> L	1	3.0	-	-	-
M <sub>3</sub> W	1	2.5	-	-	-
Mandibular depth:	2	6.9 - 8.8	7.85	-	-
Total number of specimens = 9					

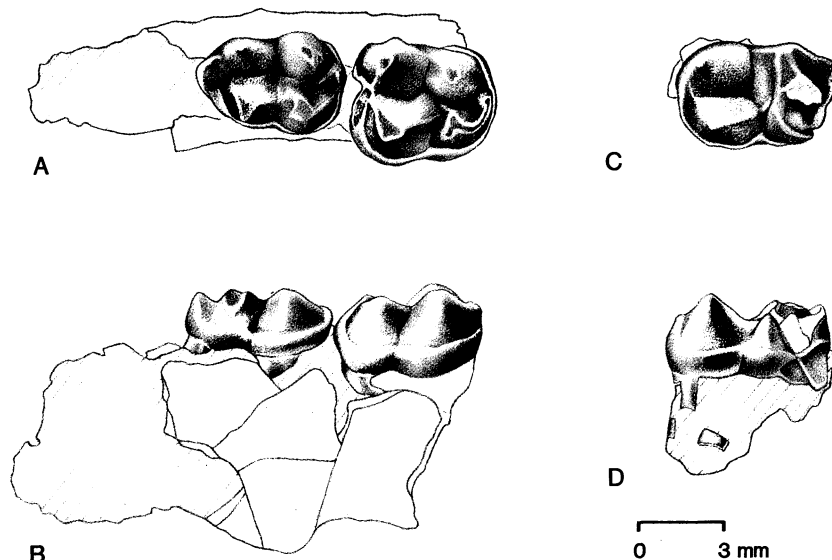


Figure 25. Lower molar dentition of *Thryptacodon barae*, new species. A and B, right M<sub>2,3</sub>, UM 85669 (holotype), in occlusal and lateral view. C and D, right M<sub>1</sub>, UM 88160m, in occlusal and lateral view.

ity SC-79: 83647m (two specimens). Locality SC-121: UM 83461 and 83463. Locality SC-342: UM 83572 is questionably referred to this species.

**Diagnosis.** Differs from Torrejonian *Chriacus pelvidens* and Tiffanian *C. oconostotae* in being some 26–37% smaller in linear dimensions and in lacking a metaconid on P<sub>4</sub>. Differs from Wasatchian *C. gallinae* in being 18–24% smaller.

**Etymology.** Named for Dr. Catherine Badgley in recognition of her important contributions to understanding fau-

nal turnover in the early Eocene. The family name Badgley is considered neutral in gender, hence *i* is the appropriate genitive suffix.

**Description.** The only maxilla is UM 83461 (Fig. 27A,B), a fragmentary specimen preserving P<sub>4</sub> and most of M<sup>1</sup> (measuring 5.5 mm in width). A second specimen, UM 83572, questionably referred, preserves a larger M<sup>1</sup> (5.7 mm in length and 5.9 mm in width). P<sub>4</sub> has a single prominent labial cusp, and a small lingual protocone. M<sup>1</sup> is nearly square, with a simple tritubercular crown and a

Table 15. Measurements of *Thryptacodon barae* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Lower dentition</i>					
M <sub>1</sub> L	1	5.6	-	-	-
M <sub>1</sub> W	1	3.8	-	-	-
M <sub>2</sub> L	1	5.0	-	-	-
M <sub>2</sub> W	1	4.2	-	-	-
M <sub>3</sub> L	1	5.3	-	-	-
M <sub>3</sub> W	1	3.8	-	-	-

Total number of specimens = 2

broad lingual cingulum. Two right upper canines are known, both catalogued as UM 83647m. Each has the base of the crown preserved. The upper canine crowns are convex on their lingual surfaces but nearly flat on their labial surfaces. The posterior edge is sharply keeled and blade-like, but it is not serrated. Enamel on these upper canines has a finely pebbled texture like that on the lower canine of the holotype.

The holotype, UM 79887 (Fig. 27E,F), is a right dentary with the alveoli for I<sub>1-3</sub> inclined at an angle of about 45° relative to the horizontal ramus. The root and base of the crown of one incisor, probably I<sub>2</sub>, is also preserved. The base of this incisor crown preserves the very posteriormost part of a central rib flanked by a lateral groove, showing that the crown was styliiform and procumbent. Thus *C. badgleyi* probably had a tooth comb like that described for *Thryptacodon* (Gingerich and Rose, 1979).

The lower canine is oval in cross-section, and its posterior edge is sharply keeled and bladelike but again it is not serrated. P<sub>1</sub> was single-rooted. P<sub>2-4</sub> all have high narrow crowns with a sharply pointed apical cusp. P<sub>4</sub> has a very small anterior basal cusp, and both P<sub>3</sub> and P<sub>4</sub> have very short talonids. Mental foramina are present beneath the crown of P<sub>1</sub> and beneath the anterior half of P<sub>3</sub>, and the mandibular ramus measures 9.9 mm in depth beneath M<sub>1</sub>.

Two specimens, UM 83463 and 87348, preserve crowns of M<sub>1</sub>. The best preserved, UM 87348 (Fig. 27C,D), has a short open trigonid with a prominent paraconid well anterior to the protoconid and metaconid. The hypoconid is sharply angled. The entoconid is smaller, and the hypoconulid is reduced to little more than a part of the shelf curving downward and labially from the entoconid. This posterior shelf is continuous with a cingulid that extends along the labial side and around the front of the tooth. Measurements of the teeth of Wa<sub>0</sub> *C. badgleyi* are summarized in Table 16.

**Discussion.** *Chriacus*, like *Thryptacodon*, is represented by an unusually small species in zone Wa<sub>0</sub> (Fig. 28). However this genus is less common than *Thryptacodon* in Wasatchian localities, meaning that its evolution cannot be traced with the same level of confidence.

### Princetononia, new genus

*Type species. Princetononia yalensis*, new species.

*Included species.* Type species only.

*Diagnosis.* Small arctocyonid distinct from all others in combining a relatively long, narrow P<sub>4</sub> lacking a metaconid, with relatively short and broad rectangular molars having low, broad, forwardly-inclined trigonids and broadly basined talonids. The lingual position of the paraconid, the anteroposterior shortness of the trigonid, and the breadth and shallowness of the talonid distinguish this form from any species of *Thryptacodon*. The low trigonids, rectangular shape of M<sub>2-3</sub>, and more rounded molar cusps and crests distinguish this form from any species of *Chriacus*.

*Etymology.* Most specimens of *Princetononia*, including the holotype, were collected by Princeton University expeditions.

### Princetononia yalensis, new species

Fig. 29

*Holotype and referred specimens.* Locality SC-121(?): YPM-PU 23629. The label with the holotype says "SW corner of Polecat Bench, Park Co., Wyo.," which could indicate either locality SC-67, SC-69, SC-121, or SC-308. The specimen is light in color and there can be little doubt that it comes from zone Wa<sub>0</sub>.

This species is also represented by YPM-PU 13943, 13957, 13976, 14115, 14316, 14321, 17643, and five unnumbered fragmentary jaws and teeth from Princeton Quarry of late Tiffanian age; YPM-PU 19398 and 19467 from Schaff Quarry of late Tiffanian age; and UM 71175, 71563, 74133, 77577, and 77289 from localities of middle and late Clarkforkian age.

*Diagnosis.* As for the genus.

*Etymology.* Named for Yale University, where the holotype and most specimens of this species are conserved.

*Description.* The holotype, YPM-PU 23629 (Fig. 29), is a right dentary preserving part of the crown of a relatively long and narrow P<sub>4</sub>. When whole, this tooth measured approximately 5.5 mm in length and 2.4 mm in width. In addition, the holotype preserves intact crowns of M<sub>2</sub> and most of the crown of M<sub>3</sub>. M<sub>2</sub> is rectangular in occlusal outline, with a short, broad, and low trigonid. The paraconid is positioned on the lingual side of the trigonid, close to the metaconid, and it is only slightly smaller than the latter cusp. The talonid is broadly basined, with a reduced hypoconulid and a curving posterior shelf. M<sub>3</sub> resembles M<sub>2</sub>, differing principally in being narrower and probably also in having a slightly larger hypoconulid (broken in this specimen). Measurements of the Wa<sub>0</sub> holotype of *P. yalensis* are listed in Table 17.

**Discussion.** Referred specimens from Princeton Quarry show that this species lacked a metaconid on P<sub>4</sub>, and that the configuration of crests connecting cusps (particularly the paraconid and metaconid) on the molar trigonids was somewhat variable. The paraconid is not centered on the

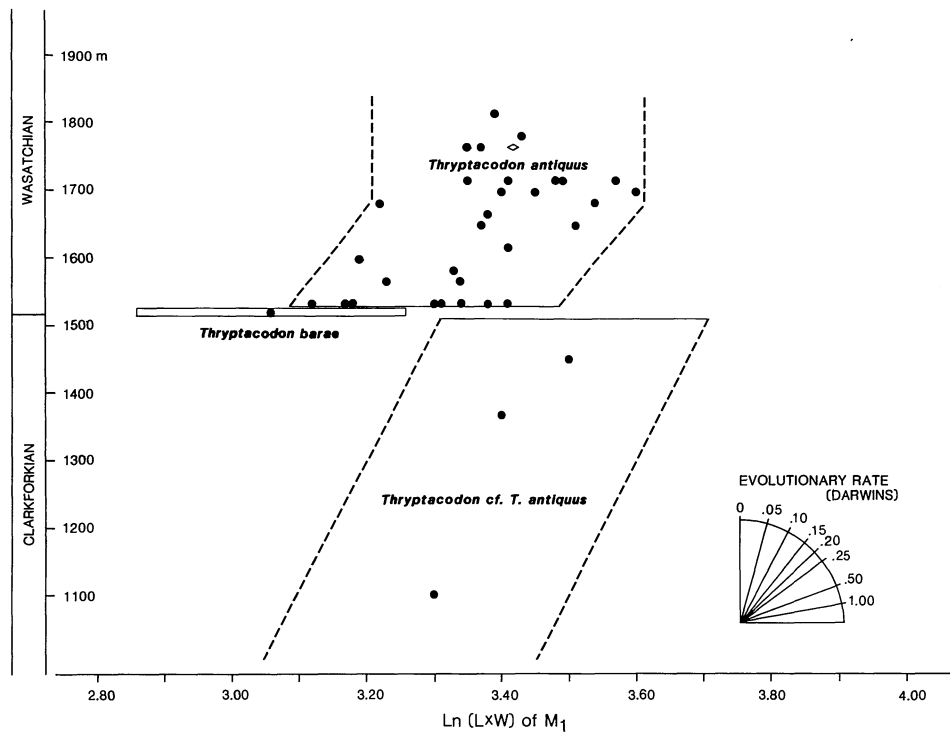
CLARK'S FORK BASIN *THRYPTACODON*

Figure 26. Stratigraphic distribution of Clarkforkian and early Wasatchian *Thryptacodon* in the Clarks Fork Basin, Wyoming. Note increasing size of Clarkforkian *Thryptacodon* cf. *T. antiquus*, and its replacement by Wasatchian *T. barae* and *T. antiquus*. The latter recapitulates, in part at least, the earlier trend toward larger size. Symbols as in Figure 14. Specimens plotted here are in the UM collection.

Table 16. Measurements of *Chriacus badgleyi* from  $W_{a_0}$

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
C <sup>1</sup> L	2	4.2 - 4.3	4.25	-	-
C <sup>1</sup> W	2	2.9 - 3.0	2.95	-	-
P <sup>4</sup> L	1	4.7	-	-	-
P <sup>4</sup> W	1	4.3	-	-	-
M <sup>1</sup> L	-	-	-	-	-
M <sup>1</sup> W	1	5.5	-	-	-
<i>Lower dentition</i>					
I <sub>2</sub> L	1	1.6	-	-	-
I <sub>2</sub> W	1	0.9	-	-	-
C <sub>1</sub> L	1	4.4	-	-	-
C <sub>1</sub> W	1	2.6	-	-	-
P <sub>3</sub> L	1	5.1	-	-	-
P <sub>3</sub> W	1	2.5	-	-	-
P <sub>4</sub> L	1	5.6	-	-	-
P <sub>4</sub> W	1	2.7	-	-	-
M <sub>1</sub> L	2	5.2 - 5.4	5.30	-	-
M <sub>1</sub> W	2	3.4 - 3.4	3.40	-	-
Mandibular depth:	1	9.9	-	-	-
Total number of specimens = 6					

trigonid as it is in *Thryptacodon*. Lower molars are not as long and narrow, and upper molars do not have the wide sweeping posterolingual cingulum characteristic of *Chriacus*. Rose (1981, p. 69 and 156) referred many of the specimens here described as *Princetonia* to cf. *Tricentes* sp., noting that the taxon involved may be closely allied to or derived from middle Paleocene *Tricentes punitor*. *Princetonia yalensis* may be derived from *T. punitor*, but it differs from that taxon in having more rectangular lower molars, in having a more lingual paraconid, and in having lower trigonids.

## Family MESONYCHIDAE

*Dissacus praenuntius* Matthew, 1915

*Referred specimens.* Locality SC-67: UM 83477, 83631, 83478m, and 87337.

*Description.* UM 87337 is an upper molar, M<sup>1</sup> or M<sup>2</sup>, with large, well separated trigon cusps, the protocone being the largest cusp and the metacone being slightly smaller than the paracone. UM 83631 includes associated crowns of C<sub>1</sub>, P<sub>2</sub>, and P<sub>4</sub>-M<sub>3</sub>. The molars are typical of early Eo-



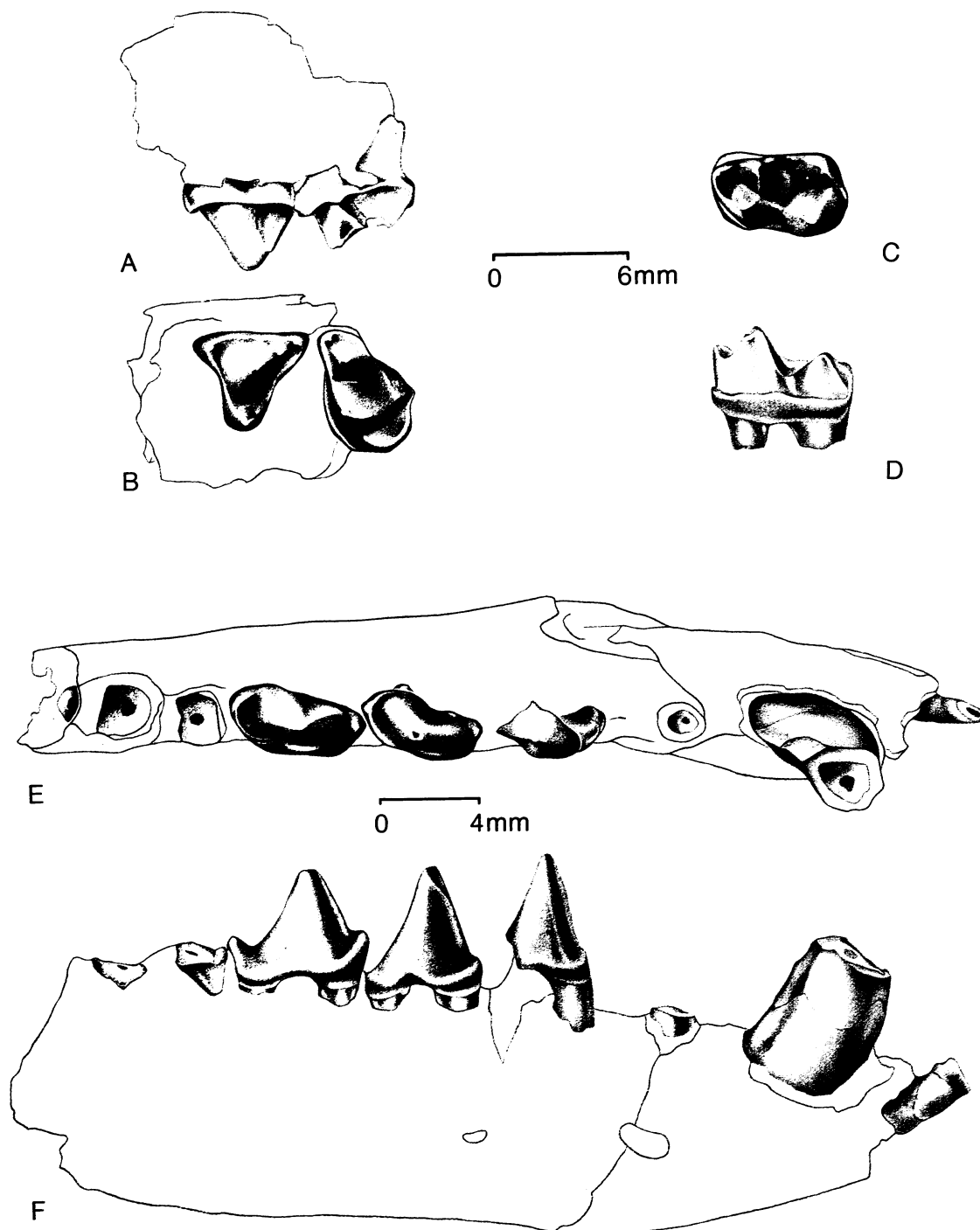


Figure 27. Dentition of *Chriacus badgleyi*, new species. A and B, left maxilla with P<sup>4</sup>-M<sup>1</sup>, UM 83461, in lateral and occlusal view. C and D, left M<sub>1</sub>, UM 87348, in occlusal and lateral view. E and F, right dentary, UM 79887 (holotype), in occlusal and lateral view.

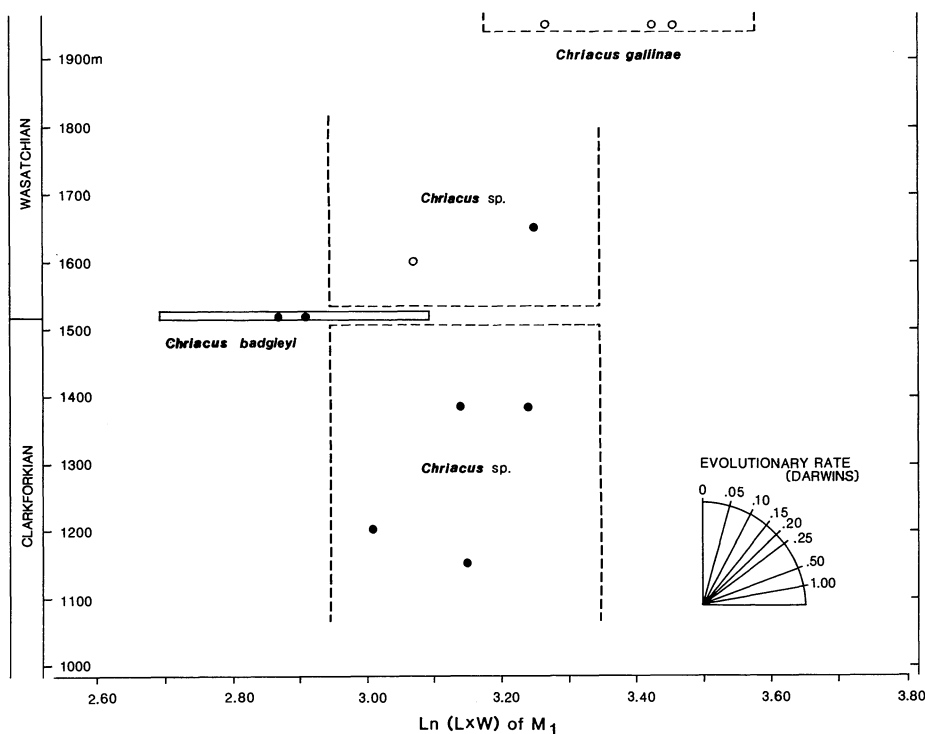
CLARK'S FORK BASIN *CHRIACUS*

Figure 28. Stratigraphic distribution of Clarkforkian and early Wasatchan *Chriacus* in the Clarks Fork Basin, Wyoming. *C. badgleyi* is well outside the range of *C. gallinae* in tooth size. *Chriacus* intermediate between the two, here designated *C. sp.*, are present in the Clarkforkian and again in the early Wasatchian, but too few specimens are known to permit determination of their evolutionary trends or relationships. Symbols as in Figure 14. Specimens plotted here are in the UM collection.

cene *Dissacus* in having distinct paraconids, in having  $M_1$  approximately the same size as  $M_2$ , and in having a reduced talonid on  $M_3$ . Measurements of  $Wa_0$  *D. praenuntius* are listed in Table 18.

**Discussion.** Matthew's (1915, p. 86) diagnoses of *Dissacus praenuntius* and *D. longaevus* are insufficient to distinguish these species; however, he does seem to be correct in recognizing two species of *Dissacus* in the Clarks Fork and northern Bighorn basins. The two differ in size, in the relative length of the lower jaw, and in the relative size and shape of  $P_3$ . Specimens in the University of Michigan collection show that the larger species ranges from zones  $Cf_1$  through  $Wa_1$ ; it has a relatively longer lower jaw, and  $P_3$  resembles  $P_4$  in size and shape. The holotype of *D. praenuntius* was collected from Clarkforkian beds at the head of Big Sand Coulee, and this name is consequently appropriate for the larger species (Rose, 1981, p. 86).

The smaller species of *Dissacus* ranges from the top of zone  $Wa_2$  through at least  $Wa_3$ : it has a relatively shorter lower jaw, and  $P_3$  is distinctly smaller than  $P_4$ , with a simpler crown. According to the American Museum of

Natural History Bighorn Wasatch field book for 1911, the holotype of *D. longaevus* was collected on August 21 from "4 mi. So. of Shoshoni R., 1st Camp, lower beds" (specimen field no. 132). In a letter dated August 24, from Walter Granger in the field to W. D. Matthew at the American Museum, Granger explains that they have been camped on the south side of the Shoshoni River, working the lower exposures on the eastern slope of the McCullough Peaks. This does not establish the type locality of *D. longaevus* very precisely, but Granger also notes that "*Eohippus*" (= *Hyracotherium*) and "*Systemodon*" (= *Homogalax protapirinus*) are abundant in this area, which indicates that the field party was collecting at the very top of zone  $Wa_2$  and in zone  $Wa_3$  or even  $Wa_4$ . Thus *Dissacus longaevus* is the appropriate name for the smaller *Dissacus* present in this interval.

There is no  $P_3$  preserved in the specimens of *Dissacus* known from locality SC-67, but the molars of UM 83631 match late Clarkforkian and early Wasatchian *D. praenuntius* very closely in size and shape, and all may be referred to this species.

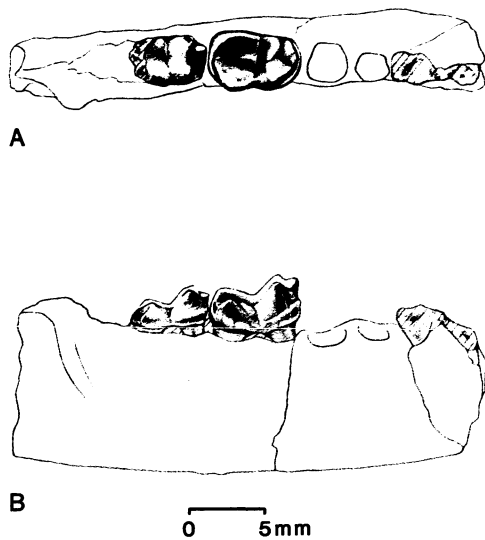


Figure 29. Dentition of *Princetonia yalensis*, new species. A and B, right dentary, YPM-PU 23629 (holotype), in occlusal and lateral view.

Table 17. Measurements of *Princetonia yalensis* from  $W_{a_0}$

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Lower dentition</i>					
M <sub>2</sub> L	1	5.3	-	-	-
M <sub>2</sub> W	1	4.0	-	-	-
M <sub>3</sub> L	1	5.3	-	-	-
M <sub>3</sub> W	1	3.4	-	-	-
Mandibular depth:	1	9.1	-	-	-
Total number of specimens = 1					

Table 18. Measurements of *Dissacus praenuntius*

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
M <sup>1/2</sup> L	1	12.2	-	-	-
M <sup>1/2</sup> W	1	10.1	-	-	-
<i>Lower dentition</i>					
P <sub>2</sub> L	1	9.2	-	-	-
P <sub>2</sub> W	1	4.9	-	-	-
P <sub>4</sub> L	1	13.2	-	-	-
P <sub>4</sub> W	1	5.8	-	-	-
M <sub>1</sub> L	1	14.2	-	-	-
M <sub>1</sub> W	1	6.6	-	-	-
M <sub>2</sub> L	1	14.0	-	-	-
M <sub>2</sub> W	1	6.6	-	-	-
M <sub>3</sub> L	1	11.3	-	-	-
M <sub>3</sub> W	1	5.4	-	-	-
Total number of specimens = 4					

*Pachyaena ossifraga* Cope, 1874

*Referred specimen.* Locality SC-348: UM 83813.

*Description.* UM 83813 is the trigonid of a right molar measuring 9.9 mm in maximum width. The specimen is worn in an unusual way, but comparison with other more complete specimens of *Pachyaena ossifraga* leaves little doubt that this is the species represented.

*Discussion.* This is the oldest record of *Pachyaena* in North America.

Family HYOPSODONTIDAE

*Hyopsodus loomisi* McKenna, 1960

Fig. 30

*Referred specimens.* Locality SC-67: UM 66614, 74075, 79886, 79891, 82382, 83612, 83625, 83664m, 85592, 85593, 85595m (three specimens), 85999, 86001, 86233m, 87343, 87345, 87347, 87351, 87352, 87354m (three specimens), 87855, 87856, 92349, 92350, 92353, and 92354. Locality SC-69: UM 86130 and 86131. Locality SC-79: UM 83640 (two specimens) and 83645. Locality SC-121: UM 83462 and 85670. Locality SC-308: UM 83465. Locality SC-342: UM 83573.

*Description.* The most complete maxillary dentition is UM 86001, a maxilla with P<sup>2</sup>-M<sup>2</sup>. P<sup>2</sup> is not well preserved, but it was clearly a very small tooth like that illustrated in the holotype described by McKenna (1960, p. 106). There is no labial cingulum on the upper molars of two specimens where this can be examined. There are numerous dentaries in various stages of wear. One, UM 87856, a left dentary fragment of a juvenile, preserves the crown of dP<sub>4</sub> (Fig. 30A,B). Other young individuals, like UM 74075, have crowns of the permanent molars in place and little worn (Fig. 30C,D).

All  $W_{a_0}$  specimens preserving M<sub>1</sub> retain a paraconid on this tooth: this is distinct in 7 out of 8 specimens (88%) and faint in 1 out of 8 specimens (12%). Some specimens retain a paraconid on M<sub>2</sub>: this is distinct in 3 out of 12 specimens (25%), faint in 5 out of 12 specimens (42%), and absent in 4 out of 12 specimens (33%). UM 74075 is one of four little-worn  $W_{a_0}$  specimens that have an isolated metaconid separated from the protoconid by a deep groove. The cristid obliqua joins the back of the protoconid and there is no crest connecting the protoconid to the metaconid. Three  $W_{a_0}$  specimens have a crest connecting the protoconid and metaconid. Hence the proportion with an isolated metaconid is 4 out of 7 (57%). Measurements of  $W_{a_0}$  *H. loomisi* are listed in Table 19.

