

600

#8

A Review of the Proteutheria  
and Insectivora of the  
Willwood Formation (lower Eocene),  
Bighorn Basin, Wyoming

---

G E O L O G I C A L   S U R V E Y   B U L L E T I N   1 5 2 3



# A Review of the Proteutheria and Insectivora of the Willwood Formation (lower Eocene), Bighorn Basin, Wyoming

By THOMAS M BOWN and DAVID SCHANKLER

---

G E O L O G I C A L S U R V E Y B U L L E T I N 1 5 2 3

*The Willwood sample of proteutherians and insectivores  
is the largest and most diverse known for lower Eocene  
rocks of the world*



UNITED STATES DEPARTMENT OF THE INTERIOR

JAMES G. WATT, *Secretary*

GEOLOGICAL SURVEY

Dallas L. Peck, *Director*

Library of Congress Cataloging in Publication Data  
Bown, Thomas M  
A review of the Proteutheria and Insectivora of the Willwood Formation (Lower Eocene), Bighorn Basin, Wyoming  
(Geological Survey Bulletin 1523)  
Bibliography p 73  
Supt of Docs No 119 3 1523  
1 Proteutheria 2 Insectivora, Fossil 3 Paleontology—Eocene 4 Paleontology—Bighorn River  
water-shed, Wyo and Mont  
I Schankler, David M II Title III Series  
QE75 B9 No 1523 [QE882 15] 557 3s 81-607068 [569' 12] AACR2

---

For sale by the Branch of Distribution, U S Geological Survey  
604 South Pickett Street, Alexandria, VA 22304

III

	Page
FIGURE 1 Stratigraphic divisions of the Fort Union and Willwood Formations of the Bighorn Basin —————	5
2 Stratigraphic plots of $\log_e (L \times W)M_2$ in Eocene <i>Didelphodus</i> —————	8
3 Stratigraphic plots of $\log_e (L \times W)M_1$ in Eocene <i>Didelphodus</i> —————	9
4 Scatter diagram for $M^1$ in some early Eocene leptictids —————	12
5 Scatter diagram for $M^2$ in some early Eocene leptictids —————	13
6 Scatter diagram of trigonid widths versus anteroposterior tooth lengths in $M_1$ of some early Eocene leptictids —————	14
7 Scatter diagram of trigonid widths versus anteroposterior tooth lengths in $M_2$ of some early Eocene leptictids —————	15
8 Stratigraphic plots of $M_2$ in some early Eocene leptictids —————	17
9 Scatter diagram of trigonid widths versus anteroposterior tooth lengths of $M_1$ in early Eocene <i>Palaeosinopa</i> —————	22
10 Scatter diagram of trigonid widths versus anteroposterior tooth lengths of $M_2$ in early Eocene <i>Palaeosinopa</i> —————	23
11 Scatter diagram of talonid widths versus anteroposterior tooth lengths of $M_1$ in early Eocene <i>Palaeosinopa</i> —————	24
12 Scatter diagram of talonid widths versus anteroposterior tooth lengths of $M_2$ in early Eocene <i>Palaeosinopa</i> —————	25
13 Histogram of $\log_e (L \times W)M_1$ in early Eocene <i>Palaeosinopa</i> —————	26
14 Stratigraphic plots of $\log_e (L \times W)M_2$ in early Eocene <i>Palaeosinopa</i> —	27
15 Stratigraphic plots of $\log_e (L \times M)M_1$ in early Eocene <i>Palaeosinopa</i> —	28
16 Histogram of $M_2$ length of Bridgerian and Uintan sample of <i>Apatemys</i> —————	33
17 Stratigraphic plots of $\log_e (L \times W)M_2$ in late Paleocene through Bridgerian specimens of <i>Apatemys</i> —————	36
18 Chart showing known stratigraphic ranges of proteutherians and insectivores in the Willwood Formation —————	48

## TABLES

	Page
TABLE 1 t values for pair-wise comparisons of early Eocene samples of <i>Prodiacodon</i> and <i>Palaeictops</i> —————	18
2 Chi-square analysis of the distribution of length measurements of $M_2$ for the Bridgerian sample of <i>Apatemys</i> (ungrouped data) —————	33
3 Chi-square analysis of the distribution of length measurements of $M_2$ for the Bridgerian sample of <i>Apatemys</i> (grouped data) —————	34
4-8 Measurements of teeth of	
4 <i>Macrocranion nitens</i> —————	47
5 <i>Scenopagus</i> sp —————	50
6 <i>Talpavoides dartoni</i> —————	53
7 <i>Plagioctenodon krausae</i> —————	62
8 Wasatchian <i>Centetodon</i> —————	66

# A REVIEW OF THE PROTEUTHERIA AND INSECTIVORA OF THE WILLWOOD FORMATION (LOWER EOCENE), BIGHORN BASIN, WYOMING

By THOMAS M BOWN and DAVID SCHANKLER

## ABSTRACT

The systematic paleontology of the Willwood Formation proteutherians and insectivores is revised, and new samples consisting of approximately 330 specimens are described. These are the largest samples of these animals from lower Eocene rocks anywhere in the world, and their occurrences indicate that they are of potential usefulness in biostratigraphic correlations once they are known from more specimens and localities.

The didelphodontine palaeoryctid *Didelphodus absarokae* is probably ancestral to the younger and smaller *D. altidens*. The leptictids *Prodiacodon* and *Palaeictops* are more closely related to each other than was recently suggested by M. J. Novacek. Two Willwood specimens show crossing characters between these genera. *Palaeictops matthewi* Novacek is probably conspecific with *P. multicuspis*, and the type of *Palaeictops pineyensis* is removed from synonymy with *Prodiacodon tauricinerei* and is placed in *Palaeictops bicuspis*. Statistical studies indicate that there were five early Eocene species of *Palaeosinopa*: *P. veterrima*, *P. didelphoides*, *P. lutreola*, *P. incerta*, sp. nov., and a large, undescribed form from the Lost Cabin Member of the Wind River Formation. *P. lutreola* is restricted to Graybullian faunas, and Student's *t* tests show that *P. didelphoides* differs statistically from *P. veterrima*. R. M. West's review of apatemyids is criticized from several viewpoints, four species of *Apatemys* are recognized in the Willwood fauna: *A. chardini*, *A. bellulus*, *A. kayi*, and *A. sp.*, cf. *A. rodens*.

Earlier concepts of the Adapisoricidae are revised. *Adapisorex* is probably an *Apfeliscus*-like condylarth, and the Dormaalinae is elevated to family status to accommodate most other taxa earlier grouped in the Adapisoricidae. *Dormaalus* and *Macrocranium* appear to be closely related, and both share similarities with late Paleocene *Litolestes*. *Mckennatherium* is not a dormaalid, rather, both it and "*Diadacodon*" *minutus* probably belong in *Adunator*. Diagnostic characters of the Nyctitheriidae are discussed in the light of the recent review of this group by L. B. Krish-talka, both *Plagioctenodon* and *Plagioctenoides* are probably nyctitheriids.

New samples of insectivores include the earliest records of *Centetodon* and the Geolabididae (two new species are described), and the Apternodontidae (a new genus and species). Other new insectivore taxa include a *Talpavus*-like dormaalid, a *Leipsanolestes*-like ernaceid, and new species of *Plagioctenodon* and *Scenopagus*. New specimens of *Pontifactor* (Nyctitheriidae) and "*Leptacodon*" *jepseni* (Ernaceidae) occur in the Willwood fauna, "*L.*" *jepseni* is an ernaceid, most closely related to Bridgerian *Entomolestes grangeri*.

## INTRODUCTION

## HISTORY AND PURPOSE OF INVESTIGATION

Cope (1881) first described a specimen of a proteutherian from the Willwood Formation of the Bighorn Basin of northwest Wyoming (*Deltatherium absarokae* (*Didelphodus* Cope, 1882; Matthew, 1918, p. 579)). Since that time, at least 500 additional specimens have been recovered from these productive rocks. Matthew (1901, 1918) and Jepsen (1930a) described the best Willwood material in the American Museum and Princeton University collections, respectively, and a few additional Willwood specimens were recorded by West (1973), Krishtalka (1976a, b), and Novacek (1977). Until recently, however, the vast majority of these fossils were undescribed. The largest single collection (about 215 specimens from the Sand Creek facies) exists in the University of Wyoming Geological Museum (No Water fauna). Most of these were discussed by Bown (1979), who named two new genera (*Plagiectenodon* and *Plagiectenoides*) and one new species (*Leipsanolestes simpsoni*) of insectivores. The No Water fauna was, in addition to the Four Mile fauna of northwestern Colorado (McKenna, 1960a), only the second comprehensive record of early Wasatchian insectivores and proteutherians.

