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WASATCHIAN POWDER RIVER  
LOCAL FAUNA, EOCENE OF  
NORTHEAST WYOMING

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## ABSTRACT

THE POWDER RIVER local fauna, collected mainly under the direction of H. E. Wood, II, is of earliest Wasatchian age, correlative with the Four Mile and early Gray Bull assemblages. The enclosing Eocene rocks are probably not referable to the Wasatch Formation. Forty-one species of mammals are represented in the collection; comparative faunal lists of the Powder River and Four Mile local faunas are presented.

A very primitive rodent is present at Powder River, as is a species of true *Leptacodon* and a probably new small pantolestine. Subspecific divisions are abandoned in the genera *Paramys* and *Hyracotherium*, but retained for *Phenacolemur*. The taxa *Adapisoricidae*, *Phenacodontidae*, *Apheliscinae*, *Paeneprolimnocyon*, *Tetoniuss*, *Haplomytus*, *Hyopsodus miticulus*, and *Esthonyx spatularius* are discussed in some detail.

## INTRODUCTION

IN THE EARLY 1950s, Horace E. Wood, II, and his wife, Florence D. Wood, collected an assemblage of fossil mammals and other vertebrates from Eocene rocks in the Powder River Basin of northeastern Wyoming. Following preliminary investigation during the summers of 1938 and 1941, intensive work was carried out during 1951, 1952, and 1953 in areas around Sussex and Pumpkin buttes, near the center of the Basin (see fig. 1).

At that time, the age of the rocks in the center of the Basin was considered Wasatchian, but of uncertain position within this North American land mammal age (Wegmann, 1917; Wood et al. 1941; Brown, 1948; Love and Weitz, 1951). Fossil mammals had been recovered from the Basin, but interpretations of their affinities varied somewhat (see Jepsen, 1963, p. 676, on the history of this problem). The collection was of further importance as it represented the easternmost extent of Wasatchian age deposits then known. For a number of reasons, however, little work was done on the collection from 1953 until the present study was begun in the late 1960s: minor collections were made in 1958 and 1961 and portions of the assemblage were briefly treated by Kitts (1956) and Radinsky (1963).

In the interim between the original collecting by the Woods and the present study, Hose (1955) published on the geology of the Crazy Woman Creek area, west of the Woods' localities, and Sharp et al. (1964) discussed the region east of the Woods' major collecting areas, but included a few of their field localities. The fossil mammalian remains reported

in those papers indicated an age of Gray Bull equivalence for the enclosing sediments. In 1960, McKenna published his analysis of the Four Mile local fauna from Colorado, in which he established a standard of comparison for earliest Eocene mammals. More recently, Guthrie (1967b) reviewed the type Lysite mammals, and Jepsen (1963) reported a collection of early Eocene mammals from the Golden Valley Formation of western North Dakota, thus extending the range of Wasatchian mammals even farther eastward.

Because there has not been any detailed geologic mapping of the area in which the Woods collected, and because almost all the localities are surface or anthill sites, it is difficult to analyze stratigraphy using modern methods. Without further collection and precise correlation of stratigraphic levels, the Woods' collection would either have to be abandoned or treated as if it all came from a single, very broad, faunal "horizon." For these reasons, and on the advice of Malcolm C. McKenna, I spent a week in the Sussex region in an attempt to resolve this dilemma. Details of this work are reported below in the section on Geology. Essentially, the faunal cohesiveness of the collection and its recovery from a relatively narrow span of rocks (and thus time) indicate that the Powder River Basin assemblage is a sample drawn from a community of animals that lived together within a relatively restricted geographical and temporal region, i.e., as a paleontological local fauna. Following Wood et al. 1941, (Chart 1), I will refer to this assemblage as the Powder River local fauna.

## CONVENTIONS AND ABBREVIATIONS

In succeeding sections of the present paper, certain conventions are followed which can best be explained here. All measurements are in millimeters (mm.); in dental measurements, width (W) precedes length (L) in all cases. The widths and lengths are maximal, defined as maximum diameters perpendicular and parallel, respectively, to the major antero-posterior axis of the tooth. In addition, the dental terms "mesial" and "distal" are employed, as they have the advantage of indicating direction toward or away from the interincisive position along the arc of the tooth row. In statistical tables, the symbols N (number of specimens in the sample), OR (observed range), M (mean), SE (standard error of the mean),  $\sigma$  (standard deviation), and V (coefficient of variation,  $V = 100\sigma/M$ ) are used.

Almost 600 specimens have been identified in the Wood collections from the Powder River Basin, but of these only 105 have been assigned American Museum of Natural History catalogue numbers: four by Radinsky (1963, p. 105), and 101 by me. The majority of specimens are isolated teeth, not of great individual importance biologically. After discussion with McKenna, it was decided to assign numbers only to those specimens figured, individually measured, or described in some detail. In order not to lose the collection data, however, each uncatalogued specimen has been stored with a reference to its source locality (see list below).

## Abbreviations of institutions:

AC, Amherst College Museum, Amherst  
 AMNH, the American Museum of Natural History  
 CM, Carnegie Museum, Pittsburgh  
 PU, Princeton University Museum  
 YPM, Yale Peabody Museum, New Haven  
 UCMP, University of California Museum of Paleontology, Berkeley

## ACKNOWLEDGMENTS

The present paper is the result of a project suggested to me by Dr. Malcolm C. McKenna,

Frick Curator of the Department of Vertebrate Paleontology, the American Museum of Natural History. Dr. McKenna has supervised the work since its inception. He has read and commented upon the entire manuscript and has offered aid in the identification of specimens. I have also discussed portions of the work with Drs. Robert M. Hunt, Giles T. MacIntyre, Leslie Marcus, James McIlett, Frederick Szalay, Leigh Van Valen, and Robert M. West, and with Messrs. Edward Atkins, and Thomas Rich. Dr. Robert E. Sloan of the University of Minnesota has identified and will further discuss the allotherians.

I thank Dr. Craig C. Black, section of Vertebrate Fossils, the Carnegie Museum, Pittsburgh, Pennsylvania; Dr. Glenn L. Jepsen, curator of the Princeton University Museum, Princeton, New Jersey; Dr. Donald E. Savage, director of the University of California Museum of Paleontology, Berkeley, California; Dr. Elwyn L. Simons, associate curator of Vertebrate Paleontology in the Yale Peabody Museum, New Haven, Connecticut; and Drs. McKenna and Bobb Schaeffer of the department of Vertebrate Paleontology, the American Museum of Natural History, for allowing me access to the relevant collections in their care.

During my field work in Wyoming, I was accompanied by my wife, Roberta Marx Delson, who also assisted with curation of the Wood collection. We thank Mrs. Helen Losey of Sussex P. O., Wyoming, for much hospitality and several other local ranchers for permission to work on their property.

The research for the present paper was undertaken while I was a graduate student in the Department of Geology, Columbia University, under the tenure of National Science Foundation predoctoral graduate fellowships and traineeships, supplemented by funds of Columbia University and its Department of Geology.

All photographs were taken by the author. Scales have millimeter divisions; stereo pairs are mounted *ca.* 60 mm. apart. Figure 1 was expertly prepared by Mr. Ray Gooris.

## STRATIGRAPHIC CONSIDERATIONS

IN THE SEVERAL years of collection, 122 field localities were examined, and each given a separate reference number. Of these, two were worked in 1938, one in 1941, 59 in 1951, 37 in 1952, and 21 in 1953, all under the supervision of Dr. and Mrs. H. E. Wood, II. In addition, in 1958 one of the areas was re-examined by Dr. Sylvia Graham (then Sylvia R. Fagan), and in 1961 Dr. Leonard B. Radinsky prospected yet another locality in this region. Most of the 122 localities were anthills, flats, or dissected badlands. Material was collected by surface pickup methods, but not all the field localities produced identifiable fossil mammal remains. With the exception of four groups of localities, the Woods' original field numbers are used herein to refer to the source of measured and/or described specimens. These group localities (Reculusa Blowout, Monument Blowout, Dry Well, and Bozeman) yielded material from more or less circumscribed areas of the Powder River "field" from which came more than two-thirds of the identifiable mammal specimens, including representatives of all but five of the known Powder River species. These four named group localities are among the dozen I located and prospected during my 1969 field reconnaissance. Geographic positions of all the Woods' localities, as well as additional information on the faunal composition of the four group localities, are given below. The original locality number cards are preserved with the collection.

As noted above, relative stratigraphic, and in some cases geographic, position of many localities was not clear from Wood's notes. Previous geological investigation of the region between Sussex and Pumpkin buttes (Sharp et al. 1964, pp. 547, 550) indicated that in this part of the Basin the Eocene rocks referred to the Wasatch Formation were essentially flat-lying, with strata dipping between 20 and 100 feet per mile to the northwest. This implies that local topography is the dominant factor controlling stratigraphic position of ground-level localities and collection spots. Most of the collection was mapped on USGS quadrangle maps, so that if localities could be accurately fixed on these maps, their elevation, and thus relative stratigraphic level, could be determined.

In this manner, at least a dozen of the Woods' most productive localities were visited and geographically identified. Their elevations were measured and a tentative interpretation of the Eocene stratigraphy was devised.

The 1585 feet of Eocene "Wasatch Formation" reported by Sharp et al. (1964) is considered to have been deposited horizontally throughout the area of interest and to have suffered postdepositional deformation leading to a constant dip of 35 feet per mile due northwest. Thus, the elevation of the "Wasatch"-Fort Union contact at the north end of North Pumpkin Butte may be estimated at approximately 4400 feet (surface elevation 6039 feet, less 1585 feet of Eocene and about 60 feet of White River Oligocene; see discussion below), whereas the contact in section 26, T. 44 N., R. 78 W., at Wood's localities 51-3, 31, 32 and Hough's locality FC 3 (Sharp et al. 1964, pl. 13), lies at roughly 4200 feet (surface elevation slightly over 4500 feet, 330 feet above the contact, Sharp et al. 1964, pl. 13). These two datum points allow the determination of 35 feet per mile as the generalized dip, and in conjunction with the elevations of the named localities permit the following interpretation of their relative stratigraphic position.

Of the four named group localities, Reculusa Blowout, the most productive, is about 400 feet above the "Wasatch"-Fort Union contact. Bozeman locality appears to include rocks from 450 feet to 500 feet above the contact, whereas Dry Well includes rocks between 600 feet and 800 feet above this level. The elevation of Monument Blowout can be only roughly estimated, but it appears to be situated slightly more than 1000 feet above the presumed local contact. Several of the less productive but still important localities occur as low as 300 feet above the contact but none occurs appreciably below this level. Above the 800-foot level (aside from Monument Blowout), the only specimens recovered were some of *Haplomylus* (from localities 51-32 and 51-52), and small adaporicids (from locality 51-34), all below the 1000-foot level; in addition, there may be some *Coryphodon* from slightly higher in the section (locality 51-50, in the buttes region). As

*Haplomylus* is considered an "indicator" for the earlier Gray Bull, it thus appears that there is no appreciable change in age between the "Wasatch"-Fort Union contact and the 1000-foot level above this datum. At least 90 per cent of all fossils recovered have come from rocks between 300 and 800 feet above this horizon, and no difference in faunal elements can be determined in this span.

Before closing the geological section of this paper, it is interesting to note some additional facts about the local geobiology and to make suggestions for future investigation. All the Pumpkin Buttes have a cap-rock 30 to 80 feet thick from which fossils of Oligocene age have been collected by individuals from the U.S. Geological Survey, the U.S. National Museum, the Frick Laboratory of the American Museum of Natural History, and others. Below this cap-rock are several hundred feet of sands which are considered part of the Eocene, although Wood did not find any fossils in them. However, Jean Hough made a collection for the U.S. National Museum at a level about 150 feet below the cap-rock on Dome Butte (near North Pumpkin Butte), which is about 1400 feet above the hypothesized "Wasatch"-Fort Union contact. From these sands have come, in addition to *Phenacodus*, *Coryphodon*, and *Hyracotherium*, a single specimen attributed to *Lambdotherium* sp., an indicator of the Lost Cabin faunal zone (Sharp et al. 1964, pl. 13, FC2; Soister, 1968, p. A42). C. Lewis Gazin wrote that there may be a single specimen referable to *Heptodon* sp. in this collection (personal commun. June 24, 1969).

Information in Sharp et al. (1964; duplicated on larger-scale maps in Sharp and White, 1957) indicated that the upper part of the Eocene may be channel sands, which might respond readily both to surface collecting and, especially, to a washing technique such as that utilized by McKenna (1960). If further work is to be carried out in the Eocene of the Sussex-Pumpkin Buttes region, the controlled study of the rocks below the Buttes cap-rock should be a primary objective. Both blowout localities described should yield much more material to either a washing or quarrying operation:

the sediment is not well consolidated, and surface indications are good. Additional controlled prospecting of badland areas, particularly at the Dry Well locality, might also prove productive, especially if quarries could be developed at several different levels.

In a discussion of regional paleogeography, Soister (1968) considered the Powder River Basin Eocene sediments in terms of the Wind River Basin and Wind River Formation. During Gray Bull time, when most of the mammals described herein were living, the Casper arch was high and separated the two basins. Soister (1968, pp. A40-A42) suggested, however, that during Lysite and Lost Cabin time there was a connection between an eastward-flowing river in the Wind River Basin and a north-northwestward-flowing river in the Powder River Basin. This river system may have linked the basins while the upper part of the Eocene rocks now preserved on the Pumpkin Buttes was being deposited.

In this connection, it is to be noted that all previous workers have considered that the Eocene rocks of the Powder River Basin belong to the Wasatch Formation (see Sharp et al. 1964, pp. 546 ff.; Jepsen, 1963). Love and Weitz (1951) named the rocks, in a limited area on the flanks of the Bighorn Mountains to the northwest of the Pumpkin Buttes area, the Moncrief and Kingsbury conglomerate members of the Wasatch Formation. No other names have been proposed in the Powder River Basin. It is most doubtful that these rocks, deposited by a river flowing north from the Hartville uplift (Soister, 1968, p. A42), were derived from the same source as those of the type Wasatch, almost 300 miles to the southwest. Investigation of this problem might also be included in a further study of the region. Having offered these suggestions for future work in the Powder River Basin Eocene, I will add my opinion that it is much more important for vertebrate paleontology and for Wyoming geology in general, that detailed work be carried out first in the Bighorn Basin region, as the fossils are so much more abundant, and the type areas of Gray Bull and Clark Fork faunal concepts are situated there.

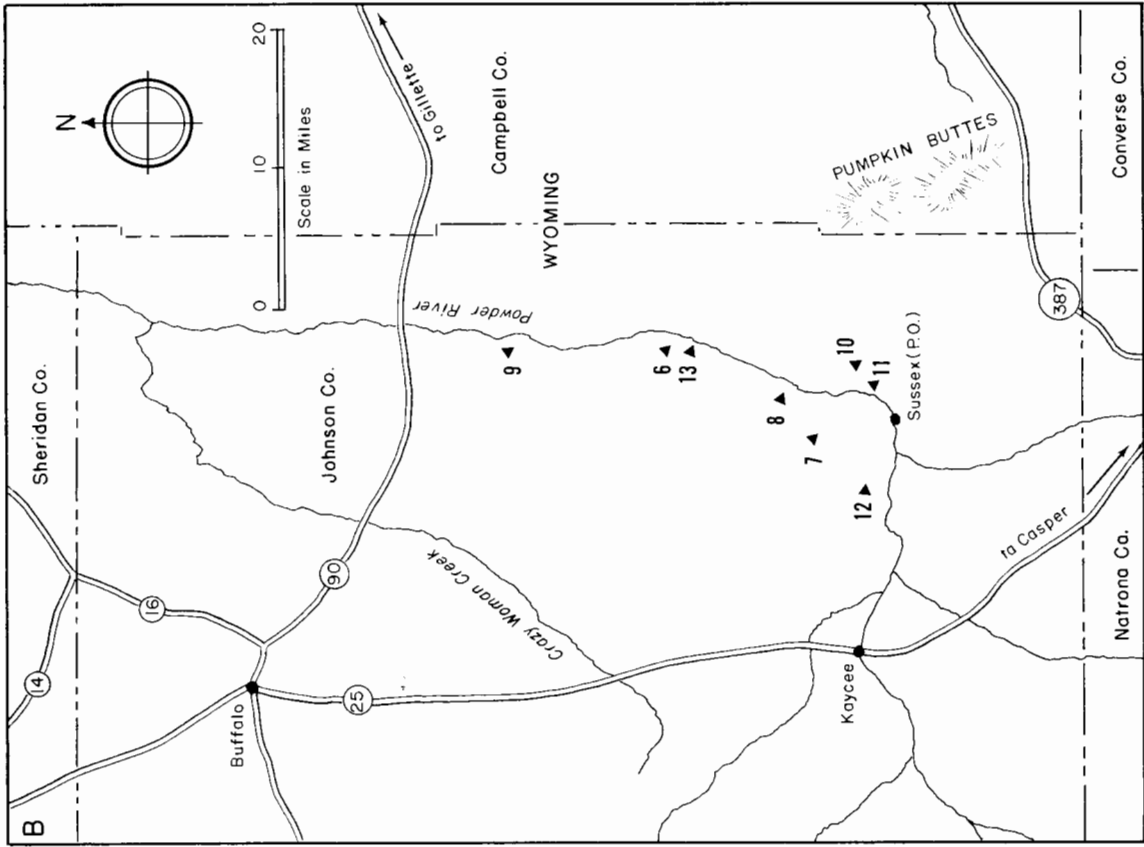
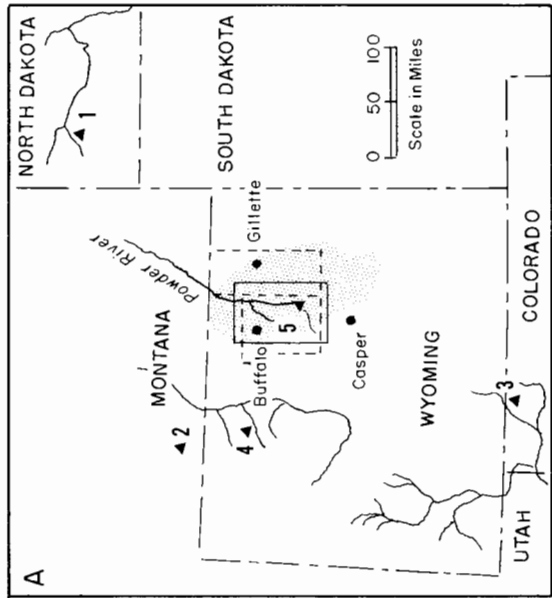


FIG. 1. A. Index map of Wyoming and neighboring states, with locations of major fossil faunas discussed in the text. 1) Golden Valley local fauna. 2) Bear Creek local fauna. 3) Four Mile local fauna. 4) Big Horn Basin local faunas (Gray Bull, Clark Fork, Sand Coulee). 5) Powder River local fauna. Hatched area indicates approximate extent of the Powder River Basin, solid rectangle outlines area enlarged in B, and dotted lines are the borders of Johnson and Campbell counties, Wyoming. B. Major collecting areas in the Powder River Basin. 6) *R. cellulosa* Blowout. 7) Dry Well locality (and neighboring localities 51-11, 51-20, 51-62). 8) Bozeman locality. 9) Monument Blowout. 10) Locality 51-3. 11) Locality 51-25. 12) Locality 52-12. 13) Locality 52-36.

## LOCALITY DATA

As noted above, 122 localities in the Powder River Basin were prospected for fossils by the Woods. They gave each locality a field number, assigned sequentially within the year of collection: e.g., 51-3 refers to the third locality collected in 1951. I have sorted these localities geographically, and all those falling inside the same surveyed section (one square mile) are treated together as a group locality. Group localities are referenced by the field number of the earliest collected field locality. Thus, 51-3, 51-31, and 51-32 all were collected in section 26, T. 44 N., R. 78 W.: the group locality is referred to as 51-3 only.

Forty-three such group or single localities have yielded identifiable remains of Eocene fossil mammals. Of these, 25 have produced one or two species; 10, from three to six species; and eight yielded seven or more. Four of these eight localities produced two-thirds of the mammal specimens among them, and I have given names to these four for easy reference (as well as abbreviations for tabular reference). For each of these four, a specimen count has been made by taxon, and an estimate has been made of the minimum number of individuals necessary to produce these specimens. The estimates are based solely on the number of teeth and jaws, taking into consideration size, wear, and tooth homology. These data are presented in table 1.

The specific locality data that follow are presented as an aid to future researchers in relocation of all fossiliferous localities, and in study of the Wood collection. The numbers of sterile field localities are not included, and those of field localities subsumed into named group localities are not listed in the section of "numbered localities." For the 39 unnamed single or group localities, a list of genera (when monotypic in this fauna) or species present is given.

## NAMED LOCALITIES

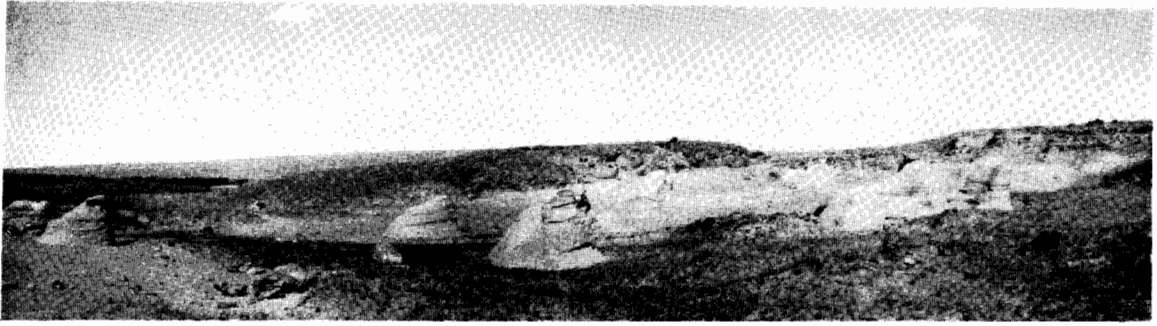
Reculusa Blowout (Rec.) so named because

it is situated on the F. Reculusa ranch, Sussex, Wyoming. Center, NE $\frac{1}{4}$ , sect. 2, T. 45 N., R. 78 W., Hoc Ranch quadrangle, Johnson County, Wyoming; surface elevation approximately 4400 feet; map four, Johnson County, general highway map, Wyoming Highway Dept. This sand blowout, about 50 feet in radius, is situated 23.1 miles north of Sussex on Fort Reno road; lying about 0.25 mile east of the road on dirt track beginning about 0.15 mile south of Irigaray Ranch cattle-guard. Other blowouts that might yield fossils may be found nearer the road. This locality was by far the most productive, yielding representatives of almost all taxa. It includes field localities 53-3, 9, 10, 13, 14, 16, 17, 20, and 22. See figure 2A, B.

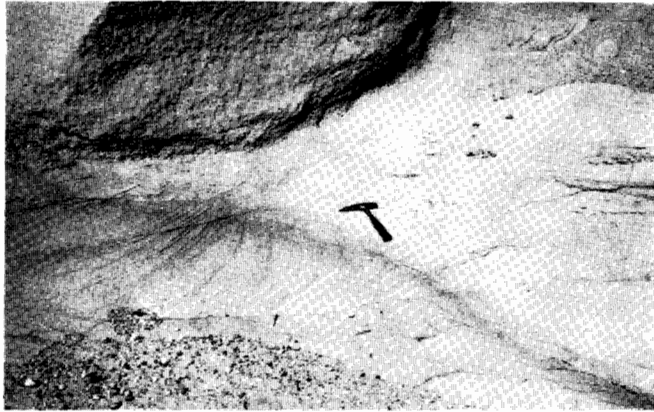
Dry Well locality (Dry), lying 1 mile south of a dry oil well from which it got its name, one of the first drilled in the now-productive Sussex region. Center, sect. 15, T. 44 N., R. 79 W., Soldier Creek quadrangle, Johnson County, Wyoming; elevation 7600 feet to 7800 feet in drainage system northeast of Fourmile Creek/Soldier Creek divide, draining into Soldier; map four, Johnson County, general highway map, Wyoming Highway Dept. Proceeding north on Fort Reno road out of Sussex, turn east 5.75 miles north of road junction with Sussex-Kaycee road (Wyoming 1002), passing Palmer Reservoir; proceed past corner marker (sects. 7, 12, 13, 18), 4.6 miles from Fort Reno road to fence and "T"-shaped road intersection; locality up small hill to north and down canyons beyond. Includes field localities 51-4, 5, 6, 7, 8, 41, 42, 43, 59, 60, 61; 52-25, 26, 27; and 53-2. See figure 3.