*Discussion.* Specimens described here appear to be typical and representative of *Hyopsodus loomisi* in every dental feature that can be studied and compared. The type sample of *H. loomisi* comes from West Alheit Pocket in northern Colorado, which is the same age as the better known East Alheit locality nearby. McKenna (1960) interpreted the sample of specimens from East and West Alheit as contain-

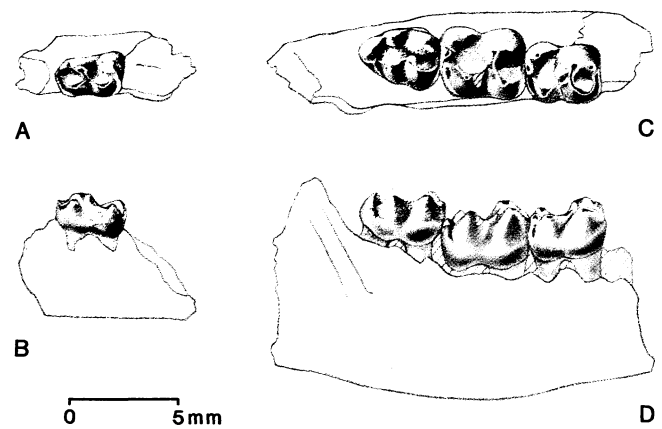
Table 19. Measurements of *Hyopsodus loomisi* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
P <sup>3</sup> L	1	3.0	-	-	-
P <sup>3</sup> W	1	3.2	-	-	-
P <sup>4</sup> L	1	2.8	-	-	-
P <sup>4</sup> W	1	3.9	-	-	-
M <sup>1</sup> L	1	3.1	-	-	-
M <sup>1</sup> W	1	4.3	-	-	-
M <sup>1/2</sup> L	2	2.9 - 3.4	3.15	-	-
M <sup>1/2</sup> W	2	3.9 - 4.9	4.40	-	-
M <sup>2</sup> L	1	3.3	-	-	-
M <sup>2</sup> W	1	4.9	-	-	-
M <sup>3</sup> L	1	2.3	-	-	-
M <sup>3</sup> W	1	3.6	-	-	-
<i>Lower dentition</i>					
dP <sub>4</sub> L	1	3.2	-	-	-
dP <sub>4</sub> W	1	2.4	-	-	-
P <sub>3</sub> L	2	2.5 - 2.6	2.55	-	-
P <sub>3</sub> W	2	2.0 - 2.1	2.05	-	-
P <sub>4</sub> L	3	2.9 - 2.9	2.90	-	-
P <sub>4</sub> W	5	2.1 - 2.3	2.22	0.08	3.8
M <sub>1</sub> L	16	2.9 - 3.3	3.08	0.15	4.8
M <sub>1</sub> W	16	2.3 - 2.7	2.48	0.12	4.7
M <sub>1/2</sub> L	2	3.2 - 3.3	3.25	-	-
M <sub>1/2</sub> W	4	2.8 - 3.0	2.88	0.10	3.3
M <sub>2</sub> L	22	3.1 - 3.9	3.34	0.19	5.7
M <sub>2</sub> W	23	2.6 - 3.4	2.91	0.17	5.9
M <sub>3</sub> L	13	3.0 - 3.7	3.25	0.22	6.8
M <sub>3</sub> W	13	2.2 - 2.8	2.52	0.19	7.4
Mandibular depth:	18	5.2 - 6.6	5.96	0.46	7.6

Total number of specimens = 40

ing two species of *Hyopsodus*, *H. loomisi* and *H. miticulus* (the combined sample included five specimens with M<sub>1</sub>). However, measurement of a larger sample of *Hyopsodus* teeth collected and made available for study by McKenna after publication of his 1960 monograph (AMNH collection, 14 specimens with M<sub>1</sub>) indicates that all belong to a single distribution of variation. This distribution resembles that in homogeneous samples of extant mammalian species, and all Alheit *Hyopsodus* are interpreted as members of a single species, *H. loomisi*. A paraconid is distinct on M<sub>1</sub> in 3 out of 3 unworn specimens in this sample (100%), and on M<sub>2</sub> in 1 out of 3 specimens (33%).

Comparison of distributions of tooth size for Alheit *Haplomylys* and *Hyopsodus* with distributions of tooth size for these genera from successive Wasatchian intervals in the Clarks Fork Basin indicates that East and West Alheit correlate with upper part of the lower *Haplomylys-Ectocion* zone of the early Wasatchian (zone Wa<sub>2</sub>), probably the 1720-1760 meter interval in the Clarks Fork Basin (the interval of localities SC-2, SC-54, SC-87, SC-133, SC-213, and others). Morphological and distributional characteristics of *Cantius* (Gingerich and Simons, 1977, p. 257), *Parectypodus* (Krause, 1982, p. 283), *Arctodontomys* (Gunnell, 1985, p. 53), and to some degree *Tetonius*

Figure 30. Dentition of *Hyopsodus loomisi*. A and B, left dentary with dP<sub>4</sub>, UM 87856, in occlusal and lateral view. C and D, right dentary with M<sub>1-3</sub>, UM 74075, in occlusal and lateral view.

(Bown and Rose, 1987, p. 52; correlation using *Tetonius* depends on how questionable presence of P<sub>2</sub> in Clarks Fork Basin specimens is interpreted) support this correlation as well. The 1720 meter level is 200 meters higher stratigraphically than the Wa<sub>0</sub> localities studied here, and *Hyopsodus* became larger and then smaller in this interval (Gingerich, 1985).

Many species in zone Wa<sub>0</sub> are different from those found in zone Wa<sub>2</sub>; however, in spite of the time elapsed between these zones (the time required for deposition of 200 m of fluvial sediments), there is no recognizable difference between the Wa<sub>0</sub> and Wa<sub>2</sub> samples of *Hyopsodus* that would indicate more than one species is involved. A sample of *H. loomisi* from SC-2 has a distinct paraconid on M<sub>1</sub> in 8 out of 9 specimens (89%, as compared with 88% in the Wa<sub>0</sub> sample and 100% in the type sample), and a faint paraconid in 1 out of 9 (11%, as compared with 12% in the Wa<sub>0</sub> sample). The SC-2 sample has a distinct paraconid on M<sub>2</sub> in 3 out of 21 specimens (14%, as compared with 25% in the Wa<sub>0</sub> sample and 33% in the type sample), a faint paraconid in 11 out of 21 specimens (52%, as compared with 42% in the Wa<sub>0</sub> sample), and no paraconid in 7 out of 21 specimens (33%, as compared to 33% in the Wa<sub>0</sub> sample). The SC-2 sample has 10 out of 20 specimens with an isolated M<sub>3</sub> metaconid (50%, as compared with 57% in the Wa<sub>0</sub> sample).

In a later sample of *Hyopsodus* (*H. latidens*, a likely descendant of *H. loomisi*) from locality SC-255 at level 2050 m in the Clarks Fork Basin, 10 out of 22 specimens (45% have a faint paraconid on M<sub>1</sub>, and 3 out of 22 specimens (14%) lack it entirely; 10 out of 31 specimens (32%) have a faint paraconid on M<sub>2</sub>, and 17 out of 31 specimens (55%) lack it entirely. There is a clear trend toward loss of the paraconid on M<sub>1</sub> and M<sub>2</sub> in early *Hyopsodus* evolution, but the first significant reduction in paraconid frequency

occurs above the level of SC-2 in the transition from *H. loomisi* to *H. latidens*.

*Hyopsodus* has been reported from the early Eocene of Europe and Asia as well as North America. Godinot (1978) named a new species of *Hyopsodus*, *H. itinerans*, based on three isolated teeth from the Sparnacian locality of Rians in southern France. He subsequently described several additional teeth and illustrated a dentary with  $P_3$ - $M_2$  from Rians (Godinot, 1981, p. 86-90). Godinot stated that one specimen, RI 409 (not illustrated), has a well formed paraconid on  $M_1$ , while the dentary shown in his figure 16bis clearly lacks any trace of a paraconid. Three specimens preserving  $M_2$  all lack a paraconid on this tooth. The absence of a paraconid is generally regarded as a derived characteristic in *Hyopsodus*, which suggests that *H. itinerans* is more derived and possibly younger than the *H. loomisi* sample described here.

Hooker (1979) named a new species of *Hyopsodus*, *H. wardi*, based on upper and lower jaw fragments and teeth from the Sparnacian locality of Abbey Wood in southern England. Teeth of this species are slightly smaller than those of North American *H. loomisi* (including the sample from  $Wa_0$  localities) but, as Hooker noted, they are otherwise very similar. *H. wardi* retains paraconids on  $M_1$  (1 distinct and 1 faint), and on  $M_2$  (both faint). Given the evidence at hand, *H. wardi* from Abbey Wood is recognizably different from *H. itinerans* from Rians, and the Abbey Wood form appears to be more primitive and probably older. *H. wardi* and  $Wa_0$  *H. loomisi* have similar frequencies of paraconid retention; both are similar in evolutionary grade, and both would appear on this evidence to be similar in age.

Dashzeveg (1977) described a species of *Hyopsodus*, *H. orientalis*, from the Bumbanian of Tsagan Khushu in southern Mongolia. This species has higher crowned, more crested molars than are typical of North American *Hyopsodus*, and  $P_4$  differs in having a much larger metaconid. These features suggest that the species is more derived and probably younger than  $Wa_0$  *H. loomisi*. Zhai (1978) mentions a specimen of *Hyopsodus* sp. from China. Zhai's specimen is a little larger than specimens of *H. orientalis* and it is somewhat worn, but it otherwise appears to resemble this species in the shape of molars and the relative development of cusps and crests. No  $P_4$  is preserved in the Chinese specimen, so this tooth cannot be compared to that in *H. orientalis*.

Rose (1981, p. 78) described two teeth, a right  $P_4$  and a right  $M_3$ , of *Hyopsodus* from the late Clarkforkian of the Clarks Fork Basin in Wyoming. The Clarkforkian  $M_3$  is significantly larger (wider) than  $M_3$  in the sample from zone  $Wa_0$ , and it may represent an earlier and more primitive species than *H. loomisi*. Whatever their specific attribution, these specimens come from localities unlikely to have been contaminated with Wasatchian fossils and they seem to indicate a brief pre-Wasatchian record for *Hyopsodus* in North America.

*Hyopsodus* is the only hyopsodontid found to date in zone  $Wa_0$ . *Haplomyilus* is common in the Clarkforkian and abundant in the early Wasatchian, but conspicuously absent in  $Wa_0$  collections.

#### Family PHENACODONTIDAE

##### *Ectocion parvus* Granger, 1915

Fig. 31

*Holotype and referred specimens.* Locality HG-3: UM 92423. Locality SC-67: AMNH 16080 (holotype, see discussion below), YPM-PU 18153 (5 specimens), UM 66138 (3 specimens), 66140m (3 specimens), 66617m (4 specimens), 71768m (2 specimens, including questionably referred  $dP_4$ ), 74076, 75423m, 77202, 79884, 79890m, 82380, 82381, 82386, 83474, 83476, 83478m, 83618m, 83626, 83636m (2 specimens), 83660, 85594 (2 specimens), 85595m (2 specimens), 86000, 86003m, 86570, 86572m (5 specimens), 87338, 87342, 87354m (6 specimens), 87859m (3 specimens), and 92356m; questionably referred are UM 74077, 74079, 82387m, and 92348. Locality SC-69: UM 83824. Locality SC-121: UM 85668. Locality SC-139: UM 67253m. Locality SC-182: UM 77020. Locality SC-308: UM 76235. Locality SC-351: UM 83871 and 83876m.

*Description.* The most complete specimen of *Ectocion parvus* is UM 77202, a crushed palate and lower jaws found in situ in greenish gray sandstone (Figure 31). The upper canine remains attached to a piece of premaxilla with roots for three incisors. Two crowns of upper incisors are associated with this specimen. Each has a spatulate crown with three distinct apical cusps. The upper canine has a long root, and a nearly straight, sharply pointed crown measuring 8.5 mm in height. There is a 1.0 mm diastema between  $C^1$  and  $P^1$ . Alveoli show that both  $P^1$  and  $P^2$  were double-rooted.  $P^1$  and  $P^2$  were separated by a diastema of 3.0 mm.  $P^3$  has a narrow crown with a moderately large protocone and confluent paracone and metacone (the paracone being the larger of the two).  $P^3$  has no parastyle or mesostyle, and no conules.  $P^4$  is broader than  $P^3$ , with a distinct parastyle, no mesostyle, a moderately large paraconule, and a small metaconule.  $M^1$  and  $M^2$  are broad molars with large labially positioned parastyles and mesostyles on the labial or buccal cingulum, moderately large paraconules and metaconules, and a large hypocone connected to the base of the protocone by a distinct lingual cingulum.  $M^3$  is generally similar to  $M^{1-2}$  in form, but it is smaller with a reduced metacone, no hypocone, and a more rounded posterior margin. UM 77202 has two infraorbital foramina, each about 1.0 mm in diameter.

Left and right lower canine roots are preserved, including the base of each crown, but the crowns are not preserved.  $P_1$  is a small tooth, single-rooted, with a simple conical crown and a very small posterolabial accessory cuspule at the base of the crown.  $P_1$  is separated from  $C_1$

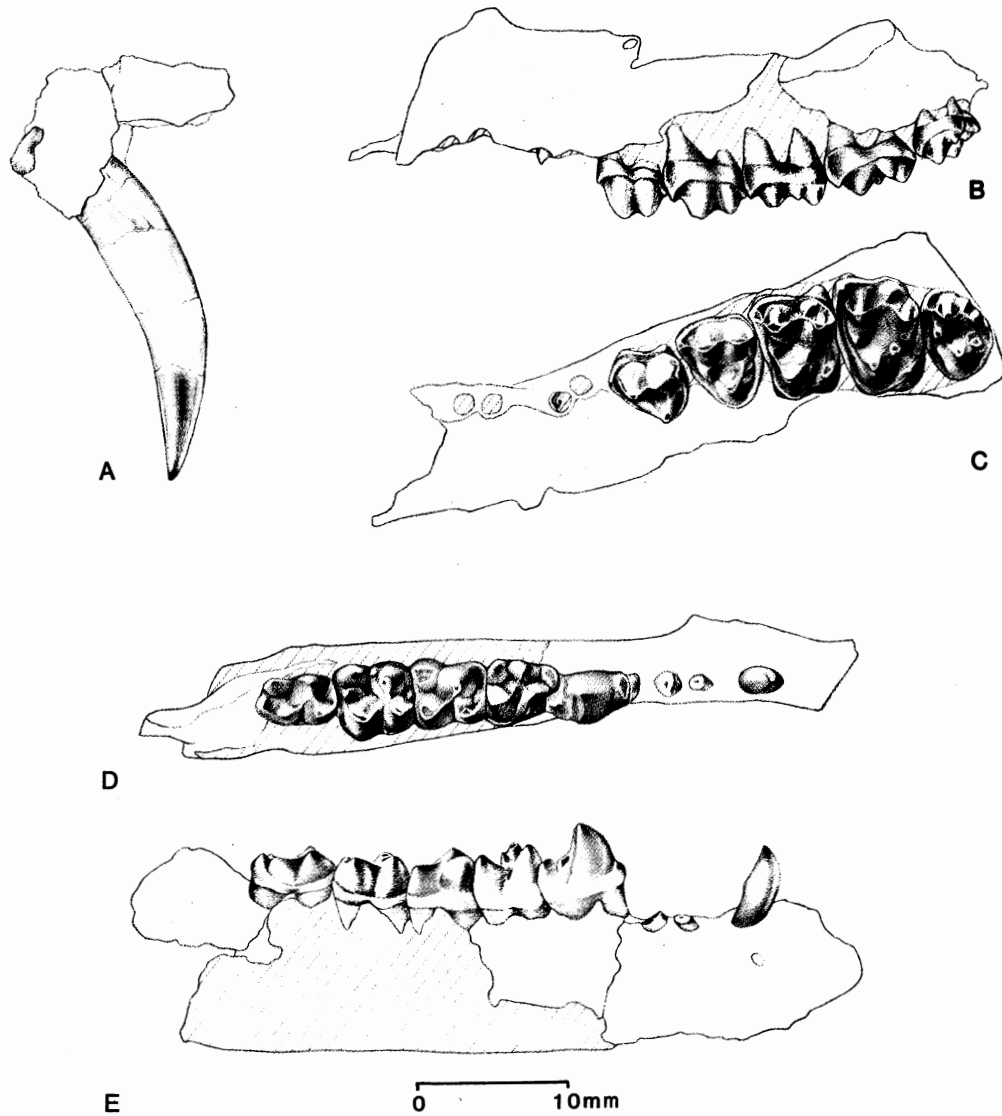


Figure 31. Dentition of *Ectocion parvus*, UM 77202. A, right premaxilla and  $C^1$ , in lateral view. B and C, left maxilla with  $P^3$ - $M^3$ , in lateral and occlusal view. D and E, right dentary with  $P_1$  and  $P_3$ - $M_3$ , in occlusal and lateral view (composite reconstruction based on both left and right sides).

by a diastema of 1.7 mm, and from  $P_2$  by a diastema of 3.0 mm.  $P_2$  is double-rooted, but the crown is not preserved in any of the known specimens.  $P_3$  has a narrow crown with a sharp protoconid, no paraconid or metaconid, and a moderately large sharp hypoconid.  $P_4$  is broader and more molarized than  $P_3$ , and it has a distinct paraconid cusp, a metaconid, and an entoconid in addition to the protoconid and hypoconid.  $M_{1-2}$  are quadrate molars with four principal cusps, the protoconid, metaconid, hypoconid, and entoconid. There is a paracristid but no paraconid. In addition,  $M_{1-2}$  usually have a small metastyloid posterolingual to the metaconid, a small hypoconulid, and a small ento-

styloid anterior to the entoconid.  $M_3$  resembles  $M_{1-2}$  but it is narrower, with a larger hypoconulid and no entostyloid. The paracristid on  $M_{1-3}$  is almost always L-shaped, curving forward and lingually from the protoconid, ending below and in front of the metaconid. However, in two specimens, UM 82381 and 83474, the paracristid is U-shaped, curving and running up the front of the metaconid, as it does in *Copecion davisii* (described below; specimens of *E. parvus* are easily confused with those of *C. davisii*). Mental foramina are located below  $P_1$  and below the posterior part of  $P_3$  or anterior part of  $P_4$ .

Table 20. Measurements of *Ectocion parvus* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
C <sup>1</sup> L	1	3.9	-	-	-
C <sup>1</sup> W	1	2.9	-	-	-
P <sup>3</sup> L	3	5.3 - 5.3	5.30	-	-
P <sup>3</sup> W	3	4.2 - 5.5	4.90	0.66	13.4
P <sup>4</sup> L	3	5.0 - 5.4	5.20	0.20	3.8
P <sup>4</sup> W	2	6.3 - 6.8	6.55	-	-
M <sup>1</sup> L	3	5.2 - 5.6	5.42	0.23	4.2
M <sup>1</sup> W	2	7.2 - 7.3	7.25	-	-
M <sup>1/2</sup> L	11	4.5 - 5.8	5.21	0.37	7.1
M <sup>1/2</sup> W	12	6.4 - 8.0	7.19	0.47	6.6
M <sup>2</sup> L	4	5.1 - 6.3	5.61	0.51	9.1
M <sup>2</sup> W	4	7.0 - 8.0	7.51	0.39	5.2
M <sup>3</sup> L	6	3.6 - 4.8	4.23	0.41	9.6
M <sup>3</sup> W	6	5.9 - 6.9	6.17	0.39	6.4
<i>Lower dentition</i>					
C <sub>1</sub> L	1	3.6	-	-	-
C <sub>1</sub> W	1	2.9	-	-	-
P <sub>1</sub> L	2	2.3 - 2.4	2.35	-	-
P <sub>1</sub> W	2	1.5 - 1.6	1.55	-	-
P <sub>3</sub> L	6	5.5 - 6.0	5.62	0.19	3.5
P <sub>3</sub> W	7	2.9 - 3.4	3.16	0.20	6.3
P <sub>4</sub> L	20	5.1 - 6.0	5.57	0.27	4.8
P <sub>4</sub> W	20	3.6 - 4.4	3.94	0.22	5.5
M <sub>1</sub> L	14	4.6 - 5.6	5.26	0.32	6.0
M <sub>1</sub> W	17	3.9 - 5.0	4.46	0.33	7.4
M <sub>1/2</sub> L	6	4.8 - 5.7	5.38	0.33	6.2
M <sub>1/2</sub> W	7	4.1 - 4.8	4.44	0.26	5.8
M <sub>2</sub> L	14	4.7 - 5.6	5.40	0.26	4.8
M <sub>2</sub> W	16	4.0 - 5.2	4.66	0.28	6.0
M <sub>3</sub> L	12	5.1 - 6.6	5.72	0.43	7.6
M <sub>3</sub> W	14	3.5 - 4.4	3.75	0.30	7.9
Mandibular depth:	14	8.7 - 14.6	11.11	1.61	14.5
Total number of specimens = 66					

Measurements of the teeth of Wa<sub>0</sub> *E. parvus* are summarized in Table 20.

*Discussion.* Granger (1915, p. 353) states that the holotype of *Ectocion parvus*, AMNH 16080, came from "Clark Fork beds, Head of Big Sand Coulee, Clark Fork basin, Wyo. Exp. 1911." This specimen is problematical in that it was not assigned a field number when it was collected, and it was never entered individually in the American Museum's Bighorn Wasatch expedition field catalogue as most specimens were. The most likely source is W. J. Sinclair's collection of August 13, 1911, listed in the field catalogue (field no. 88) as "Various genera—miscellaneous jaws. Head of Big Sand Coulee." Sinclair's field notes for 1911 (p. 63) indicate that he collected in red-banded beds in the bluff three miles north of Ralston (Polecat Bench) on August 12 and 13, while W. Granger and G. Olsen collected the new faunal horizon (Clarkforkian) in blue shales underlying these red-banded beds (Sinclair's field notebook for 1911 was examined in 1979 at Princeton University and again in 1988 in the ar-

chives of the Peabody Museum of Natural History at Yale University). Sinclair found the holotype of *Dipsalidictis platypus* on August 12, 1911, and discovery of part of this specimen seventy years later (see discussion under *D. platypus* above) confirms that Sinclair's "red-banded beds" were in what is now called locality SC-67. The holotype dentary and teeth of *Ectocion parvus* are light in color like fossils from zone Wa<sub>0</sub>. Virtually all *E. parvus* known to date come from zone Wa<sub>0</sub>, and this species is the most common fossil mammal found at SC-67. Hence it is very likely that SC-67 is the type locality, and it is virtually certain that the holotype came from earliest Wasatchian zone Wa<sub>0</sub> and not from the Clarkforkian.

*Ectocion parvus* is most similar to *E. osbornianus*, a species that is also known from zone Wa<sub>0</sub>. It appears to differ from *E. osbornianus* only in being smaller (*E. parvus* is about 18% smaller, on average, in comparable linear dimensions; Figs. 32-33). The Wa<sub>0</sub> sample of *E. parvus* is very similar in size to that of *Copecion davisii* (Fig. 32), but these two genera and species differ in premolar and in molar form.

Given available samples, there is little question that *Ectocion parvus* and *Copecion davisii* are different species belonging in different genera. However, the holotype of *E. parvus*, AMNH 16080, is a dentary that lacks premolars. Premolars are the most important teeth distinguishing *Ectocion* from *Copecion*. A decision about whether the holotype belongs in *Ectocion* or in *Copecion* must be based on its molar morphology alone. Almost all of the known specimens of *E. parvus* have an L-shaped paracristid on the lower molars that terminates at the base of the metaconid. Two specimens identified as *Ectocion* on the basis of premolar shape, UM 82381 and 83474, have a U-shaped paracristid running up the front of the metaconid. All of the known specimens of *C. davisii* have a U-shaped paracristid running up the front of the metaconid. Given present evidence, an L-shaped paracristid is diagnostic, while a U-shaped paracristid is not. The holotype of *E. parvus* has an L-shaped paracristid, hence it appears correctly referred to *Ectocion* rather than *Copecion*.

University of Michigan specimens of *Ectocion* that preserve M<sub>1</sub> and come from localities ranging from 1300 m to 2095 m in the Clarks Fork Basin section are plotted in Figure 33. *E. osbornianus* is by far the most common species and the most widely distributed stratigraphically. *E. parvus* is common in zone Wa<sub>0</sub> at level 1520 m in the Clarks Fork Basin section, and it is absent or very rare in collections from other stratigraphic levels. The co-occurrence of *E. osbornianus* with *E. parvus* in zone Wa<sub>0</sub> precludes interpretation of *E. parvus* as a shortlived dwarfed form of *E. osbornianus*. It seems more likely that *E. parvus* inhabited environments that are not normally preserved or have yet to be sampled in other parts of the Clarks Fork Basin fossil record (see discussion below).

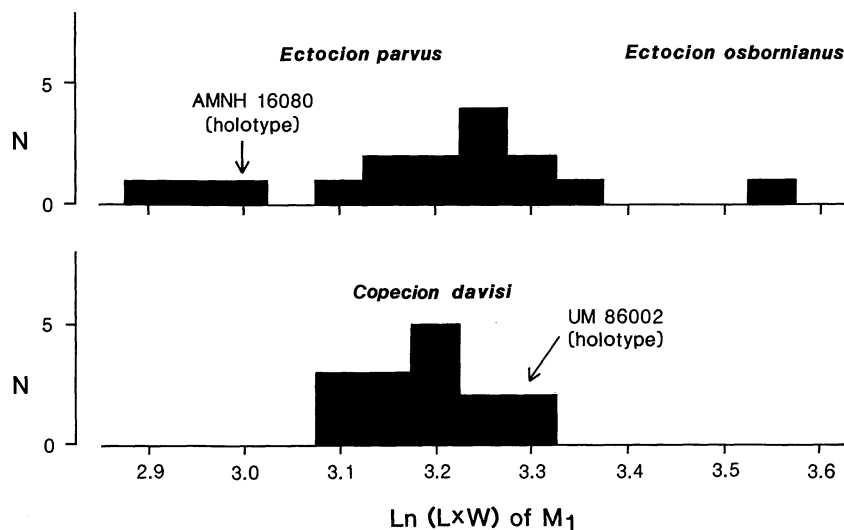


Figure 32. Comparison of tooth size in *Ectocion parvus* with that in *Ectocion osbornianus* and *Copecion davisii*. Mean  $\ln(L \times W)$  of  $M_1$  is 3.19 in both *E. parvus* and *C. davisii*.  $\ln(L \times W)$  of  $M_1$  is 3.54 in the one specimen of *E. osbornianus* from zone  $Wa_0$  that preserves an  $M_1$ . Note that while the  $Wa_0$  sample of *E. parvus* has the same mean size as *C. davisii*, its variability seems to be much greater. All specimens plotted here have  $M_1$  in place in a jaw or associated with  $M_2$ , which permits unequivocal identification as to tooth position. Most have associated  $P_4$  which permits unequivocal identification as to genus.

#### *Ectocion osbornianus* (Cope, 1882)

**Referred specimens.** Locality SC-67: UM 66612. Locality SC-351: UM 83875.

**Description.** Both of these specimens are fragmentary dentaries. The first preserves crowns of  $M_{1,2}$ , and the second preserves crowns of  $P_{3,4}$ . These differ from *Ectocion parvus* only in being significantly larger (Fig. 32). Measurements of  $Wa_0$  *E. osbornianus* are listed in Table 21.

**Discussion.** *Ectocion osbornianus* is a common species at most Clarkforkian and early Wasatchian localities, including those from the Clarks Fork Basin (Fig. 33). However, it is rare in zone  $Wa_0$ , where it is replaced by a smaller congener *E. parvus*. The abundance of *E. osbornianus* in Clarkforkian and most early Wasatchian faunal samples and its rarity in zone  $Wa_0$  suggests again that the environment being sampled in the earliest Wasatchian is unusual.

#### *Phenacodus* cf. *P. intermedius* Granger, 1915

Fig. 34

**Referred specimens.** Locality SC-67: UM 77203m, 83618m, 83622, 83636m (2 specimens), 87354m, and 87859m. Locality SC-141: UM 83570 may be from zone  $Wa_0$ .

**Description.** UM 83622, a right dentary with  $P_4$ - $M_3$  (Fig. 34), is the only specimen of this species with more than a single tooth that is unquestionably from zone  $Wa_0$ .

It was found in situ at SC-67. Measurements of UM 83622 and other  $Wa_0$  specimens referred to *P.* cf. *P. intermedius* are listed in Table 22.

**Discussion.** This *Phenacodus* species is medium-sized, differing from Clarkforkian and early Wasatchian specimens referred to *P. vortmani* in being larger, and differing from specimens referred to *P. primaevus* in being smaller. There are not yet enough specimens of *Phenacodus* known from zone  $Wa_0$  to permit definitive systematic analysis.

UM 83570 is a partial skull and lower jaw of a young individual from locality SC-141, with teeth almost identical in size and shape to those of UM 83622. However, UM 83570 is dark in color, with black teeth, and it may come from sediments of Clarkforkian age at the base of the locality.

#### *Copecion*, new genus

**Type species.** *Copecion davisii*, new species.

**Included species.** Type and *Copecion brachypternus* (Cope, 1882).

**Diagnosis.** Resembles *Phenacodus* and *Ectocion* but differs from both in having relatively square upper molars with no lingual cingula and in having a vertical furrow in the lingual surface of the crown separating a pillarlike protocone and hypocone. Lower molars are *Phenacodus*-like in having a U-shaped paracristid, but *Copecion* is distinctive in having a relatively long, narrow, wedge-shaped  $P_4$  with a very open trigonid.  $P_4$  talonid is broader than



CLARK'S FORK BASIN *ECTOCION*

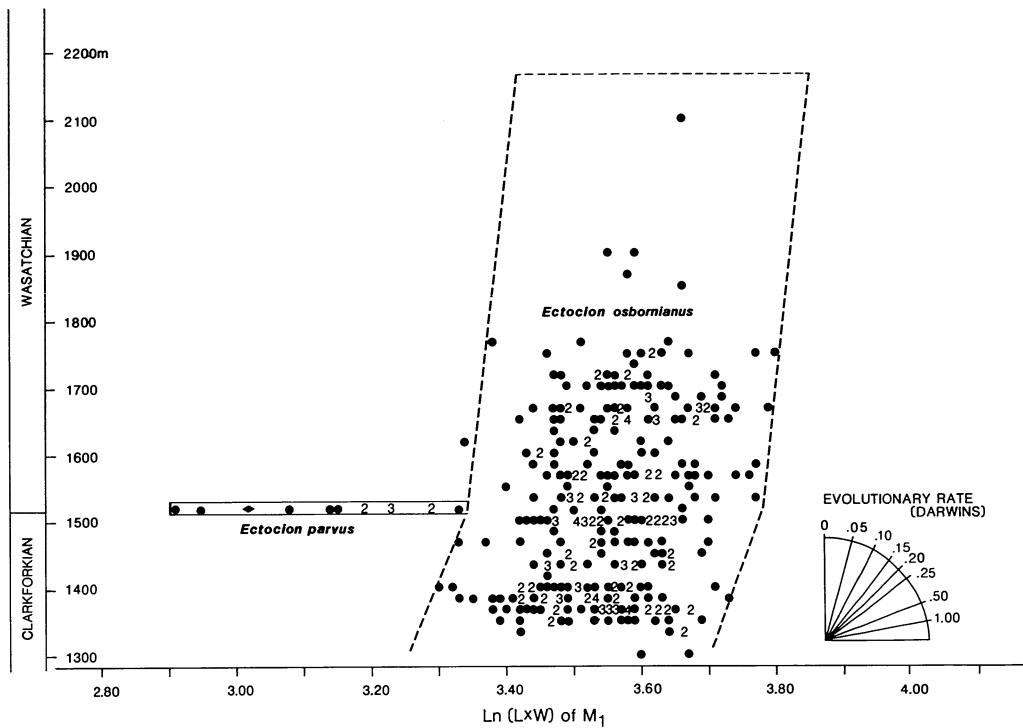


Figure 33. Stratigraphic distribution of Clarkforkian and early Wasatchian *Ectocion* in the Clarks Fork Basin, Wyoming. Note that *Ectocion parvus* is common in zone Wa<sub>0</sub>, but it is absent or very rare in other zones. *Ectocion osbornianus* is also present in zone Wa<sub>0</sub>. Symbols as in Figure 14. Specimens plotted here are in the paleontological collections of the University of Michigan.