Another large sample (about 180 specimens) in the Yale Peabody Museum was collected by Yale field parties under the direction of E. L. Simons (during 1961-65, 1968-72, 1974, 1975), and David Schankler (during 1976, 1977). This collection was obtained from numerous localities throughout the lower seven-eighths (660 m) of the Willwood Formation and contains both early (Graybullian age) and middle (Lysititan age) Wasatchian insectivores and proteutherians. These mammals have thus far not been found in Willwood rocks that yield *Lambdotherium* (Lostcabinian age).

This paper contains a documentation of the Willwood Proteutheria and Insectivora in the Yale Peabody Museum collection, a revision of some of the forms in the No Water fauna, and discussions of possible phylogenetic interpretations of these and related forms. The Willwood record of these animals is an impressive one and serves adequately to bridge the gap between known late Paleocene and Clarkforkian forms and those of the late early Eocene and middle Eocene. The Willwood sample comprises at least 18 genera, which are contained in at least 30 species, of which three new genera and seven new species are described here. It is the most diverse record of the Proteutheria and Insectivora in the North American Paleocene or Eocene.

## PRELIMINARY FAUNAL ZONATION OF THE WILLWOOD FORMATION

A comprehensive picture of the vertebrate faunal zonation of the Willwood Formation is still in progress, however, several recent studies have already contributed to a clearer understanding of Willwood biostratigraphy (for example, Neasham and Vondra, 1972; Gingerich, 1974a, 1976, 1977; Gingerich and Rose, 1977, Gingerich and Simons, 1977; Rose, 1978, Bown, 1975, 1979) Schankler (1980) has related many of the 400-odd Yale Willwood localities in the central Bighorn Basin to a measured stratigraphic section Bown (1979, 1980) has done the same for approximately 250 sites in the southern and southeastern Bighorn Basin, and ongoing studies of P. D. Gingerich and K. D. Rose at the University of Michigan have incorporated data from another 250-odd localities in the Clark's Fork Basin. Studies of Willwood mammals at each of these sites are in various stages of preparation, however, enough is now known to offer a preliminary picture of the biostratigraphic relationships of Willwood proteutherians and insectivores.

Traditionally, the Willwood Formation has been separated into three poorly defined units: the "Gray Bull Member" (faunal term: "Graybullian"), a taxon-range zone typified by *Homogalax protapirinus*; the "Lysite equivalent" (faunal term: "Lysitian"), an as yet unsubstantiated faunal assemblage zone, presently characterized only by the range of overlap of the helaetid *Heptodon* and the adapid *Pelycodus jarrovi*, and by the absence of *Homogalax*, and the "Lost Cabin equivalent" (faunal term: "Lostcabinian"), which, in the Willwood Formation, is presently distinguished only by the presence of the palaeothere *Lambdaotherium* (Wood and others, 1941; Van Houten, 1945). Wood and others (1941) were apparently unaware that these divisions in the Bighorn Basin have no rock-stratigraphic meaning. The designation of "beds", "Member", or "equivalent" for the Gray Bull, Lysite, and Lost Cabin units in that basin is, therefore, inappropriate because they cannot be distinguished without an examination of their contained faunas. Indeed, the faunal distinctiveness of the lithologically distinguished Lysite and Lost Cabin Members of the Wind River Formation is poorly understood in their type areas in spite of several recent studies, and *Homogalax*, the supposed index fossil of the Gray Bull, occurs in positively younger rocks in southern Wyoming and in association with *Heptodon* in at least twenty Willwood faunules.

In this paper, the following faunal-stratigraphic divisions are recognized for Willwood rocks and faunas and have been superimposed on existing established nomenclature to avoid confusion



that might arise if a new terminology were established without faunal documentation at this time. These divisions, which are documented in unpublished data of Schankler and Bown, facilitate discussion of the relative faunal ages of the Willwood proteutherians and insectivores, are based on unpublished faunal studies of more than 600 Willwood localities, and will be revised as subsequent investigations warrant. Measurements (in meters) are from the base of the Willwood Formation in the Elk Creek section (Schankler, 1980), central Bighorn Basin.

Lost Cabin biostratigraphic zone  
660–780 m, Lostcabinian fauna.

Lysite biostratigraphic zone: 530–660 m,  
Lysitian fauna.

Upper Gray Bull biostratigraphic  
zone: 380–530 m, late Gray-  
bullian fauna.

Middle Gray Bull biostratigraphic  
zone: 200–380 m, middle Graybullian  
fauna.

Lower Gray Bull biostratigraphic zone:  
0–200 m, early Graybullian fauna.

The stratigraphic and biostratigraphic relations of these units to rock units in the Bighorn Basin are depicted in figure 1

#### ABBREVIATIONS

Abbreviations used in this report are as follows: AMNH, American Museum of Natural History (New York); CM, Carnegie Museum (Pittsburgh); MCZ, Museum of Comparative Zoology, Harvard University (Cambridge); PU, Princeton University Museum (Princeton); TTU-P, Texas Tech University Museum (Lubbock); UCMP, University of California Museum of Paleontology (Berkeley); UMMP, University of Michigan Museum of Paleontology (Ann Arbor); USGSD, U.S. Geological Survey (Denver); UW, The Geological Museum, The University of Wyoming (Laramie); YPM, Peabody Museum, Yale University (New Haven); n, sample size.

#### ACKNOWLEDGMENTS

We are grateful to J. A. Lillegraven (UW), D. E. Russell (Institut de Paleontologie, Paris), and C. A. Repenning (U.S. Geological Survey) for their comments on the manuscript; to David Archibald

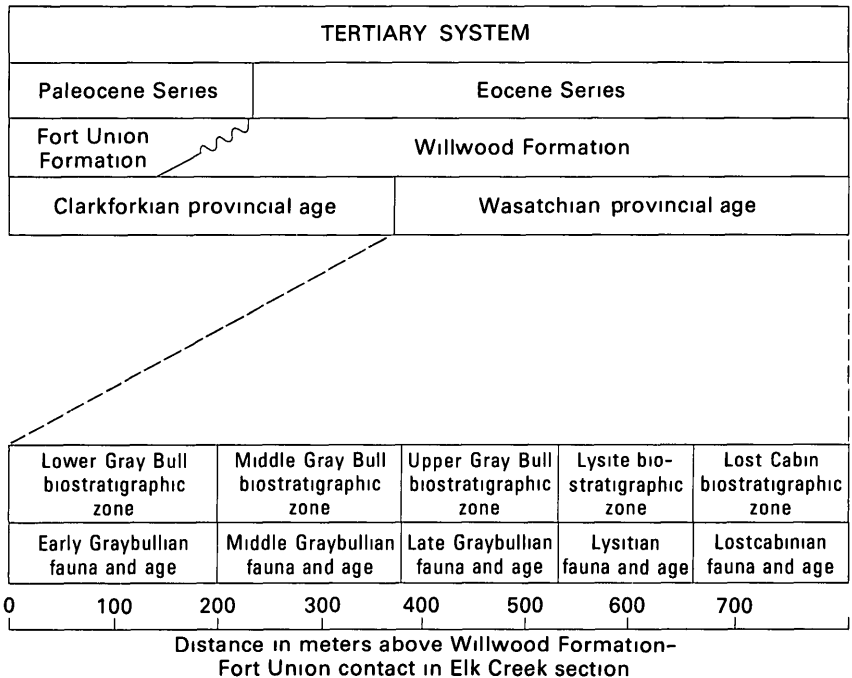


FIGURE 1—Relations of rock-stratigraphic, time-stratigraphic, and biostratigraphic units for the Fort Union and Willwood Formations of the Bighorn Basin

(YPM) and K. D. Rose (Johns Hopkins University) for discussion, and to M. C. McKenna (AMNH), J. A. Lillegraven (UW), C. C. Black and M. R. Dawson (CM), P. D. Gingerich (UMMP), D. E. Savage (UCMP), Chuck Schaff (MCZ), J. H. Ostrom and M. A. Turner (YPM), Donald Baird (PU), Eileen Johnson (TTU-P), and D. E. Russell for the generous loan of specimens and casts in their care. The section on Proteutheria is largely the work of Schankler, and the section on Insectivora is largely the work of Bown; however, both authors bear responsibility for the paper as a whole.

Robert O'Donnell (USGSD) skillfully prepared several of the specimens. Bown completed his research for this study while he was a National Research Council postdoctoral fellow with the U.S. Geological Survey and thanks N. J. Silberling, Robert Kossanek, and G. E. Lewis for access to Geological Survey facilities under their supervision. Schankler was assisted by a Sigma Xi research grant and by National Science Foundation Doctoral Dissertation Improvement Grant DEB-76-22769.

Most of the specimens described in this report were obtained

through the support of grants from the John T. Doneghy Fund (Yale University) and Boise Fund (Oxford University) to E. L. Simons, and National Science Foundation Grant GA-35754 to P. O. McGrew (UW).