Bozeman locality (Boz.) so named because it lies just off old Bozeman Pioneer trail. NE corner, sect. 1, T. 44 N., R. 79 W., Soldier Creek quadrangle, Johnson County, Wyoming; elevation approx. 4500  $\pm$  50 feet; map four, Johnson County, general highway map, Wyoming Highway Dept. Proceeding 8.7 miles

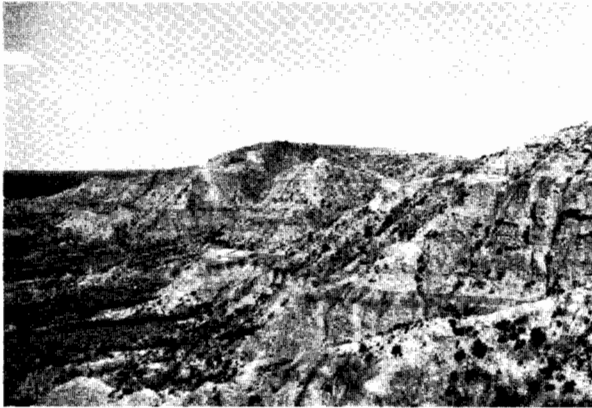
FIG. 2-5. 2. A. Panoramic view southwest across part of Reculusa Blowout; the mounds of cross-bedded channel sandstone are 3 to 4 feet high. B. Cross-bedded sands *in situ* and lag concentrate at Reculusa Blowout, geology hammer for scale. 3. View northeast of dissected variegated mudstone badland rim of Dry Well locality. 4. The cross-bedded channel sandstone "monuments" and brown concretions of Monument Blowout, geology hammer for scale. 5. View east of Monument Blowout from road.



2A



2B



3



4



5

north of Sussex on Fort Reno road, turn northwest to Bozeman trail; about 1.3 miles beyond are light-colored flats northeast of road, and 0.4 mile beyond that are badlands 25–50 yards southwest of road; both areas were productive for Wood. Includes field localities 51–9, 10, 14, 15, 16, 17, 26, 27; 52–1, 2, 3, 4, 5, 6; and 58–223.

Monument Blowout (Mon.), named by Wood because of high sand columns in center. NE $\frac{1}{4}$  (possibly), SE $\frac{1}{4}$ , sect. 14, T. 48 N., R. 78 W., Johnson County, Wyoming; elevation approx. 1050  $\pm$  50 feet, no topographic quadrangle map as yet; map one, Johnson County, general highway map, Wyoming Highway Dept. Take Schoonover road turnoff from US 90 between Gillette and Buffalo, Wyoming; 11.1 miles along main artery south, then eastward to series of sand blowouts south and east of road; most distant one is Monument; 5.1 miles beyond is Schoonover bridge across the Powder River. Includes field localities 53–19 and 21. See figures 4 and 5.

#### NUMBERED LOCALITIES

- 38–39; sect. 25, T. 44 N., R. 76 W.; *Coryphodon*.  
 38–41; sect. 28, T. 43 N., R. 78 W.; includes 41–33; "*Chriacus*," *Ectocion*, *Diacodexis*, and *Microsyops*.  
 41–33; see 38–41.  
 51–1; sect. 29, T. 43 N., R. 78 W.; includes 51–2; *Coryphodon*.  
 51–2; see 51–1.  
 51–3; sect. 26, T. 44 N., R. 78 W.; includes 51–31, 32; and Hough's FC 3 (see pp. 311–312); elevation 4500 feet, about 300+ feet above base of Eocene; rodent incisors, *Arfia*, *Coryphodon*, *Hyracotherium*, and *Pelycodus*.  
 51–11; sect. 22, T. 44 N., R. 79 W.; includes 51–12, 13; *Diacodexis*, *Arfia*, *Coryphodon*, *Hyracotherium*, *Microsyops*, and *Pelycodus*.  
 51–12; see 51–11.  
 51–13; see 51–11.  
 51–18; sect. 13, T. 44 N., R. 79 W.; includes 51–44, 45; *Didelphodus*, *Microsyops*, *Pelycodus*, rodent incisors, and *Haplomytus*.  
 51–19; sect. 23, T. 44 N., R. 79 W.; *Arfia* and *Hyopsodus*.  
 51–20; sect. 10, T. 44 N., R. 79 W., less-developed badland area to north of Dry Well locality, reached by continuing on same road around to northwest; includes 51–21, 22, 23, and 24; *Haplomytus*, *Hyopsodus*, *Apheliscus*, *Esthonyx*, *Ectocion*, *Diacodexis*, cf. "*Leptacodon*" *jepseni*, *Coryphodon*, *Hyracotherium*, and *Microsyops*.  
 51–21; see 51–20.  
 51–22; see 51–20.  
 51–23; see 51–20.  
 51–24; see 51–20.  
 51–25; sect. 4, T. 43 N., R. 78 W., continuous to south with sect. 9 and to north with sect. 33, T. 44 N., R. 78 W. (51–30), in central and eastern thirds, and also to east into western third of sect. 3, T. 43 N., R. 79 W. (61–1); House Creek quadrangle, Johnson County, Wyoming; badland rim draining into west side of Powder River; elevation 4400–4600 feet; map four, Johnson County, general highway map, Wyoming Highway Dept. Proceeding east of Sussex toward Linch 4.5 miles, turn north on road along heads of gullies on divide; drop down to west at several points. Area fauna includes: *Haplomytus*, *Hyopsodus*, rodent incisors, *Pelycodus*, *Microsyops*, *Prolimnocyon*, *Didelphodus*, *Palaeictops*, *Palaeoryctes*, and cf. "*Leptacodon*" *jepseni*.  
 51–30; see 51–25.  
 51–31; see 51–3.  
 51–32; see 51–3.  
 51–33; sect. 28, T. 44 N., R. 78 W.; *Apheliscus*, rodent incisors, undetermined miacine.  
 51–34; sect. 20, T. 44 N., R. 78 W.; *Phenacodus primaevus* and *Hyracotherium*.  
 51–35; sect. 11, T. 44 N., R. 78 W.; *Haplomytus*, *Hyopsodus*, rodent incisors, *Diacodexis*, and *Pelycodus*.  
 51–37; sect. 15, T. 44 N., R. 77 W.; includes 52–19; *Hyopsodus*.  
 51–38; sect. 23, T. 44 N., R. 77 W.; *Apheliscus*.  
 51–44; see 51–18.  
 51–45; see 51–18.  
 51–46; sect. 24, T. 44 N., R. 79 W.; *Hyopsodus*.  
 51–48; sect. 4, T. 43 N., R. 79 W.; *Diacodexis*.  
 51–49; sect. 11, T. 44 N., R. 76 W.; includes 51–50, 51, and 52; *Coryphodon* and *Haplomytus*.  
 51–50; see 51–49.  
 51–51; see 51–49.  
 51–52; see 51–49.  
 51–53; sect. 33, T. 44 N., R. 75 W.; *Haplomytus*.  
 51–58; sect. 24, T. 43 N., R. 79 W.; *Apheliscus*, rodent incisors.  
 51–62; sect. 15, T. 44 N., R. 79 W.; listed as sect. 15, but as this is area of Dry Well locality (mistakenly listed by Wood as sect. 14), 51–62 may in fact be in sect. 16 or sect.

- 10 with 51-25, or continuous with either previously collected locality (see 51-25, Dry Well); *Haplomylus*, *Hyopsodus*, *Apheliscus*, *Paramys* (small), rodent incisors (larger), *Diacodexis*, *Microsypops*, and *Pelycodus*.
- 52-7; sect. 19, T. 43 N., R. 78 W.; *Diacodexis*.
- 52-9; sect. 17, T. 43 N., R. 78 W.; rodent incisor.
- 52-10; sect. 30, T. 45 N., R. 79 W.; *Pelycodus*.
- 52-11; sect. 19, T. 45 N., R. 79 W.; *Coryphodon*.
- 52-12; sect. 5, T. 43 N., R. 79 W.; same section as 52-13, 14, and 15; 52-12 reached from Kaycee road, 5.5 miles west of Sussex, turn north opposite gate to Matthews Ranch, drive 0.85 mile on dirt trail to fence; on other side proceed to gully with 100-foot-high north face, elevation about 4600-4700 feet, Sussex quadrangle; 52-13, 14, and 15 can be reached from long, circuitous trail beginning 1.8 miles farther west on Kaycee road, 0.1 mile east of Indart gate, not reached, elevation about 4600-4700 feet, Figure 8 Reservoir quadrangle; both map four, Johnson County, general highway map, Wyoming Highway Dept. Area fauna includes: *Haplomylus*, *Hyopsodus*, "*Chriacus*," *Paramys* (larger), cf. *Diacodon*, *Coryphodon*, and *Hyracotherium*.
- 52-13; see 52-12.
- 52-14; see 52-12.
- 52-15; see 52-12.
- 52-16; sect. 15, T. 43 N., R. 80 W.; rodent incisor.
- 52-18; sect. 22, T. 43 N., R. 78 W.; *Coryphodon*.
- 52-19; see 51-37.
- 52-20; sect. 34, T. 45 N., R. 77 W.; includes 52-21; *Haplomylus*, *Hyopsodus*, rodent incisors, *Tetonijs musculus*, and *Pelycodus*.
- 52-21; see 52-20.
- 52-31; sect. 15, T. 45 N., R. 79 W.; *Haplomylus*, *Coryphodon*.
- 52-32; sect. 30, T. 47 N., R. 78 W. or sect. 25, T. 47 N., R. 79 W., exact location uncertain; includes 52-34; *Haplomylus*, cf. "*Leptacodon*" *jepseni*, and cf. *Leptacodon* sp.
- 52-34; see 52-32.
- 52-36; NE $\frac{1}{4}$ , NW $\frac{1}{4}$ , sect. 14, and SE $\frac{1}{4}$ , SW $\frac{1}{4}$ , sect. 11, T. 45 N., R. 78 W.; badland rim on north bank of east-west meander of Powder River, reached by Fort Reno road 16 miles north of Sussex (4.5 miles past Fort Reno site, 1.3 past Reculosa ranch road), turn off on dirt track to northeast; at top of rise is Bureau of Reclamation marker "BM 1950 PRU59," elevation 4300 feet; Hoe Ranch quadrangle (and Fort Reno quadrangle); map four, Johnson County, general highway map, Wyoming Highway Dept., *Apatemys*, *Haplomylus*, *Hyopsodus*, rodent incisors, *Diacodexis*, and *Pelycodus*.
- 52-37; sect. 35, T. 46 N., R. 78 W.; *Haplomylus*, rodent incisors, *Diacodexis*, and *Tetonijs musculus*.
- 52-38; sect. 23, T. 46 N., R. 78 W.; *Hyopsodus*.
- 53-4; sect. 14, T. 46 N., R. 78 W.; *Hyopsodus*.
- 53-5; sect. 11, T. 46 N., R. 78 W.; *Diacodexis*.
- 53-7; sect. 10, T. 45 N., R. 79 W.; *Hyopsodus*.
- 53-11; sect. 15, T. 46 N., R. 78 W.; rodent incisor.
- 53-12; sect. 17, T. 46 N., R. 78 W.; *Pelycodus*.
- 61-1; NW $\frac{1}{4}$ , sect. 3, T. 43 N., R. 78 W.; House Creek quadrangle, elevation about 4700 feet; locality found by L. Radinsky, specimens in Yale Peabody Museum collection, only cf. "*Leptacodon*" *jepseni* seen by the author.

#### FAUNAL LIST AND CORRELATION OF THE POWDER RIVER LOCAL FAUNA

The presence in the Powder River local fauna of perissodactyls, artiodactyls, and certain primates and deltatheridians (as used here, see pp. 322, 329) indicates a post-Paleocene age for the assemblage. On the other hand, the occurrence of multituberculates and abundant condylarths, and the stage of evolution of some other species, points to Paleocene affinities. Of the several well-described faunal assemblages of late Paleocene through early Eocene age, the Powder River local fauna shows by

far the greatest resemblance to that from Four Mile Creek, Colorado (McKenna, 1960), perhaps the earliest Eocene local fauna now known in North America. In order to show close similarity, the faunal list from Powder River will be compared with a revised and updated one from Four Mile (table 1).

Several invertebrates, numerous lower vertebrates, and at least 41 species of mammals are present in the Powder River local fauna, as now known. Only the mammals have been

TABLE 1  
 COMPARATIVE FAUNAL LISTS FROM THE POWDER RIVER AND FOUR MILE LOCAL FAUNAS  
 WITH RELATIVE SPECIES ABUNDANCES FROM POWDER RIVER  
 (Fraction numerator is number of specimens; denominator is estimated minimum number of individuals.)

	Powder River Named Localities				Powder River Totals	Four Mile Local Fauna
	Reclusa	Dry Well	Bozeman	Monument		
Order Multituberculata						
Family Eucosmodontidae						
<i>Neoliotomus ultimus</i> Granger and Simpson, 1928	—	—	1/1	—	1/1	X <sup>a</sup>
Family Ptilodontidae						
<i>Prochetodon</i> cf. <i>cavus</i>	—	—	—	—	—	X
Family Ectypodontidae						
<i>Parectypodus</i> sp. (Sloan)	—	1/1	—	—	1/1	X
<i>Ectypodus tardus</i>	—	—	—	—	—	X
<i>Neoplagiaulax</i> sp. n., cf. <i>N. hazeni</i>	—	—	—	—	—	X
Order Marsupicarnivora						
Family Didelphidae						
<i>Peratherium comstocki</i> Cope, 1884	1/1	—	—	—	1/1	cf. <sup>b</sup>
<i>Peradectes protinnominatus</i>	—	—	—	—	—	X
New genus and species	—	—	—	—	—	X <sup>c</sup>
Order Insectivora						
Family Palaeoryctidae						
<i>Didelphodus absarokae</i> (Cope, 1881b)	2/1	—	—	1/1	6/5	X
<i>Palaeoryctes</i> cf. <i>punctatus</i> Van Valen, 1965	—	—	—	—	1/1	—
Family Leptictidae						
Cf. <i>Diacodon</i> sp.	—	—	—	—	1/1	—
<i>Palaeictops tauricinerei</i> (Jepsen, 1930a)	1/1	3/1	—	—	5/3	cf.
Undescribed genus and species cf. <i>Tupaia</i>	—	—	—	—	—	X
Family Pantolestidae						
<i>Palaeosinopa didelphoides</i> (Cope, 1881a)	3/1	1/1	—	—	4/2	X
<i>Palaeosinopa</i> cf. <i>lutreola</i> Matthew, 1918	1/1	1/1	—	—	2/2	—
Cf. <i>Palaeosinopa</i> sp.	1/1	—	—	—	1/1	—
Small pantolestine genus and species	—	—	—	—	—	X
Family Apatemyidae						
<i>Apatemys</i> cf. <i>chardini</i> (Jepsen, 1930a)	—	—	—	—	1/1	—
<i>Apatemys</i> cf. <i>kayi</i>	—	—	—	—	—	X
<i>Apatemys whitakeri</i>	—	—	—	—	—	X <sup>d</sup>
Family Adapisoricidae						
“ <i>Leptacodon</i> ” <i>jepseni</i> McKenna, 1960	—	—	—	—	4/4 (cf.)	X
Cf. <i>Leptacodon</i> sp.	—	—	2/1	—	3/2	—
“Cf. <i>Metacodon</i> ”	—	—	—	—	—	X
<i>Entomolestes</i> cf. <i>nitens</i> Matthew, 1918	1/1	—	1/1	—	2/2	X
“ <i>Nyctitherium</i> ” sp.	—	—	—	—	—	X
Order Deltatheridia						
Family Hyaenodontidae						
<i>Arfia shoshoniensis</i> (Matthew, 1915a)	4/4	1/1	—	—	8/6	cf. <sup>e</sup>

Table 1—Continued

	Powder River Named Localities				Powder River Totals	Four Mile Local Fauna
	Reclusa	Dry Well	Bozeman	Monument		
<i>?Paeneprolimnocyon mordax</i> (Matthew, 1915a)	—	—	1/1	—	1/1	—
<i>?Protomus</i> sp.	—	—	—	—	—	X
<i>Prolimnocyon atavus</i> Matthew, 1915a	1/1	1/1	1/1	—	4/4	X <sup>f</sup>
Family Oxyaenidae						
<i>Oxyaena</i> sp.	—	—	—	—	—	X
Order Primates						
Family Paromomyidae						
<i>Phenacolemur praecox</i> Matthew, 1915c	5/1	2/1	4/2	—	11/4	X <sup>g</sup>
<i>Phenacolemur</i> sp., small	—	—	1/1	—	1/1	? <sup>g</sup>
Family Anaptomorphidae						
<i>Tetomys homunculus</i> (Cope, 1882a)	1/1	—	1/1	—	2/2	X
<i>Tetomys musculus</i> Matthew, 1915c	—	—	—	1/1	3/3	X
<i>Trogolemur</i> sp.	—	—	—	—	—	X
Family Microsypodidae						
<i>Microsypops wilsoni</i> Szalay, 1969a	5/1	10/2	3/2	—	30/?	X
<i>Microsypops alfi</i>	—	—	—	—	—	X
<i>Niptomomys doreenae</i>	—	—	—	—	—	X <sup>h</sup>
Family Notharctidae						
<i>Pelycodus ralstoni</i> Matthew, 1915c	13/2	8/3	1/1	—	43/?	X
Order Rodentia						
Family Ischyromyidae						
Cf. <i>Paramys atavus</i> Jepsen, 1937	—	—	—	1/1	1/1	—
Small-sized species of <i>?Paramys</i>	2/1	2/1	—	—	5/3	—
Medium-sized species of <i>Paramys</i>	4/2	—	1/1	—	6/4	—
<i>Paramys</i> sp. A, cf. <i>P. copei</i>	—	—	—	—	—	X <sup>i</sup>
<i>Paramys</i> sp. B, cf. <i>P. copei</i>	—	—	—	—	—	X
<i>Paramys</i> , undescribed species	—	—	—	—	—	X
Undescribed genus and species of <i>?Paramyinae</i>	—	—	—	—	—	X
Several additional new forms under study	—	—	—	—	—	X
Order Carnivora						
Family Miacidae						
Indeterminate genus and species of miacine	—	—	—	—	1/1	X <sup>j</sup>
<i>Miacis exiguus</i>	—	—	—	—	—	X
Cf. <i>Oodectes</i> sp.	—	—	—	—	—	X <sup>k</sup>
<i>Didymictis protenus</i> (Cope, 1874)	1/1	—	—	—	3/3	X
<i>Viverravus acutus</i>	—	—	—	—	—	X <sup>l</sup>
<i>Uintacyon</i> sp.	—	—	—	—	—	X <sup>m</sup>
Order Condylarthra						
Family Arctocyonidae						
" <i>Chriacus</i> " <i>gallinae</i> Matthew, 1915a	—	—	—	—	2/2(cf.)	X
<i>Thryptacodon antiquus</i>	—	—	—	—	—	X
Family Phenacodontidae						
<i>Phenacodus primaevus</i> Cope, 1875	1/1	4/1	—	—	7/3	X <sup>n</sup>
<i>Phenacodus brachyptermus</i> Cope, 1882a	3/1	1/1	—	—	5/3	X

Table 1—Continued

	Powder River Named Localities				Powder River Totals	Four Mile Local Fauna
	Reclusa	Dry Well	Bozeman	Monument		
<i>Phenacodus vortmani</i> (Cope, 1880)	2/1	—	1/1	—	3/2	X <sup>o</sup>
<i>Phenacodus</i> sp.	—	—	—	—	—	X
<i>Ectocion osbornianus</i> Cope, 1882a	4/1	1/1	6/2	—	14/6	X
Family Hyopsodontidae						
<i>Haplomyilus speirianus</i> (Cope, 1880b)	23/8	19/5	4/3	1/1	78/?	X
<i>Hyopsodus</i> "miticulus" (Cope, 1874)	65/9	25/5	13/5	7/4	167/?	X <sup>p</sup>
<i>Apheliscus nitidus</i> Simpson, 1937	2/1	1/1	1/1	—	9/8	X
Family Mesonychidae						
<i>Pachyaena ?ossifraga</i>	—	—	—	—	—	X
Family Anchippodontidae						
<i>Esthonyx bisulcatus</i> Cope, 1874	1/1	1/1	—	—	6/3	X
Order Pantodonta						
Family Coryphodontidae						
<i>Coryphodon</i> sp.	1/1	—	5/1	—	19/?	X <sup>j</sup>
<i>Coryphodon ?lobatus</i>	—	—	—	—	—	X
Order Perissodactyla						
Family Equidae						
<i>Hyracotherium angustidens</i> (Cope, 1875a)	58/9	13/3	9/3	4/1	90/25	X
Family Isectolophidae						
<i>Homogalax protapirinus</i> (Wortman, 1896)	6/2	—	—	6/1	12/3	cf.
Order Artiodactyla						
Family Dichobunidae						
<i>Diacodexis metisiacus</i> (Cope, 1882a)	12/6	7/2	4/2	—	35/?	X
<i>Wasatchia</i> sp.	—	—	—	—	—	X
Totals	$\frac{225}{60}$	$\frac{102}{33}$	$\frac{59}{31}$	$\frac{21}{10}$	599	

<sup>a</sup> All information on multituberculates interpolated from Van Valen and Sloan, 1966, pp. 269–270, figures 4 and 5.

<sup>b</sup> See Van Valen, 1966, p. 24; was *Didelphodus ventanus*.

<sup>c</sup> Identified in 1960 as a new genus of didelphodontine by McKenna (personal commun.).

<sup>d</sup> See p. 327 below.

<sup>e</sup> Preliminary identification by MacIntyre from the American Museum collections.

<sup>f</sup> See Van Valen, 1966, p. 70.

<sup>g</sup> See pp. 334 ff. below.

<sup>h</sup> See Szalay, 1969b, p. 28; includes *Niptomomys* sp.

<sup>i</sup> It is quite possible that the medium-sized species from Powder River is the same as sp. A from Four Mile; see p. 341 below.

<sup>j</sup> It is doubtful that we are dealing with the same species in both assemblages.

<sup>k</sup> See Van Valen, 1966, p. 24; was *Didelphodus ventanus*.

<sup>l</sup> MacIntyre (personal commun.) recognized this form as a probably new, small species of *Viverravus*; he will describe it as such in due course.

<sup>m</sup> See Van Valen, 1969b, p. 124, no documentation or specimen number mentioned. MacIntyre (personal commun.) will describe this species also; it is possibly related to the undetermined miacine from Four Mile.

<sup>n</sup> Includes *Phenacodus intermedius*; Robert M. West (personal commun.).

<sup>o</sup> Was identified by McKenna as *Phenacodus matthewi*; see p. 345 below.

<sup>p</sup> Includes *Hyopsodus loomisi*; both species are present in both local faunas, if two are recognized; see pp. 350–351 below.

studied in detail. As noted above, numbers of specimens of each species are given for the four named localities and for the total of all productive localities (as fraction numerator shows). In most cases, minimum numbers of individuals are given also (as the fraction denominator shows). All Four Mile species are as listed by McKenna (1960); additions or changes are referenced.

It will be immediately obvious from table 1 that almost all the Powder River species are represented at Four Mile, either precisely or by quite similar forms. Only four Powder River taxa, *Palaoryctes* cf. *punctatus*, cf. *Diacodon* sp., *?Paeneprolimnocyon mordax*, and cf. *Paramys atavus*, do not have close relatives in the Colorado faunule. Of these, the first is known otherwise from a single specimen of latest Paleocene or earliest Eocene age from the Bighorn Basin; the leptictid is uncertainly referred to a genus found rarely in Gray Bull beds of the Bighorn Basin and more commonly in the San Jose Formation of New Mexico; *P. mordax* is known only from two other fragmentary specimens of earliest Eocene age from the Bighorn Basin; and *Paramys atavus* is otherwise represented only in the latest Paleocene deposits from Bear Creek, Montana. All the taxa which McKenna (1960, p. 33) noted as significantly absent from Four Mile are absent also from the Powder River assemblage. The only difference of major interest is the extreme scarcity in the Wood collection of carnivorous mammals (Carnivora, mesonychid condylarths, and most large deltatheridians), both in number of taxa present and number of specimens per taxon. This difference, and the general scarcity of larger mammals, is most probably owing to the bias

in sampling: ants carry small teeth to build their hills, and sand blowouts normally sort small and medium-sized fragments. Large specimens are more common in quarries, of which none was developed by the Woods.

In addition to Four Mile, two other well-known local faunas are closely similar to Powder River. The faunas of the Willwood Formation of the Bighorn Basin, and the associated faunas of the Clark Fork Basin (both northwestern Wyoming) have been most recently reviewed by McKenna (1960) and R. Wood (1967). The Sand Coulee local fauna of the Bighorn and Clark Fork basins, also termed the early Gray Bull (see Jepsen, 1930b, p. 119; Simpson, 1937, p. 1; van Houten, 1945, p. 426), shares many species with the Four Mile and Powder River local faunas. Both stratigraphically and faunistically the Sand Coulee local fauna is much less well understood, but the large collections offer material for many of the comparisons made in the present paper.

The Bear Creek local fauna of southwestern Montana was first reported by Simpson (1928a) and most recently discussed by Van Valen and Sloan (1966). It now appears to be of quite late Paleocene age. During the course of research for this paper, I examined all specimens from Bear Creek in the Carnegie Museum, Princeton University Museum, and the American Museum of Natural History collections, and some comments on certain of these specimens will be found in the systematic section below.

I conclude that the rocks producing the Powder River local fauna are of earliest Eocene age. They share this age with the faunal assemblages from Four Mile and perhaps Sand Coulee (early Gray Bull).