Table 21. Measurements of *Ectocion osbornianus* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Lower dentition</i>					
P <sub>3</sub> L	1	6.7	-	-	-
P <sub>3</sub> W	1	4.1	-	-	-
P <sub>4</sub> L	2	6.4 - 6.9	6.65	-	-
P <sub>4</sub> W	2	4.6 - 5.0	4.80	-	-
M <sub>1</sub> L	1	6.6	-	-	-
M <sub>1</sub> W	1	5.2	-	-	-
Mandibular depth:	1	13.0	-	-	-
Total number of specimens = 2					

trigonid. Paraconid on P<sub>4</sub> is positioned well in front of the protoconid, while the metaconid is closer to the protoconid.

*Etymology.* Compound name honoring Edward Drinker Cope. Root *cion* (Gr., masculine), column or pillar, is the same root Cope used to call attention to the mesostyle in forming *Ectocion*, but pillars here appear on the inner surface of upper molars as well as the outer surface.

*Copecion davisii*, new species

Fig. 35

*Holotype and referred specimens.* Locality BR-2: UM 87594m. Locality SC-51: UM 69933. Locality SC-67: UM 66611, 71769, 71770, 74074, 75420, 75421, 75423m, 82387m, 83472, 83614, 83618m (2 specimens), 83623m, 83624, 83633, 83634, 83636m, 83663, 83664m, 86002 (holotype), 86003m, 86230, 87350, 87354m, 87853, 87859m, and questionably 82384. Locality SC-69: UM 83823, 83825m, 86133, 86137m, and questionably 83822. Locality SC-79: UM 83639, 83641, 83644, and 83647m. Locality SC-139: UM 68033m. Locality SC-308: UM 85596m. Locality SC-345: UM 83781. Locality SC-348: UM 83816. Locality SC-349: UM 83818. Locality SC-351: UM 83870 and 83872.

*Diagnosis.* Differs from *C. brachypternus* in being 17-20% smaller, on average, in linear dimensions.

*Etymology.* Named for Ms. Lesa Davis, who collected the holotype. The family name Davis is considered neutral in gender, hence *i* is the appropriate genitive suffix.

*Description.* The upper dentition of *Copecion davisii* is not as well known as that of *Ectocion parvus*. The only

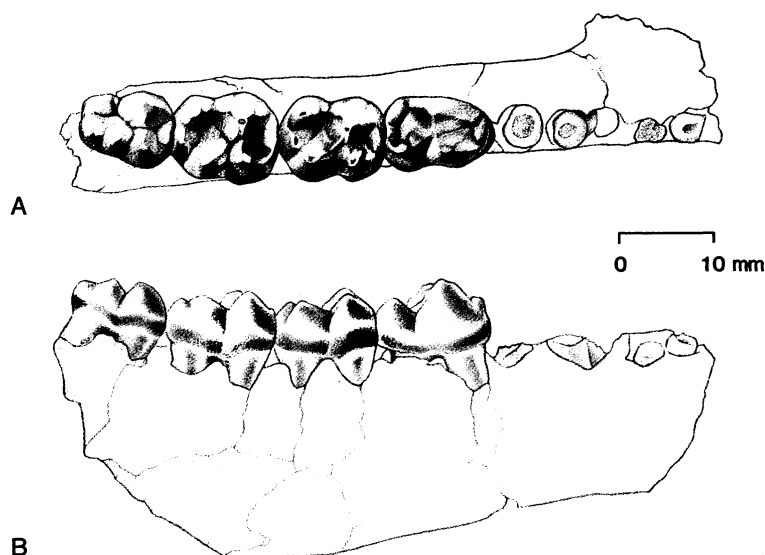


Figure 34. Right dentary of *Phenacodus* cf. *P. intermedius*, UM 83622, in occlusal (A) and lateral (B) view.

Table 22. Measurements of *Phenacodus* cf. *P. intermedius* from  $W_{a_0}$

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
I <sup>1</sup> L	1	6.3	-	-	-
I <sup>1</sup> W	1	3.2	-	-	-
M <sup>1/2</sup> L	1	10.1	-	-	-
M <sup>1/2</sup> W	1	11.5	-	-	-
<i>Lower dentition</i>					
C <sub>1</sub> L	1	6.6	-	-	-
C <sub>1</sub> W	1	5.0	-	-	-
dP <sub>3</sub> L	1	10.2	-	-	-
dP <sub>3</sub> W	1	5.8	-	-	-
P <sub>4</sub> L	2	9.8 - 10.8	10.30	-	-
P <sub>4</sub> W	2	7.0 - 7.1	7.05	-	-
M <sub>1</sub> L	1	9.6	-	-	-
M <sub>1</sub> W	1	8.4	-	-	-
M <sub>2</sub> L	1	10.3	-	-	-
M <sub>2</sub> W	1	9.0	-	-	-
M <sub>3</sub> L	1	9.5	-	-	-
M <sub>3</sub> W	1	7.5	-	-	-
Mandibular depth:	1	18.5	-	-	-

Total number of specimens = 7

upper premolar is in UM 71769, a worn left P<sup>3</sup> with a narrow anterior crown anterior to the paracone and a broad crown posterior to it. The metacone is worn but it appears to have been very small, while the protocone is larger. M<sup>1</sup> and M<sup>2</sup> are well preserved in UM 83634 (Fig. 35A,B). These upper molars are nearly identical and, when isolated, cannot be distinguished. M<sup>1</sup> and M<sup>2</sup> have relatively square crowns that are nearly the same size, and each has a large

bulbous protocone, paracone, metacone, and hypocone. Each has a smaller but distinct paraconule and metaconule, and each has a distinct parastyle and mesostyle on a narrow buccal or labial cingulum. There is no lingual cingulum and instead a vertical furrow or groove on the lingual side of the crown separates the protocone and hypocone, making them appear more pillarlike than is typical of *Phenacodus* or *Ectocion*. The crown of M<sup>3</sup> is preserved in UM 71769. It resembles that of M<sup>1</sup> and M<sup>2</sup> in being relatively square, but it is distinctly smaller, the hypocone and metaconule are greatly reduced in size, and there is no vertical furrow separating the protocone from what little remains of the hypocone.

The most complete dentary is UM 86002 (Fig. 35C,D), which preserves the canine root, a single P<sub>1</sub> root, and two roots for P<sub>2</sub>. There is a 2–3 mm diastema separating C<sub>1</sub> and P<sub>1</sub>, a space of about 1.0 mm separating the roots of P<sub>1</sub> and P<sub>2</sub>, and the remaining cheek teeth are crowded close together. P<sub>3</sub> has a narrow crown with a single apical cusp and no anterior or posterior basal cusps. P<sub>4</sub> has a long narrow trigonid with the paraconid located well in front of the protoconid. The metaconid is close to the protoconid. The talonid is broader than the trigonid, and the only talonid cusp is a moderately large hypoconid. M<sub>1-3</sub> are quadrate molars with a large protoconid and metaconid on the trigonid, and a large hypoconid on the talonid. The entocoid and hypoconulid are both small, except on M<sub>3</sub> where the hypoconulid is moderately large. All of the lower molars studied here have a curving paracristid that connects the protoconid and metaconid, running up the anterior surface of the latter. The dentary has mental foramina beneath P<sub>1</sub> and beneath the anterior root of P<sub>4</sub>.

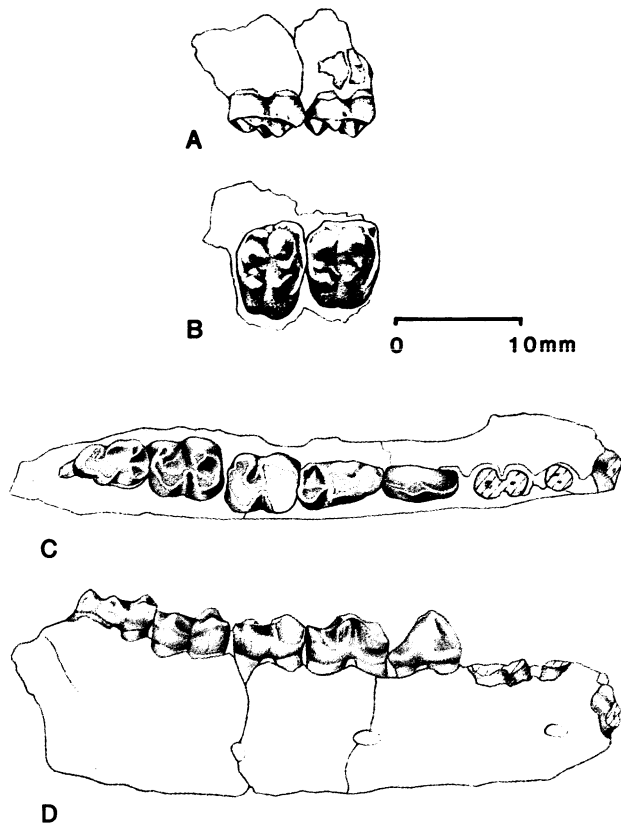


Figure 35. Dentition of *Copecion davisi*, new species. A and B, right maxilla with  $M_{1,2}$ , UM 83634, in lateral and occlusal view. C and D, right dentary with  $P_3$ - $M_3$ , UM 86002 (holotype), in occlusal and lateral view.

Measurements of the teeth of  $Wa_0$  *C. davisi* are summarized in Table 23.

**Discussion.** *Copecion davisi*, like *Ectocion parvus*, is a very small earliest Wasatchian species that is closely related to a larger congener that ranges through the late Clarkforkian and into the early Wasatchian. *C. davisi* is almost exactly the same size as *E. parvus* (Fig. 32), and the two are sometimes difficult to tell apart.  $P_4$  is markedly different in shape, and it furnishes the most important differences distinguishing the two. Upper molars usually differ in proportion, those of *C. davisi* being relatively narrower transversely. Lower molars can be sorted by examining the course of the paracristid: most specimens that have a U-shaped paracristid running up the front of the metacoid are *C. davisi*, although a few specimens of *E. parvus* have this configuration as well.

Table 23. Measurements of *Copecion davisi* from  $Wa_0$

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
$C^1L$	1	3.8	-	-	-
$C^1W$	1	3.1	-	-	-
$P^2L$	1	3.9	-	-	-
$P^2W$	1	2.0	-	-	-
$P^3L$	1	5.3	-	-	-
$P^3W$	1	4.2	-	-	-
$P^4L$	1	5.1	-	-	-
$P^4W$	1	6.4	-	-	-
$M^1L$	5	5.0 - 6.0	5.54	0.37	6.7
$M^1W$	4	6.7 - 7.2	7.02	0.24	3.4
$M^{1/2}L$	6	5.1 - 6.0	5.57	0.35	6.3
$M^{1/2}W$	6	6.0 - 8.3	7.23	0.81	11.2
$M^2L$	4	5.2 - 5.9	5.47	0.31	5.7
$M^2W$	4	7.2 - 7.6	7.45	0.19	2.6
$M^3L$	5	3.9 - 4.4	4.10	0.23	5.7
$M^3W$	5	4.6 - 5.9	5.42	0.50	9.2
<i>Lower dentition</i>					
$P_3L$	4	6.0 - 7.1	6.45	0.51	7.9
$P_3W$	5	2.9 - 3.5	3.28	0.24	7.3
$P_4L$	14	5.8 - 6.9	6.25	0.31	5.0
$P_4W$	14	3.6 - 4.2	3.86	0.17	4.4
$M_1L$	13	5.3 - 6.0	5.54	0.21	3.9
$M_1W$	14	4.2 - 4.9	4.46	0.20	4.5
$M_{1/2}L$	3	5.6 - 6.2	5.93	0.31	5.1
$M_{1/2}W$	3	4.5 - 5.2	4.83	0.35	7.3
$M_2L$	13	5.2 - 6.4	5.70	0.40	7.1
$M_2W$	14	4.3 - 5.2	4.83	0.32	6.7
$M_3L$	12	5.2 - 6.2	5.64	0.38	6.7
$M_3W$	13	3.3 - 4.6	3.95	0.33	8.3
Mandibular depth:	13	8.2 - 14.2	10.67	1.73	16.2

Total number of specimens = 42

Family MENISCOTHERIIDAE

*Meniscotherium priscum* Granger, 1915

**Holotype.** Locality SC-67(?): AMNH 16145.

**Description.** The holotype is a left dentary fragment with  $dP_4$ - $M_1$ . These teeth are more selenodont than those of contemporary *Ectocion parvus* or *Copecion davisi*, and the metastylid on  $M_1$  is more prominent. *Meniscotherium priscum* resembles *E. parvus* and *C. davisi* closely in size, with  $M_1$  measuring 5.5 mm in length and 4.5 mm in width (Granger, 1915, p. 360).

**Discussion.** Van Valen (1978) synonymized *Meniscotherium priscum* with *Ectocion parvus*, but the two are distinctly different in dental morphology, as Rose (1981) and others have recognized.

*Meniscotherium priscum* and *Ectocion parvus* were both described by Granger (1915), and the holotypes of both were said to have been found in "Clark Fork beds, Head of Big Sand Coulee, Clark Fork basin, Wyo. Exp. 1911." (see Granger, 1915, p. 353 and 360). Both specimens are light in color like others from zone  $Wa_0$ , and both lack entries in the American Museum Bighorn Wasatch expedi-

tion's 1911 field catalogue (Gingerich, 1982). It seems likely that the type of *M. priscum*, like that of *E. parvus* (see discussion above), was collected by W. J. Sinclair on August 13, 1911, from red-banded beds in the bluff three miles north of Ralston (i.e., from the southern end of Polecat Bench). The best exposures here are in what is now called locality SC-67. No new specimens of *Meniscotherium* have been found in zone  $Wa_0$  at SC-67 or elsewhere, but the combination of bone and tooth color, and circumstances of discovery paralleling those of *E. parvus* leave little doubt that the holotype of *M. priscum* came from zone  $Wa_0$  and probably from locality SC-67 (a similar argument is presented in Gingerich, 1982).

Rose (1981, p. 76) listed *Meniscotherium priscum* as being late Clarkforkian in age, based on Granger's (1915) published statement that the holotype came from the head of Big Sand Coulee. For reasons given here, it now seems more likely that the holotype came from earliest Wasatchian red beds at the southern end of Polecat Bench. However, a late Clarkforkian specimen of *M. priscum*, UM 91419, was found in 1987 at University of Michigan locality MP-71 in the northern of two outliers of Willwood Formation at locality 11 of Van Houten (1944, p. 181). This locality yielded several phenacodontids and an endocarp of *Celtis*, but no Wasatchian mammals. Granger was probably wrong about the type locality being at the head of Big Sand Coulee, but Rose appears to have been correct in including *Meniscotherium priscum* as an element of the late Clarkforkian fauna.

Order ARTIODACTYLA  
Family Dichobunidae

*Diacodexis ilicis*, new species  
Fig. 36

*Holotype and referred specimens.* Locality SC-67: UM 66613, 86232, 87854 (holotype), and 92355. Locality SC-308: UM 76236 and 85596m.

*Diagnosis.* Small species differing from all other species of the genus in having shorter lower premolars relative to molar length.  $P_4$  is shorter than  $M_1$ : the ratio of  $P_4$  length to  $M_1$  length is 0.97 ( $n = 1$ ) in *D. ilicis* compared with a range of 1.07 - 1.29 ( $n = 19$ ,  $\bar{x} = 1.17$ ) in North American *D. metsiacus* ("*Diacodexis secans* lineage segment *D. s.-metsiacus*," Krishtalka and Stucky, 1985, table 7), a range of 1.15-1.36 ( $n = 16$ ,  $\bar{x} = 1.25$  in North American *D. secans* (Krishtalka and Stucky, 1985, table 3), a range of 1.05-1.31 ( $n = 12$ ,  $\bar{x} = 1.20$ ) in North American *D. minutus* (Krishtalka and Stucky, 1985, table 11), a value of 1.05 ( $n = 2$ ) in North American *D. gracilis* (Krishtalka and Stucky, 1985, table 12), a range of 1.21-1.33 ( $n = 2$ ) in North American *D. woltonensis* (Krishtalka and Stucky, 1985, table 13), and a range of 1.00-1.19 ( $n = 8$ ,  $\bar{x} = 1.10$ ) in Asian *D. pakistanensis* (Thewissen et al., 1983, appendix 2).  $P_4$  is unknown in European *D. gazini*

and *D. varleti*. Lower molars of *D. ilicis* differ from those of *D. gazini* in having more separated paraconids and metaconids, lacking labial cingulids, and lacking a hypolophid on  $M_3$ . Lower molars of *D. ilicis* differ from those of *D. varleti* in retaining larger paraconids, and in lacking the hypoconulid-entoconid twinning characteristic of the latter species.

*Etymology.* Named for Dr. B. Holly Smith, who collected the holotype and many other  $Wa_0$  mammals. *Ilex* is Latin for holly.

*Description.* The most complete specimen of *Diacodexis ilicis* is the holotype, UM 87854 (Fig. 36), a right dentary with the posterior half of the crown of  $P_4$ , intact crowns of  $M_1$  and  $M_2$ , and the trigonid of  $M_3$ . This specimen preserves alveoli for  $P_2$ , alveoli for  $P_3$ , and the anterior root of  $P_4$ . The anterior margins of the crowns of  $P_3$  and  $P_4$  are aligned with the front edge of their respective anterior alveoli in *Diacodexis*, and the spacing of these alveoli provides a good estimate of premolar length. The spacing of alveoli indicates that  $P_3$  and  $P_4$  together measured 7.0 mm in length, and each individually probably measured 3.5 mm in length. If  $P_3$  was longer than  $P_4$ , as in later species of the genus, then  $P_4$  may have been only 3.4 mm in length.  $P_4$  measures 2.1 mm in width. The crown of  $M_1$  measures 3.6 mm in length and 2.8 mm in width.  $M_2$  measures 4.1 mm in length and 3.4 mm in width. The trigonid of  $M_3$  measures 3.3 mm in width.

The talonid of  $P_4$  is narrow and shallowly basined in the holotype, with the labial margin bounded by a slightly worn postprotocristid.  $M_1$  and  $M_2$  are different in size but otherwise very similar. Both have a distinct paraconid anterior to the metaconid. This cusp is slightly smaller than the metaconid, and well separated from it (especially on  $M_1$ ). The hypoconid is the largest talonid cusp, the entoconid is moderately large, and the hypoconulid is little more than a cuspule in the middle of the posterior edge of the crown where the posthypocristid meets the posterior cingulid. The trigonid of  $M_3$  in the holotype is constructed very much like that of  $M_2$ , with a paraconid slightly smaller than the metaconid and well separated from it. Two specimens have complete crowns of  $M_3$ : UM 85596m and 86232. These have a trigonid like that in the holotype, and both have a talonid with the hypoconid and hypoconulid large and the entoconid a little smaller. The hypoconulid is positioned very slightly to the lingual side of the midline of the crown. It is a little closer to the entoconid than to the hypoconid, but the entoconid and hypoconulid are not twinned as they are in *D. varleti*. The talonid cusps are connected by marginal crests enclosing a talonid basin, but there is no suggestion of a hypolophid connection between the hypoconid and entoconid on any of the specimens. The enamel is smooth on all lower molars, and none of them have labial cingulids. The holotype dentary measures 6.2 mm in depth below  $M_1$ , and it has mental foramina below the anterior alveolus for  $P_2$  and below a point just in front of the anterior alveolus for  $P_4$ .

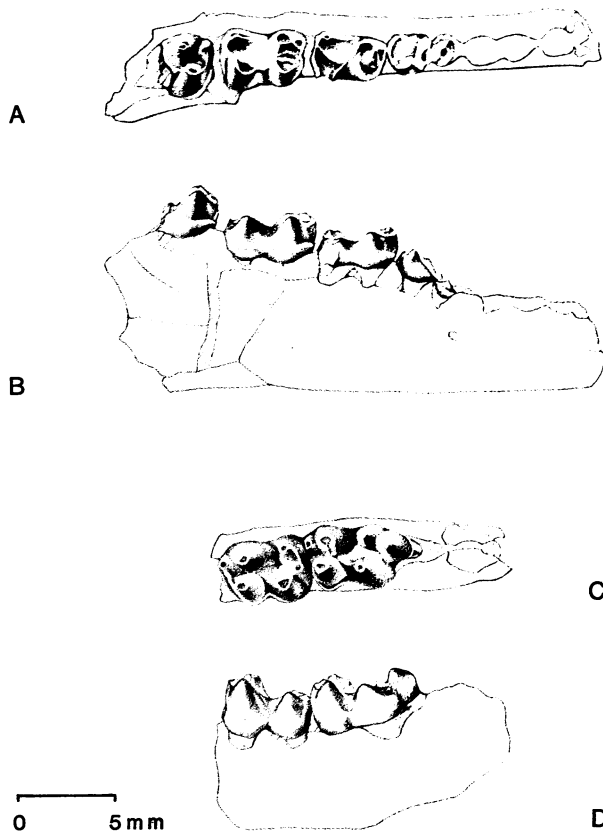


Figure 36. Dentition of *Diacodexis ilicis*, new species. A and B, right dentary with P<sub>4</sub>-M<sub>3</sub>, UM 87854 (holotype), in occlusal and lateral view. C and D, left dentary with M<sub>2,3</sub>, UM 86232, in occlusal and lateral view.

Measurements of Wa<sub>0</sub> *D. ilicis* are summarized in Table 24.

**Discussion.** *Diacodexis ilicis* is similar in size to late Wasatchian *D. minutus* described by Krishtalka and Stucky (1985), and these two together are the smallest species of *Diacodexis* known from North America. *D. ilicis* is larger than *D. gazini* described from Europe by Godinot (1978, 1981) and *D. pakistanensis* described from southern Asia by Thewissen et al. (1983), and it is about the same size as European *D. varleti* (Sudre et al., 1983). The size transition from *D. ilicis* to typical *D. metsiacus* in North America is a continuous one with early samples of *D. metsiacus* matching *D. ilicis* very closely in size (Figure 37).

In addition to this change in size, there appears to be progressive elongation of the premolars relative to molar length in North American *Diacodexis*, with earliest Wasatchian *D. ilicis* having a P<sub>4</sub>/M<sub>1</sub> length ratio less than 1.00, early and middle Wasatchian *D. metsiacus* having a mean ratio of 1.17 (range 1.07 -1.29), and late Wasatchian *D. minutus* and *D. secans* having mean ratios of 1.20

Table 24. Measurements of *Diacodexis ilicis* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Lower dentition</i>					
P <sub>4</sub> L	1	3.5	-	-	-
P <sub>4</sub> W	1	2.1	-	-	-
M <sub>1</sub> L	2	3.6 - 3.9	3.75	-	-
M <sub>1</sub> W	2	2.8 - 3.0	2.90	-	-
M <sub>2</sub> L	5	3.9 - 4.2	4.06	0.15	3.7
M <sub>2</sub> W	5	3.1 - 3.6	3.38	0.18	5.3
M <sub>3</sub> L	3	5.1 - 5.4	5.23	0.15	2.9
M <sub>3</sub> W	4	3.2 - 3.4	3.27	0.10	2.9
Mandibular depth:	2	6.2 - 6.8	6.50	-	-
Total number of specimens = 6					

(range 1.05–1.31) and 1.25 (range 1.15–1.36), respectively. The high mean P<sub>4</sub>/M<sub>1</sub> length ratio in small *D. minutus* shows that this trend is more than a simple allometric effect of increasing size. *D. ilicis* is the oldest North American species, and hence it is reasonable to infer that short premolars constitute the primitive condition. *D. pakistanensis* has a mean P<sub>4</sub>/M<sub>1</sub> length ratio of 1.10 (range 1.00–1.19), suggesting that it is also somewhat primitive in this regard. There are no fourth premolars assigned to either of the named European species, but the P<sub>2</sub> or P<sub>3</sub> of *D. gazini* described by Godinot (1981, p. 107) yields a P<sub>2</sub>/M<sub>1</sub> or P<sub>3</sub>/M<sub>1</sub> length ratio of 1.17.

European *Diacodexis gazini* does not have the prominently twinned entoconid and hypoconulid of *D. varleti*, but it is similar in having the hypoconulid on all of the lower molars more lingually placed, closer to the entoconid, by comparison with other species of *Diacodexis*. *D. gazini* from Rians (Godinot, 1981) and Silveirinha (Antunes and Russell, 1981) differs from *D. varleti* in having a stronger hypolophid on M<sub>3</sub>. The European *Diacodexis* that most closely resembles *D. ilicis* is the unnamed species from Dormaal, discussed by Sudre et al. (1983) under the appellation *Diacodexis* sp. Sudre et al. note that teeth of Dormaal *Diacodexis* are sufficiently different from teeth of Rians *Diacodexis* to consider that they belong to a distinct species. This is especially clear in comparing M<sub>3</sub>. Sudre et al. (1983, p. 294) suggest that the Dormaal *Diacodexis* may be a little younger geologically than that from Rians. However, considered in light of the generalized form of *Diacodexis* elsewhere and the morphology of earliest Wasatchian *Diacodexis* in North America, I would expect the Dormaal *Diacodexis* to be older than that from Rians. Dormaal specimens of *Diacodexis* are smaller than those of *D. ilicis* described here, and they probably represent a new species; however, premolars must be recovered from Dormaal before this form can be compared meaningfully with the Wa<sub>0</sub> species.

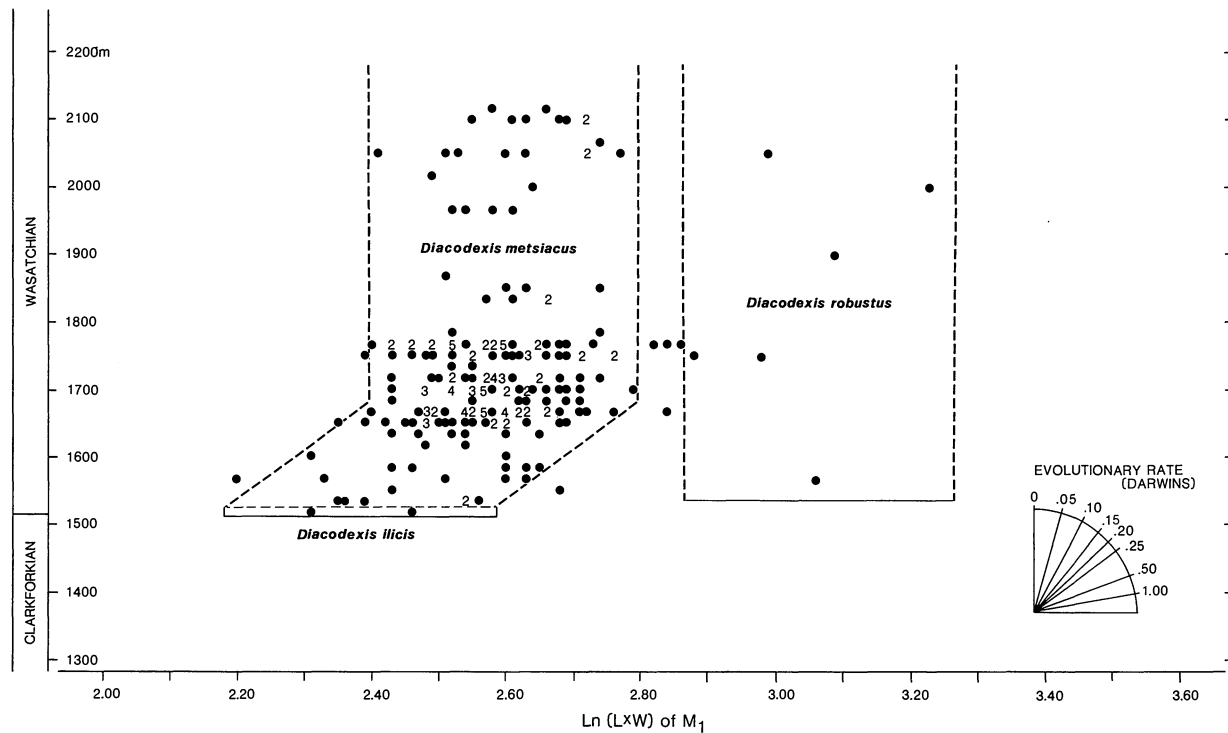
CLARK'S FORK BASIN *DIACODEXIS*

Figure 37. Stratigraphic distribution of early Wasatchian *Diacodexis* in the Clarks Fork Basin, Wyoming. Note rapid evolution toward larger size soon after introduction of *Diacodexis* in the earliest Wasatchian, and relative stability in size thereafter. Symbols as in Figure 14. Specimens plotted here are in the paleontological collections of the University of Michigan.