## SYSTEMATIC PALEONTOLOGY

Class MAMMALIA

Order PROTEUTHERIA

Family PALAEOORYCTIDAE

Subfamily PALAEOORYCTINAE

*Palaeoryctes* sp

*Referred specimens* —USGSD 1661, 2151, 3711.

cf *Pararyctes* sp

*Referred specimen* —UW 7028.

*Discussion.*—Six specimens of palaeoryctines are known from the Willwood Formation. In addition to the four teeth listed here, two superb skulls exist in the UMMP collections. Willwood palaeoryctine materials are under study by M. C. McKenna at the American Museum of Natural History. The University of Wyoming specimen of cf. *Pararyctes* was recovered from Yale locality 363 at the 190-m level of the Willwood Formation in the Elk Creek facies, the USGS materials are from Yale locality 363 (USGSD 2151), UW locality V-73037 (USGSD 3711), and UW locality V-73055 (USGSD 1661). The University of Wyoming localities are at the 34-m and 119-m levels of the Sand Creek facies of the Willwood Formation, respectively.

Subfamily DIDELPHODONTINAE

*Didelphodus absarokae* (Cope, 1881)

Plate 1, plate 2, figures 1, 2, 4

*Referred specimens.*—YPM 17289a, 17297, 17305 (including 23730 and 23731), 18971 (pl 2, figs 1, 4), 23071, 23100, 23105, 23120, 23724, 23725, 23726, 23729, 23732, 23733, 25361 (pl 2, fig. 2), 25499, 27802, 27877, 28208, 28221, 29285, 30591, 30608, 37184, 37186, USGSD 303 (pl. 1).

*Discussion.*—The type specimen of *Didelphodus absarokae* is from the Willwood Formation, but its exact locality and stratigraphic position are unknown. All the Yale specimens of *Didelphodus* are as-

signed to this species, even though the Lysitian specimens are intermediate in size between the types of *D. absarokae* and *D. altidens*. This intermediacy of size was also recorded by Guthrie (1967a) for the Lysite Member (Wind River Formation) sample, from the Wind River Basin.

In the central Bighorn Basin, *D. absarokae* is known from the lower Gray Bull to the upper part of the Lysite zones. Its absence from the Lost Cabin zone is probably due to relatively poor samples from these localities, as it is a rare species even in the faunally better represented lower horizons. The few specimens that are available tend to show a decrease in tooth size up section.

The Willwood sample has been combined with other early and middle Eocene samples in a time versus size plot in figures 2 and 3. The measure of size is adapted from that in Gingerich (1976). As can be seen from the figures, *D. absarokae* and *D. altidens* are clearly separated in size only at the end points of the temporal range. This relationship was earlier observed by Van Valen (1966, p. 32) and Guthrie (1967a, p. 13). A specimen from the Lost Cabin Member of the Wind River Formation (MCZ 3461), assigned by Van Valen (1966) to *D. altidens*, is in the middle of the size range of the Lysite zone specimens found in the Willwood Formation and the Almagre faunal sample in the San Jose Formation of New Mexico. The latter sample, presumably of Lostcabinian age, was assigned by Van Valen (1966) to *D. absarokae* and is interesting in that it contains an individual that is almost as large as the largest of the Graybullian specimens. Van Valen's argument that *D. altidens* is not an anagenetic descendant of *D. absarokae* was based largely on the existence of both species in a single fauna, that of the Lost Cabin Member of the Wind River Formation. The presence of *D. absarokae* in this fauna was indicated by a single specimen (U S National Museum 18433), whose correct assignment has been properly questioned by Guthrie (1971). Whether it is a specimen of *Didelphodus* or not, it is certainly not separable from other Lostcabinian specimens of *D. altidens* on the basis of size, which, according to Van Valen (1966), is the only valid criterion for distinguishing lower molars of the two species. The differences in morphology are of degree rather than kind. Although we do not here recommend synonymy of the two species of *Didelphodus*, we do observe that the two species are not very discrete entities and that *D. altidens*, in all likelihood, is a descendant of a population of *D. absarokae*.

The Willwood sample adds virtually nothing to Van Valen's (1966) treatment of the morphology of the genus other than to record a few variations. In the two Lysite zone specimens where  $P_1$  is known, it is two rooted, with the anterior root displaced labially. In the only other

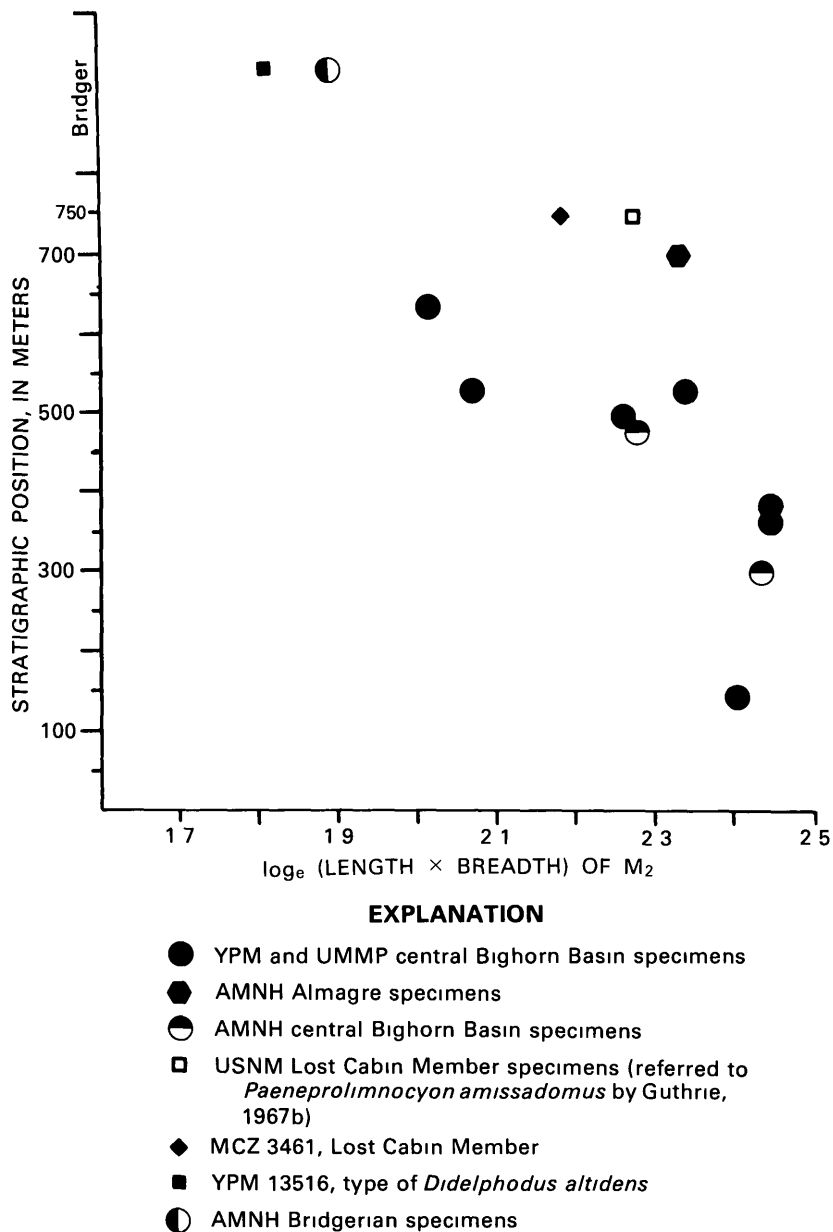
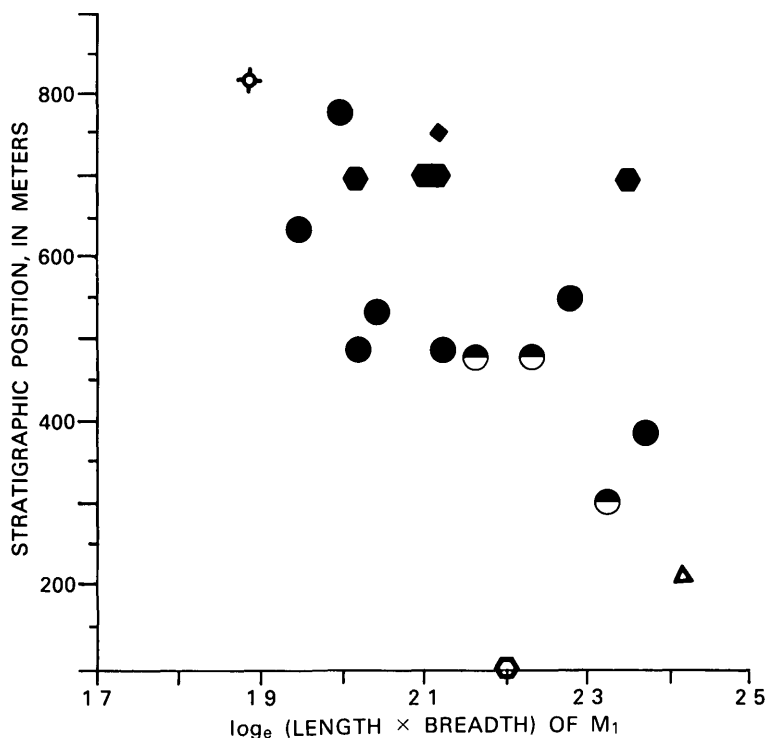


FIGURE 2—Stratigraphic plots of  $M_2$  in *Didelphodus* specimens from various Eocene localities. Measurements of stratigraphic position are from the base of the Willwood Formation. Plots in the area labeled "Bridger" are grouped.