## SYSTEMATICS

CLASS MAMMALIA

SUBCLASS ALLOThERIA

ORDER MULTITUBERCULATA

SUPERFAMILY TAENIOLABIDOIDEA  
GRANGER AND SIMPSON, 1929

FAMILY EUCOSMODONTIDAE JEPSEN, 1940

*NEOLIOTOMUS* GRANGER AND SIMPSON, 1928

*Neoliotomus ultimus* Granger and Simpson,  
1928

THE PRESENCE of a eucosmodontid multituberculate is indicated by AMNH 56305, an edentulous mandible fragment from the Bozeman locality. Behind the root of the peglike  $P_3$  typical of the genus, are three roots which R. E. Sloan has determined as being anterior and posterior roots of  $P_4$ , as well as a central accessory root. Thus, total  $P_4$  length is about 9 mm. at the alveoli, which could indicate about 11 mm. when complete. The length given for the type of *N. ultimus* is 11.4 mm. As expected, incisor size (depth 5.3 mm., width 2.3 mm.) is slightly smaller than that given for *N. conventus* ( $6.4 \times 2.5$  mm., Jepsen, 1930a). I accept and here register Sloan's identification.

SUPERFAMILY PTILODONTOIDEA  
GREGORY AND SIMPSON, 1926

FAMILY ECTYPODONTIDAE  
SLOAN AND VAN VALEN, 1965

*PARECTYPODUS* JEPSEN, 1930a

A single, isolated  $P_4$  has been identified by Sloan as belonging to a new species otherwise known from the Four Mile (East Alheit Pocket) and Mutigny local faunas (Russel, Louis, and Savage, 1967). The tooth, AMNH 56306, from Dry Well locality, measures  $0.4 \times 3.6$  mm. and shows 12 serrations. It is very heavily worn, and Sloan believes it may have belonged to an old individual.

SUBCLASS THERIA

INFRACLASS METATHERIA

ORDER MARSUPICARNIVORA

SUPERFAMILY DIDELPHOIDEA GRAY, 1821

FAMILY DIDELPHIDAE GRAY, 1821

SUBFAMILY DIDELPHINAE GRAY, 1821

*PERATHERIUM* AYMARD, 1850

*Peratherium comstocki* Cope, 1884

Figure 6

The sole marsupial specimen in the Wood collection, AMNH 56307, is one of the few from any early Eocene locality. As McGrew (1959, p. 148) has noted, size is about the only criterion for separating lower dentitions of Eocene didelphids. The morphology of the molars is rather stable, to say the least. The present specimen, an  $M_4$ , is quite fresh, although the metaconid is broken away, and the few differences it shows from the type of *P. comstocki* ( $M_{2-3}$ ) may be interpreted as those between  $M_4$  and more anterior teeth. These differences are basically in the talonid and include reduction of the entoconid, labial shifting of the hypoconulid, and conversion of this cusp into a subconical peak rather than a backward-tilting ridge.

Because the type of *P. comstocki*, AMNH 4252, has never been adequately figured, I compare it with the new specimen here. In addition, AMNH 4253, also apparently from the Gray Bull of the Bighorn Basin (cf. Simpson, 1928b, p. 5; 1968, p. 2), was referred to this species by Cope (1884). It is of the size of the type specimen but badly damaged, all of the lingual cusps being shorn off. This specimen may well represent *P. comstocki*, but could almost as easily be a small insectivore.

MEASUREMENTS: AMNH 4252, type:  $M_2$ ,  $1.90 \times 3.15$  mm.;  $M_3$ ,  $1.70 \times 3.25$  mm.; AMNH 4253,  $M_1$ ,  $1.9 \times 3.1$  mm.; AMNH 56307,  $M_4$ ,  $1.80 \times 3.25$  mm. (Reclusa Blowout).

INFRACLASS EUTHERIA

ORDER INSECTIVORA

SUBORDER PROTEUTHERIA

SUPERFAMILY PALAEOORYCTOIDEA WINGE,  
1917

Szalay (1968b, p. 2) has argued for the removal of palaeoryctids from Deltatheridia

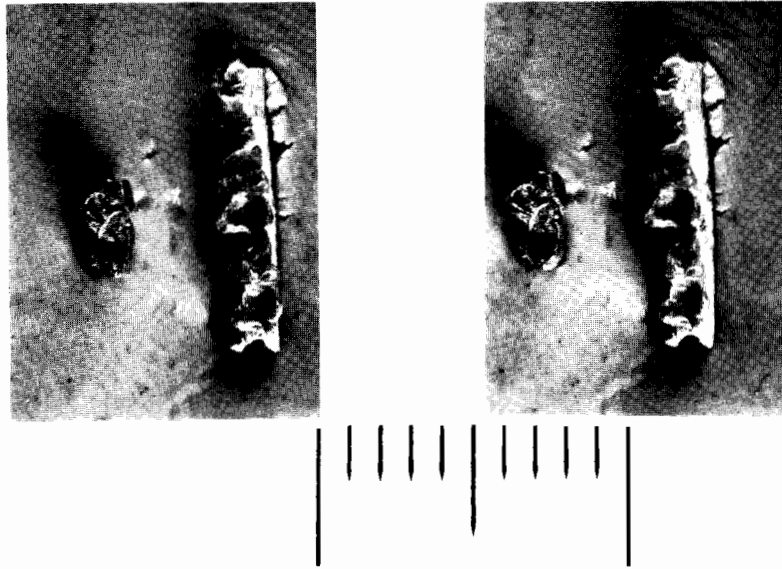


FIG. 6. *Peratherium comstocki*. Left, AMNH 56307,  $M_4$  from Reculosa Blowout, Powder River local fauna; right, AMNH 4252, type,  $M_{2-3}$ , ?Gray Bull of the Bighorn Basin.

to Insectivora on the grounds of their apparent central position in the early evolution of Eutheria. This position is tenable on the basis of recently acquired, but mostly unpublished, knowledge about the radiation of "insectivores" and other Late Cretaceous eutherians. From the standpoint of taxonomic philosophy, it would then be necessary to include within the suborder Proteutheria the "stem placental" and those animals not subordinally distinct therefrom.

FAMILY PALAEORYCTIDAE WINGE, 1917

SUBFAMILY DIDELPHODONTINEA MATTHEW, 1918

*DIDELPHODUS* COPE, 1882b

*Didelphodus absarokae* (Cope, 1881b)

This species has been reviewed by Van Valen (1966, p. 17), who gave extensive metrical data. Measurement of Van Valen's specimens shows that we obtain closely similar results, usually within 0.1 mm. Six isolated teeth from five Powder River Basin localities are identified as from this species. They show some differences in size from Van Valen's specimens, but none is significant enough to indicate a doubtful reference. The measure-

ments are given in table 2 and are those of Van Valen (1966, pp. 18 ff.).

SUBFAMILY PALAEORYCTINAE WINGE, 1917

*PALAEORYCTES* MATTHEW, 1913

*Palaoryctes* cf. *punctatus* Van Valen, 1966

A single upper molar, AMNH 56308, from locality 51-25, complements our previous knowledge of early Eocene palaeoryctines. The tooth is somewhat damaged labially, but otherwise complete and little worn. The protocone is high and labially convex; the metacone is much smaller than the paracone, and situated on the side of that cusp. There is little or no cingulum development, except on the damaged labial portion. The Powder River tooth, probably an  $M^3$ , is comparable in size to  $M^{1-2}$  of the type of *P. punctatus*. The latter specimen, AMNH 15850, was said by Van Valen to be of Clark Fork age. It is from the head of Big Sand Coulee, type locality of the Sand Coulee (=early Gray Bull) of the Clark Fork Basin. Therefore, both specimens are of closely similar age. As there is little difference in comparable morphology, the Powder River specimen is referred to the already described species.

TABLE 2  
MEASUREMENTS (IN MILLIMETERS) OF TEETH OF *Didelphodus absarokae*  
FROM THE POWDER RIVER LOCAL FAUNA

	M <sub>2</sub> 51-28 AMNH 56167	M <sub>1</sub> 51-18 AMNH 56166	M <sub>1</sub> Rec. AMNH 56165	M <sup>2</sup> Rec. AMNH 56164	?M <sup>2</sup> Mon. AMNH 56163	M <sup>3</sup> Dry AMNH 56162
Trigonid width	2.95	2.55	3.40	—	—	—
Crown length	3.85	4.15	4.90	—	—	—
Anterior margin	—	—	—	5.50	4.65	3.90
Posterior margin	—	—	—	4.65	4.30	3.55
Labial margin	—	—	—	3.00	3.15	2.50
Length at paraconule	—	—	—	2.10	2.00	—

*Symbols:* 51-28, 51-18, Rec., Mon., and Dry are localities.

MEASUREMENTS: AMNH 56308, maximum width 2.5 mm; width, apexes of paracone and protocone, 1.3 mm.; length at labial border, approximately 1.5 mm. By comparison, AMNH 15850 measures in labial length: M<sup>1</sup>, 1.95 mm.; M<sup>2</sup>, 1.70 mm. Van Valen (1966, p. 54) gave for the type of *P. puercensis*, from the Torreonian of the San Juan Basin, Nacimiento Formation, labial lengths of M<sup>1</sup>, 1.6 mm.; M<sup>2</sup>, 1.45 mm.; M<sup>3</sup>, 1.25 mm. The relative decrease in size from first to third molars indicates that the new specimen could well be a third molar.

SUPERFAMILY TUPAIOIDEA GRAY, 1825

FAMILY LEPTICTIDAE GILL, 1872

SUBFAMILY LEPTICTINAE GILL, 1872

cf. *Diacodon* sp.

A single lower molar, AMNH 56303, from locality 52-14, may represent this genus, but precise determination is extremely difficult. The tooth is wider relative to length than those of the Powder River *Palaeictops tauricinerei* (see below), measuring 1.60 × 2.40 mm. *Diacodon alticuspis* Cope, 1875a, is known from this time period, and in one specimen, AMNH 12831, although the jaws are locked, M<sub>2</sub> length is 2.5 mm. In addition to a wider (and rather shorter) talonid than in species of *Palaeictops*, the Powder River specimen appears close to *Diacodon* in possessing higher hypoconid relative to entoconid. Besides *Diacodon* or *Palaeictops*, this tooth could possibly belong to a *Leptacodon*-

like animal, but its size militates against this referral.

*PALAEICTOPS* MATTHEW, 1899

*Palaeictops tauricinerei* (Jepsen, 1930a)

Five isolated teeth from as many localities are referable to the smallest species of *Palaeictops*. As no measurements of individual teeth were given in the original description, it is not possible to make direct size comparisons, but measurements of Jepsen's figures indicate that the Powder River teeth may be slightly smaller (on the order of 10 to 15 per cent). The two lower and one upper fourth premolars are clearly leptictid, but two fragmentary upper molars show some resemblances to the Bridgerian adaposoricid *Scenopagus* (= ?*Talpavus*, see below). None of these teeth adds anything to the knowledge of the morphology of *Palaeictops tauricinerei*, but their measurements are given for reference: P<sub>4</sub>, 1.5 × 2.95 mm. (AMNH 56302, Dry Well); and 1.4 × 2.8 mm. (AMNH 56301, 51-28); P<sup>4</sup>, 2.8 × 2.4 mm. (AMNH 56300 Dry Well); M<sub>-</sub>, 3.2 × 2.6 mm., estimated (AMNH 56229, Reculosa Blowout); one upper molar (AMNH 56228, Dry Well) is too badly damaged to measure.

SUPERFAMILY PANTOLESTOIDEA COPE, 1884

FAMILY PANTOLESTIDAE COPE, 1884

*PALAEOSINOPA* MATTHEW, 1901

*Palaeosinopa didelphoides* (Cope, 1881a)

Figure 7

In his discussion of *Pantinomia*, Van Valen

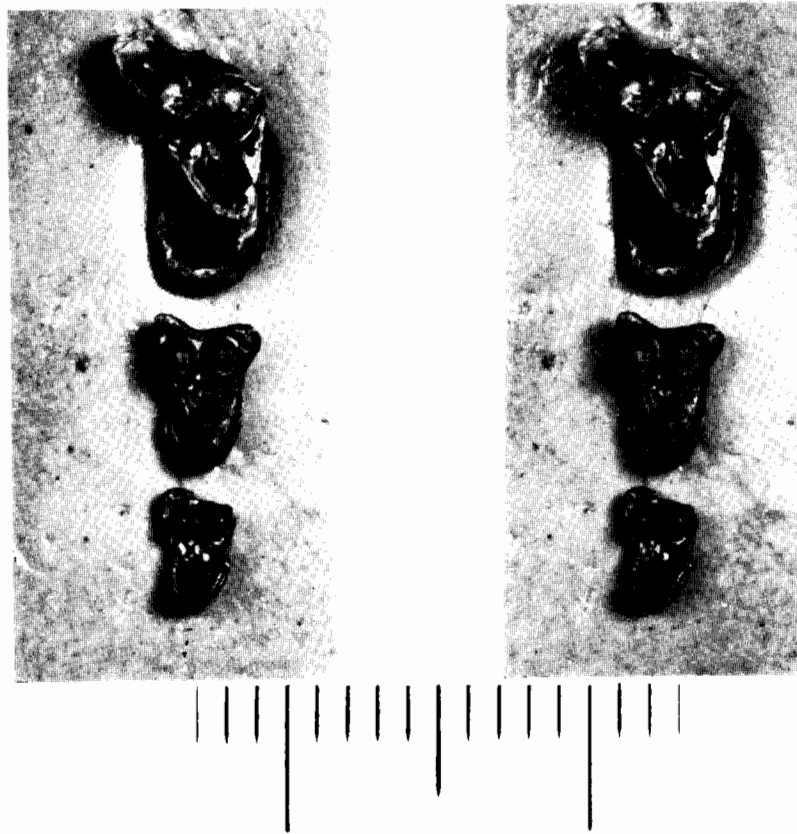


FIG. 7. *Palaeosinopa* spp. from the Powder River local fauna. Top, *P. didelphoides*, ?M<sup>2</sup>, AMNH 56224, Reculusa Blowout; center, *P. cf. lutreola*, ?M<sup>2</sup>, AMNH 56223, Dry Well; bottom, cf. *Palaeosinopa* sp., ?M<sup>1</sup>, AMNH 56309, Reculusa Blowout.

(1967, p. 225) noted that there may have been as many as four species of *Palaeosinopa* in Gray Bull time in North America: *P. veterrima* Matthew, 1901, the largest, most common form, type of Gray Bull age; *P. didelphoides*, slightly smaller than *P. veterrima*, rare in the Gray Bull, but continuing into the Lost Cabin, from which horizon the type is derived; *P. lutreola* Matthew, 1918, much smaller than *P. veterrima*, known from rare Gray Bull specimens; and a new species, termed "species E" by Van Valen, somewhat smaller than *P. didelphoides* and known from the Almagre, Four Mile, and Bitter Creek local faunas. Examination of the American Museum specimens, including the three types, leads me to doubt the distinctions drawn between *P. didelphoides*, *P. veterrima*, and species E. The geographic and intra-populational variation suggests that all three forms of

medium to large *Palaeosinopa* should be deemed populations of a single species until significant differences can be shown to indicate otherwise. All of these specimens intergrade, and a single widespread population could easily show the differences that are observed. I thus consider *Palaeosinopa veterrima* Matthew, 1901 to be a synonym of *Palaeosinopa didelphoides* (Cope, 1881a). It may be noted here that the Bear Creek specimens referred by Van Valen (1967, p. 222) to *P. didelphoides* show that the species extends back into the Paleocene and indicate another link between Bear Creek and early Wasatchian assemblages.

In the Powder River Basin collection, four teeth are referable to *Palaeosinopa didelphoides*. The specimens and their measurements are as follows: two lower molars (probably M<sub>2</sub>s), 3.7 × 4.8 mm. (AMNH 56227 and 56226,

both *Reculusa* Blowout);  $M_3$ ,  $3.75 \times 5.65$  mm. (AMNH 56225, Dry Well);  $M_2^?$ ,  $8.2 \times 5.4$  mm. (AMNH 56224, *Reculusa* Blowout). These measurements vary between those of Van Valen's "species E" and the largest specimens of *P. "veterrima."*

*Palaeosinopa* cf. *lutreola* Matthew, 1918

Figure 7

In the Powder River collection are two upper molars, probably  $M_2^?$ s, which are about two-thirds the size of the upper molars just discussed. The teeth measure  $4.7 \times 3.6$  mm. (AMNH 56223, Dry Well) and  $5.1 \times 3.4$  mm. (AMNH 56222 *Reculusa* Blowout – this tooth is broken, and the measurements may be altered by  $\pm 0.2$  mm.). These teeth possibly represent the same taxon as a probable  $M_1^?$  from Four Mile for which measurements as given by McKenna (1960, p. 43) are  $5.4 \times 4.0$  mm. In a particular individual, however,  $M_2^?$  is usually larger than  $M_1^?$ .

It is most probable that the two teeth from Powder River represent the previously unknown upper dentition of *P. lutreola*. Known from only three damaged lower jaws in the American Museum collections, this species is much smaller than *P. didelphoides*. Other possible identifications for these teeth are as very small individuals of *P. didelphoides* or even as the previously unknown upper dentition of the rare *Amaramnis gregoryi*, whose lower teeth (see Gazin, 1962, p. 24) are almost the same in size and structure as those in *P. lutreola*.

cf. *Palaeosinopa* sp.

Figure 7

An isolated upper molar, probably  $M_1^?$ , AMNH 56309 from *Reculusa* Blowout, may represent a still smaller species of *Palaeosinopa*. The tooth measures  $3.9 \times 2.4$  mm., less than half the size of *P. didelphoides* and significantly smaller than the two teeth just described.

SUPERFAMILY APATEMYOIDEA MATTHEW, 1909

FAMILY APATEMYIDAE MATTHEW, 1909

SUBFAMILY APATEMYINAE MATTHEW, 1909

*APATEMYS* MARSH, 1872

*Apatemys* cf. *chardini* (Jepsen, 1930a)

Figures 8, 9

The single apatemyid specimen in the Wood

collection does not, unfortunately, add anything to our knowledge of the Wasatchian forms. AMNH 56310, from locality 52-36, is an edentulous fragment of the right mandible, broken at the middle of the alveolus for  $M_3$  and anteriorly at or just behind the anterior border of the symphysis. All cheek tooth crowns are broken away, revealing both roots of  $P_4$ ,  $M_1$ , and  $M_2$  and the anterior root of  $M_3$ .  $P_3$  was a single-rooted tooth and was slightly procumbent, as its alveolus is inclined forward some 10 to 15 degrees to the alveolar plane. The enlarged incisiform tooth has been broken approximately 1 mm. (measured on the labial face) anterior to its passing into its alveolus.

On the labial face of the mandible, a circular foramen is present below the posterior root of  $M_1$ , situated halfway between the alveolar and the base of the jaw. Another foramen, larger and more elongate anteroposteriorly, is present immediately below the base of the (broken) alveolus of  $P_3$ . These foramina do not appear to have been confluent. The lingual face of the fragment shows no clear features, especially in the symphyseal region.

McKenna (1960, p. 47) and Guthrie (1967, p. 11) have discussed the relationships of apatemyids on the basis of number of roots of  $P_4$ , presence and development of a fossa under this tooth, and number of mental foramina. Guthrie, however, has shown that the last character may break down within a species and is thus less useful than those based on  $P_4$ . In the Powder River Basin specimen,  $P_4$  is two rooted and a strong fossa is lacking, as in McKenna's Group II, but there are two mental foramina, as in Group I. As the former criteria are the stronger, the specimen is referred to the group in which the smaller Wasatchian species, *A. chardini*, is placed.

Few measurements can be accurately taken on AMNH 56310, but all indications are that it is the smallest apatemyid yet described. Its jaw depth is only 2.7 mm. (below  $M_1$  and probably also below  $M_2$ ), as compared with 3.5-4.0 mm. for the type of *A. chardini*, the smallest previously known specimen. Incisor depth just outside the alveolus is approximately 2.05 mm. in *A. chardini* and width about 1.25 mm.; in the present specimen, these figures are 1.50 and 0.95 mm. Measurements of tooth sizes are uncertain as the crowns are lacking and apatemyid teeth often overlap, but an

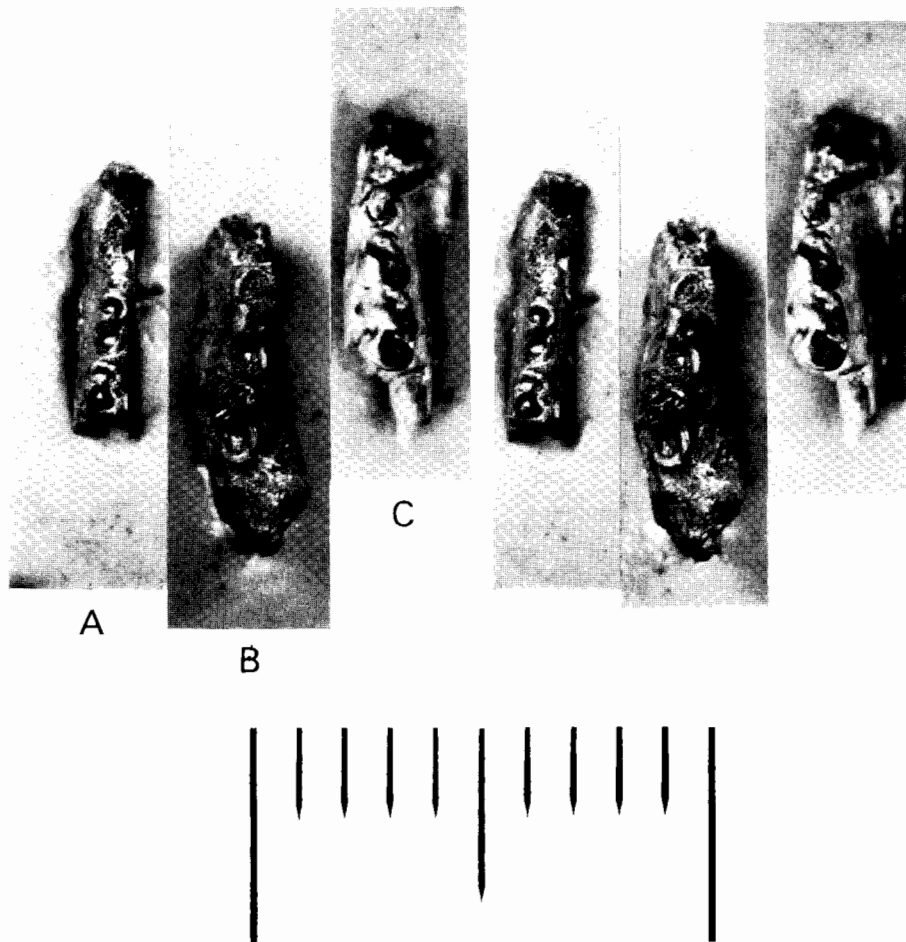


FIG. 8. *Apatemys* spp. of the Wasatchian. A. AMNH 56310, *Apatemys* cf. *chardini*, from locality 52-36, Powder River local fauna. B. UCMP 46167, *Apatemys* cf. *whitakeri*, from Alheit Pocket, Four Mile local fauna. C. AMNH 48004, *Apatemys whitakeri* type, Almagre local fauna.

estimate of length has been made based on size of alveolus:  $P_4$ , 0.9+ mm.;  $M_1$ , 1.4 mm.;  $M_2$ , 1.3 mm. The teeth, therefore, appear quite close in size to the type of *A. chardini*, PU 13236, ( $P_4$ , 1.15 mm. crown; 0.95 at alveolus;  $M_1$ , 1.3 mm.;  $M_2$ , 1.3 at alveoli). In sum, although the jaw is shallower and the incisor smaller, it seems best to refer this specimen to Jepsen's Gray Bull species, with which it agrees in root number and lack of fossa.

While studying this specimen, I also examined AMNH 48004, the type of *A. whitakeri* (Simpson, 1954) and the two Four Mile apate-

myid jaws reported by McKenna (1960, pp. 48-51). The smaller of these, UCMP 46167, now appears to be referable to *A. whitakeri*, a possibility not considered by McKenna. The only tooth preserved in these two specimens is  $M_2$ , but they agree in both tooth morphology and size. The measurements are: AMNH 48004, type, *A. whitakeri*, Almagre local fauna,  $M_2$ , 1.2 × 1.7 mm.; UCMP 46167, Four Mile local fauna,  $M_2$ , 1.10 × 1.75 mm.,  $M_3$ , 1.05 × 1.75 mm. This identification extends the range of *Apatemys whitakeri* in space, and especially in time to the earliest Wasatchian.



FIG. 9. Same specimens as figure 8, lingual views; top, as 8A; center, as 8B; bottom, as 8C (photographically reversed).