Order PERISSODACTYLA  
Family EQUIDAE

***Hyracotherium sandrae*, new species**

Figs. 38, 39A, 40

**Holotype and referred specimens.** Locality FG-61: UM 85291. Locality SC-67: UM 66139, 74078, 75423m, 79883, 79888, 79889, 79893m, 82385, 82387m (2 specimens), 83473, 83478m, 83615, 83636m, 86003m, 86229, 87336, 87858, 87859m, and 92352. Locality SC-69: UM 86137m. Locality SC-79: UM 83642 (2 specimens). Locality SC-121: UM 83459, 85667, 85671m, and 86138. Locality SC-139: 68033m and 83567 (holotype).

**Diagnosis.** Differs from most species of *Hyracotherium* in being significantly smaller (*H. sandrae* is 15–20% smaller in linear dimensions than contemporary *H. grangeri*). Similar in size to European early Sparnacian *Cymbalophus* (or *Hyracotherium*) *cuniculus*, but differs in having a less complete lingual cingulum on upper molars and a less lophodont trigonid on lower molars. Similar in size to North American Wasatchian *H. seekinsi*, but differs in having narrower upper molars with a weaker lingual

cingulum. Differs also in having narrower labial cingulids on lower molars, a weaker lower molar protolophid, and the paracristid on  $M_{1-2}$  curving up the front of the metaconid. Similar in size to North American middle and late Wasatchian *H. index* (= *H. sulcatus*, *H. angustidens*, *H. cuspidatus*, and *H. loevii*), but differs in having the paracristid on  $dP_4$  and  $M_{1-2}$  curving up the front of the metaconid, usually enclosing a distinct anterior fovea on the trigonid. Also differs in having a less elongated  $M_3$ .

**Etymology.** Named for Dr. Sandra Carlson who found the most complete specimen, the partial skeleton mentioned above. The name is also appropriate because the holotype and several referred specimens were found in the Sand Coulee area of the Clarks Fork Basin, and *H. sandrae* is known only from the early Sandcouleean subage of the Wasatchian land-mammal age.

**Description.** The holotype is a right dentary with  $M_{1-3}$ , UM 83567 (Fig. 38). This specimen exhibits several of the distinctive features of *H. sandrae*: small size, notched protolophid on  $M_{1-3}$ , continuation of the paracristid up the front of the metaconid on  $M_{1-2}$ , and a weak labial cingulid on all three molars.  $M_1$  in the holotype measures 6.4 mm in length and 4.4 mm in width,  $M_2$  measures 7.0 mm in

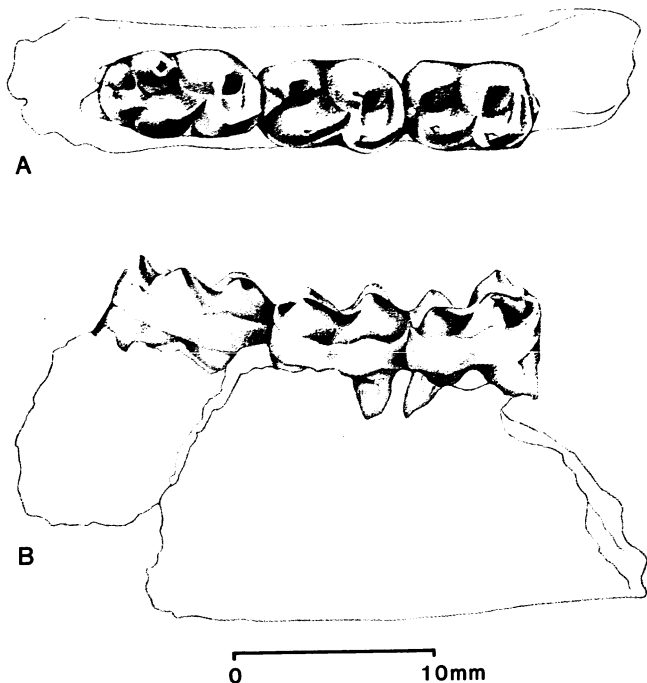


Figure 38. Dentition of *Hyracotherium sandrae*, new species. A and B, right dentary with  $M_{1,3}$ , UM 83567 (holotype), in occlusal and lateral view.

length and 4.7 mm in width,  $M_3$  measures 7.9 mm in length and 4.5 mm in width, and the mandible measures 11.3 mm in depth beneath  $M_1$ .

The anterior upper dentition of *H. sandrae* is unknown. UM 87336 is a right maxilla with  $dP^4-M^1$ .  $DP^4$  has four principle cusps (protocone, paracone, metacone, and hypocone), each about equal in size, with a distinct paraconule and metaconule connecting the anterior and posterior pairs of cusps. The centrocrista connecting the paracone and metacone is straight, and there is no trace of a mesostyle.  $P^2$  is preserved in UM 82385. It is two-rooted and has a simple narrow crown with a single prominent labial cusp (paracone), a smaller very slightly separated metacone, and a posterolingual shelf but no distinct protocone.  $P^3$  and  $P^4$  are best preserved in UM 83473. These teeth have distinct labial cusps (paracone and metacone) and a distinct protocone, but no trace of a hypocone. The paraconule is moderately large, but the metaconule is represented in both by nothing more than a small bead of enamel. Upper molars are well preserved in several specimens and these are similar to upper molars in most other *Hyracotherium*. They are distinctive only in having a weak lingual cingulum that typically appears to run up the front of the hypocone rather than passing around the base of this cusp.

Three specimens preserve evidence of the anterior lower dentition. UM 82387m is a fused symphysis with roots or

alveoli for six procumbent incisors. The symphysis itself is procumbent, long, and narrow, measuring 18–19 mm in length and 3.6 mm in width between the canine alveoli. All six incisors appear to have been about the same size (judging from roots and/or alveoli, the roots measure ca.  $1.4 \times 1.1$  mm in diameter). Left and right canine roots measure about  $2.8 \times 2.2$  mm in diameter where each is broken off near the base of the crown. There is a 7.8 mm diastema between the alveolus for  $C_1$  and the alveolus for  $P_1$ .  $P_1$  is single-rooted in the two specimens that preserve this part of the jaw (UM 79888 and 79889).  $P_1$  and  $P_2$  are positioned near each other in UM 79888, while they are separated by a short diastema of 2.5 mm in UM 79889. Crowns of  $P_1$  and  $P_2$  are not preserved in any specimen at hand. The crown of  $P_3$  is relatively long and narrow, with distinct protoconid, paraconid, and metaconid cusps on a narrow, forwardly-inclined trigonid. There is a prominent hypoconid, but no entoconid or hypoconulid.  $P_4$  is more molarized than  $P_3$ , with prominent protoconid and metaconid cusps separated by a distinct notch. The hypoconid is large but the entoconid is very small and there is no real hypoconulid. The cristid obliqua joins the back of the protoconid, and the unbasined talonid slopes lingually.

$M_1$  and  $M_2$  are very similar to each other, and isolated teeth often cannot reliably distinguished. Each has four prominent cusps. The protoconid and metaconid are separated by a distinct notch in the protolophid (Fig. 39A). The paracristid extends forward from the protoconid and then bends sharply to continue along the anterior edge of the crown. At the anterolingual corner of the crown, it bends again and extends up the front of the metaconid, enclosing a basined fovea. The hypoconid and entoconid are separated by a distinct notch that is usually large, although it is smaller in some specimens where the cusps are more closely connected (notably the holotype). The posthypoconid usually joins the hypoconulid rather than the entoconid, and there is rarely any development of a real hypolophid.  $DP_4$  is well preserved in UM 83615. It is relatively longer and narrower than  $M_1$  or  $M_2$ , but fully molarized and closely similar to these teeth in the conformation of cusps and crests. The paracristid is large, enclosing a distinct anterior fovea on the trigonid.  $M_3$  resembles  $M_1$  and  $M_2$  in trigonid construction, but it lacks the paracristid running up the front of the metaconid. There is a third or hypoconulid lobe on  $M_3$ , often with a distinct accessory cusp lingual to the hypoconulid. Here again, the strongest crest connects the hypoconid to the hypoconulid rather than the entoconid, and there is no real hypolophid on  $M_3$ .

Dental measurements of  $Wa_0$  *H. sandrae* are summarized in Table 25.

UM 79889 includes part of the postcranial skeleton one individual (Fig. 40). This specimen was found in many pieces by S. Carlson and reassembled by B. H. Smith. Further preparation will be necessary before details of foot structure will be visible. The left humerus measures 87.5 mm in length and  $8.1 \times 6.2$  mm in midshaft diameter. The

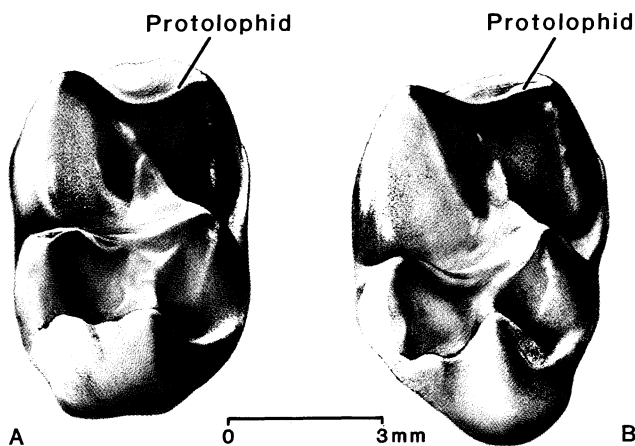


Figure 39. Comparison of lophodontology in North American *Hyracotherium sandrae* with that in European *Cymbalophus cuniculus*. A, right  $M_3$  of UM 83567 (holotype) from SC-139. B, right  $M_3$  of BMNH M-29710 (topotype) from Kyson in southern England. Both specimens in oblique posterior view. Note the distinctly notched proto-lophid connecting the protoconid and metaconid in *H. sandrae*, and the higher, straighter proto-lophid in *C. cuniculus*. Greater lophodonty is one of the principal reasons Hooker (1984) removed *C. cuniculus* from *Hyracotherium* and Hippomorpha, creating the new genus *Cymbalophus* in Ceratomorpha.

left femur measures approximately 113.5 mm in length (adding several mm to the greater trochanter, which is incomplete), and it measures  $8.3 \times 6.8$  mm in midshaft diameter. The head of the femur is 9.5–10.2 mm in diameter, depending on how it is measured. The left tibia measures 105.6 mm in length and  $7.6 \times 6.0$  mm in midshaft diameter. The left astragalus measures 14.3 mm in length and 9.0 mm in breadth across the trochlea, and the left calcaneus measures 29.8 mm in length. The left tibia, astragalus, and calcaneus remain in articulation.

The humerus is approximately the same length as the humerus of AMNH 15436, identified as *Hyracotherium angustidens* by Kitts (1956), but it is more lightly built. The humerus, the femur, and the tibia are all much smaller than corresponding elements of AMNH 15428, which Kitts (1956) also attributed to *H. angustidens*. Long bones of the  $Wa_0$  form are only 63–67% the length of the latter. The femur and tibia of *H. sandrae* are more lightly built than elements attributed to *H. angustidens*. The skeleton of *H. sandrae* compares well with the skeleton of a gracile Siamese domestic cat in terms of overall size, lengths of limb segments, and limb diameters.

**Discussion.** The stratigraphic distribution of early Wasatchian *Hyracotherium* is shown in Figure 41, which illustrates both the limited stratigraphic range of *H. sandrae* and its clear distinction from *H. grangeri*. *Hyracotherium grangeri* differs from early Wasatchian lineages of other genera and species in becoming progressively smaller rather than larger in the 1525–1700 m interval of the Clarks

Table 25. Measurements of *Hyracotherium sandrae* from  $Wa_0$

Tooth position	N	Range	Mean	S.Dev.	C.V.
<b>Upper dentition</b>					
dP <sup>4</sup> L	1	5.4	-	-	-
dP <sup>4</sup> W	1	5.6	-	-	-
P <sup>2</sup> L	1	4.3	-	-	-
P <sup>2</sup> W	1	3.4	-	-	-
P <sup>3</sup> L	1	4.9	-	-	-
P <sup>3</sup> W	1	5.6	-	-	-
P <sup>4</sup> L	3	4.9 - 5.5	5.23	0.34	6.5
P <sup>4</sup> W	3	6.0 - 6.7	6.37	0.38	6.0
M <sup>1</sup> L	5	5.9 - 6.4	6.15	0.22	3.5
M <sup>1</sup> W	5	6.9 - 7.4	7.10	0.23	3.3
M <sup>1/2</sup> L	1	5.9	-	-	-
M <sup>1/2</sup> W	1	7.1	-	-	-
M <sup>2</sup> L	5	6.3 - 7.0	6.53	0.29	4.4
M <sup>2</sup> W	5	7.7 - 8.0	7.85	0.13	1.7
M <sup>3</sup> L	6	5.8 - 6.5	6.13	0.29	4.8
M <sup>3</sup> W	6	6.7 - 7.6	7.26	0.34	4.7
<b>Lower dentition</b>					
dP <sub>4</sub> L	2	5.7 - 6.0	5.85	-	-
dP <sub>4</sub> W	2	3.5 - 3.8	3.65	-	-
P <sub>3</sub> L	3	4.9 - 5.0	4.93	0.06	1.2
P <sub>3</sub> W	3	2.7 - 3.0	2.80	0.17	6.2
P <sub>4</sub> L	4	4.9 - 5.1	5.03	0.10	1.9
P <sub>4</sub> W	5	3.3 - 3.5	3.42	0.08	2.4
M <sub>1</sub> L	5	5.8 - 6.4	6.14	0.24	3.9
M <sub>1</sub> W	5	4.0 - 4.4	4.17	0.19	4.6
M <sub>1/2</sub> L	3	6.6 - 7.5	7.03	0.45	6.4
M <sub>1/2</sub> W	3	4.7 - 5.1	4.97	0.23	4.6
M <sub>2</sub> L	8	6.1 - 7.8	6.93	0.49	7.1
M <sub>2</sub> W	9	4.3 - 5.1	4.62	0.23	5.0
M <sub>3</sub> L	5	7.8 - 8.7	8.20	0.36	4.4
M <sub>3</sub> W	8	4.1 - 5.1	4.53	0.33	7.4
Mandibular depth:	8	11.3 - 13.6	12.47	0.79	6.4

Total number of specimens = 30

Fork Basin stratigraphic section, possibly in response to the disappearance of *H. sandrae*.

*Hyracotherium sandrae* is very similar in size to European early Sparnacian *Cymbalophus cuniculus*, and it is also similar in the configuration of most cusps and crests. *C. cuniculus* was placed in the genus *Hyracotherium* when it was described and named by Owen (1842), and subsequent authors through Hooker (1980) have usually regarded it as a species of the equoid or hippomorph perissodactyl *Hyracotherium*. Recently, Hooker (1984) concluded that *H. cuniculus* is not an hippomorph but rather a ceratomorph related to tapiroids and rhinocerotoids because it is more lophodont. This required that *H. cuniculus* be placed in the new genus *Cymbalophus*.

*Cymbalophus* differs from *Hyracotherium* in the lower dentition in having higher and straighter molar proto-lophids (not "notched"); a more anteroposteriorly oriented cristid obliqua (metalophid); confluent (untwinned) metaconid and metastylid; and more vertical (less convergent or sloping) buccal, lingual, and posterior walls of principal cusps. *Cymbalophus* differs from *Hyracotherium* in the upper den-



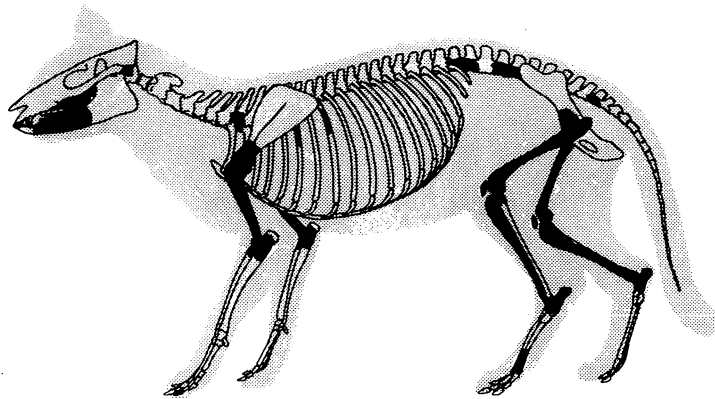


Figure 40. Skeleton of *Hyracotherium* shaded to indicate cranial and postcranial elements of *H. sandrae* preserved in UM 79889, an associated partial skeleton found at locality SC-67. Stippled outline of domestic Siamese cat superimposed for scale.

CLARK'S FORK BASIN *HYRACOTHERIUM*

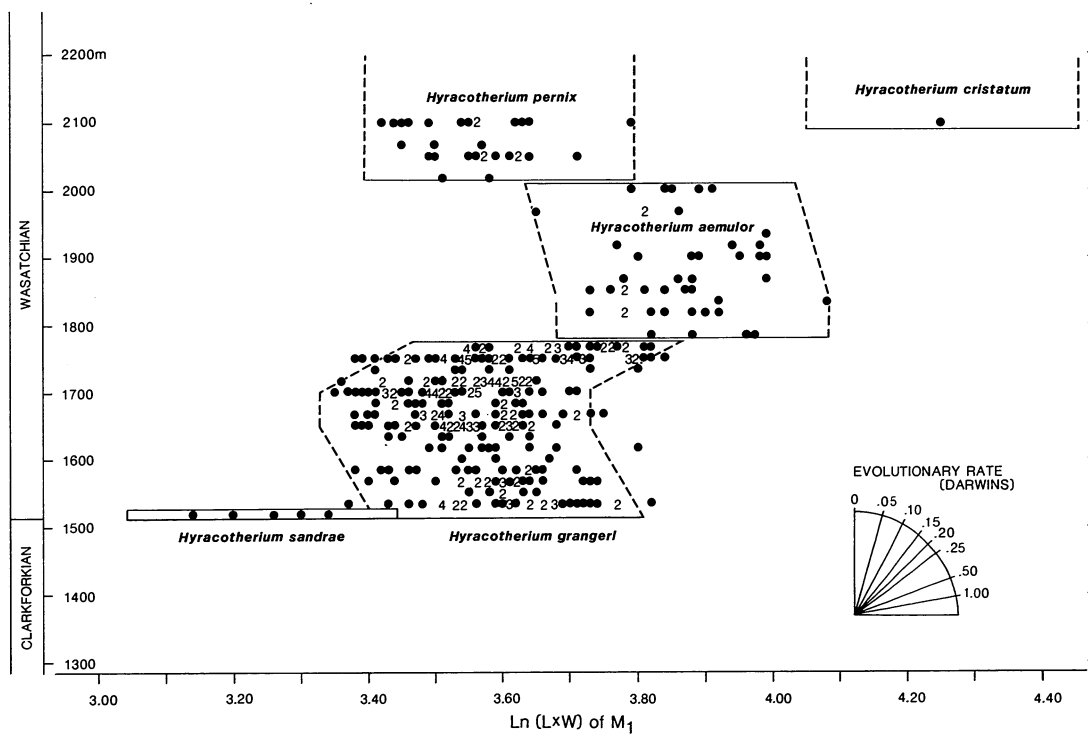


Figure 41. Stratigraphic distribution of early Wasatchian *Hyracotherium* in the Clarks Fork Basin, Wyoming. Small *H. sandrae* is known only from earliest Wasatchian zone  $Wa_0$ . *H. grangeri* is also present in this zone, although no specimens preserving  $M_1$  have been found to date. Symbols as in Figure 14. Specimens plotted here are in the paleontological collections of the University of Michigan.

tion in having weaker upper molar conules and buccally displaced paracones and/or metacones (interrupting the buccal cingulum). These distinctions are rather finely drawn and may not hold up when better material of *C. cuniculus* is available. All appear to be slight specializations in *Cymbalophus* by comparison with more primitive *Hyracotherium*. *H. sandrae* is very similar to *C. cuniculus*, but it does not show the more lophodont molar characteristics that distinguish *Cymbalophus*. It appears to be rather a slightly more primitive species comfortably accommodated within *Hyracotherium*.

North American *Hyracotherium index* is a small, middle and late Wasatchian species with cheek teeth approximately the same size as those of *H. sandrae*. However, the trigonids of lower molars of *H. index* almost always have paracristids that stop abruptly at the lingual margin of the crown.  $M_3$  is relatively long in *H. index*: the ratio of  $M_3$  length relative to  $M_2$  length varies from 1.30–1.40 in *H. index*, while this ratio is only 1.13–1.17 in *H. sandrae*.

*H. seekinsi* is another small North American species that might be confused with *H. sandrae* (if it is distinct from *H. index*). *H. seekinsi* was originally based on four associated upper molars collected from Punta Prieta in Baja California, a fossil locality interpreted to be "Paleocene" in age (Morris, 1968). New mammalian specimens indicate clearly that the Punta Prieta fauna is Wasatchian (early Eocene) in age (Flynn and Novacek, 1984; Novacek et al., 1987). New specimens include a fragmentary dentary of *H. seekinsi* with one complete molar ( $M_1$  or  $M_2$ ). This specimen has a paracristid that stops abruptly at the lingual margin of the crown, rather than curving up the front of the metacone, and it is unlikely to represent a species as primitive as *H. sandrae*. It seems more likely that *H. seekinsi* is conspecific with *H. index*.

Two other North American "Paleocene" specimens of *Hyracotherium* require discussion. The first, a Princeton University specimen (YPM-PU 18316), was described by Jepsen and Woodburne (1969) from an area northwest of Polecat Bench in the Clarks Fork Basin. The stated locality (NW  $\frac{1}{4}$ , Section 26, T 57 N, R 100 W, Park County, Wyoming, or University of Michigan locality SC-144) is now known to be late Tiffanian in age, and the specimen itself is indistinguishable from early Wasatchian *H. grangeri*. This species is very common in strata exposed 15–20 km to the southwest of SC-144; *Hyracotherium* has never been found in Tiffanian or Clarkforkian strata in the Clarks Fork Basin or elsewhere; the specimen in question was not recognized as a Tiffanian *Hyracotherium* until several years after it was collected (Rose, 1981, p. 24, points out that Jepsen and Woodburne's discussion of locality records implies in itself some doubt as to their validity); and errors in Princeton locality records have been demonstrated for other specimens collected in the same field season (1962; see Gingerich, 1977a). All things considered, it seems very unlikely that the Princeton specimen is a valid Tiffanian or Clarkforkian record of *Hyracotherium*.

The second "Paleocene" specimen of *Hyracotherium* was described from the Big Bend area of Texas by Schiebout (1974). It was identified as Paleocene because it was found with a barylambdid pantodont and, probably, because Paleocene *Hyracotherium* had been reported previously from Baja California and from Wyoming. Given two overlapping stratigraphic ranges, in this case the first appearance of an equid overlapping the last appearance of a barylambdid, a single first appearance usually takes precedence over a single last appearance in determining age. By this principle, the age of the Big Bend *Hyracotherium* was always more likely to have been Eocene rather than Paleocene. Schiebout et al. (1987) recently reidentified the "barylambdid" as *Coryphodon*, and reassigned the Big Bend "Paleocene" *Hyracotherium* to the Wasatchian land-mammal age (Eocene). Thus there is no remaining evidence to suggest that *Hyracotherium* was present in North America during the Tiffanian or Clarkforkian land-mammal ages.

#### *Hyracotherium grangeri* Kitts, 1956

*Referred specimens.* Locality SC-67: UM 66615, 82387m, and 83637m.

*Description.* These specimens include two isolated teeth identified as  $M_1$  or  $M_2$  and one isolated tooth identified as  $M^3$ . One of the former is well above the range of tooth measurements for both  $M_1$  and  $M_2$  in *Hyracotherium sandrae* and seems unlikely belong to that species. The other is smaller and could be either an  $M_1$  of *H. grangeri* or possibly an  $M_2$  of *H. sandrae*. The  $M^3$  is well above the range of tooth measurements for this tooth in *H. sandrae*.

Measurements of  $Wa_0$  *H. grangeri* are summarized in Table 26.

*Discussion.* The common species of *Hyracotherium* in zone  $Wa_0$  is clearly *H. sandrae*. Each record of *H. grangeri*, by itself, might be dismissed as a contaminant from an overlying horizon (all are dark in color, but brown and not black); however, the presence of three teeth larger than most or all *H. sandrae* suggests that *H. grangeri* is present here as well. *H. sandrae* was either very short-lived as a species in the area under study, or it inhabited environments that are not often sampled in the fossil record. It is possible that *H. sandrae* and *H. grangeri* evolved side by side in the early Wasatchian of North America, with each dominating in a different environment. Similarly, it is possible that *Cymbalophus cuniculus* and *Hyracotherium* cf. *H. vulpiceps* evolved side by side in the early Sparnacian of Europe. This would help to explain why *Hyracotherium* specimens from Meudon (France), thought to be of early or earliest Sparnacian age, are large and *H. vulpiceps*-like in form rather than small and *C. cuniculus*-like.

Table 26. Measurements of *Hyracotherium grangeri* from Wa<sub>0</sub>

Tooth position	N	Range	Mean	S.Dev.	C.V.
<i>Upper dentition</i>					
M <sup>3</sup> L	1	7.3	-	-	-
M <sup>3</sup> W	1	8.3	-	-	-
<i>Lower dentition</i>					
M <sub>1/2</sub> L	2	7.4 - 7.9	7.65	-	-
M <sub>1/2</sub> W	2	4.9 - 5.6	5.25	-	-

Total number of specimens = 3

Order EDENTATA  
Suborder PALAEANODONTA  
Family METACHEIROMYIDAE

***Palaeanodon nievelti*, new species**

Fig. 42B

*Holotype and referred specimens.* Locality SC-67: UM 83469, 83478m, 87335 (holotype), and questionably 85589. Locality SC-121: UM 83464m and 85671m.

Specimens referred to this species from higher stratigraphic levels include—Locality SC-2 (1720 m): UM 76365m and 83415m. Locality SC-4 (1570 m): UM 72864. Locality SC-6 (1530 m): UM 80598 and 83458. Locality SC-7 (1645 m): UM 63287. Locality SC-46 (1700 m): 76593. Locality SC-47 (1690 m): UM 86490. Locality SC-113 (2050 m): UM 79963. Locality SC-123 (no level): UM 76692. Locality SC-125 (1535 m): UM 66874. Locality SC-161 (1665 m): UM 79071, 82289, and 86085. Locality SC-210 (1645 m): UM 75664, 87441, and 87471. Locality SC-213 (1760 m): UM 84635. Locality SC-324 (1995 m): UM 79455.

*Diagnosis.* Smallest species of *Palaeanodon*: 11–24% smaller than *P. parvulus*, 30–35% smaller than *P. ignavus* in comparable linear dimensions. Further differs from *P. ignavus* in having the supinator crest arising higher on the shaft of the humerus (Fig. 42) and in having only three sacral vertebrae.

*Etymology.* Named for Mr. Alex van Nievelt, who found the holotype and prepared it for study.

*Description.* The holotype is the most complete specimen of *P. nievelti* known to date. It includes part of the braincase on the right side, a right dentary fragment, part of the second cervical vertebra (axis), four thoracic vertebrae, three lumbar vertebrae, a nearly complete sacrum, one proximal caudal vertebra, a nearly complete left humerus, and the proximal end of a right ulna.

The braincase is poorly preserved, and the only anatomical region of interest is the glenoid articular eminence of the squamosal. This is broad, shallowly basined, and bounded posteriorly by a small but sturdy postglenoid process. The postglenoid foramen lies directly behind the center of the articular eminence and medial to the postglenoid

process. The dentary fragment of the holotype extends from the back of the posteriormost cheek tooth alveolus to the front of the ascending ramus, including much of the medial buttress of the dentary characteristic of palaeanodonts. This dentary measures 5.2 mm in height at its shallowest point behind the posteriormost alveolus, and it measures 3.6 mm in maximum breadth across the medial buttress.

The axis is a free-standing vertebra that is not fused to the following cervicals, as reported by Matthew (1918). The sacrum provides new information about the axial skeleton of palaeanodonts. It includes three solidly fused vertebral centra, not the four present in *P. ignavus* (Matthew, 1918, p. 629, 633). The first and probably the second sacrals have lateral processes that articulated with the ilium of the innominate. The third sacral definitely did not articulate with the ilium. Neural spines of all three are solidly fused into a continuous narrow crest rising 5 mm above the level of the fused zygapophyses and extending the length of the sacrum. Postzygapophyses on the third sacral have articular surfaces well preserved, indicating that there was no fourth sacral vertebra.