## EXPLANATION

- YPM and UMMP central Bighorn Basin specimens
- AMNH Almagre specimens
- ▲ USNM central Bighorn Basin specimens
- ◻ UCMP Four Mile fauna specimens
- AMNH central Bighorn Basin specimens
- ◈ AMNH Cathedral Bluffs Member specimen
- ◆ MCZ 3461, Lost Cabin Member

FIGURE 3 —Stratigraphic plots of  $M_1$  in *Didelphodus* specimens from various Eocene localities. Ordinate is stratigraphic position (meter levels are for the Willwood Formation, other plots approximate)

specimen that preserves this tooth (YPM 23729 from the upper Gray Bull zone), it appears to be single rooted. In the four specimens that preserve  $P_4$ , the development of the metaconid varies from very weak to very strong and in some specimens it is almost equal to the protoconid in size. There is, however, no correlation of this character

with stratigraphic position. The pattern is as follows: lower Gray Bull zone, metaconid moderate; middle Gray Bull zone, metaconid very strong; upper Gray Bull zone, metaconid weak, Lysite zone, metaconid very weak.

Upper teeth of *Didelphodus* are very rare, and the only variation observed in the sample at hand is the absence of a parastyle on the P<sup>4</sup>'s of two middle Gray Bull zone specimens and the presence of a strong parastyle on one specimen from the upper Gray Bull zone

### Family LEPTICTIDAE

#### Subfamily Leptictinae

Novacek (1977) listed the following as shared derived characters of the leptictid *Palaeictops* that distinguished it from the more generalized *Prodiacodon*:

1. P<sup>5</sup>'s (traditionally P<sup>4</sup>) and upper molars are more bunodont, being more antero-posteriorly elongate and transversely compressed, with lower, more bulbous paracones, metacones, and protocones.
2. Parastylar spurs on M<sup>2-3</sup> are not prominent, and ectoflexi are relatively shallow.
3. Hypocones are well developed, being more than half the height of the protocones.
4. Conules are situated labially at the base of the paracone and metacone.
5. Molar trigonids are not greatly elevated.
6. P<sub>5</sub> paraconids are well developed.
7. The paracone on P<sup>4</sup> is moderately to greatly enlarged

With respect to these characters, the present review of early Eocene leptictids in the YPM collection and comparison of these specimens with type specimens and casts of the types and other specimens of *Prodiacodon tauricinere*, *Palaeictops bicuspsis*, and *Palaeictops multicuspsis* leads to the following observations:

1. The number of upper dentitions of either *Prodiacodon* or *Palaeictops* is very small, and generalizations about the characteristics of the upper teeth of these taxa must be made with caution. Scatter diagrams (figs. 4, 5) of the length to width of the upper molars indicate that teeth in the type of *Palaeictops bicuspsis* are only slightly less transversely broad than are those of the type

or referred specimens of *Prodiacodon tauricinerei*, and that the type of *Palaeictops matthewi* has upper molars that are wider than in either of the latter. Upper molars of Paleocene *Prodiacodon* are more transverse than any early Eocene species of *Palaeictops*.

2. The ectoflexi of the type of *Prodiacodon tauricinerei* are deeper than in the type of *Palaeictops bicuspsis*; however, a referred specimen of *P. bicuspsis* figured by Guthrie (1971) has an M<sup>2</sup> ectoflexus that is intermediately deep between these types.
3. A specimen from the Lysite biostratigraphic zone of the Willwood Formation combines several characters of both genera and is typified by its large tooth size in conjunction with transversely broad upper molars, twinned paraconules, and a large hypocone (nearly two-thirds the height of the protocone).
4. The conules of the few specimens of upper molars are situated more lingually in *Prodiacodon tauricinerei*, as observed by Novacek (1977).
5. The type specimens of the three described species of *Palaeictops* from the early Eocene are very worn, and it is difficult to accurately judge the relative degree of elevation of the molar trigonids. Guthrie's (1971) referred specimen of *P. bicuspsis* does not appear to have trigonids that are relatively less elevated than in most specimens of *Prodiacodon tauricinerei*.
6. The P<sub>6</sub> (traditionally P<sub>4</sub>) paraconid is well developed in the type and referred specimens of *Prodiacodon tauricinerei*. The paraconid appears to be better developed in *Palaeictops* species because of the larger tooth size and because the anterior portion of the trigonid is slightly more elongate (relates more to *P. bicuspsis* than to other species). This feature also gives the tooth a relatively less elevated appearance with respect to *Prodiacodon*.

The conclusion reached from these observations is that the genus *Palaeictops*, although probably constituting a natural group, is not nearly so dentally distinct from early Eocene *Prodiacodon* as Novacek (1977) believed. In particular, *Prodiacodon tauricinerei* of the early Eocene seems to be at least as closely related to *Palaeictops bicuspsis*, in an ancestral-descendant way, as it is to its probable ancestral and collateral cogeners of the Paleocene. Detailed understanding of this lineage, however, is hampered by the paucity of specimens from the critical upper Gray Bull and Lysite zones. It seems likely that early Wasatchian *P. tauricinerei*, persisting into Lysitan time, also may have given rise to a second lineage. This line led to *Palaeictops*.

Novacek's (1977) new species *Palaeictops matthewi* is probably conspecific with *Palaeictops multicuspsis*. As Novacek noted, the two



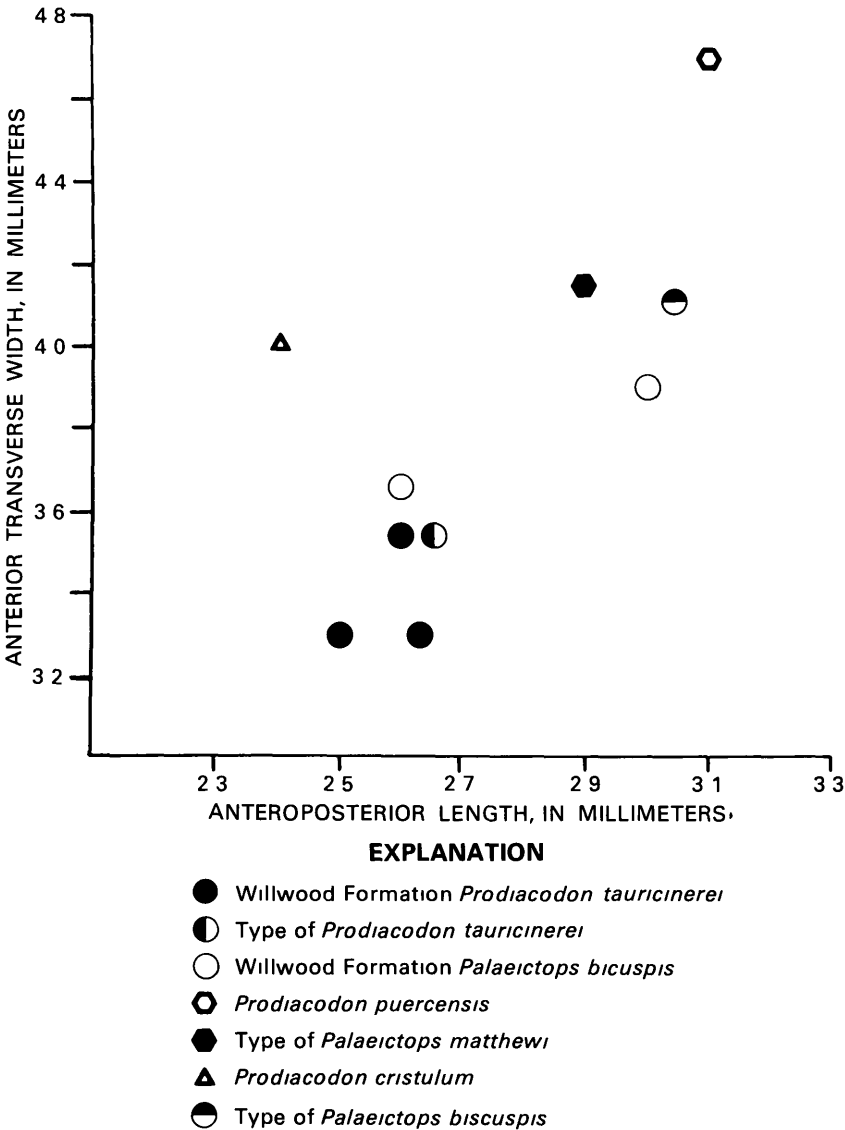


FIGURE 4—Scatter diagram of measurements for M<sup>1</sup> in some early Eocene leptictids

species are closely similar in morphology, differing only slightly in the construction of P<sub>2</sub>. The 8-percent size difference, as judged by size variation in many living and fossil species of mammals, is not considered by us to be significant. Both *P* “*matthewi*” and *P* *multicuspis* fall within the size range for *P* *bicuspis* (figs 6, 7), and a