#### SUBORDER ERINACEOTA

#### SUPERFAMILY ERINACEOIDEA FISCHER VON WALDHEIM, 1817

#### FAMILY ADAPISORICIDAE SCHLOSSER, 1887

cf. "*Leptacodon*" *jepseni* McKenna, 1960

Four partial lower jaws with more or less damaged teeth appear to be referable to the species named by McKenna from Four Mile. Although smaller than most later adapisoricids of the *Entomolestes*/*Talpavus* variety, it is nonetheless related to them rather than to the more generalized *Leptacodon*. This distinction is made on the basis of  $P_4$ , unfortunately damaged in McKenna's type specimen. McKenna (1960, p. 51) reported that the talonid was essentially a single cusp, but in fact there is a talonid basin separated from a labial hypoflexid groove for the paracone of  $P_4$ , as in all adapisoricids. This talonid is more lingually compressed than

in *Leptacodon*, however, and appears to have been basined somewhat as in species here referred to *Entomolestes*. The molar hypoconids wear flat, as in the latter genus; the metaconid may be less tall than the protoconid, as is the case in *Leptacodon*. The generic status of this species is not certain, but it appears to be structurally transitional between *Leptacodon tener* and species of both *Entomolestes* and *Talpavus* as here understood. It is possible that this species may be morphologically similar to the ancestors of Bridgerian *Entomolestes grangeri*.

Of the Powder River material, two jaws are badly damaged, with no teeth preserved completely. AMNH 56311, from locality 52-34, has the talonids of  $P_4$ - $M_2$  and the labial half of  $M_3$  preserved, the remainder of these teeth having been broken away. The talonids are unworn and somewhat more like *Leptacodon* than are those of the quite worn type. AMNH 56312, from locality 51-30 preserves a more anterior portion of the mandible, including only the talonid of  $P_4$ , but with roots and/or alveoli for  $P_3$  (two rooted) and  $P_2$ ,  $P_1$ , and an enlarged and slightly procumbent ?canine (all one rooted). It is possible that  $P_2$  may be two rooted, and that the enlarged tooth thus would be in the position of  $P_1$ ; this would differentiate this specimen from "*L.*" *jepseni*, which has a single-rooted  $P_2$ . The talonid of  $P_4$  in AMNH 56312 is narrower anteriorly than posteriorly, with three subconical cusps present. YPM 15234 (collected in 1961 by Leonard Radinsky from locality 61-1) contains  $M_2$ - $M_3$  in good condition. The second molar agrees well with that of the type in size and morphology, although it may be slightly wider in the talonid. The last molar is rather like those of the middle Eocene species of *Talpavus*. A very worn  $M_3$ , AMNH 56313 from locality 51-29 may be referable to this species but could conceivably represent a different genus; it does not add anything to known morphology.

MEASUREMENTS: AMNH 56311, length  $M_{1-3}$ , 3.05 mm.; length  $M_3$ , 1.00 mm.; AMNH 56313,  $M_3$ , anterior width, 0.75 mm., posterior width, 0.65 mm., length, 1.15 mm.; YPM 15234,  $M_2$ , anterior width, 1.00 mm., posterior width, 0.90 mm., length, 1.30 mm.;  $M_3$ , anterior width 0.80 mm., posterior width, 0.65, length, 1.15 mm.; UCMP 45949, type, Four Mile,  $M_2$ , anterior width, 0.95 mm., posterior width, 0.85 mm., length, 1.25 mm.

cf. *Leptacodon* sp.

Three additional jaw fragments appear to be referable to a larger species somewhat closer to *L. tener* than the previous group: AMNH 56314 and 56315, from Bozeman locality, and AMNH 56316, from locality 52-34. The first of these consists of a mandible fragment with  $P_4$   $M_2$  in differing states of preservation: the enamel plate behind the protoconid and metaconid is missing on  $P_4$ ,  $M_1$  is complete, and the trigonid of  $M_2$  is lacking. This specimen is quite similar to the type of *L. tener*, AMNH 17179, from the Mason Pocket Tiffanian. It is, however, somewhat closer to referred specimens of *L. minusculum* from Gidley Quarry in the Torrejonian, especially AMNH 35942. In both specimens, the paraconids of  $M_1$  are slightly less cusped, more lophlike than in *L. tener*, and the hypoflexid of  $P_4$  is deeper.

The two additional specimens are  $M_3$ s, AMNH 56315 and AMNH 56316. The former specimen also preserves the talonid of  $M_2$ , which compares well with the  $M_2$  talonid of AMNH 56314, from the same locality. In both  $M_3$ s, the metaconid is slightly higher than the protoconid, whereas the reverse is true in  $M_1$  of the more complete specimen. One might thus postulate a relative reduction in size of protoconid with respect to metaconid from  $M_1$  to  $M_3$ ; a similar change is found in both *L. tener* and *L. minusculum* as represented in the American Museum collections.

The genus *Leptacodon* is a major problem in the organization of the adapisoricids, and the relevance of these specimens to the genus is not certain. They may possibly be more closely related to the previously described species. Further consideration and systematic revision of the Paleocene species are necessary before more precise allocations are possible.

MEASUREMENTS: AMNH 56314,  $P_4$ , 0.80 × 1.85 mm.;  $M_1$ , 1.20 × 1.95 mm.; AMNH 56315,  $M_3$ , 1.05 × 1.75 mm.; AMNH 56316,  $M_3$ , 1.05 × 1.75 mm.

ENTOMOLESTES MATTHEW, 1909

*Entomolestes* cf. *nitens* Matthew, 1918

As McKenna (1960, p. 60) has noted, at least one lineage of *Entomolestes* demonstrates slow change in size and morphology, from *E. siegfriedti* Simpson, 1928a, of the late Paleocene at Bear Creek through *E. nitens* of the later

Wasatchian. These changes are especially important in  $P_4$  and will be documented in a later study. For the present, however, it is sufficient to note that the forms from Powder River and Four Mile are intermediate between those from Bear Creek and the large single-quarry sample from the San Jose Formation, New Mexico. All the animals referred to *Entomolestes* by me are separable from *Talpavus* by the development of true basins on the talonids of  $P_4$  and (apparently) by the greater separation of the end of the parolophid from the base of the metaconid in the molars. *Talpavus*, as here understood, includes *T. nitidus* Marsh, 1872 (the type species), *Scenopagus edenensis* (McGrew, 1959) (= *S. mcgrewi* McKenna and Simpson, 1959), and *Nyctitherium priscus* Marsh, 1872, all of middle Eocene age, as well, perhaps, as some early Eocene forms. Robinson (1966, 1968), however, separated *Scenopagus* (into which he placed *E. nitens* and *N. priscus*) from *Talpavus* (for him including *E. siegfriedti*), and considered that *Entomolestes* includes only *E. grangeri*, the type species, known only from a single, very worn Bridgerian specimen. This and other problems can be resolved only with the publication of large-scale revision of the adapisoricids.

MEASUREMENTS: AMNH 56317,  $M_{1-3}$ :  $M_1$ , 1.25 × 1.65 mm.;  $M_2$ , 1.25 × 1.70 mm.;  $M_3$ , 1.05 × 1.55 mm. (Reclusa Blowout); AMNH 56318,  $P_{3-4}$ :  $P_3$ , 0.95 mm. in length;  $P_4$ , 0.90 × 1.55 mm. (Bozeman).

#### ORDER DELTATHERIDIA

##### SUBORDER HYAENODONTA

##### SUPERFAMILY HYAENODONTOIDEA LEIDY, 1869

##### FAMILY HYAENODONTIDAE LEIDY, 1869

##### SUBFAMILY HYAENODONTINAE LEIDY, 1869

##### *ARFIA* VAN VALEN, 1965

##### *Arfia shoshoniensis* (Matthew, 1915a)

Van Valen (1965) has allocated the species formerly referred to *Sinopa* to four genera, three of which are present in the early Eocene of Wyoming. Separation of the several species of these three genera is quite difficult, especially with incomplete material and at the earlier time horizons such as those represented by the Powder River local fauna. Nonetheless, three

TABLE 3  
MEASUREMENTS (IN MILLIMETERS) OF JAWS AND LOWER TEETH OF *Arfia shoshoniensis*

	AMNH 56221 51-19	AMNH 56220 51-12	AMNH 56219 51-31	AMNH 56218 Rec.	AMNH 56217 Rec.	Type AMNH 16158 EGB <sup>a</sup>
Maximum width						
P <sub>3</sub>	3.70 <sup>b</sup>	3.80	—	—	—	—
P <sub>4</sub>	4.05	4.15	4.40	—	—	—
M <sub>1</sub>	3.80 <sup>b</sup>	3.75	4.60	3.65	3.80	—
M <sub>2</sub>	—	—	5.05	—	—	4.35
M <sub>3</sub>	—	—	5.50	—	—	4.80 <sup>b</sup>
Maximum length						
P <sub>3</sub>	8.10	7.70	—	—	—	—
P <sub>4</sub>	8.10	8.30	8.35	—	—	—
M <sub>1</sub>	7.15	7.30	7.15	7.00	7.00	7.90 <sup>b</sup>
M <sub>2</sub>	—	—	9.30	—	—	9.10
M <sub>3</sub>	—	—	9.90	—	—	10.40
Jaw depth below M <sub>3</sub> , labially	—	—	9.00 <sup>b, c</sup>	—	—	12.10

<sup>a</sup> From the early Gray Bull of the Clark Fork Basin, Wyoming. The more anterior teeth and mandibular portion of this specimen, figured by Matthew (1915a, p. 74), are missing.

<sup>b</sup> Estimated measurement, probably slightly less than true value.

<sup>c</sup> Opposite side of jaw from teeth; comparable portions of M<sub>3</sub> are nearly equal in size. Symbols for localities as in table 2.

partial mandibles and three isolated lower teeth are here referred to this species on the basis of size and P<sub>3</sub> and M<sub>3</sub> proportions and morphology following Van Valen (1965). In addition, two isolated upper molars are referred to *A. shoshoniensis*, and a deltatheridian-like ungual phalanx may represent this species. This limited information provides no evidence for the presence of more than one species. Measurements of the specimens are given in table 3.

*PAENEPROLIMNOCYON* GUTHRIE, 1967a

?*Paeneprolimnocyon mordax* (Matthew, 1915a)

Figures 10, 11

In a footnote to a recent functional study, Van Valen (1969a, p. 116, note 2) has made several taxonomic shifts within the Hyaenodontidae. Matthew's two somewhat "aberrant" species *Prolimnocyon robustus* and *Prototomus mordax* have been formally synonymized and *P. mordax* referred to Guthrie's genus *Paeneprolimnocyon*. The last is based on *P. amissadomus* Guthrie, 1967a, of the type Lost Cabin and *P. iudei* (Guthrie, 1967b), of the type Lysite;

both species are based on single, fragmentary mandibles of much smaller size than that in *P. mordax*.

The idea of combining the two larger species had been previously considered by Van Valen (1966, p. 70), but rejected as premature. It may still be premature but is probably correct, although only more complete specimens and especially upper teeth will prove the point. AMNH 56320, from the Bozeman locality of the Powder River local fauna, is yet another fragmentary mandible, which appears somewhat intermediate between the two named types from the Bighorn Basin. As shown in table 4, all three specimens show a ratio of M<sub>3</sub>/M<sub>2</sub> length of about 0.75, the absolute sizes are rather close, and the molar morphology is similar. These three specimens may quite correctly be considered as representatives of a single species, *P. mordax* (Matthew, 1915a).

The major question, however, is whether *mordax* should be referred to *Prototomus*, *Prolimnocyon*, or *Paeneprolimnocyon*. Van Valen (1969, p. 116) chose the last because "comparison of [Guthrie's (1967a, p. 1286)] figures . . . suggests

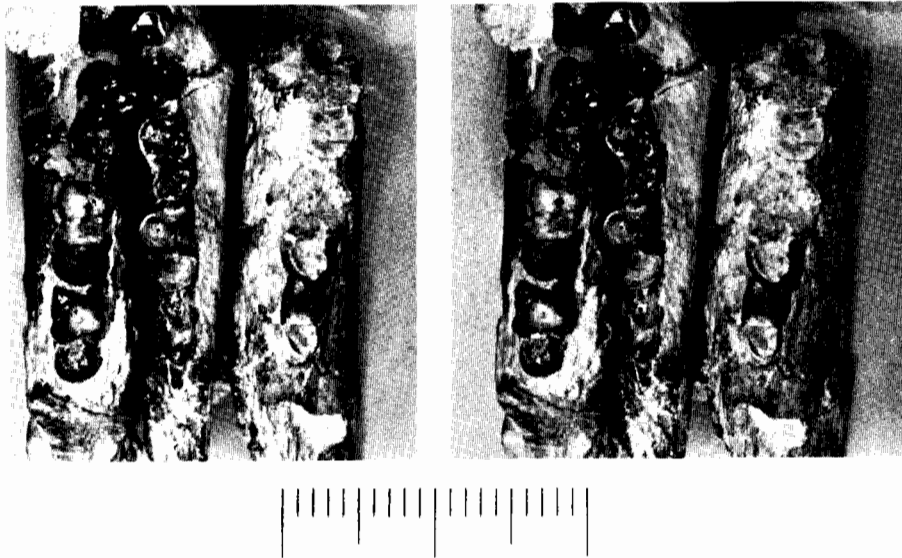


FIG. 10. ?*Paeneprolimnocyon mordax*. Left, AMNH 16157, type, right  $M_{1-3}$ , "middle" Gray Bull, Bighorn Basin; center, AMNH 56320, left  $M_{1-3}$ , Bozeman locality, Powder River local fauna; right, AMNH 15168, (type *Prolimnocyon robustus*), right  $M_{2-3}$ , "middle" Gray Bull, Bighorn Basin.



FIG. 11. Same specimens as figure 10, labial views; top, AMNH 15168; center, AMNH 16157; bottom, AMNH 56320.

that the earlier species *P. mordax* was ancestral to *Paeneprolimnocyon*." Guthrie had effectively suggested this in 1967, writing, "I feel that a

new genus could be erected to set these two species [*Prolimnocyon robustus* and *P. iudei*] apart from both *Sinopa* and *Prolimnocyon*" (1967b,

TABLE 4  
MEASUREMENTS (IN MILLIMETERS) OF JAWS AND LOWER TEETH OF ALL SPECIMENS  
REFERRED TO *Paeneprolimnocyon*

	<i>P. iudei</i> Type AC 2767 <sup>a</sup> LWRB <sup>b</sup>	<i>P. amissadomus</i> Type AMNH 55559 LCWRB <sup>c</sup>	<i>Prolimnocyon</i> <i>robustus</i> Type AMNH 15168 MGB <sup>d</sup>	<i>?Paeneprolimnocyon mordax</i>	
				<i>Prototomus</i> <i>mordax</i> Type AMNH 16157 MGB <sup>d</sup>	<i>P. cf.</i> <i>mordax</i> AMNH 56320 Bozeman
Trigonid width					
P <sub>3</sub>	—	—	—	3.50	—
M <sub>1</sub>	—	—	—	3.60	3.60
M <sub>2</sub>	2.85	—	—	4.45	3.80
M <sub>3</sub>	2.00	2.15	3.20	3.65	2.30 <sup>e</sup>
Talonid width					
M <sub>2</sub>	2.00 <sup>f</sup>	—	3.65	3.75	2.95
M <sub>3</sub>	1.80 <sup>f</sup>	1.80	2.80	2.40	2.20
Maximum length					
P <sub>4</sub>	—	—	—	6.85	—
M <sub>1</sub>	—	—	—	6.60	6.45
M <sub>2</sub>	4.40	3.30 <sup>e</sup>	7.50 <sup>e</sup>	7.75 <sup>g</sup>	6.45
M <sub>3</sub>	3.10	2.80	5.40	6.00	4.70
Labial jaw depth below M <sub>3</sub>	8.20	6.80 <sup>h</sup>	17.20 <sup>i</sup>	14.90	12.80

<sup>a</sup> Trigonid widths, maximum lengths, and jaw depth from Guthrie, 1967b, p. 15.

<sup>b</sup> Lysite, Wind River Basin.

<sup>c</sup> Lost Cabin, Wind River Basin.

<sup>d</sup> "Middle" Gray Bull, Bighorn Basin.

<sup>e</sup> Estimated measurement, probably slightly less than true value.

<sup>f</sup> Talonid widths estimated from figure 8, Guthrie, 1967b, p. 14.

<sup>g</sup> From other side of jaw.

<sup>h</sup> Below M<sub>2</sub>.

<sup>i</sup> Expanded by matrix filling cracks.

p. 14). This new genus was *Paeneprolimnocyon*, erected in a paper written later but published earlier (1967a).

At the present time, known specimens referred to *Paeneprolimnocyon* are all relatively fragmentary and have little in common except for a slightly reduced M<sub>3</sub>—the reduction is more than in *Prototomus*, but less than in *Prolimnocyon*. It is doubtful that the large species *P. mordax* could have given rise to the latter and much smaller *P. iudei*/*P. amissadomus*, but they may have shared a common ancestor apart from all other species. My examination of all specimens except the type of *P. iudei* does not indicate to me great similarity in form between M<sub>3</sub>s of these animals, the only tooth shared in common, but in all cases there is some damage present, and "*P. robustus*" especially may represent an aberrant individual. The wisest course seems tentatively to accept

Van Valen's referral and hope that no further changes will be made until more complete upper and lower dentitions of different sizes and from different time horizons are in hand. In dealing with the earliest known members of several lineages, such changes affect not only the taxonomic but also the phylogenetic position of both the Hyaenodontinae and Limnocyoninae. Measurements of all specimens discussed are given in table 4.

SUBFAMILY LIMNOCYONINAE WORTMAN,  
1902

TRIBE LIMNOCYONINI WORTMAN, 1902

*PROLIMNOCYON* MATTHEW, 1915a

*Prolimnocyon atavus* Matthew, 1915a

Figures 12, 13

This species is represented in the Powder

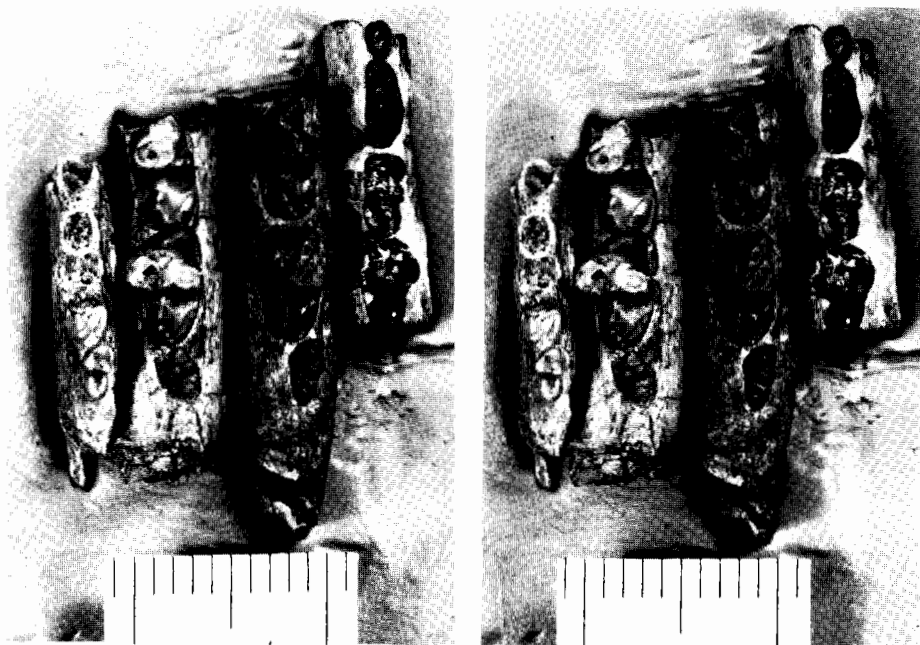


FIG. 12. *Prolimnocyon atavus*. Left to right: AMNH 56319, left  $M_{2-3}$ , Reculusa Blowout, Powder River local fauna; AMNH 16816, type, left  $M_{1-3}$ , late Gray Bull, Bighorn Basin; AMNH 16817, left  $M_{1-3}$ , "middle" Gray Bull, Bighorn Basin; AMNH 56216, right  $P_4-M_2$ , Bozeman locality, Powder River local fauna.



FIG. 13. Same specimens as figure 12, labial views; top to bottom: AMNH 16816, 56216, 16817, 56319.

River local fauna by two partial mandibles and two isolated teeth. None of the specimens shows meaningful morphologic or metrical differences from the American Museum Gray Bull sample, although they do fall at the lower end of the distribution. In fact, these specimens are the smallest reported or known to the author. Previously, Van Valen (1966, p. 71) had noted that although small size was not clearly correlated with greater age, UCMP 44864 from the Four Mile local fauna was one of the smallest known specimens. The still smaller size of the present specimens tends to reinforce both this correlation and that of the two faunal assemblages in general.

AMNH 56319, from Reculusa Blowout is especially interesting for several reasons. Although preserving only  $M_3$  and the talonid of  $M_2$  in a portion of the left mandible, it is the smallest of the Powder River specimens of *P. atavus*; these same teeth are preserved in the Four Mile specimen and are clearly larger in it. In addition, the proportions of  $M_3$  and  $M_3$  versus  $M_2$  are extremely close to those in

TABLE 5  
MEASUREMENTS (IN MILLIMETERS) OF JAWS AND LOWER TEETH OF SELECTED  
SPECIMENS OF *Prolimnocyon atavus*

	AMNH 16816 Type LGB <sup>b</sup>	AMNH 16817 MGB <sup>c</sup>	AMNH 56319 Rec.	AMNH 56216 Boz.	AMNH 56215 51-30	AMNH 56214 Dry	UCMP 44864 <sup>a</sup> Four Mile
Trigonid width							
P <sub>4</sub>	—	—	—	1.95	—	—	—
M <sub>1</sub>	3.10	3.10	—	—	2.65	—	—
M <sub>2</sub>	4.00	4.00 <sup>d</sup>	—	3.00	—	2.85	—
M <sub>3</sub>	1.65	1.75	1.40	—	—	—	2.00
Talonid width							
M <sub>2</sub>	2.70	2.55	2.25	—	—	—	—
M <sub>3</sub>	1.30	1.40	1.00	—	—	—	—
Maximum length							
P <sub>4</sub>	—	—	—	4.70	—	—	5.60
M <sub>1</sub>	5.90	6.40	—	4.60 <sup>d</sup>	4.15	—	—
M <sub>2</sub>	6.15	6.15	5.00 <sup>d</sup>	5.10	—	4.75	—
M <sub>3</sub>	2.65	3.40	2.75	—	—	—	3.70
Labial jaw depth below M <sub>3</sub>	10.70	9.70	6.50	7.60 <sup>e</sup>	—	—	7.70 <sup>e</sup>

<sup>a</sup> Measurements from McKenna, 1960, p. 93.

<sup>b</sup> Late Gray Bull, Bighorn Basin.

<sup>c</sup> Middle Gray Bull, Bighorn Basin.

<sup>d</sup> Estimated measurement, probably slightly less than true value.

<sup>e</sup> Below M<sub>2</sub>.

AMNH 16817, of the "middle" Gray Bull. These specimens and others with relatively long M<sub>3</sub> talonids reflect the ancestry of the species, and of the subfamily descended from it; the type, on the other hand, shows a "degenerate" reduced M<sub>3</sub>, foreshadowing the further reduction of the *P. antiquus*/*P. elisabetae* lineage and their descendants. Measurements of these and related specimens are given in table 5.