The left humerus is well preserved (Fig. 42B). It measures 37.5 mm in length from the proximal head to the distal capitulum. The head is ovoid, its articular surface subtends an arc of nearly 180° anteroposteriorly. The articular surface is 8.1 mm long and 5.7 mm wide, and its long axis is inclined at an angle of about 30° to the long axis of the humeral shaft. The lateral greater tuberosity is much larger than the medial lesser tuberosity. Both lie well in front of the head on their respective sides. The deltopectoral crest is prominent, broad (6.5 mm wide), and flattened, extending to a point some 71% down the front of the shaft. The length of this crest is 26.7 mm measured from the proximal end of the greater tuberosity. The supinator crest overlaps the deltopectoral crest, joining the shaft some 22.3 mm above the capitulum. The supinator crest curves smoothly downward toward the capitulum as in *Palaeanodon ignavus*. This curvature is different in cf. *Propalaeanodon schaffi* (Fig. 42). The greatest transverse breadth of the distal end of the humerus is estimated to have been 19.2 mm (estimated by combining a fragment of the right entepicondyle with the left humerus lacking this epicondyle—both preserve the entepicondylar foramen). Most of these measurements are close to those given by Rose (1979) for cf. *Propalaeanodon schaffi*. The chief difference between the two is that the supinator crest diverges higher (more proximally) on the shaft of the humerus in *P. nievelti* than it does in *P. schaffi*. The only feature of interest preserved on the proximal ulna is a sharp medial inflection of the olecranon.

UM 83469 preserves the posterior part of a right dentary, measuring 5.0 mm in depth and 3.5 mm in breadth across the medial buttress, and part of the right C<sub>1</sub> measuring 2.4 × 2.3 mm in diameter at the base of the crown. Two isolated petrosals, a distal femur, and much of a tibia are

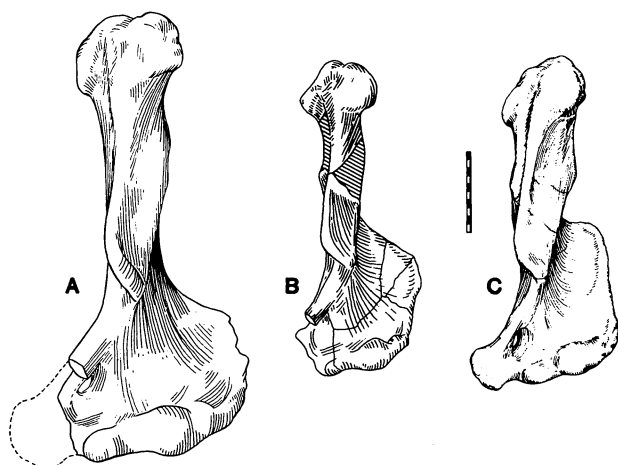


Figure 42. Left humerus of *Palaeonodon nievelti*, new species (center), compared to those of *Palaeonodon ignavus* (left) and *?Propalaeonodon schaffi* (right). All specimens drawn to same scale and shown in anterior view. A, early Wasatchian *Palaeonodon ignavus* (composite drawing based on AMNH 15008 and 16832). B, earliest Wasatchian *Palaeonodon nievelti* (UM 87335, holotype). C, late Tiffanian *?Propalaeonodon schaffi* (YPM-PU 13928). Note that deltopectoral crest of *P. nievelti* is intermediate in height and intermediate in shape by comparison with earlier *Propalaeonodon* and later *Palaeonodon*. Drawings A and C are taken from Rose (1979).

included under this number, but these do not appear to be *Palaeonodon*. UM 85589 includes three thoracic vertebrae in articulation and part of an associated rib questionably identified as *Palaeonodon*.

UM 83464 and 85671 are right dentary fragments. The first measures 4.6 mm in depth and 3.4 mm in breadth across the medial buttress, and the second measures 4.3 mm in depth and 3.6 mm in breadth across the medial buttress. UM 83478 is a left metacarpal III measuring 10.1 mm in length, 4.3 mm in breadth across the proximal end, and 4.5 mm in breadth across the distal end.

**Discussion.** *Propalaeonodon* and *Palaeonodon* are specialized digging mammals, probably partly fossorial (Rose, 1979), with many postcranial features suggesting an armadillo-like habitus (Matthew, 1918). Digging habits are reflected in the humerus by its narrow ovoid head, exaggerated development of the deltopectoral crest, and broad expansion of the supinator crest (Fig. 42), and digging habits are reflected in other aspects of cranial and postcranial morphology as well. Long thought to be rare in Wasatchian faunas, *Palaeonodon* is proving to be surprisingly common when dentary fragments and postcrania are recognized. It ranks 13th in relative abundance among mammalian species in the  $Wa_0$  fauna.

The stratigraphic distribution of early Wasatchian species of *Palaeonodon* in the Clarks Fork Basin is shown in Fig. 43. *P. parvulus* is known principally from the middle and late Clarkforkian, but it ranges into the early

Wasatchian as well (UM 66874 from SC-125, level 1535 m). *P. parvulus* has not been found in zone  $Wa_0$ . *P. nievelti* makes its first appearance in zone  $Wa_0$  and continues through the early and middle Wasatchian. The highest record at present is UM 79963 from SC-113 (level 2050 m). An unnamed *Palaeonodon* of intermediate size makes its first appearance at level 1750 m and continues upward through the middle Wasatchian. Much larger *P. ignavus* appears in the middle and late Wasatchian (e.g., UM 87227 from GR-18, and a new specimen from MP-151, both plotted near the top of Fig. 43).

Further evidence that *P. nievelti* and a larger *P. n. sp.* coexisted in the 1720–1760 m interval is provided by three metacarpal IIIs from locality SC-2. The first two, UM 76365m and 83415m, representing *P. nievelti*, measure  $9.9 \times 4.6 \times 4.7$  mm and  $9.3 \times 4.3 \times 4.6$  mm, respectively, in length, proximal breadth, and distal breadth. The third, UM 80048m, representing *P. n. sp.*, measures  $13.2 \times 5.9 \times 6.0$  mm in length, proximal breadth, and distal breadth. Matthew (1918, p. 639) gives metacarpal III lengths of 15 and 16 mm for two specimens of *P. ignavus*, the former being part of the holotype. He also illustrates metacarpal III in the holotype of *P. parvulus* (Matthew, 1918, fig. 57), which measures 12.4 mm in length. The stratigraphic distribution of dentary sizes for *Palaeonodon* shown in Figure 43 is interpreted as representing four distinct lineage segments, several of which coexisted to some degree in time. It might also be possible to interpret this pattern in terms of a lineage leading from *P. parvulus* to *P. nievelti*, with a distinct coexisting lineage leading from *P. n. sp.* to *P. ignavus*. Further evidence is required to clarify the evolutionary history of *Palaeonodon*.

#### MAMMALIA incertae sedis

Cf. *Asiabradypus* sp.

Fig. 44

*Referred specimen.* Locality SC-67: UM 87859m.

**Description.** This specimen is an edentulous right lower jaw with paired alveoli for  $M_1$  and  $M_2$  and the roots of  $M_3$  (Fig. 44). The dentary is relatively narrow and deep. It measures 2.9 mm wide and 7.3 mm deep beneath  $M_1$ . Alveoli for  $M_1$  and  $M_2$  are small, well separated, and circular in cross-section. The roots of  $M_3$  are small and circular in cross-section. Alveoli and roots indicate that  $M_1$  measured about 3.2 mm in length,  $M_2$  measured about 3.4 mm in length, and  $M_3$  measured about 2.8 mm in length. There is a mental foramen located beneath the posterior part of  $P_4$ .

**Discussion.** The specimen is distinctive enough to preclude reference to any taxon represented by teeth in the  $Wa_0$  fauna as it is known at present. The narrowness of the jaw, its depth, and the simple circular form of the roots suggest that the jaw belonged to a deep-jawed mammal with small, narrow, and delicate cheek teeth. The specimen could represent a very small *Hapalodectes*-like

CLARK'S FORK BASIN PALAEOANODONTA

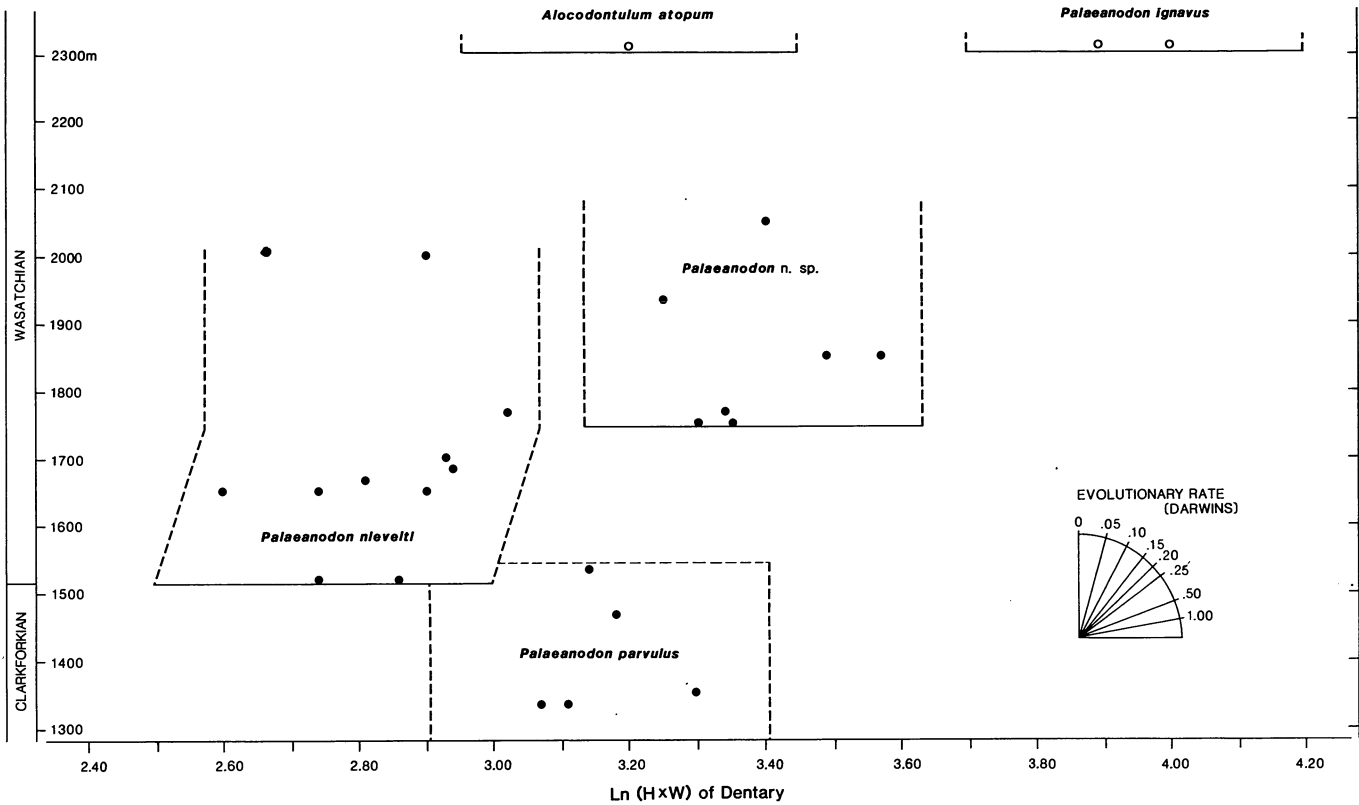
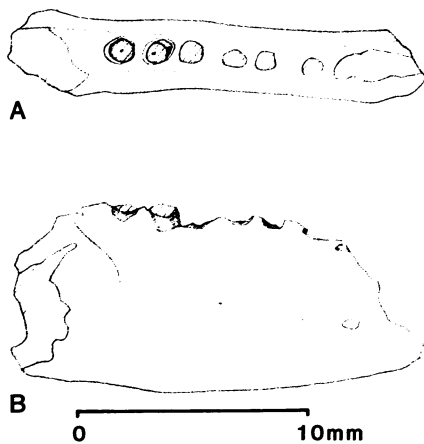


Figure 43. Stratigraphic distribution of Clarkforkian through middle Wasatchian Palaeonodonta in the Clarks Fork Basin, Wyoming. Measure of size shown here is logarithm of height multiplied by width of dentary at position of medial buttress. Clarkforkian *P. parvulus* appears to range into the early Wasatchian (although it has not been found in zone Wa<sub>0</sub>). *P. nievelti* ranges into the middle Wasatchian. Relationships of these species to each other and to middle Wasatchian *Alocodontulum atopum*, *Palaeonodon n. sp.*, *Palaeonodon ignavus* remain to be clarified by discovery of additional specimens.



mesonychid, or even, conceivably, a small *Arctostylops*-like notoungulate. However, its closest resemblance appears to be to *Asiabradypus incompositus* described by Nesson (1987) from the early Eocene of Soviet Kazakhstan. Nesson considers *Asiabradypus* to be a xenarthran, but the presence of double-rooted molars makes this unlikely.

Figure 44. Right dentary of cf. *Asiabradypus* sp. (UM 87859m) in occlusal (A) and lateral view (B). Note narrow deep jaw, and circular anteroposteriorly-aligned alveoli for double-rooted cheek teeth.



## IV COMPOSITION AND DIVERSITY

The earliest Wasatchian fauna described here is of special interest in recording the first appearance of the important mammalian orders Primates, Artiodactyla, and Perisodactyla, and the first appearance of hyaenodontid Creodonta in the North American fossil record. Fourteen mammalian orders are represented in all, with Creodonta and Condylarthra containing the greatest number of genera (6 and 10, respectively; Table 27). Eighteen out of a total of 41 evolutionary lineages (44%) make their first appearance at or near the beginning of zone  $Wa_0$ . Six lineages (15%) make their last appearance at or near the end of zone  $Wa_0$ , with four of these being species known, locally at least, only in zone  $Wa_0$ . Several orders that are usually present in Clarkforkian and early Wasatchian faunas are missing in the  $Wa_0$  fauna (Table 1): Insectivora, Proteutheria, Chiroptera, and Dermoptera have not been found in the  $Wa_0$  interval. Small mammals are difficult to find anywhere, but they appear to be even less common than usual in the  $Wa_0$  fauna. [Dr. George Junne collected a number of specimens at locality SC-67 during the 1988 field season that could not be included in the present analysis. Among these is a four-tooth maxilla of a small insectivore, the first record of Insectivora in zone  $Wa_0$ .] The common Clarkforkian and Wasatchian genus *Haplomylus* and the common Wasatchian genus *Homogalax* are conspicuously absent from the  $Wa_0$  fauna as well.

Relationships of the  $Wa_0$  fauna as a whole to preceding and succeeding faunas can be studied in terms of faunal composition, species diversity, and rank abundance of species.

### FAUNAL COMPOSITION AT THE FAMILY LEVEL

Most well-sampled Clarkforkian and Wasatchian mammalian faunas are distinctly different from each other in composition. One way to illustrate this difference is to quantify the proportional representation of each family of mammals in each well-sampled stratigraphic interval yielding a Clarkforkian or Wasatchian fauna. This yields a 33 taxon  $\times$  49 intervals matrix, where each entry in the matrix is the minimum number of individuals (MNI) representing the taxon divided by the total MNI present in the interval. Most families of Insectivora, Proteutheria, and Chiroptera are omitted because they are small and still poorly sampled at all localities. MNI provides a standard estimate of taxo-

nomic abundance that is easy to calculate, widely used, and usually appropriate for faunal assemblages in floodplain deposits (Badgley, 1986). Its principal drawback is overrepresentation of rare taxa in small samples. Results presented here are for family-level composition; similar analysis using genera or species would probably yield even greater separation of the Clarkforkian and Wasatchian since the two faunas share fewer genera and species in common.

MNIs for the  $Wa_0$  fauna were computed by counting the maximum number of length or width measurements available for every tooth, left or right, upper or lower, identifiable to species. Counts of measurements for teeth ambiguously identified as  $M_1$  or  $M_2$  were divided by two, and then this half-total was added to both appropriate  $M_1$  and  $M_2$  counts. A standard null entry was used in the data base to denote broken teeth where more than half was present so that these could be counted toward MNI but omitted when computing measurement statistics. MNIs for  $Wa_0$  species are listed in Table 1. These were totalled by family to obtain family-level MNIs for principal components analysis.

MNIs for the remaining Clarkforkian and Wasatchian intervals were estimated using the total number of specimens (TNS) of each species identified in the interval. MNI increases with increasing TNS, but not at the same rate. This is because each new specimen adds an increment to TNS, but it only contributes an increment to MNI if it adds to the most abundant element being counted (rare taxa will still be overrepresented whenever one or a few specimens of rare species are discovered fortuitously early in a sampling program, adding more to both TNS and MNI than they would given larger and more representative samples). Computation of MNI requires both a sample of identified specimens and a considerable amount of information about each specimen. Large samples of specimens are available for many Clarkforkian and Wasatchian intervals, but measurements or tallies of every tooth necessary for computation of MNI are not yet available.

Rose (1981a, tables 44–51 and 53) counted TNS and MNI for a large number of Clarkforkian and early Wasatchian surface collections (many from the same localities used in this analysis). It is possible to calculate an empirical relationship between MNI and TNS using his data, and this can be used to estimate MNI for new collections when only TNS is known. For family-level identifications:

Table 27. Stratigraphic ranges of mammalian species in Wa<sub>0</sub> fauna

Taxon	Cf <sub>2</sub>	Cf <sub>3</sub>	Wa <sub>0</sub>	Wa <sub>1</sub>	Wa <sub>2</sub>
<b>MULTITUBERCULATA</b>					
<i>Ectypodus tardus</i> (Jepsen)	—	—	—	—	—
<b>MARSUPIALIA</b>					
<i>Mimoperadectes labrus</i> Bown and Rose		?	—	—	—
<b>PROPRIMATES</b>					
Cf. <i>Niptomomys</i> sp.	—	—	—	—	—
<i>Arctodontomys wilsoni</i> (Szalay)	—	—	—	—	—
<i>Phenacolemur praecox</i> Matthew	—	—	—	—	—
<b>PRIMATES</b>					
<i>Cantius torresi</i> Gingerich			—	—	—
<b>TILLODONTIA</b>					
<i>Azygonyx gunnelli</i> n. gen. and sp.			—	—	—
<i>Azygonyx</i> sp.	—	—	—	—	—
<i>Esthonyx spatularius</i> Cope			—	—	—
<b>PANTODONTA</b>					
<i>Coryphodon</i> sp.	—	—	—	—	—
<b>TAENIODONTA</b>					
<i>Ectoganus bighornensis</i> Schoch			—	—	—
<b>CREODONTA</b>					
<i>Dipsalidictis platypus</i> Matthew	—	—	—	—	—
<i>Dipsalidictis transiens</i> (Matthew)	—	—	—	—	—
<i>Palaeonictis</i> sp.	—	—	—	—	—
<i>Acarictis ryani</i> Gingerich and Deutsch			—	—	—
<i>Prototomus deimos</i> Gingerich and Deutsch			—	—	—
<i>Arfia junnei</i> n. sp.			—	—	—
<i>Prolimnocyon eerius</i> n. sp.			—	—	—
<b>CARNIVORA</b>					
<i>Viverravus boweni</i> Gingerich	—	—	—	—	—
<i>Viverravus polius</i> Matthew	—	—	—	—	—
<i>Didymictis leptomyus</i> Cope	—	—	—	—	—
<i>Miacis winkleri</i> Gingerich			—	—	—
<b>RODENTIA</b>					
Cf. <i>Acritoparamys atavus</i> (Jepsen)	—	—	—	—	—
<i>Actioparamys atwateri</i> (Loomis)	—	—	—	—	—
<i>Paramys taurus</i> Wood	—	—	—	—	—
<b>CONDYLARTHRA</b>					
<i>Thryptacodon barae</i> n. sp.	—	—	—	—	—
<i>Chriacus badgleyi</i> n. sp.	—	—	—	—	—
<i>Princetonia yalensis</i> n. gen. and sp.	?	?	—	—	—
<i>Dissacus praenuntius</i> Matthew	—	—	—	—	—
<i>Pachyaena ossifraga</i> Cope			—	—	—
<i>Hyopsodus loomisi</i> McKenna		?	—	—	—
<i>Ectocion parvus</i> Granger		?	—	?	—
<i>Ectocion osbornianus</i> (Cope)	—	—	—	—	—
<i>Phenacodus</i> cf. <i>P. intermedius</i> Granger	—	—	—	—	—
<i>Copecion davisi</i> n. gen. et sp.	—	—	—	—	—
<i>Meniscotherium priscum</i> Granger		—	—	—	—
<b>ARTIODACTYLA</b>					
<i>Diacodexis ilicis</i> n. sp.			—	—	—
<b>PERISSODACTYLA</b>					
<i>Hyracotherium sandrae</i> n. sp.			—	—	—
<i>Hyracotherium grangeri</i> Kitts			—	—	—
<b>EDENTATA</b>					
<i>Palaeonodon nievelti</i> n. sp.	—	—	—	—	—
<b>MAMMALIA incertae sedis</b>					
Cf. <i>Asiabradypus</i> sp.			—	—	—

Note: Lineage ranges of Wa<sub>0</sub> taxa are shown from the middle Clarkforkian (Cf<sub>2</sub>) through early Wasatchian (Wa<sub>2</sub>) land-mammal ages. Heavy lines (—) show ranges of Wa<sub>0</sub> species. Light lines (—) show ranges of closely related congeners.

$$\text{MNI} = 1.02 \text{ TNS}^{0.75}$$

Substituting, this relationship means that 100 specimens (TNS = 100) are likely to represent a minimum of 32 individuals (MNI = 32), and 1000 specimens are likely to represent a minimum of 181 individuals. Parameters of the estimator change slightly when identification is to genus or species, and they change considerably for quarry and wash samples. Total number of specimens identified to family were transformed to MNI for samples of 30 or more specimens from 17 levels (1150 m, 1200 m, 1270 m, etc.) in the Clarkforkian part of the Clarks Fork Basin stratigraphic section, and for samples of 30 or more specimens from 30 levels (1530 m, 1535 m, 1550 m, etc.) in the Wasatchian part of this section (MNIs for locality SC-188 were taken directly from Rose, 1981a, table 52).

#### Principal Components Analysis

Clarkforkian and Wasatchian faunas do not overlap when composition is studied at the family level using principal components analysis (Figure 45). The first principal component (PC-I) accounts for 71% of the variance in family-level composition, PC-II accounts for 7%, PC-III accounts for 6%, and successive components necessarily account for progressively less. Most of the variance in composition is adequately represented by PC-I. The Wa<sub>0</sub> fauna studied here, intermediate in time between Clarkforkian and later Wasatchian faunas, is also intermediate in composition.

Family-level taxonomic loadings on the first principal component are ranked in Table 28, and these are scaled graphically in Figure 46. The greatest contrast in family-level composition on PC-I is clearly that between Phenacodontidae on the right with a high positive loading and Hyopsodontidae on the left with a high negative loading. Equidae, Adapidae, and Dichobunidae also have notably high negative loadings. Phenacodontidae (*Phenacodus*, *Ectocion*, *Copecion*) and Hyopsodontidae (*Haplomytus*, *Hyopsodus*) are both present in most Clarkforkian and early Wasatchian faunas, so the contrast in loadings seen here reflects a major reorganization of existing composition as well as the addition of new families.

Lesser contrasts are evident within Proprimates, where positive PC-I loadings for Plesiadapidae and Paromomyidae contrast with negative loadings for Microsomyidae; and within Creodonta, where positive loadings for Oxyaenidae contrast with negative loadings for Hyaenodontidae. Some important families, Paramyidae and Coryphodontidae for example, contribute virtually nothing to compositional differences between Clarkforkian and Wasatchian faunas. The intermediate position of the Wa<sub>0</sub> fauna on PC-I undoubtedly reflects the unusual balance that it exhibits between Phenacodontidae on one hand and Hyopsodontidae, Equidae, Adapidae, and Dichobunidae on the other, balance that is uncharacteristic of either Clarkforkian or Wasatchian faunas in general.



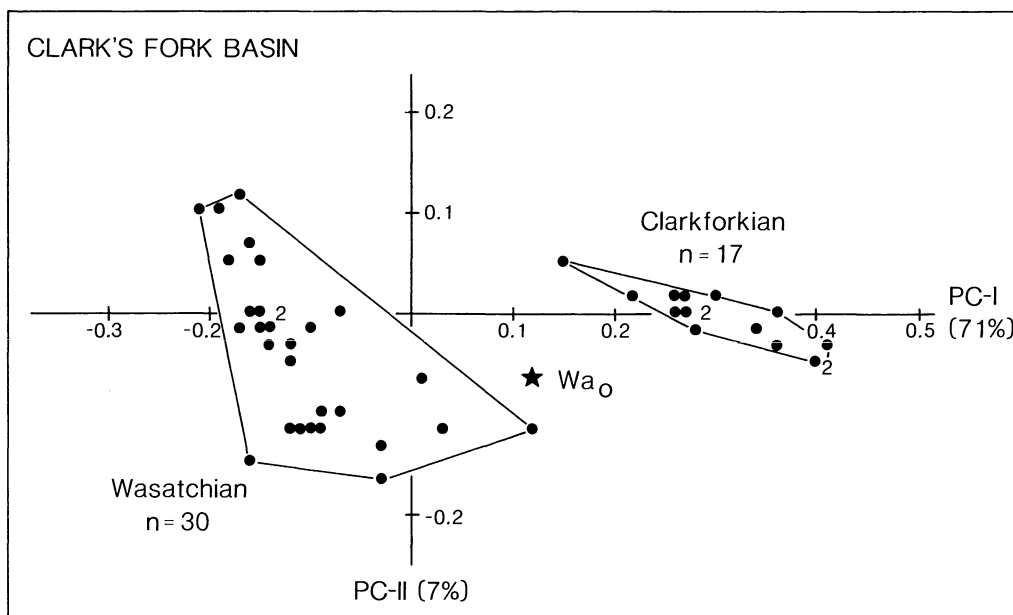


Figure 45. Principal components analysis comparing 49 Clarkforkian and Wasatchian mammalian faunas on the basis of family composition. Value of first principal component (PC-I) score for each faunal sample is plotted on the abscissa, and second principal component (PC-II) score is plotted on ordinate. Clarkforkian ( $C_{f_{2-3}}$ ) and Wasatchian ( $W_{a_{1-4}}$ ) samples are enclosed in convex polygons. Note that  $W_{a_0}$  sample (star) falls between the two, but closer to the Wasatchian polygon. PC-I contrasts Clarkforkian faunas dominated by Phenacodontidae at right with Wasatchian faunas dominated by Hyopsodontidae, Equidae, Adapidae, and Dichobunidae at left (see Table 28 and Fig. 46 for ranked PC-I loadings).

Interpretation of loadings on PC-II and PC-III is difficult. The principal contrast in PC-II loadings is between Hyopsodontidae on one hand and Equidae and Adapidae on the other. The principal contrast in PC-III loadings is between Hyopsodontidae and Phenacodontidae on one hand and Plesiadapidae on the other. Conceivably these contrasts reflect important differences in ecological associations and paleoenvironments. However, it seems appropriate to look for such differences within Clarkforkian faunas or within Wasatchian faunas, thereby removing major compositional contrasts between them, an endeavor beyond the scope of this study.

#### Change through Time

Change in mammalian faunal composition across the Clarkforkian-Wasatchian boundary is illustrated graphically in Figure 47, where 49 successive values of PC-I family-level composition are plotted against stratigraphic level. A line connecting successive PC-I scores shows the pattern of change. The Clarkforkian fauna was relatively stable, with PC-I scores varying between 0.2 and 0.4. The change from Clarkforkian to Wasatchian faunal composition involved a rapid transition. This was followed again by relative stability in the Wasatchian, with PC-I scores

varying between about 0 and -0.2 (and a trend from the former toward the latter over time). The  $W_{a_0}$  fauna described here is intermediate in having a PC-I score of about 0.1.

As one would expect from their position in Figure 47, the lowest sample in Figure 47 is unusual for a Clarkforkian fauna in having a high proportion of Hyopsodontidae (*Haplomylus*), and the sample falling almost directly above the  $W_{a_0}$  sample is unusual for a Wasatchian fauna in having a high proportion of Phenacodontidae (principally *Ectocion*). These outliers confirm the strong effect Hyopsodontidae and Phenacodontidae have in determining faunal position on PC-I, but they do not provide any further insight into differences between Clarkforkian and Wasatchian faunas.

#### SPECIES DIVERSITY

Species diversity can be calculated in several different ways. The  $W_{a_0}$  mammalian fauna is listed in order of relative abundance, based on minimum number of individuals (MNI) in Table 29. Using MNI, the most common mammalian species in the  $W_{a_0}$  fauna is *Hyopsodus loomisi*, represented by 40 specimens comprising a minimum of 19 individuals or 12.5% of the fauna. More specimens of *Ec-*

Table 28. Ranked family-level principal component loadings distinguishing Clarkforkian and Wasatchian mammalian faunas

Family	PC-I (71%0)	PC-II (7%)	PC-III (6%)
<i>Clarkforkian end of spectrum based on PC-I</i>			
Phenacodontidae	0.777	-0.164	-0.418
Plesiadapidae	0.130	0.152	0.647
Viverravidae	0.113	0.073	-0.171
Prodinoceratidae	0.071	0.041	0.017
Paromomyidae	0.045	0.029	0.070
Esthonychidae	0.044	0.065	0.085
Oxyaenidae	0.035	0.000	0.200
Arctocyoniidae	0.034	-0.007	-0.049
Mesonychidae	0.032	0.009	-0.063
Carpolestidae	0.026	0.024	0.140
Cyriacotheriidae	0.023	0.029	0.008
Plagiomenidae	0.012	0.092	0.015
Didelphidae	0.009	0.016	0.039
Arctostylopidae	0.006	0.009	0.007
Miacidae	0.005	-0.019	-0.077
Coryphodontidae	0.004	-0.027	-0.022
Neoplagiulacidae	0.003	0.022	0.009
Pantolambidae	0.001	0.002	0.012
Stylinodontidae	0.001	0.013	-0.002
Pantolestidae	-0.000	0.027	0.024
Paramyidae	-0.001	0.013	0.110
Didymoconidae (Wyolestinae)	-0.004	0.001	-0.005
Metacheiromyidae	-0.006	-0.004	0.017
Eucosmodontidae	-0.009	-0.075	0.008
Apatemyidae	-0.009	0.004	0.010
Microsypidae	-0.038	0.140	-0.005
Isectolophidae	-0.060	0.022	0.024
Hyaenodontidae	-0.069	-0.108	0.019
Omomyidae	-0.084	0.272	0.019
Dichobunidae	-0.157	-0.040	-0.052
Adapidae	-0.213	-0.302	-0.068
Equidae	-0.299	-0.734	-0.031
Hyopsodontidae	-0.419	0.426	-0.517

*Wasatchian end of spectrum based on PC-I*

*tocion parvus* and *Copecion davisi* are known (66 and 42, respectively), but each of these samples yields a smaller calculated MNI of 18. The total number of species (species richness) in the  $W_{a_0}$  fauna is 40 (41 if *Meniscotherium priscum* is counted), which is similar to that counted for early Wasatchian faunas and greater than the number typically found in the Clarkforkian (Rose, 1981a,b; Badgley and Gingerich, 1988).