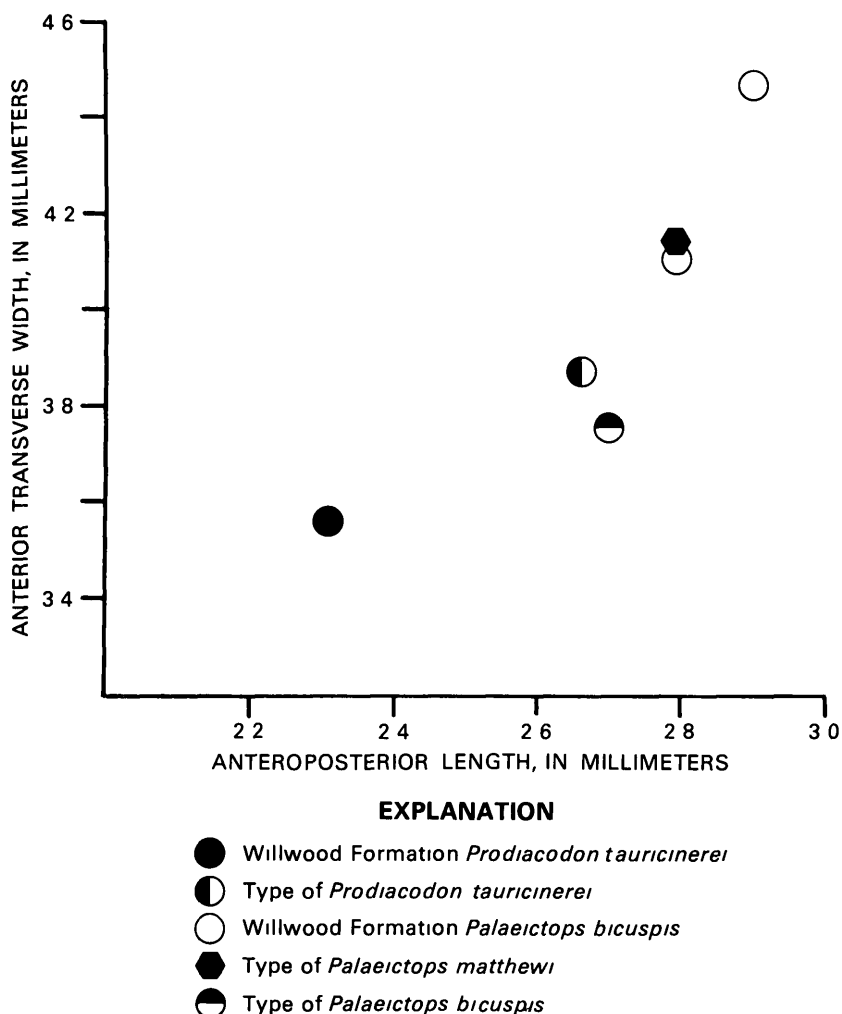
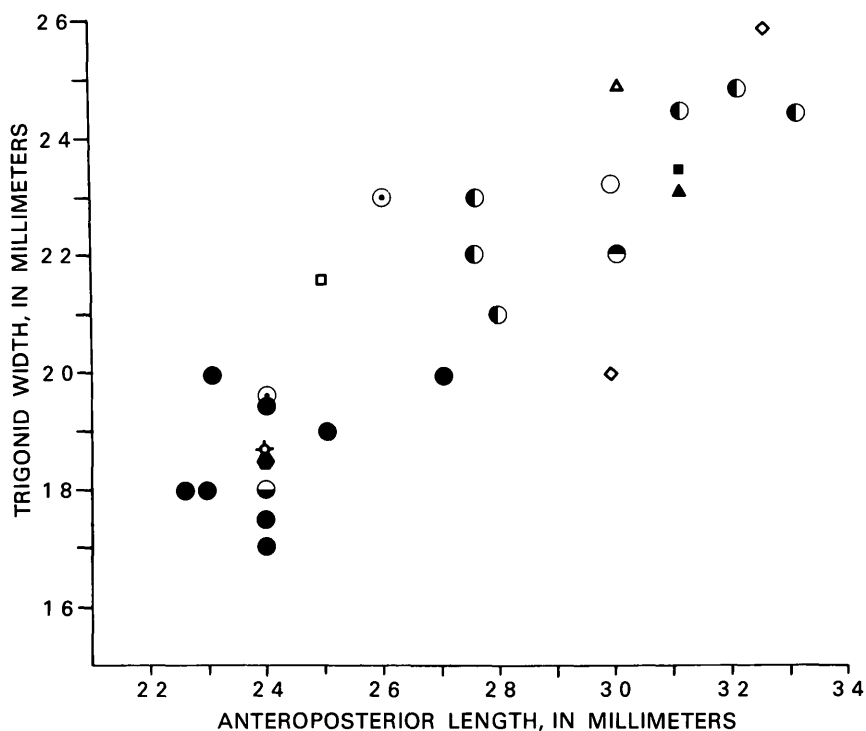


FIGURE 5—Scatter diagram for measurements of  $M^2$  in some early Eocene leptictids

better understanding of the variation and significance of the supernumerary cusps on the anterior premolars might eventually result in their inclusion in that species.

***Prodiacodon tauricinerei* (Jepsen, 1930a)**

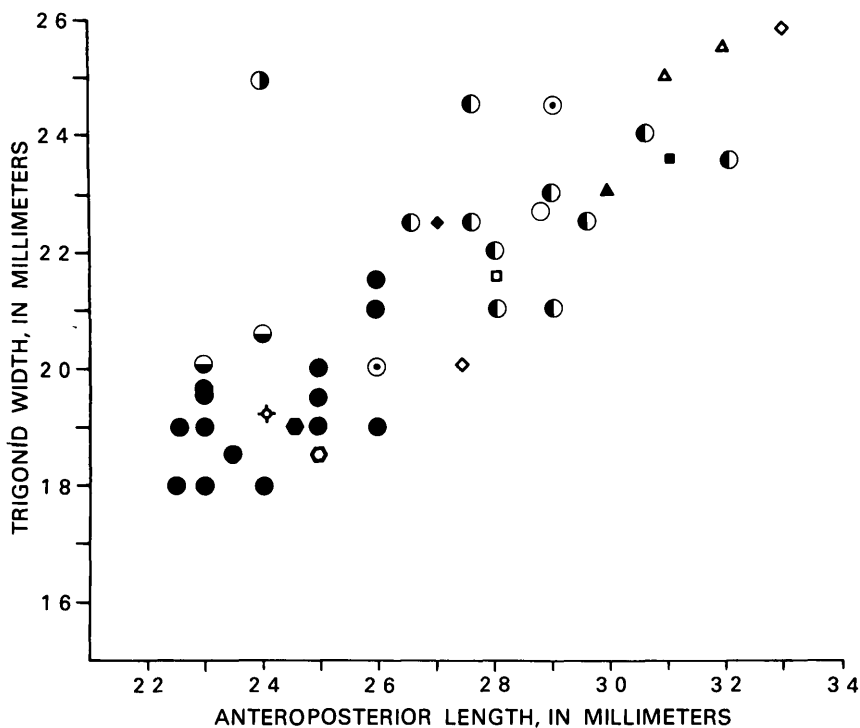
*Referred specimens.*—YPM 23073, 23081, 23090, 23093, 23115, 23119, 27212, 30521, 30556, 30565, 30571, 30601, 30606, 30619, 30621, 30633, 30638, 30640, 30650, 32098, 32104, 34256, 34259,