ORDER PRIMATES

SUBORDER PROSIMII

SUPERFAMILY INCERTAE SEDIS

FAMILY PAROMOMYIDAE SIMPSON, 1940

SUBFAMILY PAROMOMYINAE SIMPSON, 1940

TRIBE PAROMOMYINI SIMPSON, 1940

*PHENACOLEMUR* MATTHEW, 1915c

*Phenacolemur praecox* Matthew, 1915c

Figure 14B

Matthew (1915c) named two species of *Phenacolemur* from different levels in the Bighorn

Basin Gray Bull. Simpson (1955) considered the larger and earlier (*P. praecox*) and the smaller and later (*P. citatus*) Bighorn Basin forms as subspecies of a single species—*P. praecox*. He separated *P. jepseni* from New Mexico based on size (the single specimen is slightly smaller than the range of roughly contemporary *P. p. citatus*) and small morphological differences, mostly in the upper teeth. McKenna (1960) referred the Four Mile *Phenacolemur* (age roughly equivalent to *P. p. praecox*) to the New Mexican species on morphological grounds, noting also a great size range. Robinson (1966) named a new subspecies, *P. jepseni simpsoni*, from Huerfano, again based on a single specimen. Guthrie (1967b) recorded several teeth from the Lysite as small as those of the *P. jepseni* type and separated the two subspecies of Simpson's *P. praecox* at the specific level. The variation demonstrated by known specimens does not exceed that expected in a variable species with populations separated by space and time. I therefore suggest that the known early Eocene populations of *Phenacolemur* be considered as

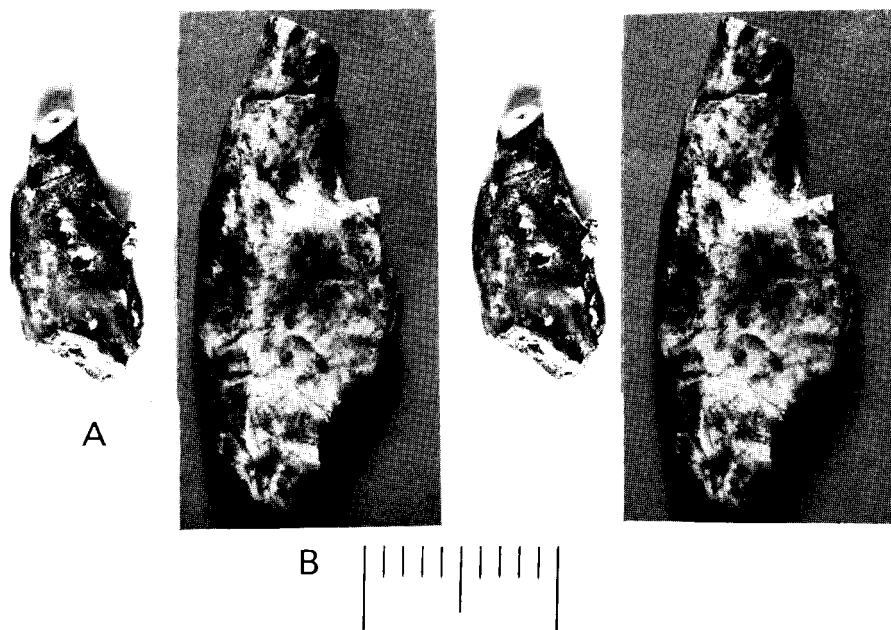


FIG. 14. *Phenacolemur* spp. from Powder River. A. AMNH 56322, edentulous left mandible from Bozeman locality; labial view. B. AMNH 56321, edentulous right mandible from Bozeman locality; labial view (photographically reversed).

subspecies in time and space of a single species. The four named populations would thus be: *Phenacolemur praecox praecox* Matthew, 1915c, early Gray Bull of Wyoming; *Phenacolemur praecox citatus* Matthew, 1915c, late Gray Bull of Wyoming; *Phenacolemur praecox jepseni* Simpson, 1955, Wasatchian of New Mexico and *Phenacolemur praecox simpsoni* Robinson, 1966, later Wasatchian of Colorado. The range of variation at Four Mile is large, but more than one species may be represented there, as at Powder River (see below). The larger animals in both of these early Gray Bull age local faunas can best be considered as *P. praecox*, with subspecific designation possible (if warranted) only after further study.

An edentulous lower jaw and 10 isolated teeth represent this species in the Powder River local fauna. These specimens are large, but agree well with lower teeth in the American Museum early Gray Bull and Four Mile collections, in morphology as well as size. In  $M_3$ , for example, the reported Four Mile lengths (McKenna, 1960, p. 72) were 2.3–4.0 mm.; the  $M_3$  lengths of Powder River specimens are

3.60 mm. (AMNH 56213, Bozeman), 4.10 mm. (AMNH 56212, Reculosa Blowout), and 4.15 mm. (AMNH 56211, also Reculosa Blowout). No  $M_3$  is known from early Gray Bull specimens in the American Museum, but the type of *P. praecox* (AMNH 16102) had a third molar between 4.0 and 4.5 mm. long, based on the length of the alveolus. All other teeth compare well with Simpson's (1955) data for *P. praecox*.

The lower jaw, AMNH 56321, from the Bozeman locality, contains the roots of  $P_4$  and  $M_1$  and a small portion of the incisor. The alveolar border is broken away behind  $M_1$  and no remnants of  $M_{2-3}$  are left. Reference to *Phenacolemur* is made on the basis of the lack of teeth anterior to  $P_4$ , full sheathing of incisor in enamel and mesio-distal compression of the tooth, mental foramina under the posterior part of the diastema and under  $M_1$ , presence of a ridge above the symphyseal region, and size similar to Powder River and early Gray Bull teeth and jaws of *Phenacolemur*. This jaw is perhaps the largest specimen referred to the genus: alveolar lengths of  $P_4$  and  $M_1$  are 4.3 and 3.4 mm., respectively; the incisor measures

2.7 × 4.6 mm., and the jaw is some 10 mm. deep between P<sub>4</sub> and M<sub>1</sub> labially. For comparison, in AMNH 16102, the type of *P. praecox*, these measurements are: 3.7, 3.2, 2.2, 4.1, and 8.5 mm.

?*Phenacolemur* sp.

Figure 14A

A second species of *Phenacolemur* may be represented by a single mandibular fragment, edentulous except for a small part of an enlarged anterior tooth in its alveolus. The specimen, AMNH 56322, also from the Bozeman locality, shows alveoli for four cheek teeth, the last being merely indicated, whereas roots of the other three are present. No sign of a more anterior tooth (i.e., P<sub>3</sub>) is discernible, although the jaw is well preserved in this region. Reference to *Phenacolemur* is supported by many features: over-all size, incisor morphology, presence of a ridge on the upper edge of the symphyseal area, and condition of the mental foramen (slightly posterior to its position in AMNH 16102, the type of *P. praecox*, but of the same shape and direction) are some. In direction of P<sub>4</sub> alveolus and pattern of incisor enamel, this specimen differs from AMNH 16102, but agrees with e.g., AMNH 15078.

Given that this specimen is a *Phenacolemur*, its specific placement is more difficult. In length of M<sub>1</sub> and M<sub>2</sub>, the specimen fits easily into the ranges for late Gray Bull specimens given by Simpson. But the jaw is shallow (6.0 mm. below M<sub>1</sub> as opposed to 7.5–8.0 mm. in Gray Bull specimens and 6.7 mm. for San Jose specimens) and, of more interest, P<sub>4</sub> appears to be the shortest tooth. An examination of many specimens shows that although M<sub>1</sub> may have a greater crown length than alveolar length, P<sub>4</sub> never does. Thus, estimating tooth length from the alveolus, P<sub>4</sub> in the Powder River specimen is roughly 1.8–1.9 mm long, whereas M<sub>1</sub> is about 2.2 mm. long; the ratio of lengths is thus between 0.8 and 0.9, but certainly below 1.0. This condition is found only in the Tiffanian *P. frugivorus*, which itself is too small to include this specimen. Judged, however, from the contemporaneity of *P. frugivorus* with *P. pagei* (more like *P. praecox* in P<sub>4</sub>), it is possible that AMNH 56322 may represent the end of a small lineage of *Phenacolemur* in which P<sub>4</sub> was relatively small. On the other hand, it could conceivably repre-

sent one of the smallest individuals of early *P. praecox*. Further specific analysis cannot be made at this time, but the specimen is reported to indicate the possibility of two lines of *Phenacolemur* extending into the Wasatchian.<sup>1</sup> In addition, the range in size between AMNH 56321 and 56322 (see fig. 14A and B) is quite similar to that in the Four Mile specimens, and may indicate the common presence of two forms. Determination of P<sub>4</sub>/M<sub>1</sub> length ratio in the smaller Four Mile specimens will be of great importance in this question.

#### *Phenacolemur* FROM BEAR CREEK

Figure 15

AMNH 22244 from Bear Creek Coal Mine, a right P<sub>4</sub>, was made the type of *Parapheliscus bjorni* by Van Valen (1967a, p. 248). Re-examination of this specimen in the course of consideration of *Apheliscus* from the Powder River local fauna led me to question its referral to an allied genus. Instead, it appeared more like the homologous tooth in *Phenacolemur*, not certainly known from Bear Creek (see below). Van Valen had considered AMNH 22244 to be somewhat intermediate between *Apheliscus* and *Phenacodaptes*, but I question this reference also.<sup>2</sup>

In morphology and size, the Bear Creek specimen is close to the later Gray Bull representatives of *Phenacolemur praecox*, those which Simpson (1955) termed *P. p. citatus*. It is probably too small to represent the same population as the specimens of *P. pagei* from the slightly antecedent Silver Coulee quarry, of the Polecat Bench Tiffanian (table 6), and certainly too large for *P. frugivorus* of similar age. It does, however, add a new element to the Bear Creek local fauna.

An additional note about the primate fauna of Bear Creek may be inserted here. Van Valen and Sloan (1966, p. 273) noted that AMNH 22154 represents a paromomyine, either *Phenacolemur* or *Paromomys*, and not *Plesiadapis*, as originally identified by Simpson (1928a). On the specimen label are both these identifications, and a third, signed by Martin of Florida, noting

<sup>1</sup> *P. fuscus*, of the French Sparnacian, is known from isolated P<sub>4</sub> and M<sub>1</sub> of this size and proportion; cf. Russell et al. 1967.

<sup>2</sup> Since this was written I have compared the specimen with *Apheliscus*, *Phenacodaptes*, and *Phenacolemur* in the company of Van Valen, and he has accepted my identification.

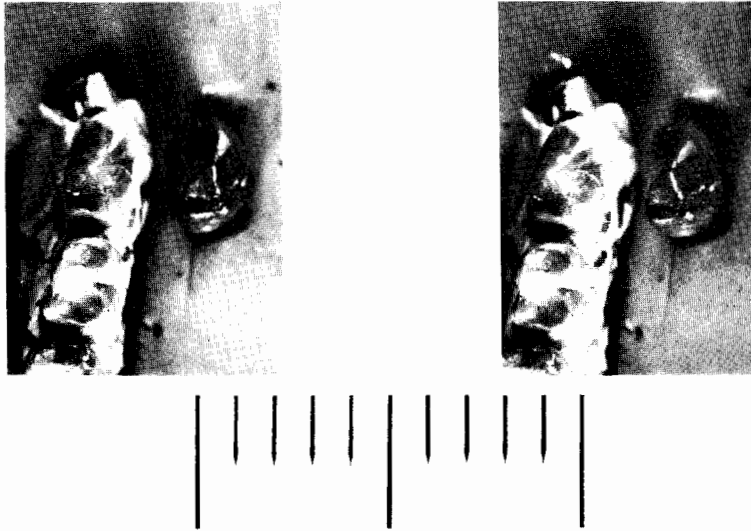


FIG. 15. *Phenacolemur* spp. from Bear Creek and the Bighorn Basin. Left, AMNH 16833, *Phenacolemur praecox citatus*, late Gray Bull, Bighorn Basin, right P<sub>4</sub>-M<sub>2</sub>; right, AMNH 22244, *Phenacolemur* sp. from Bear Creek local fauna, right P<sub>4</sub> (type of "*Parapheliscus bjorni*").

TABLE 6  
MEASUREMENTS (IN MILLIMETERS) OF PRIMATE P<sub>4</sub> AND M<sub>3</sub>  
FROM THE BEAR CREEK LOCAL FAUNA AND SELECTED COMPARISONS

	Maximum Width	Maximum Length
P <sub>4</sub>		
AMNH 22244, <i>Phenacolemur</i> sp., Bear Creek: measured by Van Valen (1967, p. 248)	2.0	2.8
Delson	1.80	2.60
AMNH 16833, Type, <i>Phenacolemur praecox citatus</i> , late Gray Bull: measured by Simpson (1955, p. 425)	1.8	2.8
Delson	1.70	2.80
<i>Phenacolemur pagei</i> , Princeton Silver Coulee Quarry Sample, Tiffanian; measured by Simpson (p. 423)		
Mean (N=16)	2.57	3.31
Observed Range	2.3-2.9	3.0-3.5
M <sub>3</sub>		
AMNH 22154, <i>Plesiadapis</i> sp. (or <i>Paromomys</i> sp.), Bear Creek	3.00	4.95

"not *Phenacolemur*." I am in agreement with the latter statement, but without further extensive study find it impossible to identify the specimen as *Paromomys* or *Plesiadapis* with certainty. The trigonid of the Bear Creek tooth is somewhat more like *Plesiadapis*, the hypo-

conulid-heel rounded as in *Paromomys*, and the hypoconid intermediate. Anterior and upper teeth would be necessary to confirm any allocation. Measurements of this tooth appear in table 6.

## FAMILY ANAPTOMORPHIDAE COPE, 1883

*TETONIUS* MATTHEW, 1915c*Tetonijs musculus* Matthew, 1915c

Four supposedly new and distinct small anaptomorphids, actually of closely similar morphology, have been described and named since Matthew's revision of 1915. These are: *Tetonijs tenuiculus* Jepsen, 1930a; *Paratetonijs steini* Seton, 1940; *Paratetonijs sublettensis* Gazin, 1952; and *Tetonioides pearcei* Gazin, 1962. Additional important specimens have been figured and discussed by McKenna (1960, p. 65), Guthrie (1967, p. 17), and Robinson (1967), and most species assigned to *Anemorhysis* Gazin, 1958. Examination of the illustrations in all of these papers, especially those of Gazin, and comparison of original American Museum, Berkeley, and Princeton specimens, and new material from Powder River, has led me to believe that all are referable to a single species. Gazin's (1962, pp. 34-37) distinctions between the several genera and species on the basis of lower teeth do not stand up to examination of his own figures or referred specimens. I conclude that all four species are to be considered as junior synonyms of *Tetonijs musculus* Matthew, 1915c (see also Guthrie, *loc. cit.*).

Jepsen's (1930a) type of *T. "tenuiculus"* is effectively indistinguishable from a Powder River Basin specimen, AMNH 56323, from Monument Blowout. The maxilla of the latter, with  $M^{1-2}$ , allows two additions to be made to Jepsen's description (1930a, p. 126): the cingulum is essentially continuous around the outside of the molars, and there is really no indication of a hypocone—some crests come off the protocone to the area which a hypocone would occupy, but they do not reach the shelflike area present in these specimens. These crests and area are not related to the development of a hypocone except incipiently, much as in the early *Pelycodus* versus *Notharctus* relationship. In this case, a structurally later development appears to be represented by *Tetonijs homunculus*, which (as Jepsen noted) differs in no other way except size from *musculus*.

The last point brings up the matter of generic assignment. The only differences I can discern between this species and *Tetonijs homunculus* are: less development of hypocone, smaller size, slightly different  $P_4$  morphology, and apparently

less reduced anterior dentition in *T. musculus*. I believe that the differences in  $P_4$  are due partly to the size distinction and partly to the different anterior teeth, whereas lack of a hypocone indicates more generalized status for the smaller form. These conditions are to be expected in a structural ancestor, as is perhaps the case here. Without further knowledge of the skull in *T. musculus*, it does not seem necessary to separate this species generically from *Tetonijs homunculus*. The synonymy of *Tetonijs* therefore includes *Paratetonijs* Seton, 1940; *Anemorhysis* Gazin, 1958; and *Tetonioides* Gazin, 1962.

MEASUREMENTS: AMNH 56323,  $M^1$ ,  $1.95 \times 1.60$  mm.;  $M^2$ ,  $2.20 \times 1.60$  mm.; also two isolated lower molars.

*Tetonijs homunculus* (Cope, 1882a)

Two teeth of this larger species are present in the Wood collection. One shows slightly rounder trigonid cusps than the Gray Bull specimens from the Bighorn Basin, but this is considered to represent merely inter-populational variation.

SUPERFAMILY MICROSYOPOIDEA  
OSBORN AND WORTMAN, 1892FAMILY MICROSYOPIIDAE  
OSBORN AND WORTMAN, 1892*MICROSTYOPS* LEIDY, 1872*Microstypops wilsoni* Szalay, 1969a

This species, the smallest and most primitive of the genus, was previously known only from the Bighorn Basin Gray Bull (type and one other specimen) and the Alheit Pocket Quarry of Four Mile. Twenty-seven isolated teeth from 18 Powder River local fauna localities are referable to *M. wilsoni* on the basis of size. Szalay (personal commun.) has noted that the length of  $M_3$  is a useful criterion and supplied the following figures (1969a, p. 251): in *M. wilsoni* from Four Mile,  $M_3$  ranges from 2.8 to 3.2 mm. in 35 specimens; in *M. alfi* from all other Four Mile localities,  $M_3$  length in 11 specimens ranges from 3.55 to 4.0 mm. The Wood collection sample of three  $M_3$ s shows lengths of 3.05, 3.10, and 3.15 mm., within, but at the upper range of, the *M. wilsoni* sample. Of two  $P_4$ s from Powder River, measurements are: lengths, 2.73 and 2.60 mm.; widths, 1.80 and 1.65 mm., respectively. Twelve Four Mile *M. wilsoni* show lengths, 2.4 to 2.7 mm.; widths, 1.3 to 1.7 mm.;

a single *M. alfi* has length, 3.10; width, 1.90 mm. The Powder River specimens are within or just above the upper limits for *M. wilsoni*. In other measurements, a similar situation holds.

SUPERFAMILY LEMUROIDEA GRAY, 1821

FAMILY NOTHARC'HIDAE TROCESSART, 1879

*PELYCODUS* COPE, 1875a

*Pelycodus ralstoni* Matthew, 1915c

Figure 16

Placement of American lemuroids with respect to European forms is still uncertain. *Pelycodus* (—*Cantius*; see Russell, 1968; Russell et al. 1967; Simons, 1962) occurs in the earliest Eocene of France and England, as well as in the United States, but is uncertainly related to contemporaneous European *Protoadapis*. If it can be shown that these two genera shared a middle or late Paleocene common ancestor, I would advocate placing notharc'hids and adapids in a single family (or as families in a separate superfamily). Because it has not yet been shown, they may be retained as distinct at a higher taxonomic level, in accord with Gazin (1958) and McKenna (1968).

Forty isolated teeth and a maxilla with

P<sup>4</sup>–M<sup>3</sup>, from 26 localities, are referable to *Pelycodus ralstoni*. The teeth are small for *Pelycodus*, being similar in size to those reported by McKenna (1960) from Four Mile and to the Sand Coulee sample of the Willwood Formation (see Guthrie, 1967, p. 20). In the same size range are teeth of *Pelycodus* (*Cantius*) from the early Eocene of Europe, as reported by Simons (1962) and Russell et al. (1967). If the European teeth were found isolated in the Powder River Basin, I doubt that they would be separable on any grounds from the specimens I am now reporting.<sup>1</sup> Selected measurements and statistics of the Wood collection *Pelycodus* are given in table 7.

ORDER RODENTIA

SUBORDER SCIUROMORPHA

FAMILY ISCHYROMYIDAE ALSTON, 1876

SUBFAMILY PARAMYINAE

MILLER AND GIDLEY, 1920

On the authority of Black (1968, pp. 273–

<sup>1</sup> With reference to Russell et al. 1967, Szalay has noted (1969a, p. 281, note 1) that the labels of figures 12 and 13 are switched. It may be added that the specimen illustrated on page 42, Leve-29 Py, is apparently an artiodactyl referable to *Diacodexis* (cf. *D. metsiacus* on size grounds).

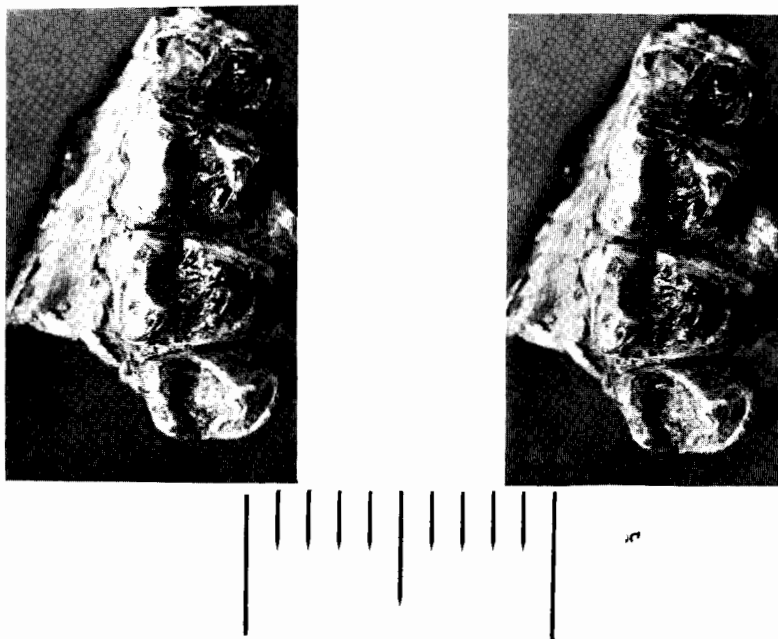


FIG. 16. *Pelycodus ralstoni* from the Powder River local fauna; right P<sup>4</sup>–M<sup>3</sup> from locality 52–36, AMNH 56210.

TABLE 7  
STATISTICAL DATA ON THE TEETH OF *Pelycodus ralstoni*  
IN THE POWDER RIVER LOCAL FAUNA

	N	OR	M	SE	$\sigma$	V
M <sub>1</sub>						
AW	3	2.80-2.90	2.83	0.03	0.06	2.0
PW	3	3.20-3.25	3.23	0.01	0.03	0.9
L	3	4.15-4.25	4.18	0.03	0.06	1.4
M <sub>2</sub>						
AW	8	2.85-3.65	3.23	0.11	0.31	9.7
PW	9	3.00-3.85	3.37	0.11	0.33	9.8
L	5	3.70-4.40	3.94	0.13	0.31	7.4
M <sub>3</sub>						
AW	12	3.00-3.60	3.30	0.06	0.21	6.4
PW	11	2.75-3.55	3.14	0.08	0.28	8.9
L	10	4.85-5.95	5.34	0.13	0.40	7.5
P <sup>4</sup>						
W	4	3.20-4.40	3.75	0.28	0.55	14.7
L	4	2.25-2.90	2.59	0.14	0.28	10.7
M <sup>1</sup>						
W	1	— —	4.80	—	—	—
L	1	— —	3.90	—	—	—
M <sup>2</sup>						
W	6	5.15-6.00	5.59	0.16	0.39	7.0
L	6	3.45-4.15	3.83	0.10	0.25	6.5
M <sup>3</sup>						
W	2	4.40-4.85	4.63	—	—	—
L	2	2.75-3.00	2.88	—	—	—

275), the paramyids of Wood (1962) are here considered a subfamily of Ischyromyidae. At least three types of rodent are distinguishable in the Powder River fauna on the basis of morphology and size, all represented only by isolated teeth, totaling 12 in number, from five separate localities. All are provisionally referred to species of *Paramys* as revised by Wood, 1962.<sup>1</sup>

*PARAMYS* LEIDY, 1871

cf. *Paramys atavus* Jepsen, 1937

Figure 17

A single upper tooth, AMNH 56324 from Monument Blowout, may represent the most primitive Eocene rodent. It is about 1½ times as large as the upper tooth of *P. atavus* described by McKenna (1961), which is the most similar known specimen. The tooth is roughly triangular, with well-developed posterior, but faint anterior, cingulum. The protocone, paracone,

<sup>1</sup>The many isolated incisors cannot now be allocated further.

and metacone are nearly equal in size, and they form a right triangle with legs labiolingually and mesiodistally directed. Wear facets are present on the anterior faces of the paracone and metacone, and at the apex of the protocone. A small mesostyle lies buccomesial to the metacone, separated from it by a groove. The "paraloph" curves anteriorly convex, and a paraconule is indicated by parallel grooves perpendicular to the loph, but there is no conular swelling. The "metaloph" is less distinct, but a fair-sized metaconule lies between the protocone and metacone. The distolingual corner of the tooth shows no sign of a hypocone or other cingular development; this feature may indicate that the tooth is a P<sup>4</sup>. The enamel has been broken away in a small area at the mesio-buccal corner of the tooth. The roots have been broken away, but their canals indicate that the lingual or protoconal root was significantly more robust than the external roots.

Differences from the Bear Creek specimen include presence of a mesostyle, lack of a hypocone, smaller paraconule, and metaconule closer to the protocone. In most or all other characters, the two teeth are very similar. AMNH 56324 is not sufficiently diagnostic to be made a type, but it may well represent an undescribed species.

MEASUREMENTS: AMNH 56324, upper cheek tooth: maximum length, 2.45 mm., anterior width, 3.10 mm., posterior width, 3.25 mm.; AMNH 22195, *P. atavus* from type locality, Bear Creek, Montana, upper cheek-tooth: maximum length, 1.50 mm., anterior width, 1.70 mm., posterior width, 1.80 mm.

MEDIUM-SIZED SPECIES OF *Paramys*

Figure 18

Six teeth, two upper and four lower, appear to represent a single species of intermediate size. Of the two upper molars, both from Reculosa Blowout, one (AMNH 56204) is nearly fresh and may be briefly described. The protocone is large, separated from the anterior cingulum, and its apex is lingual to the most lingual extent of this cingulum. There are two subequal metaconules, much larger than the subequal two paraconules. The mesostyle is doubled and complex, and the hypocone is separated lingually from the protocone by a groove. These features are much like those of the

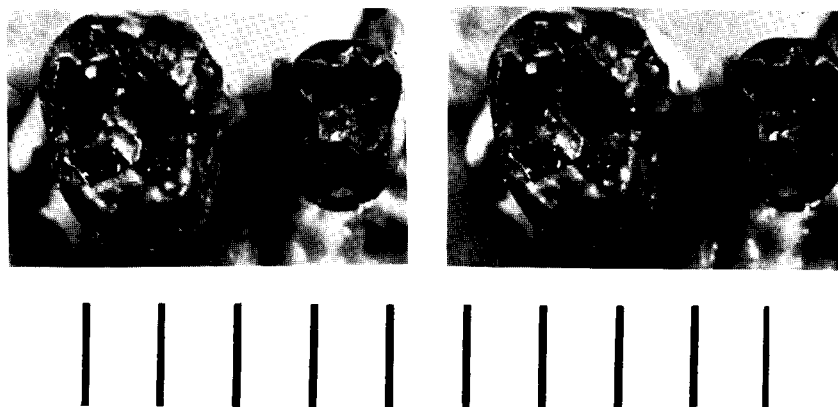


FIG. 17. Left, AMNH 56324, cf. *Paramys atavus*, upper right cheek tooth from Monument Blowout, Powder River local fauna; right, AMNH 22195, *Paramys atavus*, upper left cheek tooth from Bear Creek local fauna.