Other measures of faunal diversity (see Rose, 1981a,b) include the *Simpson index* reflecting the concentration of dominance in the fauna: this has a value  $L$  of 0.06. The complementary index of dispersion of dominance  $1-L$  is thus 0.94. The *Shannon-Wiener index* of heterogeneity or mixed diversity  $H$  is 3.20, and *Pielou's index* of evenness  $J$  (derived from  $H$ ) is 0.87. The *Whittaker index* of evenness  $E$  is 31.95. All of the indices of richness, dispersion, heterogeneity, and evenness are high by comparison with values derived both from underlying Clarkforkian and most overlying Wasatchian faunas sampled in the same way (see Rose, 1981a, p. 175). Rose, following May (1976), inter-

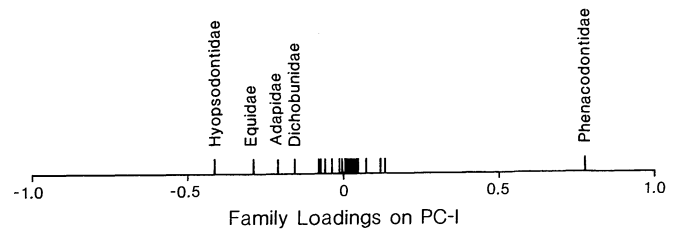


Figure 46. Ranked family loadings on PC-I, based on information in Table 28. Note that PC-I separates faunas dominated by Phenacodontidae from faunas dominated by Hyopsodontidae, Equidae, Adapidae, and Dichobunidae. Clarkforkian faunas fall in the former category and Wasatchian faunas fall in the latter. The intermediate position of the  $W_{a_0}$  fauna on PC-I clearly reflects its unbalanced nature in having all five of these families well represented: Phenacodontidae as well as Hyopsodontidae, Equidae, Adapidae, and Dichobunidae.

preted high diversity indices to reflect general ecological stability and development of a complex and delicately balanced ecosystem in which specialist species are more common and generalist species less common than usual.

Rose (1981a) calculated high diversity indices for the earliest part of the Wasatchian fauna then known in the No Water Creek area of the southeastern Bighorn Basin (level 150 of Bown, 1979). Values obtained here for the fauna from zone  $W_{a_0}$ , a faunal interval unknown at the time of Rose's study, corroborate his finding that earliest Wasatchian mammalian diversity was exceptionally high.

RANK ABUNDANCE OF SPECIES

Rank abundance provides another way of looking at evenness in the distribution of species. MacArthur (1960) discussed a model in which the relative abundance of any one species in a fauna depends on the relative abundances of all other species. From this he predicted that the relative abundance  $N_r/m$  of the  $r$ -th rarest species should be:

$$\frac{N_r}{m} = \frac{1}{n} \cdot \sum_{i=1}^r \frac{1}{n-i+1}$$

where  $m$  is the total number of individuals in a fauna (here total MNI),  $n$  is the total number of species in the fauna, and  $N_r$  is the abundance (MNI) of the  $r$ -th species ( $r$  varies from 1 to  $n$ ).

For the  $W_{a_0}$  fauna, using information in Table 29, where  $m = 152$  and  $n = 40$  (or 41):

$$N_1/m = 1/40 \cdot (1/(40-1+1)) = 1/1600 = 0.0006$$

$$N_2/m = 1/40 \cdot [(1/(40-1+1)) + (1/(40-2+1))] = 0.0013$$

CLARK'S FORK BASIN

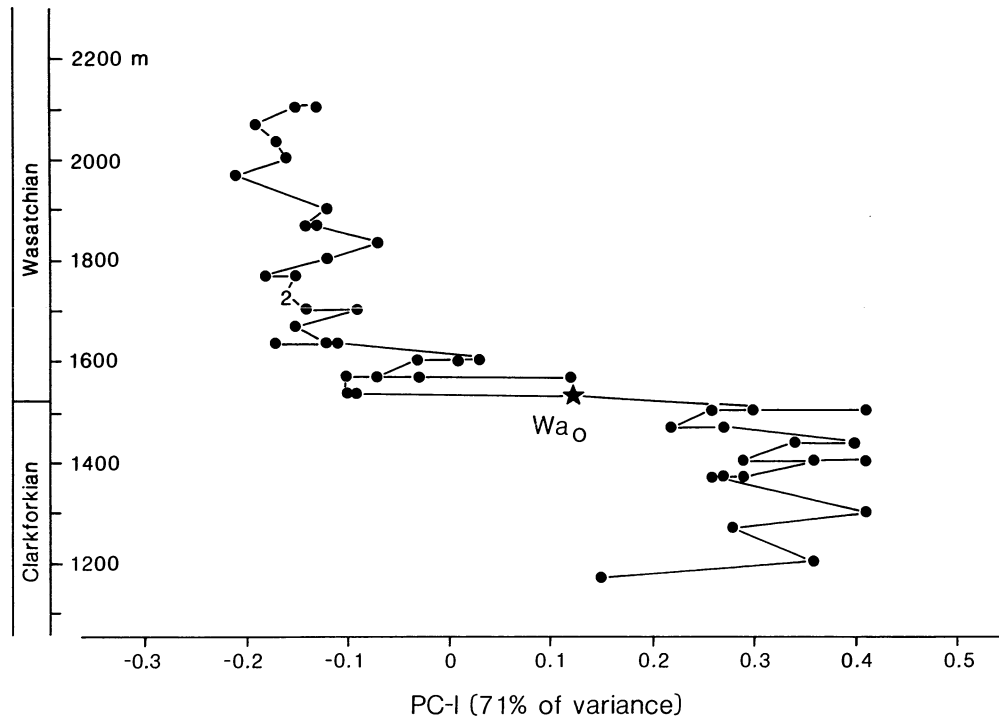


Figure 47. Principal component—stratigraphic (prinstrat) plot showing the evolution of mammalian faunal composition across the Clarkforkian-Wasatchian boundary. First principal component scores are plotted on the abscissa (PC-I, including 71% of variance), and the ordinate is stratigraphic level above Cretaceous-Tertiary boundary in Polecat Bench—Clarks Fork Basin stratigraphic section. PC-I contrasts faunas dominated by Phenacodontidae at right with faunas dominated by Hyopsodontidae, Equidae, Adapidae, and Dichobunidae at left (see Table 28 and Fig. 46 for ranked PC-I loadings). Lines connect successive faunal samples. Note rapid shift from positive to negative scores on PC-I across the Clarkforkian-Wasatchian boundary, reflecting rapid reorganization of faunal composition with little evidence of intermediate stages.  $Wa_0$  fauna (star) at level 1520 m is intermediate but closer to Wasatchian faunas. Note relative stability of faunal composition in the middle and late Clarkforkian, but clear secular trend toward more negative scores in the early and middle Wasatchian. Change in Wasatchian faunal composition probably reflects real decrease in proportional representation of Phenacodontidae.

$$N_3/m = 1/40 \cdot [(1/(40 - 1 + 1)) + \dots + (1/(40 - 3 + 1))] = 0.0019$$

and so forth, until:

$$N_{39}/m = 1/40 \cdot [(1/(40 - 1 + 1)) + \dots + (1/(40 - 39 + 1))] = 0.0820$$

$$N_{40}/m = 1/40 \cdot [(1/(40 - 1 + 1)) + \dots + (1/(40 - 40 + 1))] = 0.1070$$

The empirical rank abundance distribution for the  $Wa_0$  fauna is illustrated by the solid line in Figure 48. The distribution expected using MacArthur's *dependent model* for relative abundance is shown by the heavier of two dashed lines. The observed distribution of rank-abundances deviates from this expected distribution in that the three

most abundant species (labelled) are more abundant than predicted by MacArthur's equation, lying above the heavier dashed line. Middle rank species deviate also in being less abundant than expected, lying below the heavier dashed line.

MacArthur (1960) also discussed a second model for rank-abundance, one in which the relative abundances of species are independent (lighter dashed line in Figure 48). MacArthur's *independent model* has a less even distribution than the dependent model, with one or a few species being much more common than the others.

The  $Wa_0$  distribution appears to lie between the distributions predicted by MacArthur's dependent and independent models, but closer to the dependent model. The root-mean-square or RMS deviation (square root of the mean of squared deviations—the "standard deviation") from values predicted by the dependent model is somewhat less (0.011)

Table 29. Mammalian faunal list for  $Wa_0$  ordered by relative abundance of species

Rank	Taxon	TNS	MNI	Percent
1	<i>Hyopsodus loomisi</i> McKenna	40	19	12.5
2	<i>Ectocion parvus</i> Granger	66	18	11.8
3	<i>Copecion davisi</i> n. gen. et sp.	42	18	11.8
4	<i>Hyracotherium sandrae</i> n. sp.	30	10	6.6
5	<i>Arfia junnei</i> n. sp.	20	8	5.3
6	<i>Didymictis leptomytus</i> Cope	13	6	4.0
7	<i>Caninus torresi</i> Gingerich	7	6	4.0
8	<i>Paramys taurus</i> Wood	9	5	3.3
9	<i>Acritoparamys atwateri</i> (Loomis)	8	5	3.3
10	<i>Coryphodon</i> sp.	11	4	2.6
11	<i>Dipsalidictis platypus</i> Matthew	7	4	2.6
12	<i>Chriacus badgleyi</i> n. sp.	6	4	2.6
13	<i>Palaeonodon nievelti</i> n. sp.	5	4	2.6
14	<i>Ectoganus bighornensis</i> Schoch	11	3	2.0
15	<i>Diacodexis ilicis</i> n. sp.	6	3	2.0
16	<i>Miacis winkleri</i> Gingerich	3	3	2.0
17	<i>Azygonyx gunnelli</i> n. gen. and sp.	6	2	1.3
18	<i>Prototomus deimos</i> Gingerich and Deutsch	4	2	1.3
19	<i>Ectypodus tardus</i> (Jepsen)	3	2	1.3
"	<i>Hyracotherium grangeri</i> Kitts	3	2	1.3
21	<i>Mimoperadectes labrus</i> Bown and Rose	2	2	1.3
"	<i>Phenacolemur praecox</i> Matthew	2	2	1.3
"	<i>Thrypiacodon barae</i> n. sp.	2	2	1.3
"	<i>Ectocion osbornianus</i> (Cope)	2	2	1.3
25	<i>Phenacodus</i> cf. <i>P. intermedius</i> Granger	7	1	0.7
26	<i>Dissacus praenuitius</i> Matthew	4	1	0.7
27	<i>Acarictis ryani</i> Gingerich and Deutsch	2	1	0.7
28	Cf. <i>Niptomomys</i> sp.	1	1	0.7
"	<i>Arctodontomys wilsoni</i> (Szalay)	1	1	0.7
"	<i>Esthonyx spatularius</i> Cope	1	1	0.7
"	<i>Azygonyx</i> sp.	1	1	0.7
"	<i>Dipsalidictis transiens</i> (Matthew)	1	1	0.7
"	<i>Palaeonictis</i> sp.	1	1	0.7
"	<i>Prolimnocyon eeri</i> n. sp.	1	1	0.7
"	<i>Viverravus boweni</i> Gingerich	1	1	0.7
"	<i>Viverravus politus</i> Matthew	1	1	0.7
"	Cf. <i>Acritoparamys atavus</i> (Jepsen)	1	1	0.7
"	<i>Princetonia yalensis</i> n. gen. and sp.	1	1	0.7
"	<i>Pachyaena ossifraga</i> Cope	1	1	0.7
"	Cf. <i>Asiabradypus</i> sp.	1	1	0.7
"	<i>Meniscotherium priscum</i> Granger	-	-	-
Totals:		334	152	100.6

## Diversity indices

Species richness (number of species):	S = 40
Simpson index (concentration of dominance):	L = 0.06
(dispersion of dominance):	1 - L = 0.94
Shannon-Wiener index (heterogeneity, mixed diversity):	H' = 3.20
Pielou index (evenness):	J = 0.87
Whittaker index (evenness):	E = 31.95

than the RMS deviation from values predicted by the independent model (0.016). (RMS deviation is used because it gives more weight to greater deviations than to lesser ones in calculating an average.)

MacArthur found "dependent" distributions of relative abundance for species living in homogeneous habitats (e.g., a particular woodland, grassland, or wetland), and "independent" distributions for species living in mixed habitats (e.g., an area of the same size spanning woodland, grassland, and wetland). The  $Wa_0$  mammalian fauna was

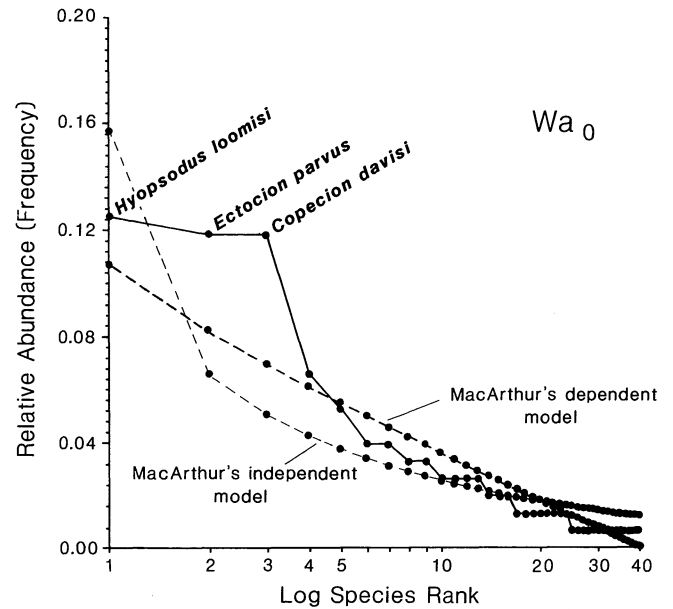


Figure 48. Rank-abundance curve for earliest Wasatchian ( $Wa_0$ ) fauna, showing relative abundance of each species ( $N_i/m$ ) on the ordinate plotted against its rank (rank here is based on abundance rather than rarity, i.e.,  $i = n - r + 1$  rather than  $r$  itself). MacArthur expectation for a fauna of 40 species, where the abundance of any one species depends on the abundance of all others, is shown by the heavy dashed line (see text). Three species exceeding this expectation are labelled. Light dashed line shows MacArthur's model for a fauna of 40 species where species abundances are independent of each other. Logarithmic scale on abscissa serves only to make MacArthur's biotic dependence model more linear.

an integrated one in which the relative abundances of mammalian species were more biotically dependent on each other than not, which suggests in turn that this fauna lived in a relatively homogeneous habitat.

## Change through Time

The minimum number of individuals has been quantified in 24 mammalian faunal samples ranging from middle Paleocene through early Eocene in age. The faunal samples are all from the Bighorn Basin, Clarks Fork Basin, or Crazy Mountain Basin (data from Rose, 1981a; Krause and Maas, 1989; this study). These can be used to compare the  $Wa_0$  fauna to earlier and later faunas, and to test MacArthur's "dependent" versus "independent" models for the relative abundances of species in faunas evolving through time (Table 30; the question being asked is not how observed patterns of relative abundance of species match one or the other model, but simply which of the two models gives the best fit to data).

Both middle Paleocene faunas fit MacArthur's dependent model better than the independent model. Late Paleocene faunas, with two exceptions, fit the independent

Table 30. Test of rank-abundances of mammalian species in middle Paleocene through early Eocene faunas against predictions of MacArthur's dependent and independent models of species abundance

Locality	Species	Total MNI	RMS Deviation	
			Depend. model	Independ. model
<i>Middle Paleocene</i>				
Rock Bench Quarry	57	497	0.008*	0.012
Gidley Quarry	57	387	0.008*	0.011
<i>Late Paleocene</i>				
Douglass Quarry	48	208	0.007*	0.010
Scarritt Quarry	24	145	0.048	0.043*
Cedar Point Quarry	41	503	0.031	0.028*
Princeton Quarry	36	185	0.010*	0.016
Bear Creek	20	75	0.023	0.021*
Early Clarkforkian	28	131	0.037	0.030*
Middle Clarkforkian 1	24	93	0.047	0.037*
Sand Coulee SC-188	30	70	0.013	0.009*
Middle Clarkforkian 2	23	72	0.030	0.020*
Middle Clarkforkian 3	27	173	0.027	0.024*
Late Clarkforkian 1	28	152	0.040	0.033*
Late Clarkforkian 2	27	140	0.026	0.023*
Late Clarkforkian 3	27	108	0.024	0.016*
Late Clarkforkian 4	29	187	0.037	0.030*
<i>Early Eocene</i>				
Earliest Wasatchian (Wa0)	40	152	0.011*	0.016
Sand Coulee SC-4	31	129	0.014*	0.021
Sand Creek facies 150 ft	48	243	0.012*	0.013
Sand Coulee SC-54	28	159	0.018*	0.022
Sand Creek facies 288 ft	32	90	0.008*	0.009
Sand Coulee 250-350 m	28	119	0.013*	0.019
Sand Coulee 400-500 m	32	203	0.011*	0.018
Sand Creek facies 590 ft	29	90	0.014*	0.019

\*Lesser deviation of model and data is marked with asterisk. Data from Rose (1981a), Krause and Maas (1989), and Table 29.

model better. The  $Wa_0$  fauna and other early Eocene faunas uniformly fit the dependent model better than the independent one. This pattern is consistent with other results (Rose, 1981a,b; Krause and Maas, 1989) in showing that middle Paleocene and early Eocene mammalian faunas are more evenly distributed than are intervening late Paleocene faunas.



## V PALEOENVIRONMENTAL INTERPRETATION

The paleoenvironmental setting of the earliest Wasatchian  $Wa_0$  fauna can be interpreted from several lines of evidence: sedimentology and paleosol development, flora and fauna, and cenogram analysis of the distribution of body sizes among mammalian species.

### SEDIMENTOLOGY AND PALEOSOL DEVELOPMENT

The  $Wa_0$  fauna is unusual in that it is found in a deeply weathered red bed sequence deposited within and on the lateral margins of an unusually well developed sheet sandstone complex.

#### Sheet Sandstone and Mature Paleosols

Kraus (1979, 1980) interpreted the Clarkforkian-Wasatchian boundary sandstone, the multistory sheet sandstone deposited over much of the Clarks Fork Basin during  $Wa_0$  time, as indicating a time of relatively slow sediment accumulation and, by inference, relatively slow subsidence of the Clarks Fork Basin. Kraus' interpretation was made after it was known that the unit marks the boundary between two land-mammal ages, but before there was any indication that fine-grained sediments within and lateral to the boundary sandstone contain a distinctive  $Wa_0$  fauna.

Kraus (1987) subsequently described ancient soil profiles at  $Wa_0$  locality SC-67, where fine-grained sediments are well exposed in relation to the boundary sandstone. She found an association of mature stage-4 paleosols (which are not known elsewhere in Clarkforkian or early Wasatchian sediments of the Clarks Fork Basin) with incorporated crevasse-splay deposits. This association is consistent with slowed sediment accumulation and slowed basin subsidence previously inferred from sandstone architecture. The light color of bones and teeth in the  $Wa_0$  fauna probably reflects chemical alteration during formation of exceptionally mature paleosols.

An interval of slowed basin subsidence is one explanation for development of a sheet sandstone with mature paleosols lateral to it. Observed sandstone architecture and associated paleosol maturity might also result from basin tilting or broad regional uplift relative to base level (Bridge and Leeder, 1979). The critical change necessary to produce a sheet sandstone is a shift in the balance of aggradation (sediment accumulation) and degradation (erosion),

allowing erosion to balance fine-sediment accumulation. In a fluvial system, a slight change in the net combination of accumulation and erosion may have the same local effect whether it is caused by slowed basin subsidence, basin tilting, or broad regional uplift.

### Basin Model

Kraus' study of the history of sedimentary facies deposited during  $Wa_0$  time provides a context for understanding important features of faunal change observed across the Clarkforkian-Wasatchian boundary. A graphic model incorporating her results is presented in Figure 49. It is based on broad-scale Fort Union - Willwood stratigraphic relationships in the Clarks Fork Basin, illustrated, for example, by Wiltschko and Dorr (1983: fig. 2). The model is embellished, anticipating the faunal discussion to follow, in having high and well drained distal floodplains for which there is often little direct evidence in the sedimentological or paleontological record. The model compares sedimentation in the Clarks Fork Basin at three successive stages: the late Clarkforkian ( $Cf_3$ ), the earliest Wasatchian ( $Wa_0$ ), and subsequently in the early Wasatchian ( $Wa_1$ ).

A "high" floodplain, as the term is used here, is a floodplain that stands higher in elevation and higher above the water table than a "low" floodplain. In general, high floodplains will be distal floodplains, and low floodplains will be proximal floodplains, but the critical difference is one of elevation and drainage rather than distance from a river channel. The proximal and distal floodplains diagrammed by Bown and Kraus (1987: fig. 4) are both low floodplains, but farther from a river channel (and alluvial ridge) the distal floodplain must eventually rise to become high. High floodplains lie above normal river level, at about the same elevation as the tops of levees or alluvial ridges, whereas low floodplains lie at or below normal river level. Both high and low floodplains are flooded periodically, but high floodplains are flooded less often. Both are near the water table, but a high floodplain stands higher above it, with drier, better drained soils. The difference in elevation need not be great, but soil development, the flora, and the fauna are all likely to be different on high and low floodplains.

In late Clarkforkian ( $Cf_3$ ) time, the part of the depositional basin that can now be sampled paleontologically included river channels separated by levees, backswamps,

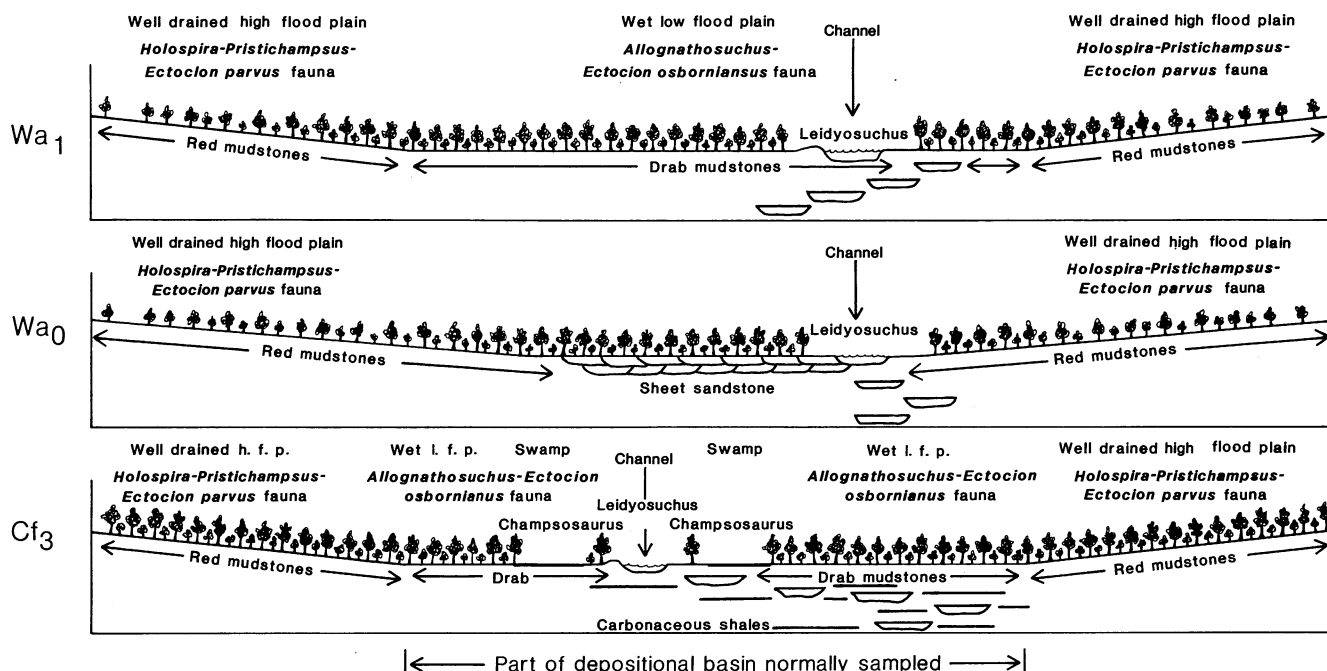


Figure 49. Sedimentological and paleontological model for faunal change from the late Clarkforkian to the early Wasatchian, with intervening zone  $Wa_0$ , in the Clarks Fork Basin. Model is based on distribution and architecture of sedimentary facies discussed by Kraus (1979, 1980, 1987) and Bown and Kraus (1987). Bottom figure labelled  $Cf_3$  represents much of Clarkforkian time, middle figure labelled  $Wa_0$  represents  $Wa_0$  time, and upper figure labelled  $Wa_1$  represents much of early and middle Wasatchian time. High floodplains are high relative to normal river level and the local water table, meaning that they flood less frequently and that they are better drained. Slowed subsidence of the Clarks Fork Basin or regional uplift during  $Wa_0$  time changed the balance of aggradation and degradation of mudstone in the basin, and a multistory sheet sandstone accumulated near the basin's depositional center. The change from a more aggradational to a more degradational fluvial regime enhanced the drainage of all floodplain environments, and even proximal floodplains stood high relative to channel level. A *Holospira-Pristichampus-Ectocion parvus* fauna typical of high distal floodplains moved to the center of the basin with loss of wet proximal floodplains. Wetter floodplain environments and their associated *Allognathosuchus* and *Ectocion osbornianus* faunas were displaced during this interval, but these returned when low wet floodplains reappeared in zone  $Wa_1$ . Early and middle Wasatchian floodplains probably included more open forests than were evident in zones  $Cf_3$  or  $Wa_0$ . Carbonaceous shales are rare in zone  $Wa_1$ , and *Champsosaurus* did not survive the  $Wa_0$  restriction of wet floodplain environments.

and low wet floodplains. Channel deposits were separated horizontally and vertically in the stratigraphic record, and most intervening sediments are drab floodplain muds that accumulated during times of flooding and were buried rapidly enough to prevent development of mature paleosols. Carbonaceous shales are common, representing backswamps. The system is rich in calcium carbonate, which is concentrated in soil nodules and also in lenses and pods in a variety of other settings. Oxidized red mudstones probably accumulated in higher, better drained distal floodplain and alluvial fan settings, but these environments are rarely preserved and almost never sampled.

In the earliest Wasatchian ( $Wa_0$ ), the part of the depositional basin that can now be sampled paleontologically included river channels and floodplains. However, in this setting, channel sands were superimposed on each other horizontally and vertically over much of the basin because degradation of mud exceeded aggradation (sand was still accumulating). This shift in the balance of mud aggradation and degradation means that channels are more likely to

have been bordered by eroding banks rather than levees, and that the entire floodplain was probably better drained. Muds, where they did accumulate, were more likely to develop mature soil profiles, and the  $Wa_0$  mudstones that remain are brightly colored.

The proximal floodplain that was wet in the Clarkforkian became better drained during  $Wa_0$  time, and there is little evidence of drab mudstones, carbonaceous shales, or freshwater limestones. The presence of highly oxidized stage-4 paleosol red and purple beds within and lateral to the Clarkforkian-Wasatchian boundary sandstone indicates that wet floodplains were largely missing. Distal basin facies converged, in effect, on the channel environment from both sides, and wet floodplains virtually disappeared.

Later in the early Wasatchian, in zone  $Wa_1$ , the part of the depositional basin that can now be sampled paleontologically resembled that in  $Cf_3$  time, before  $Wa_0$ , except that there is less evidence of backswamps accumulating carbonaceous shales (although these were still present; Wing, 1984). Channel deposits are again well separated by mudst-



ones in the stratigraphic record. Mudstones constitute most of the record, and these are again drab with development of immature paleosols. Calcium carbonate is concentrated in soil nodules, and also in lenses and pods in a variety of other settings. Here again, oxidized red mudstones probably accumulated in well drained distal floodplain and alluvial fan settings, but these environments are rarely preserved and rarely sampled.