## EXPLANATION

- *Prodiacodon tauricinerei* (Gray Bull zone, Willwood Formation)
- Type of *Prodiacodon tauricinerei* (measurements from Novacek, 1977)
- ✦ Mean of Willwood Formation *Prodiacodon tauricinerei*
- ◐ *Prodiacodon* sp., YPM locality 290
- ◑ *Palaeictops bicuspsis* (Lysite zone, Willwood Formation)
- Mean of Willwood Formation *Palaeictops bicuspsis*
- Type of *Palaeictops matthewi* (measurements from Novacek, 1977)
- ⊙ Range of Lysite Member (Wind River Formation) *Palaeictops pineyensis* (measurements from Guthrie, 1967a)
- ◻ Mean of Lysite Member (Wind River Formation) *Palaeictops pineyensis* (from Guthrie, 1967a)
- ◇ Range of Lost Cabin Member *Palaeictops bicuspsis* (from Guthrie, 1971)
- ▲ Mean of Lost Cabin Member *Palaeictops bicuspsis* (from Guthrie, 1971)
- ▲ Type of *Palaeictops multicuspsis*
- ◐ Type of *Palaeictops bicuspsis*

FIGURE 6 —Scatter diagram of measurements for  $M_1$  of some early Eocene leptictids



## EXPLANATION

- *Prodiacodon tauricinerei* (Gray Bull zone, Willwood Formation)
- Type of *Prodiacodon tauricinerei* (measurements from Novacek, 1977)
- *Prodiacodon tauricinerei* (Lysite zone, Willwood Formation)
- ✧ Mean of Willwood Formation *Prodiacodon tauricinerei*
- ◐ *Prodiacodon* sp., YPM locality 290
- ◑ *Palaeictops bicusps* (Lysite zone, Willwood Formation)
- ◆ Type of *Palaeictops pineyensis* (measurements from Novacek, 1977)
- Mean of Willwood Formation *Palaeictops bicusps*
- Type of *Palaeictops matthewi* (measurements from Novacek, 1977)
- ⊙ Range of Lysite Member (Wind River Formation) *Palaeictops pineyensis* (measurements from Guthrie, 1967a)
- Mean of Lysite Member (Wind River Formation) *Palaeictops pineyensis* (from Guthrie, 1967a)
- ◇ Range of Lost Cabin Member *Palaeictops bicusps* (from Guthrie, 1971)
- ▲ Mean of Lost Cabin Member *Palaeictops bicusps* (from Guthrie, 1971)
- ▲ Type of *Palaeictops multicusps*

FIGURE 7 —Scatter diagram of measurements of  $M_2$  of some early Eocene leptictids

35146, 35151, 35160, 37238, 37239, 37240, 37243, 37247, UMMP 64482, MCZ 18958, USGSD 2566, possibly YPM 27931

*Discussion.*—*Prodiacodon tauricinerei* is the second most common species of a proteutherian or an insectivore in the Gray Bull biostratigraphic zone of the Bighorn Basin. The type specimen (PU 13104) was recovered from a shale "pocket" south of Dorsey Creek in the central part of the Bighorn Basin (Jepsen, 1930a), and this locality is thought to be near YPM locality 295, in the middle Gray Bull zone. In the Bighorn Basin Lysite zone, *P. tauricinerei* is represented by only one or possibly two specimens. For the most part, it appears to be replaced in these beds by the larger and more abundant leptictid *Palaeictops bicusps*.

Outside the Bighorn Basin, *Prodiacodon tauricinerei* is known from the Powder River local fauna, from rocks of early Wasatchian age at Bitter Creek, Wyo., and from the Four Mile fauna of northwestern Colorado. Measurements given by Novacek for AMNH 80023 from the Four Mile fauna are either typographical errors or indicate a species other than *P. tauricinerei*. In this specimen, the talonid width of  $M_1$  and the trigonid width of  $M_2$  are anomalously small and large, respectively.

Novacek (1977) synonymized the type of *Palaeictops pineyensis* with *Prodiacodon tauricinerei*, noting the larger size of the former but a general similarity of morphology. As discussed previously, the differences between *Prodiacodon* and *Palaeictops* are not great, and what differences do exist (for example, placement of conules on the upper molars and elongation of the  $P_3$  trigonid) cannot be observed in the type of *Palaeictops pineyensis* because they are not preserved in that specimen. A scatter diagram of length versus trigonid width of  $M_2$  for early Eocene leptictids (fig. 7) shows that the type of *P. pineyensis* from the La Barge fauna (Lostcabinian age) is most closely associated in this character with specimens from the Lysite Member of the Wind River Formation that were referred to *P. pineyensis* by Guthrie (1967a), and with specimens from the Lysite zone of the Willwood Formation. The two Lysite zone populations are significantly different from the largely Gray Bull sample of *Prodiacodon tauricinerei* in both length and width (Lysite zone: length  $t=7.92$ ,  $n=24$ ;  $p=0.0001$ , width  $t=8.12$ ,  $n=24$ ,  $p=0.0001$ ; Lysite Member, Wind River Formation: length  $t=8.14$ ,  $n=20$ ,  $p=0.0001$ , width  $t=4.92$ ,  $n=20$ ;  $p=0.0001$ ; see table 1). Similar results were obtained from analyses of the dimensions of  $M_1$ , except for the length comparisons of specimens from the Lysite Member of the Wind River Formation to *P. tauricinerei*, in which case they do not differ significantly ( $t=1.18$ ,  $n=10$ ,  $p=0.25$ ). Perhaps this lack of difference is due to the small sample size from the Wind River Formation, which appears to include only specimens in the lower end of the size range of  $M_1$  length.

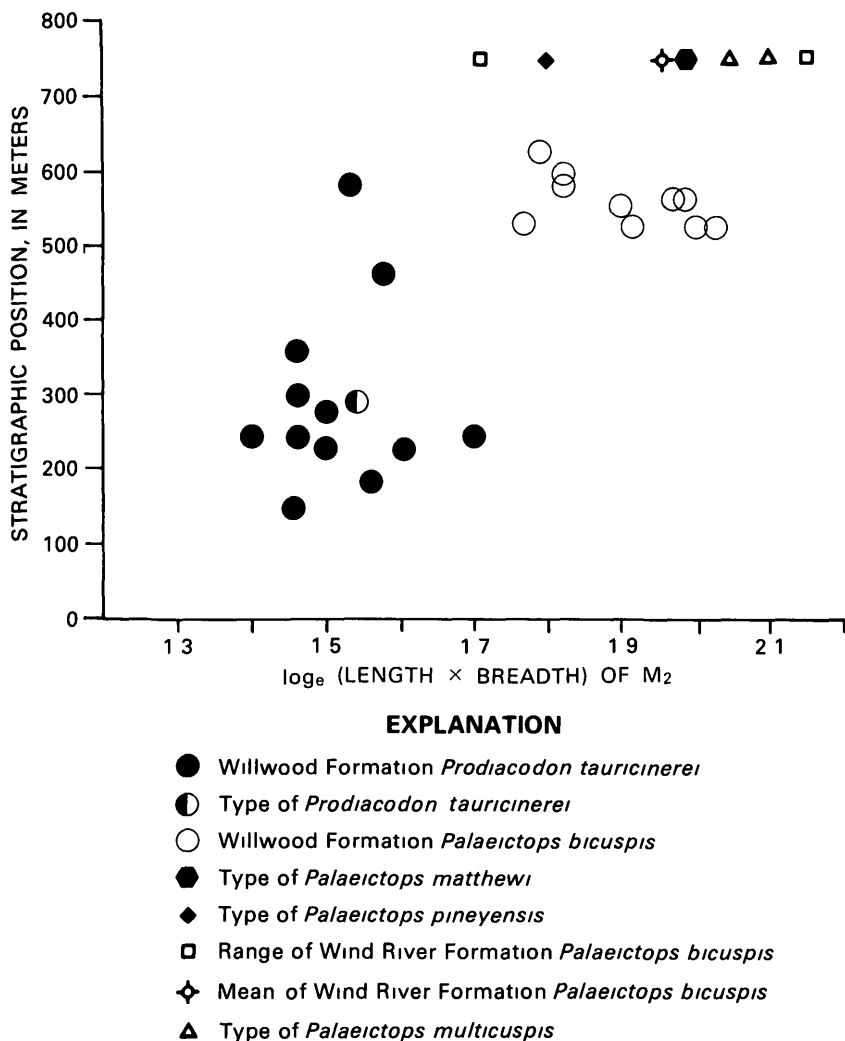


FIGURE 8—Stratigraphic plots of  $M_2$  in some early Eocene leptictids. Measurements of stratigraphic position are from the base of the Willwood Formation. Positions of non-Willwood specimens are hypothesized.

The type specimen of *P. pineyensis* also is closer in size to the mean of the Lost Cabin Member sample of *P. bicuspsis* than it is to the mean of the *Prodiacodon tauricinerei* sample, and it falls within the  $\log_e(L \times W)$  range of the former species (fig. 8).