M<sup>2</sup> of *P. copei bicuspis* (Wood, 1962, p. 47), but the last character distinguishes upper molars of *P. excavatus taurus* (*op. cit.*, p. 57). Measurements of both teeth are smaller than the former "subspecies" and larger than the latter (for either M<sup>1</sup> or M<sup>2</sup>).

The single P<sub>4</sub> (AMNH 56209, Rec.) is much like *P. e. taurus*, but the hypoconid is even more enlarged, almost as in some *Reithroparamys*. The best-preserved lower molar (?M<sub>1</sub>, AMNH 56208, loc. 52-14) shows a large metaconid, far forward on the narrow trigonid basin, a smooth posterior edge (?cingulum) of the tooth, and a not very well-developed entoconid. Both of the above-mentioned "subspecies" are characterized by these patterns, but the teeth seem again somewhat closer to those of the American Museum specimens labeled *P. e. taurus* (by Wood?). In size, all four lowers fall within the ranges of *P. e. taurus*, being rather smaller than teeth of *P. c. bicuspis*.

On such meager material, it is impossible to determine if these teeth belong to one of Wood's named "subspecies" (or, as I would prefer, local populations), or to a new form. Considering the very early date of this assemblage and the apparent intermediacy of these specimens, they may represent a population ancestral to both named forms; this assumes, of course, that all teeth are referable to a single population. Such a population might, in Wood's classification, be best considered a subspecies of *Paramys*

*excavatus*, but this step is not taken at the present time.<sup>1</sup> Comparative measurements will be found in table 8.

#### SMALL-SIZED SPECIES OF ?*Paramys*

##### Figure 18

Five smaller teeth are in some ways similar to the above specimens. Of two upper molars, the best preserved is AMNH 56200 (Rec.) It has single conules; the metaconule is larger than the paraconule, but similar in size to the hypocone; there is a single small mesostyle; the lingual features are as in the above description. The sole upper premolar (AMNH 56201, Rec.) is heavily worn, the hypocone, paraconule, and mesostyle being effectively erased if ever there; the paraloph is straight and directed labiolingually, the metaloph curves mesially interior to the metaconule. The lower teeth, one of which may be a P<sub>4</sub>, are even more worn and no special features are distinguishable; the hypoconid is not so well developed as on the larger fourth premolar.

Referral of these teeth to a single form is quite uncertain. The upper molars are similar to each other and perhaps to P<sub>4</sub>; the two lowers are close; lower-upper reference is the most doubtful. P<sub>4</sub> is somewhat similar to the much

<sup>1</sup> It is possible that this species is the same as that from Four Mile termed by McKenna (1960, p. 82) *Paramys* sp. A, cf. *P. copei*.

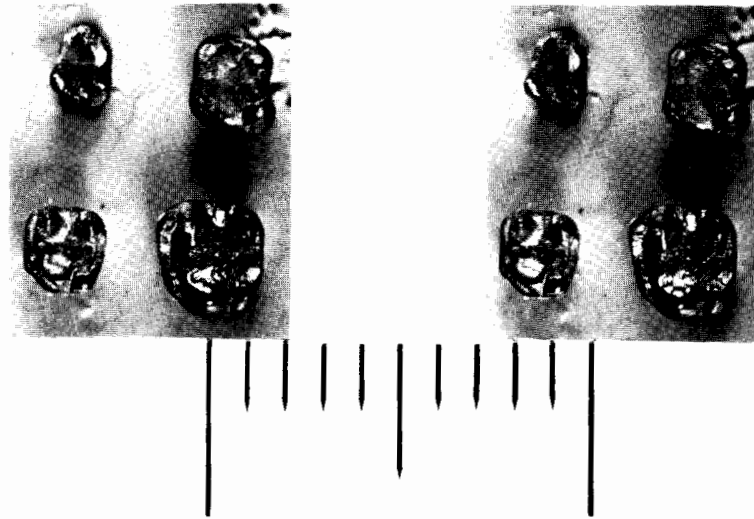


FIG. 18. *Paramys* spp. from the Powder River local fauna. Left, small-sized species: above, AMNH 56202, right ?M<sub>1</sub>, locality 51-62; below, AMNH 56200, left upper molar, Reculosa Blowout. Right, medium-sized species: above, AMNH 56208, right ?M<sub>1</sub>, locality 52-14; below, AMNH 56204, left upper molar, Reculosa Blowout.

TABLE 8  
MEASUREMENTS (IN MILLIMETERS) OF MEDIUM-SIZED AND SMALL-SIZED *Paramys*  
FROM THE POWDER RIVER BASIN

	P <sub>4</sub>	?M <sub>1</sub>	?M <sub>2</sub>	P <sup>4</sup>	M-		
Medium-sized							
AMNH	56209	56208	56207	56206	—	56205	56204
Locality	Reculosa	52-14	Reculosa	Bozeman	—	Reculosa	
Maximum length	2.70	2.55	2.80	2.80	—	2.80	2.90
Anterior width	2.10	2.50	2.40	2.55	—	2.95	2.80
Posterior width	2.50	2.10	2.55	2.80	—	3.30	3.00
Small-sized							
AMNH	56203	56202	—	—	56201	56200	56199
Locality	Dry	51-62	—	—	Rec.	Rec.	Dry
Maximum length	1.85	1.95	—	—	1.65	2.05	2.10
Anterior width	1.25	1.45	—	—	2.20	2.30	2.20
Posterior width	1.60	1.70	—	—	2.20	2.30	2.30
<i>P. copei bicuspis</i> <sup>a</sup>							
Maximum length	—	—	2.99-3.50	—	—	2.90-3.13	—
Anterior width	—	—	2.49-3.03	—	—	2.62-3.80	—
Posterior width	—	—	2.32-2.50	—	—	2.93-3.75	—
<i>P. excavatus taurus</i> <sup>b</sup>							
Maximum length	—	—	2.42-2.90	—	—	2.20-2.53	—
Anterior width	—	—	2.03-2.60	—	—	2.50-3.30	—
Posterior width	—	—	2.35-2.80	—	—	2.48-3.00	—

<sup>a</sup> From Wood, 1962, pp. 47-48.

<sup>b</sup> From Wood, 1962, pp. 57-58.



FIG. 19. Indeterminate genus and species of miacine from the Powder River local fauna; AMNH 56325, left  $M_2$  or  $M_3$ , locality 51-33.

younger *P. huerfanensis*, and the upper molars could refer to their as yet unknown homologues in this species, but the lower teeth do not seem like the badly worn mandibles from Huerfano. They appear closer to the early species of *Reithroparamys*, *Lophiparamys*, and *Microparamys* from the American Museum collections. For the moment, it is sufficient to note small paramyine(s), possibly *Paramys* sp., in the Powder River fauna. Their measurements are listed in table 8.

#### ORDER CARNIVORA

##### SUBORDER FISSIPEDA

##### SUPERFAMILY MIACOIDEA COPE, 1880a

##### FAMILY MIACIDAE COPE, 1880a

##### SUBFAMILY MIACINAE COPE, 1880a

##### Indeterminate genus and species

##### Figure 19

The only miacine from Powder River is AMNH 56325, from locality 51-33, an isolated  $M_3$  or perhaps  $M_2$  of rather small and "primitive" aspect. The trigonid is compressed anteroposteriorly, the talonid compressed laterally and curved, and the cusps distinct. The tooth might be of *Miacis*, but not the common lower Gray Bull species, *M. exiguus*; it might be similar to the small *M. jepseni* of the Lysite

(cf. Guthrie, 1967, p. 30). On the other hand, this specimen could be similar to those of the ancestor of *Vulpavus* or *Oodectes*. The tooth measures  $2.05 \times 2.60$  mm.

##### SUBFAMILY VIVERRAVINAE WORTMAN AND MATTHEW, 1899

##### *DIDYMICTIS* COPE, 1875a

##### *Didymictis protenus* (Cope, 1874)

Three isolated and damaged teeth are referable by size to this species of *Didymictis*. The genus is being revised by Giles T. MacIntyre, and his identification and suggested terminology are accepted. The teeth and their measurements are: AMNH 56198, lower molar, Reculosa Blowout,  $4.75 \times 8.95$  mm.; AMNH 56197, lower molar trigonid, Dry Well, width, 5.65 mm.; AMNH 56196,  $P^3$ , Monument Blowout, maximum length along axis, 10.40 mm. Several additional molar trigonids may pertain to this genus or to various deltatheridians.

##### ORDER CONDYLARTHRA

Van Valen (1963, 1966, 1969b) has reorganized the condylarths, adding to the order the apparently ancestral arctocyonids as well as the mesonychids and tillodonts. He advocated, and I follow, separation of three suborders for the mesonychids, the tillodonts, and all

other families including arctocyonids. Tillodontia is obviously usable as a subordinal nomen, and Van Valen (1969b) has proposed names, Mesonychia and Arctocyonia, for the other suborders. Although a case could be made for the use of Acreodi (Matthew, 1909, p. 327) as the nomen for mesonychids and Procreodi (Matthew, 1915a, p. 5) as the nomen for more "normal" condylarths, Van Valen's new names are less ambiguous and clearly distinguish the taxa from Matthew's outmoded concept of the Creodontia.

#### SUBORDER ARCTOCYONIA

FAMILY ARCTOCYONIDAE GIEBEL, 1855

SUBFAMILY OXYCLAENINAE SCOTT, 1892

cf. "*Chriacus*" *gallinae* Matthew, 1915a

Figure 20

Two isolated and damaged molars, AMNH 56326 and 56327, represent an animal similar to that described by Matthew as *Chriacus gallinae*, from the "Wasatch" of New Mexico. The type of this species, AMNH 16223, from the Almagre fauna, San Jose Formation, has not been found in a recent search of the collection, but Matthew's illustration of the upper molar indicates clearly that this is a not a species of *Chriacus*. The type of *Chriacus* is *C. pelvidens*, from the Torrejonian of the Nacimiento Formation, San Juan Basin, which is based on a mandible;

the upper dentition is known in AMNH 2384, which also has lower teeth that match the holotype. In this maxilla, the hypocone is present as a true cusp on  $M^{1-2}$ , projecting distally; the distobuccal corner of the tooth is also enlarged, thus giving a concave-anterior aspect to the distal margin. Matthew (1915a, p. 6) illustrated the type of "*C.*" *gallinae* with only  $M^2$  present, and the exact structure of the hypocone is not clearly discernible; it appears, however, to be more of a cingular ridge than a true cusp.

AMNH 48006, also from the Almagre, is a partial skeleton, with lower jaws and a single fragmentary upper molar, which appears referable to Matthew's species. In this animal, the molar hypocone is well preserved and consists solely of a broad cingular shelf extending around the lingual aspect of the tooth from conule to conule. A faint crest connects the protocone to this shelf; the lingual edge of the shelf is higher than the lingual base of the protocone, so that the former slopes down to the latter, producing a groove. The metacone and associated distobuccal area of this tooth is missing, so its exact position is uncertain. The parastyle is not expanded.

The type of hypocone just described is similar to that on  $M^3$  of *C. pelvidens*, but in this animal the parastyle is greatly enlarged and produced mesiobuccally. It is possible that the Wasatchian specimen is an  $M^3$ , but the difference in form



FIG. 20. "*Chriacus*" from the Wasatchian. Left, AMNH 48006, right ? $M^3$  of "*Chriacus*" *gallinae*, from the Almagre local fauna; right, AMNH 56326, right ? $M^3$  of "*Chriacus*" cf. *gallinae*, locality 52-14, Powder River local fauna.

of the parastyle is probably as indicative of distinction as is the form of the cingular hypcone.

The lower teeth of Matthew's type are worn badly, but probably would not be too different from the well-preserved molars in AMNH 48006. These teeth are similar to those of Paleocene *Chriacus* and all *Thryptacodon*, but are narrower. The talonids especially are compressed laterally but of similar length.

The necessity of separating "*Chriacus*" *gallinae* from the Paleocene species referred to this genus has also been noted by Van Valen (letter, October, 1968). I do not erect a new genus at this time, because Matthew's type specimen is missing and because a thorough study of postcranial elements is necessary first. The matter will be discussed further in a future paper by Van Valen or myself, and the Four Mile material will also be included.

The two teeth from the Powder River local fauna are similar to, but smaller than, those from the New Mexican Eocene; AMNH 56326 from locality 52-14 is perhaps an M<sup>3</sup>; its paracone and parastyle are broken away, but the metacone is present. The distobuccal corner of the tooth is bent distolingually even more than in the Torrejonian specimen, and the buccal face of the tooth is not hollowed as in that animal. The lower molar (AMNH 56327, locality 41-33), probably M<sub>1</sub>, is closer in size to the New Mexican specimen.

MEASUREMENTS: AMNH 56326, ?M<sup>3</sup>, 5.60 × 4.0 + mm.; AMNH 56327, ?M<sub>1</sub>, 4.0 + × 6.0 + mm.; AMNH 48006, M<sub>1</sub>, 4.30 × 7.00 mm. (M<sub>2</sub>, 4.40 × 6.60 and 4.45 × 6.40 mm.); ?M<sup>3</sup>, 8.90 × 5.1 + mm.

#### FAMILY PHENACODONTIDAE COPE, 1881d

##### *PHENACODUS* COPE, 1873

##### *Phenacodus primaevus* Cope, 1873

The rather rare *Phenacodus* from Powder River consists mostly of isolated teeth, but these are separable on grounds of size into three series. Five large teeth are similar to those broadly termed *P. primaevus*, but relation to one or another of the several subspecific taxa previously described (by Granger, 1915; Simpson, 1937) is not possible with such fragmentary material.

MEASUREMENTS (fairly complete teeth): P<sup>4</sup>, 11.10 × 10.40 mm. (AMNH 56195, 51-34) and 11.15 × 10.65 mm. (AMNH 56194, Dry Well);

M<sup>3</sup>, 12.40 × 8.90 mm. (AMNH 56193, 51-34) and 12.05 × 8.70 mm. (AMNH 56192, Recclusa Blowout). The last specimen is quite similar to AMNH 17192, from Mason Pocket Tiffanian, an M<sup>3</sup> referred to *P. grangeri* but not mentioned by Simpson (1935) in his discussion of these specimens. The Tiffany tooth, measuring 12.50 × 8.70 mm., serves to tie the Powder River animal, if not the *P. primaevus* complex, to Paleocene forms.

##### *Phenacodus brachypternus* Cope, 1882a

Two mandible fragments and a number of isolated teeth appear referable to this species. The teeth are relatively narrow, as is common in the species, and are smaller than any specimen measured by Guthrie (1967, p. 40, fig. 29).

MEASUREMENTS: jaws, AMNH 56191: P<sub>3</sub>, 4.15 × 7.30 mm., P<sub>4</sub>, 4.50 × 7.35 mm., M<sub>1</sub>, 5.50 × 7.10; AMNH 56190: M<sub>1</sub>, 5.35 × 6.50 mm., M<sub>2</sub>, 6.00 × 6.60 mm. (both Dry Well); isolated first or second lower molars, 5.25 × 6.60 mm. (AMNH 56189, 51-31) and 4.95 × 6.30 mm. (AMNH 56188, Recclusa Blowout); M<sup>3</sup>, 7.15 × 5.05 mm. (AMNH 56187, Recclusa Blowout).

##### *Phenacodus vortmani* (Cope, 1880b)

##### Figure 21

*Phenacodus vortmani* originally was employed for all Wasatchian medium-sized *Phenacodus*. In 1915, Granger separated *P. copei* for the larger, mostly Gray Bull specimens. Guthrie (1967, p. 40) has shown that these specimens intergrade and has combined the two species. Simpson (1935) described *P. matthewi* and *P. gidleyi*, as well as the larger *P. grangeri*, from the Tiffany area of Colorado, but not from Mason Pocket; McKenna (1960, pp. 97-99) has referred to *P. matthewi* two jaws from Four Mile, from where he does not recognize either *P. copei* or *P. vortmani*. Reexamination of the Tiffany specimens shows that the two types have only one tooth in common, M<sub>3</sub>. The observed differences in size (*P. matthewi* is slightly larger) and morphology (little, if any) indicate that nothing more than interpopulational variability is represented (the two specimens do not come from the same locality). I therefore suggest combination of *P. matthewi* and *P. gidleyi* into a single species.

The important question now is to relate the Tiffanian and Wasatchian forms to each other or to deny such relation. McKenna has referred the two Four Mile mandibles to the earlier species on the basis of simpler teeth, especially the lack of a strong metastylid. It is to be noted that only four molars and a badly worn  $P_4$  are known of Paleocene *P. matthewi*, so McKenna's use of premolars to indicate relationship is not so strong as it might seem. In addition, in a Sand Coulee specimen (AMNH 16125, with most of both upper and lower teeth) and a jaw from Powder River (AMNH 56328, Bozeman locality, with  $P_2$ - $M_2$  and a few other teeth), the morphology described by McKenna is duplicated precisely. The Four Mile specimens are small, but within the range of those measured by Guthrie on all counts. It seems that these specimens are the earliest members of the medium-sized Wasatchian species, which would be expected to be somewhat more primitive in some characters than their assumed descendants. For these reasons, I would prefer not to use *Phenacodus matthewi* for any Wasatchian animals, but instead to use *P. vortmani*. In time, with revision<sup>1</sup> and collec-

<sup>1</sup> Since this section was written, Robert M. West of Adelphi College has commenced a thorough revision of the Phenacodontidae. His conclusions, based on all available specimens, will certainly supplant mine.

tion of latest Paleocene specimens, I would think that *P. matthewi* and *P. vortmani* will be shown to intergrade, as the former seems to be the ancestor of the latter. The question will then arise, as it has in so many other lineages, of whether to divide the species or simply to have one evolving lineage of a single species.

Comparative measurements of all Paleocene and earliest Eocene middle-sized *Phenacodus* known to the author are given in table 9.

*ECTOCION* COPE, 1882b

*Ectocion osbornianus* (Cope, 1882a)

The taxonomy of *Ectocion* has been dealt with in depth four times. Granger (1915) accepted Cope's type species *E. osbornianus* (of Gray Bull age) and defined three others: *E. superstes*, a large form from the Lost Cabin (with two referred specimens of Gray Bull age); a smaller *E. ralstonensis*, with "Clark Fork" type and specimens from Sand Coulee and Gray Bull; and the very small *E. parvus* of the "Clark Fork." In 1937, Simpson reviewed the American Museum Clark Fork collection and considered *E. parvus* as distinctive (only the type mandible, AMNH 16080, has ever been described), but possibly aberrant. He noted the essential continuity and unity of the "Clark Fork"-Sand

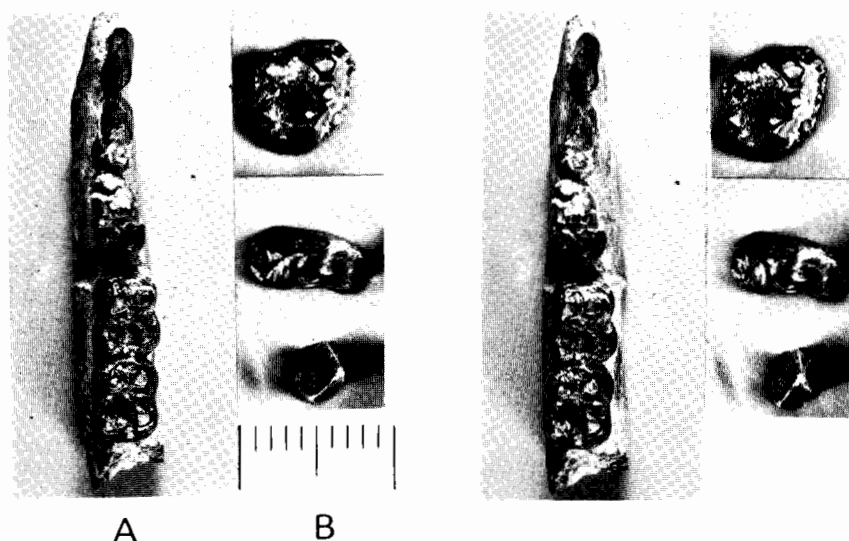


FIG. 21. *Phenacodus vortmani* from the Powder River local fauna; AMNH 56328, Bozeman locality. A. Right mandible with  $P_2$ - $M_2$ . B. Top to bottom, right  $M^3$ , left  $P_2$ , incisor.

TABLE 9  
MEASUREMENTS OF SELECTED EARLY MEDIUM-SIZED *Phenacodus*

		Powder River		Sand Coulee		Four Mile		Tiffany	
		<i>P. vortmani</i>		<i>P. vortmani</i>		<i>P. "matthewi"</i>		<i>P. matthewi</i>	
		AMNH 56328 Bozeman	AMNH 56186 Reclusa	AMNH 16125 Right	Left	UCMP 4034 <sup>a</sup>	UCMP 46168	AMNH 17191 <sup>b</sup>	AMNH 17193 <sup>c</sup>
P <sub>2</sub>	W	3.10	—	4.05	4.05	—	—	—	—
	L	6.40	—	8.25	8.00	—	—	—	—
P <sub>3</sub>	W	4.30	4.35 <sup>d</sup>	4.80	4.85	—	4.20	—	—
	L	7.45	7.85 <sup>d</sup>	8.35	8.20	—	7.40	—	—
P <sub>4</sub>	W	5.30	5.95	6.25	6.15	—	5.30	—	4.70
	L	8.85	8.70	8.30	8.50	—	7.90	—	6.80
M <sub>1</sub>	W	7.15	—	7.10	7.10	—	6.60	—	5.75
	L	8.50	—	9.05	8.70	—	8.00	—	6.85
M <sub>2</sub>	W	6.95	—	6.95	7.25	6.60	6.80	6.80	—
	L	8.40	—	8.90	8.65	8.00	7.85	7.50	—
M <sub>3</sub>	W	—	—	6.15	6.15	6.10	5.60	5.65	5.15
	L	—	—	8.85	8.60	8.20	8.10	7.65	7.40
P <sup>4</sup>	W	—	—	—	7.70	—	—	—	—
	L	—	—	—	7.25	—	—	—	—
M <sup>1</sup>	W	—	—	9.05	9.30	—	—	—	—
	L	—	—	8.25	8.60	—	—	—	—
M <sup>2</sup>	W	—	—	—	9.70	—	—	—	—
	L	—	—	—	8.00	—	—	—	—
M <sup>3</sup>	W	8.20	—	7.90	7.80	—	—	—	—
	L	6.50	—	6.20	6.20	—	—	—	—

<sup>a</sup> Measured from drawing, McKenna, 1960, p. 98, fig. 52.

<sup>b</sup> Type of *P. matthewi*.

<sup>c</sup> Type of *P. gidleyi*.

<sup>d</sup> From opposite side of AMNH 56328.

Coulee-Gray Bull series and considered *E. ralstonensis* as a subspecies of *E. osbornianus*. *Ectocion superstes* was retained as a possible end member of the sequence.

In 1943, in his definitive discussion of chronoclines, Simpson used *Ectocion* as the example, relegating all specimens to *E. osbornianus* with a temporal subspecies at each of four horizons. *Ectocion parvus* was lumped into *E. o. ralstonensis* at one end of the distribution and *E. o. superstes* considered a late form of the broader species.

The defining character of the subspecies was temporal horizon, although Simpson used a single linear variate, length of M<sub>1</sub>, to illustrate the variational range of the groups.

In McKenna's (1960) work on the Four Mile fauna, he reviewed Simpson's classification, finding it untenable on several counts (p. 102):

1. "Overlapping measurements of a single character need not mean that successive taxa are of subspecific rank.

2. "There is no compelling reason for lumping

*E. parvus* with '*E. osbornianus ralstonensis*.'

3. "*Ectocion superstes* need not be considered a subspecies of *E. osbornianus* on the basis of available evidence." P<sub>3</sub>, McKenna noted, has a distinct high paraconid and P<sub>4</sub> a distinct entoconid. He further reasoned that since Simpson (1943) listed only one Gray Bull specimen as belonging to Granger's *E. superstes*, the other probably is smaller. Finally, McKenna considered that *E. superstes* probably is specifically distinct from *E. osbornianus* and perhaps represents a late variant of *Phenacodus vortmani*.

4. "To lump all 'Gray Bull' specimens of *Ectocion* as one subspecies is undoubtedly premature," because of the long time involved and possibility of more than one evolving lineage.

Thus McKenna accepted two "Clark Fork" species (*E. parvus* and *E. ralstonensis*); the Sand Coulee subspecies, *E. o. complens* (defined by Simpson in 1943 to complete the pattern of one subspecies per horizon); the Gray Bull typical subspecies; and *E. superstes*, questionably, in the Lost Cabin.