During much of Clarkforkian time, the axis of the Clarks Fork Basin subsided and sediments accumulated at an average rate estimated to have been about 280 m/my. During much of the early Wasatchian, the average rate of basin subsidence and sediment accumulation is estimated to have been about 250 m/my (Gingerich, 1983). These rates correspond to net accumulation of a meter of sediment every 3,000–4,000 years. There is at present no way to determine rates of basin subsidence and sediment accumulation during deposition of the Clarkforkian-Wasatchian boundary sandstone, or to determine the duration of faunal zone  $Wa_0$ . If one assumes that the rate of sediment accumulation in zone  $Wa_0$  was one-half that before and after, between 140 m/my and 125 m/my, then  $Wa_0$  time was probably on the order of 250,000 years in duration.

#### FLORA AND FAUNA

##### Plants, Invertebrates, Fish, and Reptiles

Calcareous endocarps of *Celtis* have long been used as guide fossils to indicate the beginning of Wasatchian time in the Bighorn and Clarks Fork basins. In recent years, endocarps of *Celtis* have been found in the uppermost few meters of Clarkforkian sediments. Clarkforkian endocarps are moderately large (ca. 6 mm in maximum diameter), and  $Wa_0$  endocarps are conspicuously smaller (ca. 5 mm in maximum diameter). This difference in mean size is statistically significant in spite of considerable variation (Figure 8), and it may reflect a difference in the species of *Celtis* represented (or a change in the proportional representation of species), it may reflect a purely ecophenotypic response to changing environmental conditions, it may reflect differential hydraulic sorting during transport and burial, or all three factors may be involved. The difference is likely to be related to differences between high and low floodplains in any case. The  $Wa_0$  pollen and leaf flora is still unknown.

The  $Wa_0$  gastropod fauna is different from that in underlying and overlying sediments. First, aquatic elements (principally *Elimia* or *Pleurocera* sp., = "*Goniobasis*") are common. These are found principally in sandstone, and they are interpreted as part of an aquatic fauna well represented due to a predominance of channel deposits in the  $Wa_0$  sedimentary record. The gastropod fauna also includes the terrestrial urocopid *Holospira* sp., which is very rare or absent in overlying and underlying sediments. Shells of

*Holospira* are always found as isolated individuals, probably weathering out of mudstones, and these are never found in association with aquatic gastropods. Extant *Holospira* live in calcium-rich environments in warm dry climates, and  $Wa_0$  *Holospira* are interpreted as part of a dry terrestrial fauna living on high, well drained floodplains.

Ganoid scales and opisthocoelous vertebrae of the gar *Lepisosteus* sp. are seemingly ubiquitous in  $Wa_0$  localities. Amphicoelous vertebrae of the bowfin *Amia* sp. are less common but also present. Two additional aquatic elements are the turtles *Plastomenus* sp. and *Echmatemys* sp. The most common lizard in zone  $Wa_0$  is *Melanosaurus* sp., a terrestrial faunal element common in the Clarkforkian and early Wasatchian, where it is usually found in sediments reflecting better-drained local environments.

Amphibious gavial-like *Champsosaurus* is present in the Clarks Fork Basin through late Clarkforkian time, but it is conspicuously absent from  $Wa_0$  and later deposits. *Champsosaurus* is plausibly interpreted as having been a wet floodplain inhabitant that became extinct, locally at least, when wet floodplains disappeared at the end of the Clarkforkian (it is not known anywhere after Clarkforkian time, see below).

The crocodylid *Leidyosuchus* is an aquatic element that is much more commonly found in  $Wa_0$  deposits than it is earlier in the Clarkforkian or later in the Wasatchian. The alligatorid *Allognathosuchus* has the opposite distribution, being much more common earlier in the Clarkforkian and later in the Wasatchian than it is in the  $Wa_0$  fauna. *Allognathosuchus* is interpreted as a wet floodplain inhabitant that is very rare in  $Wa_0$  deposits because wet floodplain environments were so restricted. The hoofed ziphodont *Pristichampsus*, which makes its first appearance in the fossil record at this time, is interpreted as a terrestrial faunal element inhabiting dry floodplains.

Thus snails and lower vertebrates in the  $Wa_0$  fauna are either aquatic or they are elements of a dry floodplain fauna. Wet floodplain elements like *Allognathosuchus* are conspicuously rare. Paleocene and Eocene mammals do not have such clear paleoenvironmental preferences, but it is possible to make some inferences about specialized genera based on their association with ancient sediments.

##### Trends in the Relative Abundance of Mammals

The  $Wa_0$ -fauna lies at the boundary between the Clarkforkian and Wasatchian land-mammal ages, which makes paleoenvironmental interpretation using mammalian faunal composition somewhat complicated: the  $Wa_0$  fauna includes taxa making their first appearance in this zone whose presence may be related to factors beyond the local environment. These must be set aside when attempting to clarify paleoenvironmental differences between the Clarkforkian,  $Wa_0$ , and the later Wasatchian within the Clarks Fork Basin. Similarly, taxa whose relative abun-

dance changes significantly across the Clarkforkian-Wasatchian boundary must be interpreted in a context wider than local environmental differences.

Sixteen of the families of mammals listed in Table 28 are present in the Clarkforkian, in zone  $Wa_0$ , and in later Wasatchian faunas of the Clarks Fork Basin. Comparison of the relative abundances of each of these families in each faunal interval (using relative abundances for families discussed under faunal composition above) indicates that most show no trend or follow a unidirectional trend across the Clarkforkian-Wasatchian boundary, either increasing or decreasing in abundance. The four groups that do not follow a unidirectional trend in relative abundance, given present evidence, are Paramyidae, Metacheiromyidae, Paromomyidae, and Stylinodontidae.

Paramyids are 2–3 times as common in zone  $Wa_0$  as they are before or after; metacheiromyids are about 10 times as common; and stylinodontids are more than 10 times as common. Paromomyids are less than half as common in zone  $Wa_0$  as they are before or after. These deflections in trend, interpreted in context of the sedimentological and paleontological sampling model in Figure 49 and discussions above, suggest that paramyids, metacheiromyids, and stylinodontids may have lived predominantly on well drained high floodplains, while paromomyids may have lived predominantly on (or in trees above) wet floodplains. Hyopsodontids increase in relative abundance across the Clarkforkian-Wasatchian boundary, but this unidirectional trend at the family level obscures the very conspicuous absence of *Haplomytus* in zone  $Wa_0$ . *Haplomytus*, like paromomyids, may have lived predominantly on wet floodplains.

A two-fold change in relative abundance may be considered equivocal in the cases of Paramyidae and Paromomyidae, but a 10-fold change in the relative abundances of Metacheiromyidae (*Palaeonodon*) and Stylinodontidae (*Ectoganus*) provides strong evidence that these groups inhabited high floodplains. Metacheiromyids are similar in size and body form to extant armadillos (which has been noted since virtually the time they were first described, e.g., by Osborn, 1904). Stylinodontids are sometimes compared to extant aardvarks (McKenna, 1980). Armadillos and aardvarks are burrowing forms that live on high floodplains today. Patterson (1949) and Schoch (1986) have suggested independently that stylinodontids may have been "upland" forms.

#### High and Low Floodplain Faunas

The idea that faunas on high floodplains differ from those on low floodplains is not new. It has been much discussed in recent years in connection with dinosaur nesting grounds in "upland" areas (e.g., Sternberg, 1956; Horner and Makela, 1979; Dorr, 1985). Patterson (1949) was concerned with this problem. Winkler (1983) compared faunal samples from a mature red-gray paleosol couplet and

immature orange-gray paleosol couplets at an early Wasatchian locality (SC-210) in the Willwood Formation of the Clarks Fork Basin. He found differences, including restriction of the stylinodontid *Ectoganus* and the mesonychid *Pachyaena* to the red-gray paleosol couplet, and concluded that the mature red paleosol represents a different environment, with a somewhat different fauna, than the immature orange paleosols.

Bown (1987) published an abstract on Willwood Formation mammals in which he stated:

Examination of bone element composition, general faunal composition, and even intrafamilial and intrageneric composition across the pedofacies shows that these parameters correlate well with lateral position on the ancient floodbasin. . . . [T]he adapid primates *Cantius* and *Copelemur* appear to reverse their relative abundances with respect to each other across 1.8 km of stage 1–2 soils at the 625 m level [in the Willwood Formation of the central Bighorn Basin].

Studying the correlation of Willwood Formation faunal composition and soil maturity (as an indication of location on a floodplain), Bown and Beard (1989) found that at their 442 m level: (1) the hyopsodontid *Hyopsodus miticulus* predominates in immature soils and *H. minor* predominates in mature soils; and (2) the adapid *Cantius* sp. nov. predominates in immature soils and *Cantius frugivorus* predominates in mature soils. Similar patterns of difference are shown for hyopsodontids and adapids at the 546 m and 556 m levels.

Bown and Beard (1989) also compared ordinal-level composition of faunal samples from locality D-1198 (paleosol stage 1–2; 2,972 specimens) at the 470 m level and locality D-1177 (paleosol stage 4; 458 specimens) at the 481 m level. Both localities lie or near the Graybullian-Lysitean boundary. Bown and Beard found that Condylarthra were significantly more abundant at locality D-1198 than at locality D-1177 (67% more abundant—the ratio of the proportions 49% and 30% at the two localities). Combined Arctocyonina-Carnivora were significantly more abundant at D-1177 than at D-1198 (78% more abundant—a ratio of unspecified proportions). Other differences were not significant (ratios and negative autocorrelation make evaluation of statistical significance a complex problem here).

Bown and Beard concluded from this that "differential ordinal representation of mammals between stage 1–2 and stage 4 paleosols . . . is suggestive of lateral controls on distribution at an appreciably higher taxonomic grade." The meaning and significance of this would be clearer if the localities compared were at the same level within either the Graybullian or the Lysitean (not at an important faunal transition), if the sizes of faunal samples drawn from each were more nearly equivalent (proportional representation at any taxonomic level changes with sample size), and if the proportions compared were based on minimum number

of individuals (MNI) rather than total number of specimens (TNS).

Bown and Beard (1989) found that combined Tillodontia-Taeniodonta were more common in mature soils than in immature soils, consistent with Winkler's finding and results presented here. They also found that *Palaeanodon* was more common in immature soils than in mature soils, which contradicts results here. The relative abundances of Paleocene and Eocene mammals living on different parts of a floodplain clearly warrant further study.

There are few studies of extant mammals contrasting high and low floodplain faunas from the same basin. Myers (1982) describes such differences in the mammals of Paraguay (see also Myers and Wetzel, 1983). The fauna living on the low floodplain Chaco Boreal west of the Rio Paraguay is different in composition and species richness from that living on high floodplains east of the Rio Paraguay. Myers attributed observed faunal differences to differences in vegetation, and ultimately differences in drainage and soils east and west of the river. Interestingly, the low floodplain Chaco fauna on poorly drained soils is the fauna with fewer species. The low floodplain Chaco environment is further characterized as being less "predictable" ecologically, which helps to explain lower diversity.

Differences between Clarkforkian and Wasatchian mammalian faunas may be related, in some degree, to differences in basin drainage and soil development, with the Clarkforkian being more Chaco-like. Similarly, in the early Wasatchian, differences between the  $Wa_0$  fauna and later  $Wa_1$  and  $Wa_2$  faunas may be related to differences in basin drainage and soil development, with  $Wa_{1-2}$  being more Chaco-like. Environmental differences related to drainage and soil formation influence the diversity of extant faunas and these factors need to be considered in interpreting patterns of diversity in the fossil record.

#### Small Mammalian Species with Large Clarkforkian or Wasatchian Congeners

One of the most striking features of the  $Wa_0$  mammalian fauna is the presence of numerous small species of genera normally represented in Clarkforkian or Wasatchian faunas by larger forms. This "dwarfing" affects 11 of the 40 species (28%) that have Clarkforkian or Wasatchian congeners or other close relatives. Five small species are first records of new genera characteristic of later Wasatchian faunas (*Cantius*, *Arfia*, *Prolimnocyon*, *Diacodexis*, and *Hyracotherium*). These species may be small because their radiations started at small body size, and they cannot be considered dwarfed forms without additional evidence not presently available.

The remaining six "dwarfed"  $Wa_0$  species are represented by larger species in both immediately preceding late Clarkforkian and immediately succeeding early Wasatchian faunas. The six genera with unusually small species are *Azygonyx*, *Thryptacodon*, *Chriacus*, *Ectocion*, *Copecion*,

and *Palaeanodon*. These small species account for 48 out of 152 MNI (Table 29), or 32% of the  $Wa_0$  fauna. The larger congener is present in the  $Wa_0$  fauna in the cases of *Azygonyx* and *Ectocion*, and in the remaining genera the large form is sufficiently rare (both before and after  $Wa_0$ ) that there is a reasonable expectation that it will be found when the  $Wa_0$  fauna is better known. Consequently, even though they are small, these cannot really be considered dwarfed forms either.

The small size of many species in the  $Wa_0$  fauna is striking by comparison with sizes usually found in Clarkforkian and Wasatchian congeners, but no special explanation for body size differences is required if the paleoenvironmental setting of the  $Wa_0$  fauna was different from that normally sampled in the Clarks Fork and Bighorn basins. Smaller species may have replaced larger low-floodplain congeners on high floodplains because the vegetation was different, or smaller species may have been present in addition to larger (and rarer) congeners simply because high floodplains support greater species diversity.

#### CENOGRAM OF MAMMALIAN BODY SIZE

The environmental setting of a mammalian fauna can be investigated using a cenogram of body size. *Cenogram* or *coenogram* is derived from classical Greek *koinos*, community, and *gramme*, a line (from *grapho*, to draw). The term was proposed by the ecologist Jose Valverde (1964, p. 140) as a name for the line obtained when species in a fauna ("community") are arranged by size (e.g., Figure 50). Valverde separated carnivorous mammals from insectivores, herbivores, and omnivores (at the base of the mammalian food chain) in drawing cenograms. In recent years, cenograms have been developed by Serge Legendre to the point that the form of the cenogram line for body weights of insectivorous, herbivorous, and omnivorous mammalian species can be used to infer environmental ecological parameters (Legendre and Sudre, 1984; Legendre, 1986, 1987, 1988). Legendre's work is particularly important in demonstrating that cenograms can be used to interpret fossil faunas, providing new insight into mammalian faunal evolution through the late Eocene and early Oligocene.

Cenograms illustrate a remarkable uniformity that exists in the distribution of body sizes among species in extant mammalian faunas. Each species differs from the next larger or smaller species by a nearly constant proportion, which is appropriately illustrated on a logarithmic scale ( $\log_e$  or  $\log_{10}$ , the base is irrelevant). Breaks in the uniform distribution, when they occur, are always at about 500 gm and at about 250 kg. Thus mammals are naturally divided into three body size categories: small (less than 500 gm), medium (more than 500 gm but less than 250 kg), and large (more than 250 kg). Large species are always few in number, and large species do not enter into interpretation of a cenogram.

The break between small and medium-sized mammals at 500 gm corresponds to "Kay's threshold" in the distribution of primate body weights (Kay, 1975; Gingerich, 1984b), a break separating primates according to their source of dietary protein. Small primates derive their protein primarily from insects, and larger primates derive their protein primarily from leaves. The 500 gm break can be traced, in primates, from the Eocene to the present (Fleagle, 1978). Fleagle's results, and those of Legendre, indicate that patterns in the distribution of body size that we observe in extant faunas can be traced back in time to the Eocene, which suggests in turn that scaling processes operating in ecology today were also operating then.

Cenograms are interpreted in terms of their slope and continuity. Species-rich faunas, and species-rich parts of faunas have their weight distribution spread over many species, and they thus have a relatively low slope per unit rank. Species-poor faunas, and species-poor parts of faunas, have the same weight distribution spread over fewer species, and they thus have a steeper slope per unit rank.

Closed-forest environments have species from a full range of habitats and a full range of body sizes, and they have continuous slopes. Faunas from open woodland and savanna environments usually lack species in the 500–600 gm range, and they have relatively few medium-sized species. Thus faunas from open woodland and savanna environments usually have a break in slope and an offset in the middle of the cenogram. If we can generalize from Kay's (1975) study of primates, the 500 gm breakpoint is related in some way to the range of size, the density, and the diversity of insects and leaves, both of which are greatest in forests. Humid environments have more mammalian species in a given size range, and thus lower slopes per unit rank. Dry environments have fewer species in a given size range, and thus steeper slopes per unit rank. There is, of course, a close association between vegetation and moisture: forests are almost always humid, and savannas are usually drier.

Legendre (1987, 1988) stated that there are many species in the middle part of a cenogram in closed environments (forests) and fewer species in the middle part of the range in open environments (open woodlands and savannas), yielding a break or offset in the overall distribution. Legendre also stated that greater aridity means that there are fewer species in the upper part of the cenogram, yielding a greater slope above the breakpoint. Legendre did not quantify either the breakpoints, the offsets at these breakpoints, or the slopes of his cenograms, but these can be quantified using data he provides. Parameters of interest are (1) the slope of the cenogram over the range of small mammals; (2) the slope of the cenogram over the range of medium-sized mammals; (3) the difference, if any, between 1 and 2; and (4) the vertical offset in body size at the 500 gm breakpoint (if any) in the cenogram, that is, the magnitude of the gap between small and medium-sized mammals. Slope and vertical offset parameters for

cenograms of extant mammalian faunas are quantified in Table 31, based on body size information Legendre (1988) compiled for 42 extant faunas from a range of habitats in Europe, Asia, Africa, North America, and South America.

Legendre's data show that an offset, when it is present, always occurs at a breakpoint between ranks of species weighing more and less than about 500 gm (discussed above). Regression lines fit to small species below the breakpoint have slopes ranging from -0.079 to -0.628 units of  $\ln$  weight (gm) per unit rank. Regression lines fit to medium species above the breakpoint (and below 250 kg) have slopes ranging from -0.111 to -1.345 units of  $\ln$  weight (gm) per unit rank. The offset in regression lines at the breakpoint may be as great as 3.28 units of  $\ln$  weight (gm). Analysis confirms Legendre's conclusion that the offset is small in forest faunas (mean = 0.236  $\ln$  weight units) and large in more open woodland and savanna faunas (mean = 1.154 to 1.367  $\ln$  weight units; Table 31). Analysis also confirms Legendre's statement that there are fewer large species in increasingly arid environments. Slopes for medium-sized species average -0.208 in humid environments, -0.313 in subhumid environments, -0.616 in semiarid environments, and -1.058 in arid environments. Slopes for small species are stable over this moisture gradient, meaning that the difference in mean slopes also increases with increasing aridity (Table 31).

Body weights can be estimated from tooth size in fossil mammals (Gingerich and Smith, 1984), an approach extended significantly by Legendre (1986, 1988). The smallest mammalian species in the  $W_{a_0}$  fauna for which body size can be reliably estimated is *Cf. Acritoparamys atavus*, with an estimated body weight of about 40 gm. The largest mammalian species in the  $W_{a_0}$  fauna is *Coryphodon eocaenus*, with an estimated body weight of about 400 kg. A cenogram constructed for the 24 herbivorous and omnivorous  $W_{a_0}$  mammalian species is illustrated in Figure 50.

The largest species in the  $W_{a_0}$  fauna is *Coryphodon* sp., rank 1 on the cenogram of Figure 50, which exceeds 250 kg and is omitted from further analysis. The 500 gm breakpoint falls between ranks 19 and 20. Regression of  $\ln$  estimated body weight (gm) on rank for the five species of small mammals of rank 20–24 lying below the 500 gm breakpoint yields a slope of -0.432. Regression of  $\ln$  estimated body weight (gm) on rank for the 18 species of medium-sized mammals of rank 2–19 lying above the 500 gm breakpoint yields a slope of -0.228. Offset between the two regression lines at the breakpoint is 0.21  $\ln$  weight (gm) units. Comparison of the negligible offset at the breakpoint in the  $W_{a_0}$  cenogram with those characteristic of extant faunas living in forest, woodland, and savanna (vegetation gradient in Table 31), indicates that the  $W_{a_0}$  fauna was a forest fauna. Comparison of the cenogram slope for medium-sized mammals in the  $W_{a_0}$  fauna, -0.228, with those characteristic of extant faunas living in humid, subhumid, semiarid, and arid environments (mois-

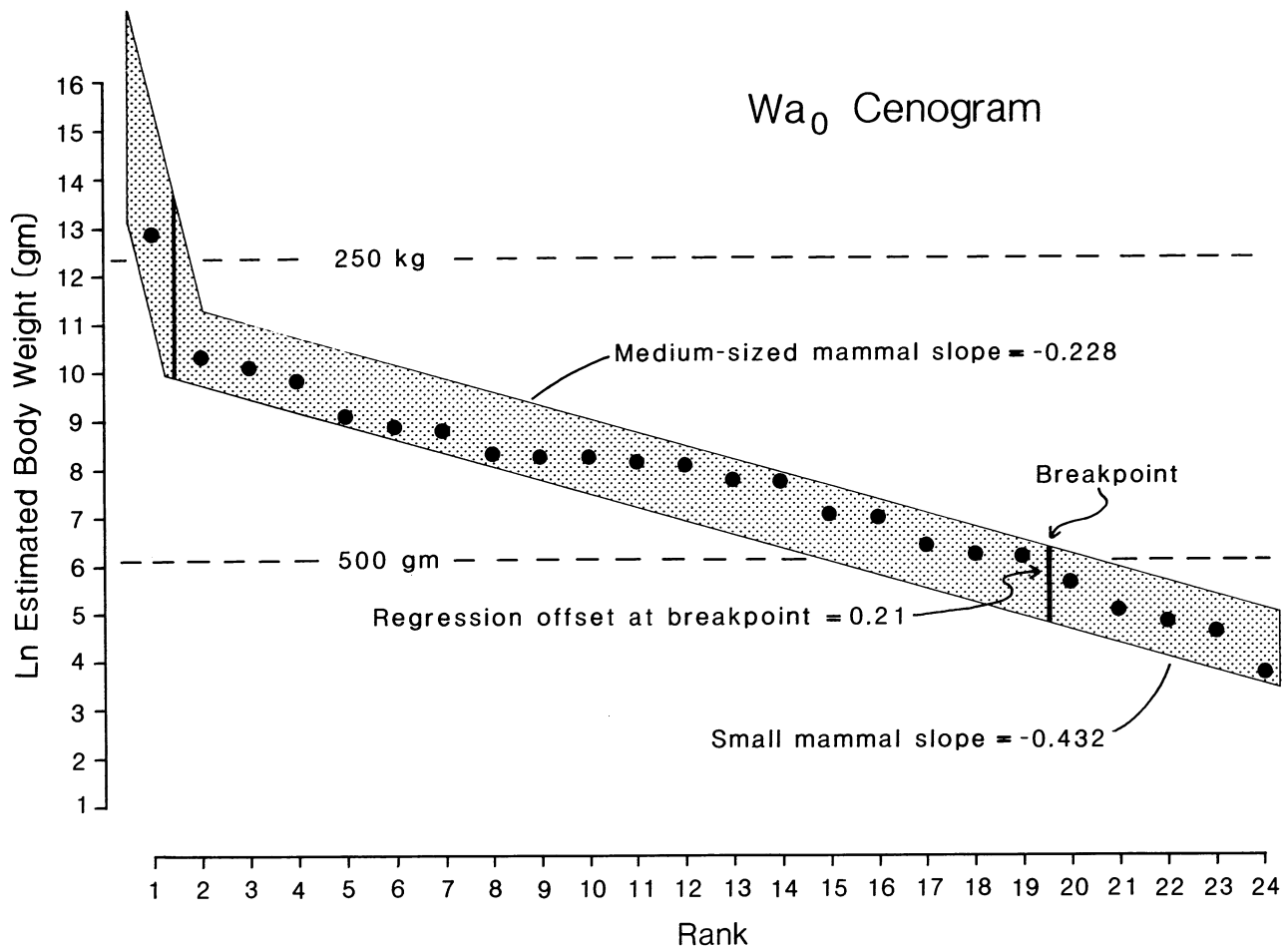


Figure 50. Cenogram showing ranked distribution of body weights estimated from tooth size for 24 herbivorous and omnivorous mammalian species in the Wa<sub>0</sub> fauna. Largest species (rank 1) is *Coryphodon* sp. Medium-sized species occupy ranks 2–19; these are, in order: *Azygonyx* sp., *Phenacodus* cf. *P. intermedius*, *Azygonyx gunnelli*, *Esthonyx spatularius*, *Hyracotherium grangeri*, *Ectocion osbornianus*, *Hyracotherium sandrae*, *Meniscotherium priscum*, *Copecion davisi*, *Ectocion parvus*, *Thryptacodon barae*, *Princetonia yalensis*, *Chriacus badgleyi*, *Cantius torresi*, *Diacodexis ilicis*, *Hyopsodus loomisi*, *Phenacolemur praecox*, and *Arctodontomys wilsoni*. Small species occupy ranks 20–24; these are, in order: *Paramys taurus*, *Acritoparamys atwateri*, cf. *Niptomomys* sp., *Mimoperadectes labrus*, and cf. *Acritoparamys atavus*. Note the similarity of regression slopes for medium-sized species and small species, and negligible offset at 500 gm breakpoint, which are characteristics of extant faunas inhabiting forests. Note also the low regression slope for medium-sized species, which is characteristic of extant faunas inhabiting humid environments (see text and Table 31).

ture gradient in Table 31), indicates that the Wa<sub>0</sub> fauna inhabited a humid environment. The cenogram slope for small mammals in the Wa<sub>0</sub> fauna is higher than usual for extant faunas, reflecting poor sampling of the small-mammal part of the fauna, but this slope does not enter into interpretation of the cenogram.

Table 31. Slope and offset parameters for cenograms of extant mammalian faunas in different environmental settings

	Number of faunas N	Mean slope small mammals  ————— (Ln weight gm/unit rank)	Mean slope medium mammals  ————— (Ln weight gm/unit rank)	Mean slope difference small-medium mammals  ————— (Ln weight gm/unit rank)	Mean offset at break between small-medium mammals  ————— (Ln weight gm)
<i>Vegetation gradient</i>					
Forest	14-15	-0.165	-0.292	0.138	0.236*
Woodland	14	-0.167	-0.257	0.090	{1.367}* 1.154}
Savanna	13	-0.233	-0.690	0.457	
<i>Moisture gradient</i>					
Humid	13-14	-0.157	-0.208*	0.056*	0.151
Subhumid	15	-0.172	-0.313*	0.140*	1.788
Semiarid	10	-0.244	-0.616*	0.372*	0.565
Arid	3	-0.201	-1.058*	0.857*	1.000

\*Parameters showing trends consistent with environmental gradients. All parameters estimated by regression, using data in Legendre (1988).

## VI CORRELATION WITH EUROPE AND ASIA

The geological time scale is based on faunal succession, supplemented by paleomagnetic correlations and radiometric calibrations whenever possible. Epochs like the Paleocene and Eocene, and epoch boundaries like the Paleocene-Eocene boundary, are intervals, and events, of faunal succession. One problem with the Paleocene-Eocene boundary concerns its several definitions by paleobotanists, invertebrate paleontologists, and vertebrate paleontologists. A second problem concerns recognition and correlation of the boundary, however defined, around the world.

### PALEOCENE-EOCENE BOUNDARY

The Paleocene-Eocene boundary is understood differently in different subdisciplines of paleontology. The term Paleocene was first used by Schimper (1874), but it was characterized ambiguously: floras that Schimper called Paleocene subsequently proved to be contemporary with those he called Eocene (and vice versa). Koenen (1885) drew the Paleocene-Eocene boundary between the Woolwich-Reading beds and the overlying London Clay in England, and between the *Lignites* and overlying *Sables inférieurs de Cuise* in France. There is no type section of the Paleocene, and a hiatus marks the Paleocene-Eocene boundary in many stratigraphic sections. Thus the boundary is recognized by common use (and this varies by subdiscipline) rather than any workable common definition or reference type section.

The beginning of the European Sparnacian substage/age is regarded as the beginning of the Eocene epoch by most vertebrate paleontologists (e.g., Russell et al., 1982a,b; Schmidt-Kittler, 1987) and by many geologists, especially those working in the Paris Basin in France (e.g., Pomerol, 1969; Cavalier and Pomerol, 1986). Russell, Pomerol, and Cavalier include the Sparnacian within a broadly drawn Ypresian stage/age. Invertebrate paleontologists and micropaleontologists often regard the Sparnacian as Paleocene (Berggren, 1965), and consider the beginning of Eocene time to coincide with the base of a more narrowly drawn Ypresian stage/age (including the Cuisian substage/age but not the Sparnacian; e.g., Costa et al., 1978; Curry et al., 1978; Berggren et al., 1985). Paleobotanists differ in where they draw the Paleocene-Eocene boundary. Schimper (1874) included both the Sparnacian and Cuisian of the Paris Basin in the Paleocene when he first proposed the term. More recently in North America, Hickey (1977,

1980) placed the Paleocene-Eocene boundary at the base of the Wasatchian land-mammal age, while Wing (1984) has reasoned that it should be placed within the Wasatchian.

European Sparnacian mammalian faunas are so different from preceding Thanetian faunas, and Sparnacian faunas are so similar to those of the succeeding Cuisian that it is difficult to imagine grouping Sparnacian mammals in the same epoch with archaic Thanetian forms. Hence I follow vertebrate paleontological tradition in drawing the Paleocene-Eocene boundary at the beginning of the Sparnacian. No Paleocene-Eocene boundary definition is "correct" at this stage, but each is useful for particular groups of organisms studied in particular settings. Agreement on a single boundary is probably less important than recognition that multiple definitions exist, with clear designation of the definition being followed.