For these reasons, *Palaeictops pineyensis* is removed from synonymy with *Prodiacodon tauricinerei* and is tentatively referred to *Palaeictops bicuspsis*. (See following text.) This new appraisal re-

# 18 PROTEUTHERIA AND INSECTIVORA, WILLWOOD FORMATION, WYO.

TABLE 1.—*t* values for pair-wise comparisons of early Eocene samples of *Prodiacodon* and *Palaeictops*

[Willwood sample of *Prodiacodon tauricinerei* is mostly Graybullian in age. Computation of *t* values used the standard deviation of sample. Where not given by Guthrie (1967b, 1971) for Wind River Formation samples, they were estimated using either  $S_1 = \frac{1}{4} \text{ range}$  or  $s_1 = s_2$ , where  $s_2$  was the standard deviation of other sample. Estimate used in each case was chosen to maximize robustness of conclusion (that is, if it was desired to demonstrate that two samples were not significantly different, a minimum estimate of "s" was used.  $n = n_1 + n_2 - 2 = \text{degrees of freedom}$ ). Probability values (*p*) were determined from a graph and are necessarily approximate. \*, significant; \*\*, highly significant]

Biostratigraphic unit and taxon	M <sub>1</sub> L	M <sub>1</sub> W	M <sub>2</sub> L	M <sub>2</sub> W
Willwood Formation	t: 6.4	6.8	7.9	8.1
<i>P. tauricinerei</i> , Bighorn Basin Lysite zone.	n: 14 p: .0001**	13 .0001**	24 .0001**	24 .0001**
Willwood Formation	t: 1.18	3.2	8.14	1.92
<i>P. tauricinerei</i> , Wind River Formation, Lysite Member.	n: 10 p: .25	9 .01*	20 .0001**	20 .0001**
Willwood Formation <i>P. tauricinerei</i> , Wind River Formation, Lost Cabin Member.	t: 9.75 n: 11 p: .0001**	6.2 12 .0001**	10.2 22 .0001**	7.23 21 .0001**
Bighorn Basin Lysite zone, Wind River Formation, Lysite Member.	t: 3.62 n: 8 p: .01*	1.62 6 .15	1.08 14 .25	1.81 14 .08
Bighorn Basin Lysite zone, Wind River Formation, Lost Cabin Member.	t: .94 n: 9 p: .35	.42 9 .70	1.7 16 .12	.54 15 .65
Wind River Formation Lysite Member, Wind River Formation, Lost Cabin Member.	t: 14.4 n: 5 p: .0001**	1.36 5 .2	3.19 12 .01*	1.89 11 .09

stricts the known temporal range of *Prodiacodon tauricinerei* to early and middle Wasatchian time in the northern Rocky Mountains, though it is represented in a Lostcabinian fauna from the San Jose Formation of New Mexico (AMNH 48763 from Arroyo Blanco).

## *Prodiacodon* sp.

Plate 2, figure 6

*Referred specimens*.—YPM 26013, 26040 (pl. 2, fig. 6), possibly 26026.

*Discussion.*—Two specimens from the middle Gray Bull zone of the central Bighorn Basin Willwood Formation have a morphology distinct from that of contemporary *Prodiacodon tauricinerei*. The specimens fall within the size range of that species (text figs 6, 7), though the  $M_2$ 's are slightly more robust. The most distinctive characters, however, are the very large entoconulid on  $P_4$  ( $P_5$  of Novacek, 1977) through  $M_3$ , and the colinearity of the remaining talonid cusps. These characters are contrasted with a weak to absent entoconulid and a hypoconulid that is more posterior than the entoconid and hypoconid in typical *P. tauricinerei*.

Both specimens are from a single locality (YPM loc. 290) where *P. tauricinerei* is not known. A third specimen of a leptictid from this site (YPM 26026) is missing the lingual portion of the tooth, rendering specific identification impossible. Locality 290 has a number of unusual faunal elements; for example, there is a very high abundance of the otherwise rare dermopterian *Plagiomene multicuspis*. Presence of this fossil in abundance indicates the locality might represent an unusual Willwood ecology. This insularity of occurrence, coupled with the possibility that *Prodiacodon* sp. might be geographically sympatric with, but ecologically distinct from, *P. tauricinerei*, has here led to separation of the species on characters that otherwise might be attributed to intraspecific variation

***Palaeictops bicuspis* (Cope, 1880)**

Plate 2, figures 3, 5

*Referred specimens.*—YPM 17508, 17521, 17522, 18584, 18588, 18592, 23070, 23072, 23079, 23118, 23723 (pl. 2, figs 3, 5), 23805, 24964, 27918 (including YPM 28783), 27937, 29638, 30618, 30652, possibly YPM 26852, 28111, U.S. National Museum 19204.

*Discussion.*—The type of *Palaeictops bicuspis* is from the Lost Cabin Member of the Wind River Formation, though all referred specimens from the Willwood Formation (Van Houten, 1945; Novacek, 1977) are from older rocks. Scatter diagrams of length versus trigonid width of  $M_1$  and  $M_2$  of the Lost Cabin Member of the Wind River sample and the sample from the Lysite zone in the Bighorn Basin overlap considerably (figs. 6, 7). The means for the Bighorn Basin sample are slightly smaller in most dimensions, but the differences are not significant (table 1). The means of the Willwood sample are intermediate between those of the Wind River Lost Cabin Member sample assigned to *P. bicuspis* by Guthrie (1971) and in the Lysite Member sample assigned by the same author (1967a) to *P. pineyensis*. The Willwood sample from the Lysite biostratigraphic



zone is significantly different from the Lysite Member sample only in the dimension of  $M_1$  length (see text on previous page), though the Lysite Member sample is significantly different from that of the Lost Cabin Member in both  $M_1$  and  $M_2$  length.

Retention of the name *P* "*pineyensis*" for specimens from the Lysite Member of the Wind River Formation would imply that two lineages of leptictines were present in the middle and late Wasatchian; whereas, the combined stratigraphic and morphologic evidence points to the existence of a single lineage that showed an increase in individual size through time. *Palaeictops bridgeri*, a probable middle Eocene member of this lineage, is larger than Lost Cabin Member *P bicuspis*. The type specimen of *P* "*pineyensis*" from the La Barge fauna is an individual from the small end of this stratigraphically controlled size spectrum.

If *Palaeictops* "*pineyensis*" is distinct from *P bicuspis*, as suggested in 1977 by Novacek (although not a synonym of *Prodiacodon tauricinerei*), a southerly migration of these two species may have taken place. *Palaeictops bicuspis* first appears in the Lysite zone of the Willwood Formation and occurs in the younger, more southerly Wind River Basin Lost Cabin Member, where it was apparently absent during Lysitian time. *P* "*pineyensis*" first occurs in the Lysite Member of the Wind River Formation. The species disappears there in Lostcabinian time, but does occur in the Lostcabinian La Barge fauna of the northern Green River Basin. Alternatively, this same evidence could be interpreted as the southerly migration of a single species that had a north-to-south size cline

#### Family PANTOLESTIDAE

##### *Palaeosinopa incerta*, sp nov

Plate 3, figures 3, 4, plate 10

*Synonyms*.—*Palaeosinopa didelphoides* Matthew (1918), in part; cf. *Palaeosinopa didelphoides* of McKenna (1960a); *Palaeosinopa* sp. of Gazin (1962); *Palaeosinopa* sp. E of Van Valen (1967); *Palaeosinopa didelphoides* of Delson (1971), in part, *Palaeosinopa lutreola* of Guthrie (1971).

*Etymology*.—Latin *incertus*, uncertain, for the uncertain taxonomic status that specimens included in this species long held

*Holotype*.—UMMP 69722, partial skull and lower jaws (pl. 10).

*Locality*.—UMMP locality SC-211, lower part of Willwood Formation, sec. 3, T. 55 N., R. 101 W., Park County, Wyo

*Hypodigm*: The type specimen and YPM 25506, 25648, 25892, 30613 (pl. 3, fig. 3), 32258, 37246, AMNH 15701, 16239, 16823,

94457, UCMP 44047, CM 22039, 22040, 22041, possibly AMNH 39565 (pl. 3, fig. 4), 56226, 56227

*Distribution*.—Lower to upper Gray Bull zones, Bighorn Basin, Wyo.; Graybullian equivalents in Washakie and Powder River(?) basins, Wyo., and Sand Wash Basin, Colo.; Lost Cabin Member of Wind River Formation, Wind River Basin, Wyo.; San Jose Formation, N. Mex.

*Diagnosis*.—Intermediate in tooth size between its contemporaries *P. veterrima* and *P. lutreola* in early Wasatchian faunules; smaller than contemporary *P. didelphoides* in late Wasatchian faunules.  $M_1$  trigonid subequal in width to talonid and  $M_1$  relatively narrower than in *P. veterrima* or *P. didelphoides*.  $M_2$  talonid generally much narrower than trigonid (YPM 25506 and 25892), and trigonid relatively as wide as in *P. veterrima* and *P. didelphoides*.