As it has with many other taxa, Roger Wood's (1967) demonstration that some "Clark Fork" specimens are probably of Sand Coulee age, if determinable at all, has wrought havoc with the systematics of *Ectocion*. Wood showed that almost all *Ectocion* listed as Clark Fork are seemingly Sand Coulee (=early Gray Bull). The types of *E. ralstonensis* and *E. parvus* are both from the head of Big Sand Coulee, type locality of these beds in the Clark Fork Basin, as are most other specimens. In addition, determining exact levels within the Gray Bull for Bighorn Basin specimens is difficult, as labels and comments may disagree and exact definition has never been made. For these reasons it seems best to consider the entire sample of Gray Bull specimens as a single unit for the present. The specimens previously termed *E. o. osbornianus*, *E. o. complens*, and *E. o. ralstonensis* should now be referred to as *E. osbornianus* with no further division. The more recent Yale and perhaps Princeton collections, with more attention to stratigraphy, might form a basis for future breakdown of this (and other?) evolutionary species. It is to be noted here, in defense of Simpson, that with the data available to him in 1943, his arrangement was satisfactory and not based, as McKenna implied, on length of M<sub>1</sub>, which was only employed as an illustrative device. This also explains why only one Gray

Bull specimen of *E. superstes* (of Granger) was listed; the other specimen, AMNH 15324, only has M<sub>2-3</sub>.

The type of *Ectocion superstes* is larger than either Gray Bull specimen, but does appear to be an *Ectocion* dentally. In opposition to McKenna, I note that all *Ectocion* P<sub>4</sub>s have a strong entoconid. P<sub>3</sub> of *E. superstes* is distinct in possessing a strong high paraconid, but it is rather removed in time from the *E. osbornianus* complex (Guthrie, 1967b, reported no *Ectocion* from the type Lysite); it appears to be the end-point of the lineage and of the genus. *Ectocion superstes* might be considered a subspecies of *E. osbornianus*, but for the present, without more data on variation, it is best left as a full species, represented only by the type.

"*Ectocion*" *parvus* is only represented by a rather worn mandible with M<sub>1 3</sub>. The entoconid wear on M<sub>3</sub> is not typical of *Ectocion* and suggests comparison with *Hyopsodus*, as do all the teeth on the bases of molar wear and size. It is farther from *Ectocion osbornianus* than *Phenacodus brachypternus* is from typical *P. vortmani* (cf. McKenna, 1960, p. 101), and certainly much more distinct than is *E. superstes*.

The *Ectocion osbornianus* sample from Powder River consists of eight isolated teeth and three fragments of upper and lower jaws. The teeth average somewhat small, as expected for an early Gray Bull deposit, with M<sub>1</sub> lengths of 6.0, 7.1, and possibly 5.9 and 6.3 mm.; the last two teeth are isolated and could be M<sub>2</sub>. These values tally best with the combined "Clark Fork" and Sand Coulee values of Simpson, 1943.

MEASUREMENTS (well-preserved teeth in jaws): P<sub>3</sub>, 4.35 × 6.75 mm.; P<sub>4</sub>, 5.30 × 7.30 mm.; M<sub>1</sub>, 6.00 × 7.10 mm. (AMNH 56161, Bozeman); M<sub>1</sub><sup>1</sup>, 8.60 × 7.15 mm.; M<sub>2</sub><sup>2</sup>, 9.80 × 7.40 mm. (AMNH 56160, Bozeman). For comparison with Four Mile, single loose M<sub>3</sub>s measured 5.90 × 8.35 mm. from Powder River (AMNH 56159, Bozeman) and 4.60 × 7.30 mm. from Four Mile (UCMP 44799).

FAMILY HYOPSODONTIDAE TROUESSART,  
1879

SUBFAMILY HYOPSODONTINAE TROUESSART,  
1879

*HAPLOMYLUS* MATTHEW, 1915b

*Haplomylus speirianus* (Cope, 1880c)

In Cope's original description of this species,

TABLE 10  
 STATISTICAL DATA ON THE TEETH OF *Haplomylys speirianus*  
 FROM THE POWDER RIVER BASIN

	N	OR	M	SE	$\sigma$	V
P <sub>3</sub>						
W	4	1.35-2.00	1.61	0.14	0.28	17.2
L	4	2.85-2.95	2.90	0.02	0.04	1.4
P <sub>4</sub>						
W	10	1.45-1.80	1.63	0.03	0.10	6.2
L	10	2.70-3.20	2.97	0.05	0.15	5.1
M <sub>1</sub>						
W	3	2.00-2.35	2.18	0.10	0.18	8.0
L	3	2.60-3.00	2.73	0.13	0.23	8.4
M <sub>2</sub>						
W	2	2.20-2.40	2.30	0.10	0.14	6.1
L	2	2.75-2.85	2.80	0.05	0.07	2.5
M <sub>3</sub>						
W	5	1.65-2.00	1.80	0.06	0.13	7.1
L	5	2.55-3.05	2.48	0.06	0.13	5.3
P <sup>4</sup>						
W	5	2.60-3.05	2.82	0.07	0.16	5.7
L	5	2.50-2.90	2.66	0.07	0.15	5.8
M <sup>1</sup>						
W	1	— —	3.65	—	—	—
L	1	— —	2.85	—	—	—
M <sup>2</sup>						
W	1	— —	4.00	—	—	—
L	1	— —	2.60	—	—	—
M <sup>3</sup>						
W	3	2.15-2.60	2.38	0.13	0.23	9.5
L	3	1.85-2.10	2.00	0.08	0.13	6.6

he gave the type locality as Wind River Basin. Matthew (1915b, p. 314) and Gazin (1953, p. 22) have shown that this type, as well as the types of *Esthonyx spatularius* (see below) and *Didymictis leptomylys*, probably was found in the Bighorn Basin, especially as all three are almost "index fossils" of the (early) Gray Bull horizon. Although the other two forms may be no more than small variants of the Gray Bull species, *Haplomylys* is generically distinct from *Hyopsodus*, its closest relative at this horizon.

In his review of the "Clark Fork" assemblage, Simpson (1937) indicated that the three specimens of *Haplomylys* from this level appeared significantly larger than the supposedly later Sand Coulee (= early Gray Bull) material, and more in line with specimens from later in the Gray Bull. In support of this indication, he published statistical data for 23 M<sub>2</sub> lengths of Gray Bull (including ?Sand Coulee) specimens. Neither raw data nor additional statistics were

published, but Simpson stated that they reinforced the differences from the Clark Fork specimens. I have re-measured all the American Museum specimens of *Haplomylys* from the Bighorn and Clark Fork basins incorporating Roger Wood's (1967) work on the stratigraphic position of the Clark Fork, as well as the specimens from Powder River and Four Mile. Statistics are given in tables 10-12. In addition, Student's t-test was calculated for several measurements between these three samples.

Of the Bighorn/Clark Fork specimens, 39 are lower jaws, and four upper, one with associated P<sup>4</sup>. Exact horizons in the Gray Bull are not presently possible to determine, but no specimen appears to come from a definitely late Gray Bull horizon (counting Sand Coulee as early). There is no significant change in size with horizon in any tooth; the large "Clark Fork" specimens noted by Simpson are offset by the smaller ones from the Sand Coulee

TABLE 11

STATISTICAL DATA ON THE TEETH OF *Haplomyllus speirianus* FROM THE BIGHORN AND CLARK FORK BASINS

	N	OR	M	SE	$\sigma$	V
P <sub>3</sub>						
W	2	1.10-1.20	1.15	0.05	0.07	6.1
L	2	2.45-2.75	2.60	0.15	0.21	8.2
P <sub>1</sub>						
W	13	1.30-1.90	1.66	0.05	0.19	11.7
L	13	2.70-3.40	3.06	0.06	0.23	7.6
M <sub>1</sub>						
W	27	1.85-2.70	2.21	0.04	0.21	9.6
L	27	2.45-3.20	2.71	0.04	0.22	8.0
M <sub>2</sub>						
W	36	1.95-2.85	2.37	0.04	0.23	9.9
L	38	2.40-3.10	2.75	0.03	0.21	7.5
M <sub>3</sub>						
W	23	1.55-2.15	1.79	0.03	0.17	9.2
L	23	2.20-2.90	2.55	0.04	0.17	6.9
P <sub>1</sub>						
W	2	2.50-2.55	2.53	0.02	0.04	1.4
L	2	2.35-2.45	2.40	0.05	0.07	2.9
M <sup>1</sup>						
W	3	3.10-3.30	3.20	0.06	0.10	3.1
L	3	2.55-2.85	2.72	0.09	0.15	5.6
M <sup>2</sup>						
W	5	3.50-4.00	3.72	0.09	0.20	5.4
L	5	2.40-2.75	2.55	0.06	0.15	3.7
M <sup>3</sup>						
W	3	2.15-2.60	2.37	0.13	0.23	9.5
L	3	1.60-1.95	1.75	0.10	0.18	10.3

(often from the same localities). Comparisons among the three samples show no cases of difference at less than or equal to the 0.08 level of probability, and most samples (especially those with sample sizes of 10 or more) gave values in the range of 0.2 to 0.5, not at all meaningful.

In the Powder River collection, *Haplomyllus* and *Hyracotherium* are the second most common mammals after *Hyopsodus*. Of 86 *Haplomyllus* teeth, however, 47 were isolated first or second molars, which are not clearly differentiable. The 39 other teeth, mostly in jaws, show no morphological distinctions. The Four Mile specimens used included all the teeth in jaws in the American Museum, as well as those measured by McKenna (1960, p. 105). There does not appear to be any distinction between McKenna's measurements and my own.

*HYOPSODUS* LEIDY, 1870

*Hyopsodus* cf. *miticulus* (Cope, 1874)

*Hyopsodus* is by far the most common mammal in Wood's Powder River Basin collections. Almost 150 isolated teeth and eight jaws with two to five teeth have been recognized. Specific allocation of this material is somewhat difficult, however, due to some uncertainty about populations of the earliest *Hyopsodus*. McKenna (1960, p. 106) proposed *H. loomisi* for a rather rare, small form of the genus known from Four Mile and (as *H. simplex*) from the early Gray Bull of the Clark Fork, Bighorn, and Wind River basins. In addition to size, the upper teeth of *H. loomisi* were characterized by small hypocones (lacking in M<sup>3</sup>), connected to the protocone, and by lack of labial cingulum. Lower teeth were not recognizably different from the contemporaneous *H. miticulus*, with which there

TABLE 12

STATISTICAL DATA ON THE TEETH OF *Haplomyllus speirianus* FROM FOUR MILE

	N	OR	M	SE	$\sigma$	V
P <sub>3</sub>						
W	1	—	1.30	—	—	—
L	3 (2) <sup>a</sup>	2.95-3.30	3.12	0.10	0.18	5.6
P <sub>4</sub>						
W	1	—	1.40	—	—	—
L	4 (3)	2.85-3.50	3.21	0.13	0.27	8.5
M <sub>1</sub>						
W	5	1.85-2.15	2.04	0.05	0.11	5.8
L	16 (11)	2.40-3.00	2.63	0.04	0.15	5.8
M <sub>2</sub>						
W	5	2.05-2.60	2.31	0.09	0.20	8.6
L	25 (20)	2.50-3.20	2.76	0.03	0.18	6.4
M <sub>3</sub>						
W	5	1.55-1.90	1.72	0.06	0.13	7.3
L	20 (15)	2.40-2.90	2.54	0.03	0.16	6.2
P <sub>4</sub>						
W	2	2.90-3.25	3.08	0.07	0.25	8.0
L	2	2.60-2.90	2.75	0.15	0.21	7.7
M <sup>1</sup>						
W	1	—	3.55	—	—	—
L	1	—	3.20	—	—	—
M <sup>2</sup>						
W	1	—	4.20	—	—	—
L	1	—	3.00	—	—	—
M <sup>3</sup>						
W	1	—	2.90	—	—	—
L	1	—	2.20	—	—	—

<sup>a</sup>Specimens in parentheses measured by McKenna, 1960, p. 105.

was an intergradation in size; as *H. simplex* was based on a somewhat "aberrant" lower jaw, all uppers and more normal lowers referred to it were re-allocated by McKenna to *H. loomisi*. Gazin (1962, pp. 62-63) recognized this species for small specimens and a single upper molar showing the defining characters; other uppers from the same locality were more typically *H. miticulus* in morphology. Guthrie (1967b, pp. 36-38) discussed the matter further, and gave measurements of one character in many specimens. He concluded that *H. loomisi* was apparently distinct from, but perhaps ancestral to, Gray Bull *H. miticulus*. He argued that since the larger group from Four Mile had M<sub>2</sub> length (and possibly other features) larger than the sample from the Sand Coulee level (some of which are referred to *H. loomisi* by McKenna), the former population is not related to the latter, but may be ancestral to the large Lysite form. Gazin (1968) accepted *H. loomisi* as distinct (and more primitive) without further comment.

Much more material from East Alheit Pocket and other Four Mile localities is now available, however, which can be analyzed both in terms of size and morphology. In terms of size, it is necessary to determine if there is truly a bimodality in any measurements which would indicate more than one species. Furthermore, it must be determined if morphology as in *H. loomisi* occurs in larger specimens. A maxilla with P<sup>4</sup>-M<sup>3</sup>, from Sand Quarry at Four Mile, appears to show such morphology, but is the same size as that "typical" of *H. miticulus* according to the measurements of McKenna (1960, pp. 106, 109). AMNH 80034, the specimen in question, measures as follows: P<sup>4</sup>-M<sup>3</sup>, 13.65 mm.; P<sup>4</sup>-M<sup>2</sup>, 11.00.; M<sup>1-3</sup>, 10.10 mm.; M<sup>1-2</sup>, 8.00 mm.; M<sup>2-3</sup>, 6.75 mm.

With the large sample of a single population now available, it will be possible to investigate several aspects of this problem and to determine if the small and apparently "primitive" variants of early *Hyopsodus* are a separable species or whether they are merely the smaller members of a single widely varying species. As the Powder River Basin specimens show a great range in size, as well as both types of upper molar morphology, I am provisionally referring them to a broadly construed *Hyopsodus miticulus*, with precise allocation reserved until further study has been completed.

SUBFAMILY APHELISCINAE MATTHEW, 1918

*APHELISCUS* COPE, 1875a

*Apheliscus nitidus* Simpson, 1937

Figure 22

As noted above, the type of *Parapheliscus bjorni* has been shown to be a tooth of *Phenacolemur*. As the former genus was differentiated from *Apheliscus* mainly on the basis of morphology of P<sub>4</sub> and related adaptive differences, the demonstration that the sole P<sub>4</sub> referred to *Parapheliscus* is not apheliscine indicates that the genus is not valid.

Nine specimens of *Apheliscus* have been recognized in the Powder River collection, eight of them isolated teeth. The ninth, AMNH 56329, from Dry Well locality, is a maxilla fragment with P<sup>4</sup>-M<sup>2</sup> present. These teeth match those in AMNH 16935 (type of "*Parapheliscus*" *wapitiensis*) very closely in both size and morphology (see fig. 22B, C). Although these two specimens are smaller, they duplicate the morphology of AMNH 15849, the type of *A. nitidus* (fig. 22A). In these three maxillae, the molars show a small hypocone and the P<sup>4</sup>s have rather well-developed mesial, distal, and labial cingula (considering wear differences) and a protocone which is not expanded mesially. In these features they differ from AMNH 15696, which Matthew (1918, p. 592) referred to Cope's type species, *A. insidiosus* (Cope, 1874).

The three previously described specimens were all collected in the Bighorn Basin Gray Bull, but at somewhat uncertain horizons. The type species was based on a now-lost fragment of mandible from the late Wasatchian of New Mexico, the only individual from this region.

Setting aside the problem of *A. insidiosus* for a later and more detailed revision, the question remains as to distinction between *A. nitidus* and "*P.*" *wapitiensis*. The morphology of the upper teeth of the types is similar (considering wear), and relative age does not seem correlated with size. In addition, a series of P<sup>4</sup>s from East Alheit Pocket at Four Mile shows a size range that links the two extremes from the Bighorn Basin. I therefore consider that *Parapheliscus wapitiensis* Van Valen, 1967a, is a junior synonym of *Apheliscus nitidus* Simpson, 1937.

MEASUREMENTS: *Apheliscus nitidus*, P<sup>4</sup>s—AMNH 15849, type, 3.00 × 2.75 mm.; AMNH

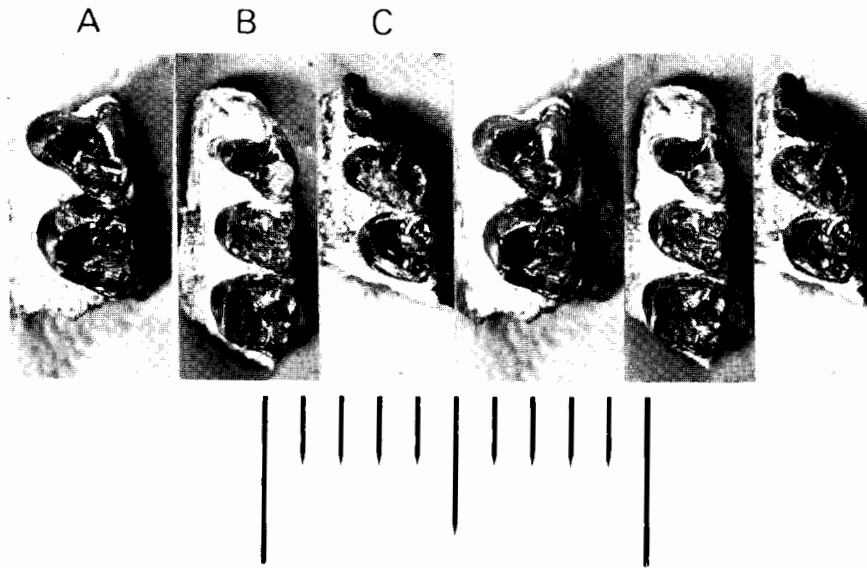


FIG. 22. *Apheliscus nitidus* from the early Wasatchian. A. AMNH 15849, type, left  $P^4-M^1$ , Gray Bull (?Sand Coulee), Bighorn Basin. B. AMNH 56329, left  $P^4-M^2$ , Dry Well locality, Powder River local fauna. C. AMNH 16935, right  $P^3-M^1$  (photographically reversed), Gray Bull (South Elk Creek), Bighorn Basin, type of "*Parapheliscus wapitiensis*."

16935,  $2.15 \times 1.95$  mm.; AMNH 56329,  $2.10 \times 2.05$  mm.; Four Mile specimens, AMNH unnumbered, range  $2.20-2.90 \times 1.90-2.45$  mm.

The ancestry of *Apheliscus* is still an unsolved problem. I agree with Gazin (1959) and other authors (e.g., Van Valen, 1967a) that the immediate ancestor is to be found in the genus *Phenacodaptus* Jepsen, 1930b. This genus has been known to date only from the late Paleocene Princeton quarry in the Polecat Bench Formation. It is also present, however, in the latest Paleocene of the Eagle Coal Mine at Bear Creek, Montana (AMNH 22172, 22181, 22245 [referred to *Parapheliscus bjorni* by Van Valen, 1967a], and 22246, and CM 11669). The two genera can best be placed in a higher taxon, the subfamily Apheliscinae, as they show a clearly new trend in adaptive pattern and ecology, as reflected in dental morphology.

The question thus devolves to the derivation of *Phenacodaptus*. Gazin (1959) has suggested a relationship to pentacodontids such as *Aphronorus*, which have somewhat similar fourth premolars, but highly distinct molars. McKenna (1960) and Van Valen (1967a) argued that

greater similarities in all cheek teeth are to be found with mioclaenine hyopsodonts, and they placed Apheliscinae as a subfamily of the hyopsodonts. Van Valen (*op. cit.*, pp. 249-250) went so far as to suggest affinity with *Haplaletes*, but in a rather uncertain manner.

More detailed comparison must be left to a complete revision of the subfamily, but it is worth noting here that of known hyopsodonts, *Haplaletes* does indeed appear most similar to early apheliscines in those parts known in both. The type species, *H. disceptatrix* of the middle Paleocene, is precluded from actual ancestry as it possesses heavy buccal cingula on the lower molars, a feature altogether lacking in *Phenacodaptus*. On the other hand, *H. pelicatus* Gazin, 1956, lacks cingulum on the type lower molars; this species is from the early Tiffanian of Bison Basin, however, and may be too late in time and too large to provide more than a structural indication of ancestry. It thus appears that apheliscine similarity of form to the pentacodontids is convergent, unless this family is also a derivative of early hyopsodonts.

## SUBORDER TILLODONTIA

FAMILY ANCHIPPONENTIDAE GILL, 1872

SUBFAMILY ESTHONYCHINAE COPE, 1883

*ESTHONYX* COPE, 1874*Esthonyx bisulcatus* Cope, 1874

As noted above, I accept Van Valen's (1963) placement of the tillodonts as a suborder of condylarths. The family for all tillodonts is given as Esthonychidae by Gazin (1953), who most recently reviewed the group, although he noted that Anchippodontidae Gill, 1872, has priority. This family was based on a genus and species with indeterminate type, however, and thus Gazin (as had Simpson, 1945) selected Esthonychidae. By the current edition of the Code (Stoll and others, 1964) this is not valid without a formal request for suspension, and I therefore have employed the older nomen.

TABLE 13;

STATISTICAL DATA ON THE TEETH OF *Esthonyx bisulcatus* FROM THE GRAY BULL OF THE CLARK FORK BASIN

	N	OR	M	SE	$\sigma$	V
P <sub>3</sub>						
W	2	3.50-4.10	3.80	0.30	0.42	11.2
L	3	5.40-6.25	5.78	0.25	0.43	7.5
P <sub>4</sub>						
W	6	4.45-6.15	5.17	0.27	0.66	12.8
L	5	6.10-7.60	7.04	0.28	0.63	9.0
M <sub>1</sub>						
W	6	5.70-6.40	6.08	0.13	0.31	5.1
L	7	7.15-8.05	7.56	0.13	0.35	4.6
M <sub>2</sub>						
W	7	5.50-6.75	6.25	0.15	0.40	6.4
L	7	6.90-8.60	8.04	0.22	0.57	7.1
M <sub>3</sub>						
W	4	4.50-5.70	5.08	0.26	0.52	10.2
L	4	8.50-10.00	9.25	0.32	0.65	7.0
M <sup>1</sup>						
W	2	9.90-10.90	10.40	—	—	—
L	2	6.45-6.60	6.53	—	—	—
M <sup>2</sup>						
W	1	— —	11.60	—	—	—
L	1	— —	6.90	—	—	—

Note: Although t-tests are probably not meaningful here, as noted in the text, they were calculated on the two larger samples for possible interest. In only two characters was the difference significant: P<sub>4</sub> length at the 0.04 level and M<sub>1</sub> length at the 0.015 level of probability. This agrees with the course of joining the two "populations."

TABLE 14

STATISTICAL DATA ON THE TEETH OF *Esthonyx bisulcatus* FROM THE (LATER) GRAY BULL OF ELK CREEK, CAMP 1, BIGHORN BASIN

	N	OR	M	SE	$\sigma$	V
P <sub>3</sub>						
W	4	3.75-3.90	3.83	0.03	0.06	1.7
L	4	6.00-6.65	6.33	0.14	0.27	4.3
P <sub>4</sub>						
W	9	4.60-5.30	4.91	0.07	0.22	4.5
L	11	6.80-8.10	7.67	0.12	0.40	5.2
M <sub>1</sub>						
W	8	5.50-6.25	5.84	0.11	0.30	5.2
L	11	7.30-8.45	8.04	0.10	0.33	4.1
M <sub>2</sub>						
W	10	6.00-6.50	6.28	0.05	0.18	2.8
L	12	7.90-9.00	8.35	0.09	0.33	3.9
M <sub>3</sub>						
W	3	5.30-5.50	5.37	0.07	0.12	2.1
L	5	9.50-10.20	9.88	0.12	0.26	2.6
P <sup>4</sup>						
W	1	— —	9.60	—	—	—
L	1	— —	7.50	—	—	—
M <sup>1</sup>						
W	4	10.90-11.10	11.00	—	—	—
L	4	7.90-8.15	8.06	—	—	—
M <sup>2</sup>						
W	3	11.40-13.30	12.20	—	—	—
L	3	8.20-8.60	8.37	—	—	—
M <sup>3</sup>						
W	3	12.40-12.70	12.57	—	—	—
L	3	7.20-7.70	7.37	—	—	—

Only three specimens of *Esthonyx* are known from the Powder River Basin, but their small size reopens a controversy about earliest Eocene tillodonts. The species *Esthonyx spatularius* was named by Cope (1880c), who gave the type locality as the Wind River Basin. As corrected by Matthew (1915b, p. 314) and Gazin (1953, p. 22), it is more likely that the type was found in the Gray Bull levels of the Bighorn Basin, probably the early Gray Bull as the type of *Haplomylus* was apparently collected at the same locality. The type specimen of *E. spatularius*, AMNH 4809, consists of an M<sub>3</sub> and several broken and not certainly associated other teeth.