### FAUNAL SIMILARITY

Earliest Wasatchian mammals are very similar to earliest Sparnacian mammals both individually as genera and species, and taken together as a fauna. Wasatchian and Sparnacian faunas have long been known to be similar (Cope, 1878), but new discoveries on both sides of the Atlantic have made the closeness of this resemblance more clear in recent years. The  $Wa_0$  fauna described here is particularly important in this regard.

Many mammalian genera found in the  $Wa_0$  fauna are also known from Europe and Asia. The greatest similarity in Europe is with the fauna of the Sparnacian substage/age: 17 out of 34  $Wa_0$  genera (50%) are found in the Sparnacian of Europe (Russell et al., 1982a, p. 48; Russell et al., 1982b). The greatest similarity in Asia is with the mammalian fauna of the Bumbanian land-mammal age: 5 out of 34  $Wa_0$  genera (15%) are found in the Bumbanian of Asia (Russell and Zhai, 1987, p. 414). All five  $Wa_0$  genera found in Asia (*Coryphodon*, *Miacis*, *Hyopsodus*, *Diacodexis*, and *Hyracotherium*) are found in Europe, indicating that a significant component of the fauna was cosmopolitan. Dashzeveg (1982, 1988) correlated the early Bumbanian in Asia with the early Sparnacian in Europe and with the early Wasatchian in North America, but Bumbanian *Homogalax* and *Hyopsodus* that form part of the evidence for the correlation appear to be more advanced

and more specialized than congeners in the early Sparnacian or early Wasatchian, which suggests that the earliest Bumbanian may not yet be sampled. As is often the case, more and better evidence is required.

The number of genera shared in common suggests that the  $W_{a_0}$  mammalian fauna was more similar to the European Sparnacian fauna than it is to the Asian Bumbanian fauna (Flynn, 1986, provides an independent analysis with a similar result). However, this is, at best, a tenuous conclusion. Some 57 mammalian genera are known from the Sparnacian, while only about 26 genera are known from the Bumbanian. The Bumbanian probably spans an interval twice as long as the Sparnacian, it includes taxa from localities distributed over a much larger geographic area, and it cannot be considered adequately known for purposes of intercontinental comparison. Equivalent sampling of the earliest Bumbanian might well reveal the presence of additional cosmopolitan taxa, increasing its faunal resemblance to both the  $W_{a_0}$  fauna in North America and the earliest Sparnacian fauna in Europe.

#### FAUNAL SUCCESSION IN EUROPE

The principal European mammalian faunas included in the early Sparnacian substage/age (European mammalian reference level MP-7; Schmidt-Kittler, 1987; Godinot, 1987) are the following: Meudon, Pourcy, Rians, and Palette in France; Dormaal and Erquelinnes in Belgium; Suffolk Pebble beds at Kyson and Ferry Cliff, and Blackheath beds at Abbey Wood in England; and Silveirinha in Portugal.

Mammalian fossils have been known from the *Conglomérat de Meudon* at the base of the *Argile Plastique* since 1836, when d'Orbigny published a stratigraphic section and described numerous teeth of "*pachydermes*," "*carnassiers*," and "*rongeurs*." The *Conglomérat de Meudon* has long been regarded as the earliest Sparnacian known in the Paris Basin. Teilhard (1922, p. 54) listed *Pachyaena*, *Coryphodon*, *Hyracotherium*, *Palaeonictis*, *Paramys*, and *Plesiadapis* as genera known with certainty to have come from the *Conglomérat de Meudon* beneath the *Argile Plastique*. He considered the *Conglomérat de Meudon* to be "*sûrement au Sparnacien le plus inférieur*" (1922, p. 53). This view has never been challenged, the problem with Meudon being the very small fauna known from this locality and the long-imagined impossibility of collecting more.

Several other mammalian faunas are considered to be earliest Sparnacian in age. These include Dormaal (reviewed by Godinot et al., 1978), Kyson and Ferry Cliff (Hooker, 1980), Rians (Godinot, 1981), Silveirinha (Antunes and Russell, 1981), and Palette (Godinot et al., 1987). Dormaal appears to be an earliest Sparnacian fauna, about equivalent to Meudon in age, with a primitive omomyid *Teilhardina belgica* retaining four premolars in virtually all specimens (Gingerich, 1977b), a primitive

*Arfia* (see above), and a primitive dichobunid *Diacodexis* (Sudre et al., 1983). Kyson and Ferry Cliff are considered earliest Sparnacian on the basis of their *Cymbalophus* (or *Hyracotherium*) and *Hyopsodus*, although it is not clear that these localities are very much older than Abbey Wood. Rians is considered to be earliest Sparnacian in age largely because its *Hyracotherium* and *Diacodexis* are small. However  $P_2$  or  $P_3$  of *Diacodexis* is 17% longer than  $M_1$  and the hypolophid on  $M_3$  is well developed. These characteristics of *Diacodexis*, and full reduction of the paraconid on  $M_1$  of *Hyopsodus*, suggest that the fauna from Rians is probably not as old as that from Dormaal. Preliminary evaluation of Silveirinha as the earliest Eocene fauna in Europe was based on identification of a characteristically Paleocene genus, *Louisina*, in the fauna. Restudy indicates that this is a new species of *Microhyus* (Antunes et al., 1987), which removes the Paleocene element from the Silveirinha fauna. Development of an incipient hypolophid on  $M_3$  of Silveirinha *Diacodexis* suggests that this too is a more advanced species than that found at Dormaal. *Donrussellia* from Palette appears to be intermediate between a primitive early Sparnacian *Cantius* and the *Donrussellia* found at Rians, and further evidence will be required to substantiate the claim that Palette is older than Dormaal.

Russell et al. (1982a, p. 74) list *Coryphodon grosseleti* as coming from the *Sables de Bracheux* in France, which are Thanetian in age. However, Malaquin (1899) described this species from "Landenian" beds at Vertain, and these are sometimes (usually?) regarded as early Sparnacian in age (e.g., by Cavelier, 1987, table 7). Malaquin states that *Coryphodon* was found with champsosaur remains at Vertain, but this association in the *Sables d'Erquelinnes* has been questioned by Heinzelin (1979), who suggested that the champsosaur specimens were reworked. The same question of reworking can be raised for specimens of *Champsosaurus* from the "sable roux à gros grains" at Vertain. Lucas (1986) described *Coryphodon* remains from the "upper Paleocene" *Sable fluvio-marin de Landen* of Orp-le-Grand in eastern Belgium. This stratigraphic unit too is regarded as early Sparnacian in age by Cavelier (1987, table 7). Hence there is no evidence that *Coryphodon* appeared in Europe before the beginning of the Sparnacian, nor is there any clear evidence that champsosaurs survived into the Sparnacian (I am indebted to D. Russell and D. Sigogneau-Russell for reconsidering both of these questions in light of present evidence—they confirm, in litt., 1988, that *Coryphodon* is unknown in Europe before the Sparnacian, and champsosaurs are unknown after the Thanetian).

#### COMPARISON OF EARLIEST WASATCHIAN SPECIES

Species in the  $W_{a_0}$  fauna share many detailed similarities with Sparnacian species in Europe. There are also some differences. To the extent that available material can be



compared, early Wasatchian *Ectypodus tardus* appears less specialized than Sparnacian *E. childi* in having a lower first serration and in having a less expanded exodaenodont lobe (Krause, 1982). *Cantius torresi* is very similar to early Sparnacian *Cantius eppsi*, but more primitive in having relatively shorter and broader lower premolars (Gingerich, 1986). Earliest Wasatchian *Esthonyx spatularius* is similar to *Esthonyx* sp. from Abbey Wood. Earliest Wasatchian *Coryphodon* is similar to early Sparnacian *C. eocaenus*. Both species of  $W_{a_0}$  *Dipsalidictis* are similar to early Sparnacian "*Oxyaena*." *Arfia junnei* is probably conspecific with the *Arfia* found at Dormaal. Cf. *Prolimnocyon* has been reported from Dormaal, but this form has not yet been described. *Miacis winkleri* is similar to *M. latouri* from Dormaal, but differs (to the extent they can be compared), in the relative development of cingula on upper molars. *Hyopsodus loomisi* is a little larger but otherwise similar in evolutionary grade to *Hyopsodus wardi* from Abbey Wood. Earliest Wasatchian *Diacodexis ilicis* is most similar to the undescribed species of this genus from Dormaal. It is primitive for North American species in having relatively short premolars. One isolated premolar has been described for *D. gazini* from Rians: it is relatively long by comparison with the length of molars from the same site, a more advanced characteristic. *Hyracotherium sandrae* and *H. grangeri* are very similar to *Cymbalophus cuniculus* from Kyson and Ferry Cliff and *Hyracotherium* aff. *H. vulpiceps* from Abbey Wood, respectively. *H. sandrae* appears to be more primitive than *C. cuniculus* in being slightly less lophodont.

#### NEW EVIDENCE ON CORRELATION OF THE CLARKFORKIAN

Cope (1878) was one of the first to suggest that the mammalian fauna from Meudon was correlative with the North American Wasatchian, and virtually all subsequent authors equated the beginning of the Wasatchian with the beginning of Sparnacian time (e.g., Matthew, 1914; Teilhard, 1922; Simpson, 1929). When Granger (1914) named the "Clark Fork beds" he suggested that this faunal interval might represent the latter part of the Paleocene. Most subsequent authors followed Granger in considering the Clarkforkian land-mammal age to be part of the Paleocene, the Tiffanian and Clarkforkian together being correlative with the Thanetian rather than Sparnacian in Europe (e.g., Jepsen, 1930; Wood et al., 1940; Russell, 1964).

Rodents (*Paramys* and its relatives) and perissodactyls (principally *Hyracotherium*), both found at Meudon, are the two taxa most often mentioned as marking the beginning of the Sparnacian and hence the beginning of Eocene time (e.g., Granger, 1914; Matthew, 1914; Teilhard, 1922; Simpson, 1929; Jepsen, 1930). Jepsen (1937) described a new rodent from Bear Creek in North America, a fauna then regarded as being Tiffanian late Paleocene in age.

Morris (1966) described a North American *Hyracotherium* from beds in Baja California thought to be Clarkforkian in age. Wood (1967) published his conclusion that the Clarkforkian did not warrant recognition as even a faunal zone, and Morris (1968) revised the age of his *Hyracotherium* to Tiffanian. Jepsen and Woodburne (1969) described a putative Tiffanian *Hyracotherium* from Wyoming, and Schiebout (1974) described a putative Clarkforkian *Hyracotherium* from Texas.

Revising Plesiadapidae, I concluded (Gingerich, 1976b), contrary to Wood (1967), that there is a distinct Clarkforkian faunal interval in North America, that the Bear Creek fauna with its early record of rodents belongs in the Clarkforkian, and that Jepsen and Woodburne's *Hyracotherium* might be from the early part of the Clarkforkian rather than the Tiffanian (Gingerich, 1976b). Restudying the mammalian fauna from the European early Sparnacian Conglomérat de Meudon, I noted that all six of the genera then known (*Coryphodon*, *Hyracotherium*, *Plesiadapis*, *Phenacolemur*, *Paramys*, and *Oxyaena*) appeared to be present and at about the same stage of evolution in the North American Clarkforkian (Teilhard included *Pachyaena* in this list, but Boule (1903) clearly stated that the specimen in question was found "*vers la base de l'argile plastique*," not from the *Conglomérat de Meudon*). Consequently, I proposed correlation of the Sparnacian with the Clarkforkian (or the Clarkforkian with the Sparnacian) based on the six *Conglomérat de Meudon* genera. Pursuing this logic, the North American Clarkforkian was early Eocene rather than late Paleocene in age (Gingerich, 1975, 1976b).

Intensive field work and museum study of the North American Clarkforkian from 1975–1979 greatly augmented the evidence and our understanding of this fauna, which made possible a more refined correlation with the European Thanetian and early Sparnacian. Rose (1980, 1981a) subdivided the Clarkforkian into three faunal zones, correlating the lower Clarkforkian with the European Thanetian and the middle and upper Clarkforkian with the Sparnacian. Thus it appeared that the Paleocene-Eocene boundary lay within the Clarkforkian.

At the same time, however, field work made it questionable that the Clarks Fork Basin *Hyracotherium* described by Jepsen and Woodburne (1969) came from either the late Tiffanian or the Clarkforkian: we were unable to find even a fragment of a tooth of *Hyracotherium* in the area where the find was said to have been made. Flynn and Novacek (1984) collected additional mammalian species from Morris' *Hyracotherium* locality in Baja California and concluded that this fauna is Wasatchian in age. Finally, Schiebout et al. (1987, p. 371) reidentified the *Barylambda* tooth that formed the basis for the Clarkforkian age assigned to the Texas *Hyracotherium*, concluding that the "*Barylambda*" is probably a Wasatchian *Coryphodon*. The only remaining record of *Hyracotherium* from a pre-Wasatchian locality in North America is the Jepsen-Wood-

burne specimen, and this record is suspect because the specimen was not recognized as a pre-Wasatchian *Hyracotherium* until it had been in the Princeton museum for a year or more, by which time it might easily have been misassociated with an incorrect locality label.

New evidence comes too from the *Conglomérat de Meudon* itself. Several years ago M. Alain Galoyer rediscovered a pocket of *Conglomérat* in the collapsed chamber of one of the many subterranean galleries excavated in the Cretaceous chalk underlying Meudon. New genera added to the *Conglomérat de Meudon* fauna as a result include the primates *Teilhardina* and *Cantius* (Russell, et al., 1988), genera known from the Wasatchian but not the Clarkforkian in North America.

Reevaluation of supposed pre-Wasatchian records of *Hyracotherium* in North America and addition of two more *Conglomérat de Meudon* genera found in the North American Wasatchian but not Clarkforkian remove some of the evidence on which a Clarkforkian-Sparnacian correlation was based, raising new obstacles to such a correlation. Further, discovery of a new earliest Wasatchian fauna in North America, the  $Wa_0$  fauna described here, sharing half its genera and several species with early Sparnacian faunas in Europe, indicates that the earliest Wasatchian in North America should be correlated with the earliest Sparnacian in Europe. This is not simply a return to an earlier intercontinental faunal correlation using evidence previously available, but rather a result of much better evidence of mammalian faunal succession on both sides of the Atlantic.

One consequence of correlating the earliest Wasatchian with the earliest Sparnacian is that the Clarkforkian land-mammal age is again entirely Paleocene rather than Eocene in age. Clarkforkian equivalent faunas appear to be partly or entirely missing in Europe (Dashzeveg, 1982, 1988). Rose (1980, 1981a) correlated the early Clarkforkian with the latest Thanetian because of the close resemblance of North American *Plesiadapis gingerichi* and European *Plesiadapis tricuspis*, and this remains the most reasonable interpretation. Equivalents of the North American *Plesiadapis cookei* and *Phenacodus-Ectocion* zones of the Clarkforkian appear to be missing in Europe. Discovery of many new teeth of *Plesiadapis russelli* at Meudon indicates that this species should probably be transferred to *Platychoerops*. *P. russelli* is, in any case, more specialized and probably younger than North American middle Clarkforkian *Plesiadapis cookei*.

Jepsen (1930b, p. 494) claimed that *Champsosaurus* was discovered repeatedly above the lowest occurrences of *Hyracotherium* in North America, but this has never been substantiated. To the best of my knowledge, *Champsosaurus* has never been found in a Wasatchian fauna.

#### PALEOMAGNETIC STRATIGRAPHY

Paleomagnetic stratigraphy has been studied in three areas relevant to intercontinental correlation of land-mammal

faunas at the Paleocene-Eocene boundary: the Clarks Fork Basin in Wyoming, the Big Bend area of Texas, and the Hampshire and London basins in England.

Butler et al. (1981) recognized two paleomagnetic anomalies in the Clarks Fork and northern Bighorn basins. Both were based on multiple normally polarized samples in stratigraphic succession. The first was associated with late Tiffanian mammals and the second with latest Tiffanian and early Clarkforkian mammals. These were identified, respectively, as magnetochrons C26N and C25N. Samples were taken every 20 feet (7.4 m), on average, using a protocol that avoided red beds. Samples were taken from the southwest end of Polecat Bench in the interval now recognized as  $Wa_0$ , but this interval was not sampled intensively. A single anomalous normally-polarized sample was found just above  $Wa_0$  locality SC-67, but this was not regarded as sufficient evidence of a paleomagnetic anomaly. No paleomagnetic anomaly was recognized at the Clarkforkian-Wasatchian boundary.

Rapp et al. (1983) recognized two anomalies intercalated between mammalian faunas in the Big Bend area (see also Schiebout et al., 1987). One, interpreted as magnetochron C26N, was reported to overlie a middle Tiffanian fauna and underlie a late Tiffanian fauna (independent study of plesiadapids confirms these age assignments; Gingerich, 1976b). The second anomaly, interpreted as magnetochron C25N, was reported to include later Tiffanian mammals. These interpretations are consistent with interpretations in the Clarks Fork Basin, and again no anomaly was found at the Clarkforkian-Wasatchian boundary (this boundary has not been located paleontologically and may be missing in Big Bend stratigraphic sections).

Townsend and Hailwood (1985) studied a series of stratigraphic sections in the Hampshire and London basins of England and produced a composite paleomagnetic polarity sequence across the Paleocene-Eocene boundary. Their objective was regional comparison and they did not attempt to correlate observed magnetochrons to the worldwide reversal sequence. Townsend and Hailwood recorded an anomaly in the Thanet Formation of Thanetian age; an anomaly in the Oldhaven Formation of Sparnacian age (a probable lateral equivalent of the Blackheath beds at Abbey Wood and possible equivalent of the Suffolk Pebble beds at Kyson and Ferry Cliff; Hooker, 1980); and three anomalies in the London Clay of late Sparnacian and early Cuisian age. Subsequently, Aubry et al. (1986) numbered the Thanetian anomaly C26N, considered C25N to be missing in the Hampshire-London Basin, and included all three London Clay anomalies in C24N. The Oldhaven anomaly was regarded as a discrete Oldhaven normal-polarity event lying within C24R.

The most important aspect of Townsend and Hailwood's work relevant here is that their Oldhaven event should be found in or near zone  $Wa_0$  if the revised North American-European faunal correlation proposed in this paper is correct.  $Wa_0$  sediments are well exposed, but they have never

been intensively sampled paleomagnetically. Full analysis of the paleomagnetic polarity of zone  $Wa_0$  would provide an important test of the  $Wa_0$ -Oldhaven correlation based on fossil mammals: zone  $Wa_0$ , like the Oldhaven beds, should be partly or entirely of normal polarity.

Aubry et al. (1988) placed the Paleocene-Eocene bound-

ary at the base of the Oldhaven beds. Paleomagnetic confirmation of an Oldhaven- $Wa_0$  correlation would help to resolve longstanding differences in the Paleocene-Eocene boundary recognized by marine and continental paleobotanists, invertebrate paleontologists, and vertebrate paleontologists.



## VII ORIGIN OF ARTIODACTYLA, HYAENODONTIDAE, PERISSODACTYLA, AND PRIMATES

One of the most interesting problems in evolution concerns the origin of major taxonomic groups of organisms. The modern orders Artiodactyla, Perissodactyla, and Primates, and the creodont family Hyaenodontidae made their first appearance in the fossil record together in zone  $Wa_0$ . These four major groups seem also to have appeared together at the same time, or very nearly the same time, in Europe and in Asia. Possible precursors have been identified in the middle Paleocene but not the late Paleocene of North America, so they must have come from somewhere else.

### CLIMATE AND GEOGRAPHY

The late Paleocene was a time of enhanced faunal endemism and reduced cosmopolitanism on the northern continents. This interval of enhanced endemism coincided, broadly, with an interval of climatic cooling (e.g., Wolfe and Hopkins, 1967; Wolfe, 1978), and it coincided with an interval of lower mammalian species diversity (Rose, 1981a,b) and reduced biotic dependence (Table 30). It is possible to explain reduced cosmopolitanism in continental faunas of the late Paleocene by (partial) faunal retreat toward the equator as climates cooled. Equatorial continental areas were isolated from each other by oceans, enhancing opportunities for the evolution of endemics. Later, when climates warmed again as the Paleocene-Eocene transition began, new taxa dispersed poleward to recolonize the northern continents, cross high-latitude land bridges, and become a new cosmopolitan early Eocene fauna.

This climate-driven hypothesis for the origin of modern mammalian orders was first outlined by Sloan in 1969. Sloan (1969) regarded Central America as the late Paleocene center of origin of the cosmopolitan holarctic perissodactyl-rodent-omomyid-adapid mammalian fauna of the early Eocene. The late Paleocene climate-driven hypothesis has been refined and restated in terms of increasingly better faunal evidence by Gingerich (1976b), Gingerich and Rose (1977), Gingerich (1980a,b, 1982), Godinot (1982), Gingerich (1985b, 1986, 1987a), and Krause and Maas (1989). It is important to emphasize that the hypothesis has now been generalized to the point that any late Paleocene equa-

torial continental area (northern South America and Central America, northern Africa, or South Asia) is a possible center of endemism and source for later holarctic higher taxa.

North American middle Paleocene mammals represent a grade and interval of mammalian evolution that is poorly known elsewhere in the world. They provide a model for the stage of evolution of middle Paleocene mammals worldwide, but they do not indicate that modern orders like Artiodactyla, Perissodactyla, or Primates necessarily originated in North America from North American middle Paleocene ancestors.

The clustered pattern of first appearances of modern orders of mammals worldwide at the time of the Paleocene-Eocene transition is similar to the clustered patterns of first appearances of modern families at the time of the Eocene-Oligocene transition and modern genera in subsequent faunal transitions. Taxonomic hierarchy is imposed in hindsight, and the origin of modern orders is no more profound a problem than the origin of modern families or the origin of modern genera. Earlier pulses of diversification are expressed at higher taxonomic levels because the groups involved survived more subsequent pulses, not because the pulses themselves were necessarily any more profound (Gingerich, 1987a). This means that the origin of modern orders of mammals should be studied in the context of pulses of origination at other times and other taxonomic levels. It does not mean that the context will necessarily be the same for all.

I interpreted the appearance of Perissodactyla in North America and the order's early rise to dominance among ungulates as a response to development of an environmental mosaic including open park woodland and savanna habitats replacing humid forests (Gingerich, 1981). This is similar to the context Legendre (1986, 1987) documented for the Eocene-Oligocene transition or *Grande Coupure* in Europe, which also involved replacement of humid forest faunas by those characteristic of dryer and more open woodland and savanna. Study of the  $Wa_0$  fauna here indicates that the first North American fauna with perissodactyls inhabited a humid forest. More work remains to be done to place the whole Paleocene-Eocene faunal transition in paleoclimatological and paleoenvironmental context.

## HIGH FLOODPLAIN AND LOW FLOODPLAIN ENVIRONMENTS

It is well known that sedimentary basins bury and preserve a small subset of the whole mammalian fauna living at a given time. Little is known about faunas that inhabited large areas outside sedimentary basins on each continent in the geological past. Zone  $Wa_0$  provides an opportunity to look at the fauna in an environment, the high floodplain, that is otherwise rarely sampled.

One of the most interesting results of this study is demonstration that the earliest Eocene Clarks Fork Basin fauna living in a high-floodplain environment differed in characteristic ways from faunas living before and after in low-floodplain environments. Differences include the presence of a substantial number of unusually small congeners of species normally found in low-floodplain environments, and an unusually high relative abundance of burrowing metacheiromyids and stylinodontids.

Differences between high-floodplain faunas and contemporaneous low-floodplain faunas are significant at the ordinal and family level for a few specialized taxa, and they are different at the species level for up to about one-quarter of the species. However, overall, contemporaneous high-floodplain and low-floodplain faunas are very similar taxonomically, and they are probably similar in most other ways as well. The low floodplain normally sampled does not seriously misrepresent the high floodplain that is rarely sampled. The farther any unknown locality is from known localities, the greater the likelihood that it will differ faunally, but there is at present no way to estimate how great this difference might have been in the Eocene.

Artiodactyla, hyaenodontid Creodonta, Perissodactyla, and Primates made their first North American appearance together in the  $Wa_0$  high-floodplain fauna. Since the high-floodplain fauna is so rarely sampled, it is possible to question whether these groups really appeared together in North America at the same time. As an alternative, one might postulate that they originated in or entered North America at different times and only seemed to appear together because a high-floodplain fauna was being sampled for the first time.

Staggered entry into the Clarks Fork Basin is unlikely because Artiodactyla, hyaenodontid Creodonta, Perissodactyla, and Primates are all missing in low-floodplain samples of the preceding Clarkforkian, and all four groups are present in succeeding Wasatchian low-floodplain environments when these are first sampled after  $Wa_0$  time. The

evidence of their sudden appearance together is really based on sudden appearance together in low-floodplain faunas for which we have reasonably continuous sampling through the Clarkforkian and Wasatchian, not on their appearance together in the  $Wa_0$  fauna. We do not have a low-floodplain fauna of  $Wa_0$  age, but given that all four groups are present in overlying faunas it is reasonable to expect that Artiodactyla, hyaenodontid Creodonta, Perissodactyla, and Primates were present in a  $Wa_0$ -equivalent low-floodplain fauna as well. Here again, high- and low-floodplain faunas of the early Wasatchian were probably significantly but not greatly different.

Sudden appearance together, without precursors in known late Paleocene faunas of North America, is the best evidence that Artiodactyla, hyaenodontid Creodonta, Perissodactyla, and Primates evolved on some other continent. Appearance together suggests that they may have evolved on the same continent. I have proposed that these groups may have originated in Africa and entered North America by dispersal through Asia, subsequently dispersing to Europe as well (Gingerich, 1986). Africa is a good candidate as a center of origin because it was one of three equatorial land masses in the late Paleocene, hyaenodontid creodonts dominate Oligocene African faunas in the Fayum region of Egypt to the exclusion of true Carnivora, early perissodactyls resemble hyraxes, especially Eocene hyraxes (Sudre, 1979; Hartenberger et al., 1985), and Africa has long been known as a center of primate evolution. There is no independent chronology dating first appearances of these taxa on each northern continent, but North American  $Wa_0$  species appear slightly more primitive than their European counterparts. It is possible that Artiodactyla, Hyaenodontidae, Perissodactyla, and Primates dispersed from Africa through Europe to North America, but present evidence, limited as it is, appears to favor dispersal from North America to Europe, implying that the route from Africa to North America was through Asia rather than Europe.

We may never be able to resolve temporal differences between Paleocene and Eocene faunas living on different continents with enough precision to demonstrate the direction of dispersal of any particular group. However, some progress has been made. Global geochronology has developed rapidly, and our understanding of Paleocene-Eocene mammalian faunas and faunal succession on all three northern continents is now much better than it was in 1969.

## VIII CONCLUSIONS

Clarkforkian and Wasatchian faunas are clearly distinct in family-level composition. The earliest Wasatchian  $Wa_0$  fauna, with a high proportion of phenacodontid condylarths as well as hyopsodontids, adapids, dichobunids, and equids, is intermediate in faunal composition. However, the presence of new taxa (Artiodactyla, Perissodactyla, Primates, hyaenodontid Creodonta), calculated high and even diversity values, and a biotic-dependence pattern of species abundances indicate that the  $Wa_0$  fauna is most like other Wasatchian faunas.

Sedimentological studies of the Clarkforkian-Wasatchian multistory sheet sandstone and laterally correlative mature paleosols indicate that the  $Wa_0$  fauna lived during a time when rivers were less aggradational and more degradational than usual in the late Paleocene and early Eocene of the Clarks Fork Basin. Cenogram analysis indicates that the  $Wa_0$  fauna lived in humid forests, and consequently development of mature paleosols was probably due more to good drainage than to dry climate.

Low wet floodplain environments supporting the common Clarkforkian and early Wasatchian *Allognathosuchus*-*Ectocion osbornianus* fauna appear to have been restricted in distribution during  $Wa_0$  time. Higher, better drained floodplain environments supporting a distinct *Holospira*-*Pristichampsus*-*Ectocion parvus* fauna predominated, and these are found adjacent to channel environments supporting an aquatic fauna.

The  $Wa_0$  fauna includes small species of several genera

that are normally represented by larger forms in Clarkforkian and Wasatchian faunas, and the metacheiromyid *Palaeonodon* and stylinodontid *Ectoganus* are more common than usual in zone  $Wa_0$ . These features are interpreted as general characteristics of high floodplain faunas in the early Eocene and not characteristics unique to  $Wa_0$  time.

Given present evidence, the  $Wa_0$  fauna is correlative with earliest Sparnacian mammalian faunas in Europe, and the North American Clarkforkian is now regarded as being entirely Paleocene in age. To the extent that differences in closely related taxa are real, they suggest that the  $Wa_0$  fauna may be more primitive and possibly slightly older than known European Sparnacian faunas. This hypothesis can be tested by location of the Oldhaven normal polarity event in the North American continental stratigraphic record.

Finally, this study confirms that Artiodactyla, hyaenodontid Creodonta, Perissodactyla, and Primates appeared together at the beginning of the Wasatchian. Climate undoubtedly played some role in their origin and in their subsequent dispersal to all of the northern continents, but evidence is limited. High-floodplain faunas differ significantly in characteristic ways from contemporary low-floodplain faunas normally sampled in the early Eocene, but these differences are not great and they are not likely to affect our understanding of major features of faunal composition and evolution.





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