Simpson (1937) and Gazin (1953) have referred to this species several jaws and teeth from the "Clark Fork" and Sand Coulee faunal levels of the Clark Fork Basin region. Most of these specimens are smaller, as is the type, than

TABLE 15  
STATISTICAL DATA ON THE TEETH OF *Esthonyx bisulcatus* FROM THE POWDER RIVER BASIN

	N	OR	M	SE	$\sigma$	V
P <sub>1</sub>						
W	1	—	4.00	—	—	—
L	1	—	6.95	—	—	—
M <sub>1</sub>						
W	2	—	5.60	—	—	—
L	2	7.20–7.80	7.50	—	—	—
M <sub>2</sub>						
W	1	—	6.35	—	—	—
L	1	—	8.30	—	—	—
M <sub>3</sub>						
W	1	—	4.50 <sup>a</sup>	—	—	—
L	1	—	8.45	—	—	—
P <sup>1</sup>						
W	1	—	7.50	—	—	—
L	1	—	6.00	—	—	—
M <sup>2</sup>						
W	1	—	6.60	—	—	—
L	—	—	—	—	—	—
M <sup>3</sup>						
W	1	—	11.30	—	—	—
L	1	—	6.20	—	—	—

<sup>a</sup>AMNH 4809, the type of *E. spatularius*, is an M<sub>3</sub> measuring 4.80 × 8.45 mm. All referred specimens are listed in the Clark Fork Basin sample.

Bighorn Basin Gray Bull specimens. The situation is thus similar to that in such diverse genera as *Didymictis*, *Hyopsodus*, and *Pelycodus*. The small forms can be considered either as small variants, a subspecies, or a distinct species.

I have examined the American Museum collections of *Esthonyx* and separated out two somewhat localized "populations." One consists of seven specimens from five localities in the Clark Fork Basin (obviously large specimens referred to *E. latidens* and *E. grangeri* were not included in this sample); included specimens are AMNH 16065, 16144, 16165, 16873, 56620, and two unnumbered specimens. The second sample is a group of nine specimens collected by Granger in 1910 at camp 1 on Elk Creek—the exact level of this locality is uncertain, although it is probably of later Gray Bull age, but at least all nine individuals appear to be from a rather localized area in space and presumably in time; specimens are AMNH 15111, 15113, 15114, 15119, 15120, 15122, 15123, 15126,

and one unnumbered. Selected statistics of P<sub>3</sub>–M<sub>3</sub> are given in tables 13–15. The Clark Fork Basin specimens, with which both the type of *E. spatularius* and the Powder River sample agree most closely, are generally smaller in size than the Elk Creek group, but there is overlap to some extent. Tests of statistical significance (c.g., student's t) are probably not meaningful as the samples are only relatively cohesive. Until precise data on stratigraphic level and relative occurrence of such size-grades are available, it seems best to consider the smaller forms as (possibly early) variants of the typical species, and this course is followed here. *Esthonyx spatularius* Cope, 1880c, is thus a junior synonym of *Esthonyx bisulcatus* Cope, 1874. Obviously some data are lost for purposes of correlation, but comparison of measurements and not just names will allow almost complete retrieval of this information. The retention of *E. spatularius* as a subspecies of *E. bisulcatus* was considered but rejected as not based on sufficiently complete data.

#### ORDER PANTODONTA

#### FAMILY CORYPHODONTIDAE MARSH, 1876

#### *CORYPHODON* OWEN, 1845

#### *Coryphodon* sp.

"Specific identification of fossil remains of *Coryphodon* is a difficult if not impossible task. A thorough revision of the genus is necessary, but, as Patterson (1939, p. 109) has pointed out, 'it would seem that a much better knowledge than we now possess of the skeletons of the various "species" is necessary before any satisfactory revision of the genus can be attempted'" (McKenna, 1960, p. 114). What was true in 1960 (and 1939!) is no less true today. Some 20 fragmentary specimens or groups of specimens from Powder River localities may be referable to one or more species of *Coryphodon*. No M<sub>3</sub> is present, so criteria based on this tooth are of no use in determining the affinities of the specimens. Few teeth are complete enough to measure, but these few indicate a size intermediate between Patterson's and McKenna's specimens. It is possible that some of the material here referred to *Coryphodon* may represent fragments of a Uintathere or other large mammal, but this is doubtful in most cases as even small fragments of *Coryphodon* show the

rugose and lincated enamel typical of the genus. Morphology of more complete specimens indicates pantodont and not dinoceratan affinities.

MEASUREMENTS:  $I_1^?$ , mesiodistal length, 21.0 mm. (AMNH 56185, Bozeman);  $P_1$ , length, 17.5 mm., width, 14.0 mm.;  $P_2$ , length, 19.5 mm., width, 17.5 mm. (AMNH 56184, 51-1);  $dP_3$ , length, 17.0 mm., width, 14.0 mm. (AMNH 56183, 52-11);  $P_4$ , length, 23.0 mm., width, 18.5 mm. (AMNH 56182, 51-11);  $M_1$ , length, 25.3 mm., anterior width, 16.5 mm., posterior width, 17.2 mm. (AMNH 56181, Bozeman);  $M_2$ , length, 36.4 mm., anterior width, 28.6 mm. (distal end of tooth damaged) (AMNH 56180, 52-12); anterior widths of fragmentary  $M_1$ , 20.5 mm. (AMNH 56179, 51-11); 22.5 mm. (AMNH 56178, 51-32);  $M_2$ , 26.5 mm. (AMNH 56177, 51-11);  $P_4^?$ , buccal length, 20.8 mm. (AMNH 56176, 51-50).

ORDER PERISSODACTYLA

FAMILY EQUIDAE GRAY, 1821

SUBFAMILY HYRACOTHERIINAE COPE, 1881c

*HYRACOTHERIUM* OWEN, 1840

*Hyracotherium angustidens* (Cope, 1875a)

Figure 23

Kitts (1956) reviewed American *Hyracotherium*

and divided *H. angustidens*, the earliest and most primitive species,<sup>1</sup> into three subspecific units. McKenna (1960) described another population of *H. angustidens* and questioned the allocation of Kitts's units to meaningful biological groupings much less to subspecies; a sample of 11  $M_3$ s from Alheit Pocket showed a lower coefficient of variation than any of Kitts's subspecies, which led him to question the unity of the latter "populations." I am in general agreement with McKenna on the meaning of Kitts's subspecies.

Altogether, the Powder River Basin specimens of *Hyracotherium* number some 90 teeth. Of these, 59 are from Reculosa Blowout; all are isolated except for a maxilla with  $dP_3$ - $M_4$ . An additional 38 teeth from other localities are mostly isolated but include one maxilla with  $P_4$ - $M_3$ ,

<sup>1</sup> One specimen referred to *H. angustidens* has recently been reported from the late Paleocene of the Polecat Bench Formation (Jepsen and Woodburne, 1969). Interestingly enough, the teeth are larger in all cases than the average from Powder River, in some cases even larger than the maxima. *Hyracotherium seekinsi* Morris, 1968, from late Paleocene (or early Eocene) beds in Baja California has been termed even more primitive than *H. angustidens* on the basis of shape indexes of the few known upper molars; by this test, the Powder River hyracothere is clearly *H. angustidens*.

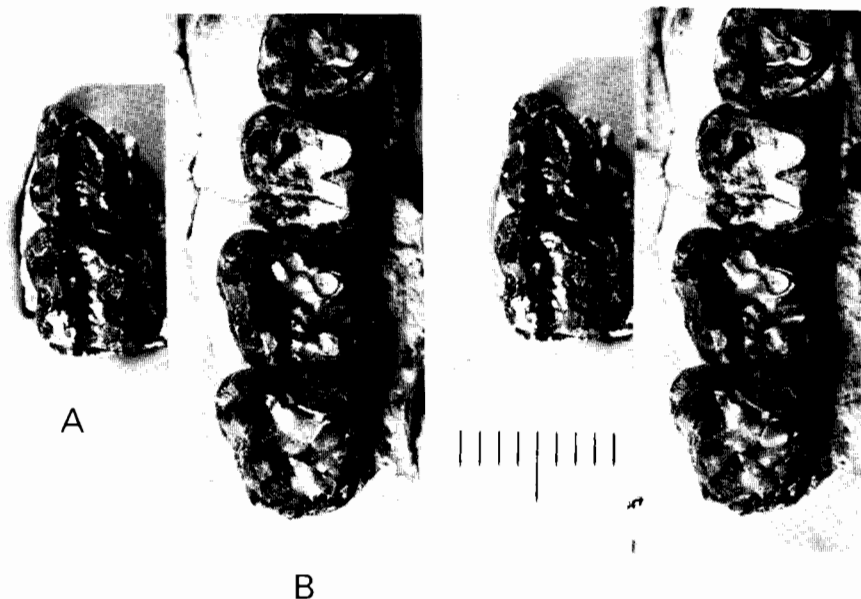


FIG. 23. *Hyracotherium angustidens* from the Powder River local fauna. A. AMNH 56175,  $dP_3$ - $M_4$ , Reculosa Blowout. B. AMNH 56174, right  $P_4$ - $M_3$ , Dry Well locality.

another with  $M^1$  <sup>2</sup>, and several fragments of lower jaw.

Kitts examined about a dozen of these teeth for his study, and at that time concluded (p. 40) that they were most like the sample from the Almagre facies of the San Jose Formation; this latter sample is most probably mixed, as Kitts explained. Examination of the complete sample of Powder River *Hyracotherium* indicates to me that a closer relationship may exist with the Sand Coulee sample. This would be expected as the two Wyoming "populations" are closer in both time and space.

In order to test this similarity, Student's-t was calculated for the samples of  $M_3$ ,  $M^1$ , and  $M^2$ . These teeth were chosen as the identifications are fairly secure and Kitts has given values of  $\sigma$  for them;  $M^3$  and  $P^4$  are secure, but Kitts did not calculate them fully;  $P_4$ ,  $M_1$ , and  $M_2$  are the least secure of the Powder River identifications. The results show that there is no significant difference in  $M_3$  width or length or in  $M^2$  length. In  $M^2$  width, the samples differ at the 0.05 ÷ level of significance (about 0.055), whereas both  $M^1$  measures differ at the 0.005 level, showing rather significant difference in this character. In general, the lower teeth of the Powder River sample were close to, or slightly larger than the Sand Coulee sample, whereas the uppers were usually smaller.

A further test was made comparing the Four Mile sample of  $M_3$  lengths (McKenna, 1960, p. 118) with those from Powder River and with Kitts's Sand Coulee and Gray Bull samples. The results are interesting in that they show (for whatever the interpretation might be) that the Four Mile sample differs from that from Powder River at a level of significance greater than 0.0001, from Sand Coulee at an even greater level, and from the Gray Bull sample at about 0.0001. Perhaps the best interpretation of these tests is that all the samples are different from each other and that special relationships should be investigated with morphological and stratigraphical rather than statistical methods. As I have often repeated here, it is only with temporally and stratigraphically controlled sequences of populations that such correlations can be really meaningful. For the present, it is sufficient to note that the Powder River Basin *Hyracotherium angustidens* is a small form, tending to indicate early Gray Bull age. Selected statistics are given in table 16. As most of the speci-

mens are isolated and as  $P_4$ - $M_2$  and  $M^1$  <sup>2</sup> differ mostly on relative size, assignment of specimens to these categories is not as certain as for  $M_3$  and  $P^4$ .

TABLE 16  
STATISTICAL DATA ON THE TEETH OF *Hyracotherium angustidens* FROM THE POWDER RIVER BASIN

	N	OR	M	SE	$\sigma$	V
$P_1$						
W	1	—	2.40	—	—	—
L	1	—	4.40	—	—	—
$P_3$						
W	2	3.20-3.80	3.50	—	—	—
L	2	5.50-5.80	5.65	—	—	—
$P_4$						
W	5	3.30-4.20	3.78	0.17	0.38	10.1
L	3	5.45-6.80	6.22	—	—	—
$M_1$						
W	11	4.10-5.50	4.85	0.14	0.47	9.8
L	11	6.60-8.00	7.32	0.15	0.49	6.7
$M_2$						
W	6	5.00-6.20	5.65	0.21	0.51	9.1
L	6	8.00-9.40	8.83	0.21	0.51	5.8
$M_3$						
W	7	4.80-6.00	5.46	0.15	0.39	7.2
L	7	9.60-10.50	10.13	0.13	0.34	3.4
d $P_3$						
W	3	2.60-3.25	3.00	—	—	—
L	3	5.40-5.90	5.60	—	—	—
d $P_4$						
W	3	4.80-5.20	4.93	—	—	—
L	3	7.00-7.80	7.47	—	—	—
$p_3$						
W	3	5.70-6.30	5.97	—	—	—
L	3	5.40-5.80	5.67	—	—	—
$P^1$						
W	6	6.30-8.50	7.18	0.30	0.74	10.2
L	6	5.40-7.20	5.96	0.26	0.64	10.8
$M^1$						
W	6	7.00-8.60	7.43	0.26	0.63	8.4
L	6	5.90-7.40	6.62	0.20	0.48	7.3
$M^2$						
W	14	8.20-10.10	9.03	0.14	0.52	5.8
L	14	7.30-9.00	7.96	0.14	0.52	6.5
$M^3$						
W	7	8.50-9.90	8.99	0.24	0.64	7.1
L	7	7.40-8.40	7.80	0.13	0.34	4.4
d $P^3$						
W	3	5.20-6.00	5.70	—	—	—
L	3	5.50-6.50	6.13	—	—	—
d $P^4$						
W	2	5.30-7.30	6.30	—	—	—
L	2	5.00-6.20	6.10	—	—	—

SUBORDER CERATOMORPHA  
 SUPERFAMILY TAPIROIDEA GRAY, 1821  
 FAMILY ISECTOLOPHIDAE PETERSON, 1919  
*HOMOGALAX* HAY, 1899  
*Homogalax protapirinus* (Wortman, 1896)

Radinsky, in his 1963 review of early tapiroids, discussed a few Powder River Basin specimens of this species (p. 16, AMNH 55520-55523). In addition to the four specimens described by Radinsky, several fragments and fairly complete teeth are referable to *H. protapirinus*. The scarcity of this species may be due to the method of collecting and not to a true deficiency in the fauna, but it may reflect an actual rarity of tapiroids, as at Four Mile. Measurements are given in table 17.

ORDER ARTIODACTYLA  
 SUBORDER SUIFORMES  
 INFRAORDER PALAEDONTA  
 SUPERFAMILY DICHOBUNOIDEA TURNER,  
 1849  
 FAMILY DICHOBUNIDAE TURNER, 1849  
 SUBFAMILY DIACODEXINAE GAZIN, 1955  
*DIACODEXIS* COPE, 1882c  
*Diacodexis metsiacus* (Cope, 1882a)  
 Figure 24

This species is represented in the Wood collection by 34 isolated teeth and a maxilla with M<sup>1-3</sup>. As M<sup>1</sup> and M<sup>2</sup> are not clearly distinguishable when isolated, 16 isolated upper molars were not included in the measurement data of table 18. The specimens are small, but appear to be within the expected range of variation for the species as construed by Guthrie (1967; cf. p. 50, fig. 36; also McKenna, 1960, p. 122, table 10).

TABLE 17

MEASUREMENTS (IN MILLIMETERS) OF *Homogalax protapirinus* IN THE POWDER RIVER LOCAL FAUNA

AMNH Number	Tooth	Locality	Maximum Width	Maximum Length
55520	M <sup>3</sup>	Monument Blowout	13.40	10.60
55521	M <sub>2</sub>	Monument Blowout	7.10	10.70
56173	M <sup>1?</sup>	Monument Blowout	11.10	8.75
56172	M <sup>2?</sup>	Monument Blowout	12.40	10.20
56171	P <sub>2</sub>	Monument Blowout	4.20	8.30
55522	M <sub>3</sub>	Reclusa Blowout	8.10	14.30
55523	dP <sup>3</sup>	Reclusa Blowout	8.20	8.00
56170	P <sup>4</sup>	Reclusa Blowout	—	8.9 <sup>a</sup>
56169	dP <sub>3</sub>	Reclusa Blowout	4.50	8.30

<sup>a</sup>Only the portion lingual to the parastyle is preserved.

TABLE 18

STATISTICAL DATA ON THE TEETH OF *Diacodexis metsiacus* IN THE POWDER RIVER LOCAL FAUNA

	N	OR	M	SE	$\sigma$	V
M <sub>1</sub>						
AW	6	2.65-3.50	3.18	0.16	0.39	12.4
PW	6	2.90-3.75	3.33	0.13	0.33	9.8
L	5	3.95-4.45	4.15	0.08	0.19	4.6
M <sub>2</sub>						
AW	4	3.40-3.95	3.63	0.13	0.25	7.0
PW	5	3.40-4.40	3.78	0.20	0.44	11.7
L	5	3.30-4.90	4.21	0.28	0.63	15.1
M <sub>3</sub>						
AW	3	2.80-3.40	3.20	0.20	0.35	10.8
PW	3	2.60-3.15	2.95	0.18	0.30	10.3
L	3	4.80-5.40	5.10	0.17	0.30	5.9
P <sup>4</sup>						
W	1	—	3.50	—	—	—
L	1	—	3.30	—	—	—
M <sup>1</sup>						
W	1	—	5.25	—	—	—
L	1	—	3.80	—	—	—
M <sup>2</sup>						
W	1	—	5.60	—	—	—
L	1	—	4.30	—	—	—
M <sup>3</sup>						
W	3	4.20-5.70	5.05	0.44	0.77	15.2
L	3	3.30-4.40	3.90	0.32	0.56	14.3

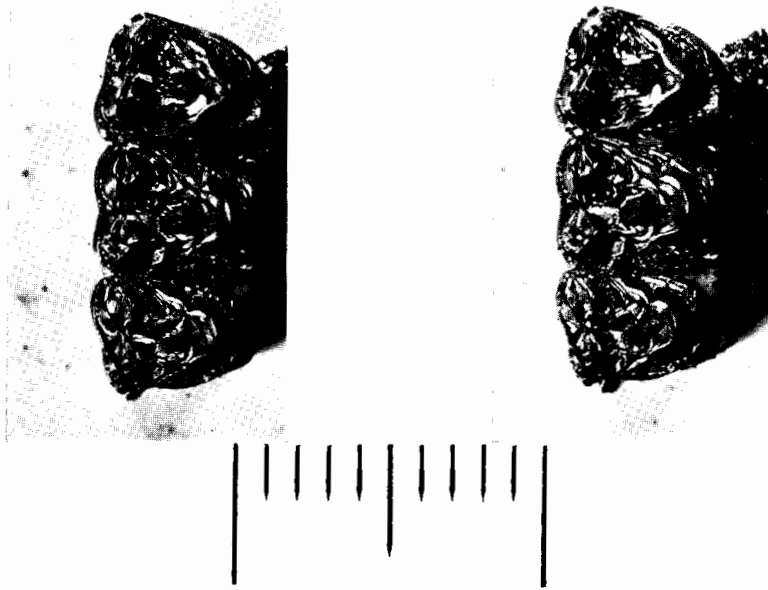


FIG. 24. *Diacodexis metsiacus* from the Powder River local fauna; AMNH 56168, right M<sup>1-3</sup>, Reculosa Blowout.

## SUMMARY

THE POWDER RIVER local fauna, collected mainly in 1951–1953 under the direction of H. E. Wood, II can be treated as a unified assemblage despite its mostly surficial character. It is most closely correlative with the Four Mile and early Gray Bull faunas of earliest Wasatchian age. The Eocene beds of the Powder River Basin, which also produce late Wasatchian mammals from higher levels, probably do not belong to the Wasatch Formation as currently understood.

Van Valen's (1967a) discussion of *Palaeosinopa* is reconsidered, and *P. veterrima* and Van Valen's "species E" are included within *P. didelphoides*. In addition to this species, upper teeth possibly of *P. lutreola* and of an even smaller species of ?*Palaeosinopa* are present at Powder River.

A small edentulous specimen of *Apatemys*, referable to *A. chardini*, is present in the Powder River local fauna. The species of apatemyid from Four Mile previously thought indeterminate is referred to *A. whitakeri*.

"*Leptacodon*" *jepseni* McKenna, 1960, is removed from *Leptacodon*—it may represent a new genus; members of this species are present at Powder River. An additional species may represent true *Leptacodon* or a close relative. The genus *Entomolestes* is considered to include "*Leipsanolestes*" *siegfriedti*, as well as *E. nitens* and *E. grangeri*, the generic type; the form present at Four Mile and Powder River shows intermediacy between the first two species, but the Bridger type may be of a different lineage. *Talpavus* Marsh, 1872, probably includes *Scenopagus* McKenna and Simpson, 1959, despite the arguments of Robinson (1968) to the contrary.

One damaged specimen helps to link *Protomus mordax* and *Prolimnocyon robustus* into a single species, as in Van Valen, 1969a. The generic reference of this species to *Paeneprolimnocyon* is questioned. Very small specimens of *Prolimnocyon atavus* are reported.

The species *Phenacolemur praecox* is considered to include *P. citatus*, *P. jepseni*, and *P. j. simpsoni*, treated as subspecific local populations sampled in time and space. In addition to a form of this species, a smaller *Phenacolemur* may be present at Powder River, similar to, but slightly larger

than, the Pliocene *P. frugivorus* and possibly a descendant of that lineage; it may, however, represent merely a small variant or extreme of early *P. praecox*, as may be the case also at Four Mile. The type  $P_4$  of *Parapheliscus bjornii* Van Valen, 1967a, from Bear Creek, is a specimen of *Phenacolemur* similar to *P. praecox citatus*; it is important in adding this genus to the list of Bear Creek primates. The primate  $M_3$  previously reported from Bear Creek is not a *Phenacolemur*, but may be either *Plesiadapis* (as in Simpson, 1928a) or a large *Paromomys* (as in Van Valen and Sloan, 1966).

The several species previously referred to *Anemorhysis* Gazin, 1958 (*Tetonius musculus* Matthew, 1915; *T. tenuiculus* Jepsen, 1930a; probably *Paratetonius steini* Seton, 1940; *P. sublettensis* Gazin, 1952; and *Tetonoides pearcei* Gazin, 1962) are considered to be a single species, *Tetonius musculus* Matthew, 1915. As at Four Mile, both *T. musculus* and *T. homunculus* are present in the Powder River local fauna.

A specimen of a rodent close to, but slightly larger than, the single known upper molar of *Paramys atavus* from Bear Creek is present at Powder River. It differs from the earlier specimen in having a mesostyle and lacking a hypocone. Two additional very generalized species of *Paramys* are also present.

"*Chriacus*" *gallinae* Matthew, 1915a, from the late Wasatchian of New Mexico, is considered to represent a genus distinct from the type of *Chriacus*, mid-Pliocene *C. pelvidens*. A smaller representative of this undescribed genus is known at Powder River.

Following Guthrie (1967b), *Phenacodus vortmani* is considered to include *P. copei*. The specimens from Powder River and Four Mile are referred to this species rather than to the Tiffanian *P. matthewi*, here considered to include *P. gidleyi*. The status of the species of *Ectocion*, reviewed by Simpson (1937, 1943) and by McKenna (1960) and considered as a typification of the chronocline, is re-examined. *E. osbornianus*, without further subdivision, is considered to include the "Clark Fork" and Gray Bull *E. ralstonensis* and *E. o. complens*. *Ectocion superstes*, of the Lost Cabin, is retained for the type only. "*E.*" *parvus*, apparently of

early Gray Bull age, is distinct and only questionably referable to the family.

Biometrical data on *Haplomyilus speirianus* are given, and no changes observed in the species in space or time; it appears to be definitely present only in the early and "middle" Gray Bull. The validity of *Hyopsodus loomisi* McKenna, 1960, is questioned. It may be only a small variant of *H. miticulus*. The latter species is considered to be the sole *Hyopsodus* in the early Wasatchian, pending detailed revision.

*Apheliscus nitidus* Simpson, 1937, is considered to include *Parapheliscus wapitiensis* Van Valen, 1967a, thus invalidating *Parapheliscus*. *Apheliscus* appears to be derived from a species of *Phenacodaptus* (following Gazin [1959] and others); *Phenacodaptus* is the apheliscine present at Bear Creek. The subfamily may originate from a species of *Haplaletes* dentally similar to *H.*

*pelicatus*, and not from convergent pentacodontids. Apheliscinae is thus a subfamily of Hyopsodontidae, as in McKenna, 1960, and others.

*Esthonyx spatularius* Cope, 1880c, is analyzed biometrically and considered merely as the small and perhaps early variant of *E. bisulcatus*, not deserving of taxonomic separation at any rank. Anchippodontidae Gill, 1872, is revived as the correct family *nomen* for the Tillodontia, a suborder of Condylarthra.

Kitts's (1956) subspecific division of *Hyraotherium angustidens* is abandoned and the several local populations sampled shown biometrically to be similarly distinct from one another. Although Kitts placed the Powder River sample with his probably mixed Almagre sample, it is apparently closer to that from the Sand Coulee on the basis of size.

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