*Discussion*.—As early as 1918, Matthew observed that all the large Willwood specimens of *Palaeosinopa* could not be reasonably accommodated in *P. veterrima*. He assigned the smaller, less robust specimens to *P. didelphoides* and remarked that they might eventually prove to be variants of *P. veterrima*. McKenna (1960a) and Gazin (1962) also recorded a medium-size species of *Palaeosinopa* in the Four Mile and Bitter Creek faunas, respectively. Van Valen (1967), in a discussion of Paleocene pantolestids, grouped these specimens together in a new species that he designated *Palaeosinopa* sp. E, distinct from *P. didelphoides*. Delson (1971), in his examination of the pantolestids in the Powder River local fauna, decided that the three species were merely populations of a single species that were dispersed over a wide geographic area. He referred both *P. veterrima* and *Palaeosinopa* sp. E to *P. didelphoides*.

After examining the Willwood collection of *Palaeosinopa* in the Peabody Museum and American Museum collections, the specimens referred to *P. sp. E* by Van Valen, and a few specimens from the Wind River Basin earlier referred to *P. didelphoides*, we conclude that there are at least five Eocene species of *Palaeosinopa*. *P. veterrima*, *P. didelphoides*, *P. incerta*, sp. nov., *P. lutreola*, and a new large species, incorrectly referred to *P. veterrima* (CM 24042) by Guthrie (1971). Evidence for this viewpoint is largely derived from scatter distributions and on statistical data on the ranges and coefficients of variation of these samples.

A scatter diagram of length versus trigonid width of  $M_1$  (fig. 9) shows that the Willwood specimens represent three groups: *P. lutreola* on the small end, *P. veterrima* on the large end, and *P. incerta* in the middle. A similar plot for  $M_2$  (fig. 10) less clearly separates these groups, possibly owing to three specimens with very wide trigonids. When length is plotted against talonid width for  $M_2$  and  $M_1$  (figs. 11, 12), the separation is more distinct for  $M_2$  but remains the

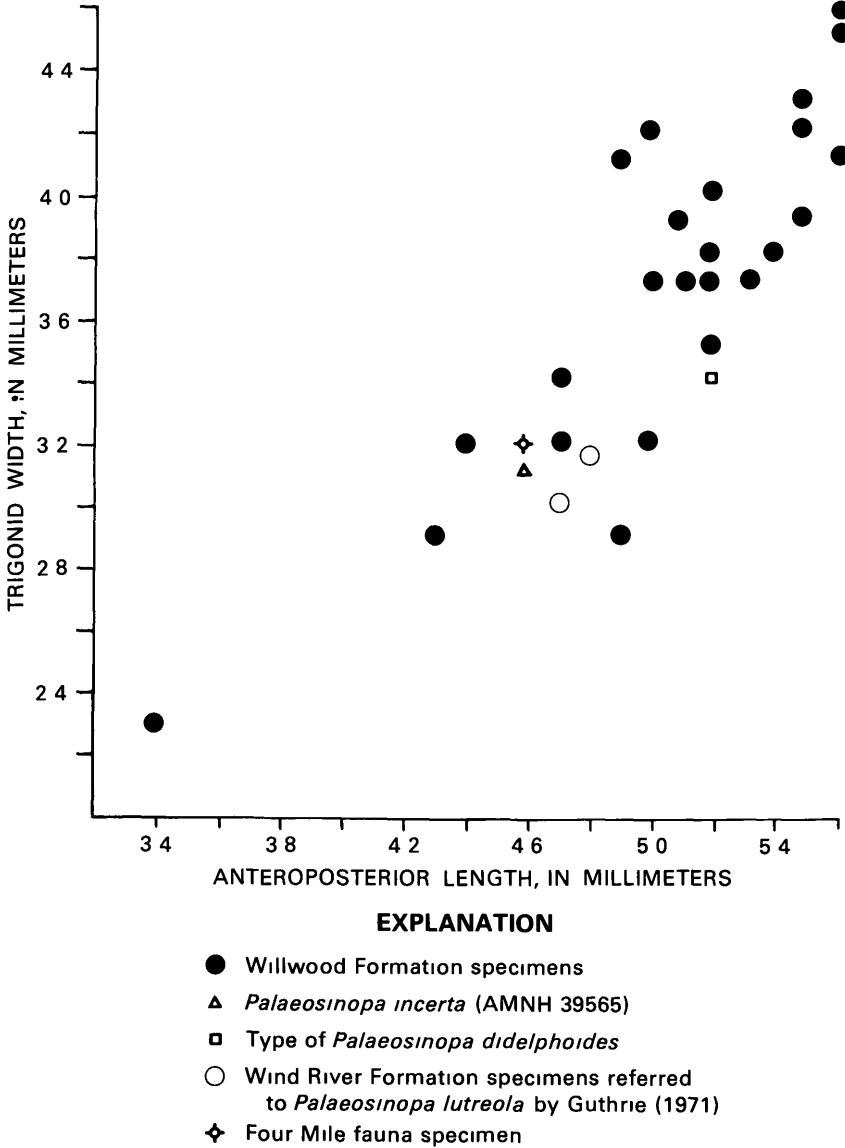
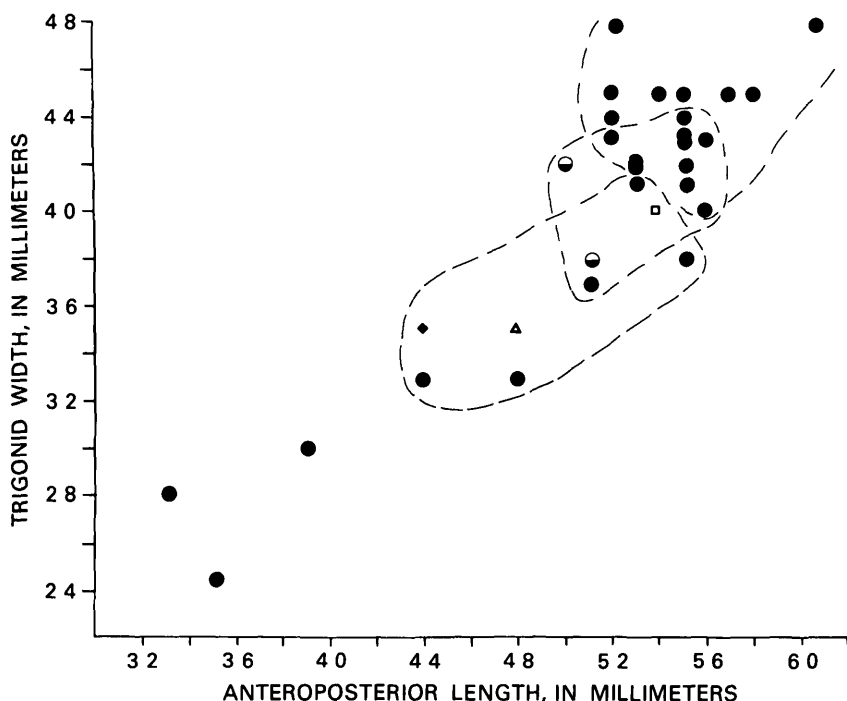


FIGURE 9 —Scatter diagram of measurements of  $M_1$  in early Eocene *Palaeosinopa*

same for  $M_1$ . The specimens referred to *Palaeosinopa* sp. E by Van Valen (1967) from the Four Mile fauna and San Jose Formation lie clearly within the *P. incerta* grouping, as do specimens referred to *P. lutreola* by Guthrie (1971). If Delson's (1971) specimens are, in fact,  $M_2$ 's, then they also belong in *P. incerta*. If, on the other hand, they



## EXPLANATION

- Willwood Formation specimens
- ▲ *Palaeosinopa incerta* (AMNH 39565)
- Type of *Palaeosinopa didelphoides*
- ◆ New Mexico specimen
- ⊖ Lost Cabin Member specimens, *Palaeosinopa lutreola* is at the bottom, *Palaeosinopa incerta* (middle), and *Palaeosinopa veterrima* (top)
- - - Range of Wind River Formation *Palaeosinopa didelphoides*
- — — Upper, *Palaeosinopa veterrima*, lower, *Palaeosinopa incerta*

FIGURE 10—Scatter diagram of measurements of  $M_1$  in early Eocene *Palaeosinopa*. Dashed dotted line is range of Wind River Formation *P. didelphoides*. Upper dashed line is *P. veterrima*, lower dashed line is *P. incerta*. Three specimens in lower left corner are *P. lutreola*.

are  $M_1$ 's, they would, conversely, be more appropriately assigned to *P. veterrima*. The type and two other specimens of *P. didelphoides* from the Lost Cabin Member of the Wind River Formation were also plotted, and these occur between *P. incerta* and *P. veterrima*, evidence of the size overlap mentioned by Delson (1971).

If the sample for all three species is combined, the coefficient of

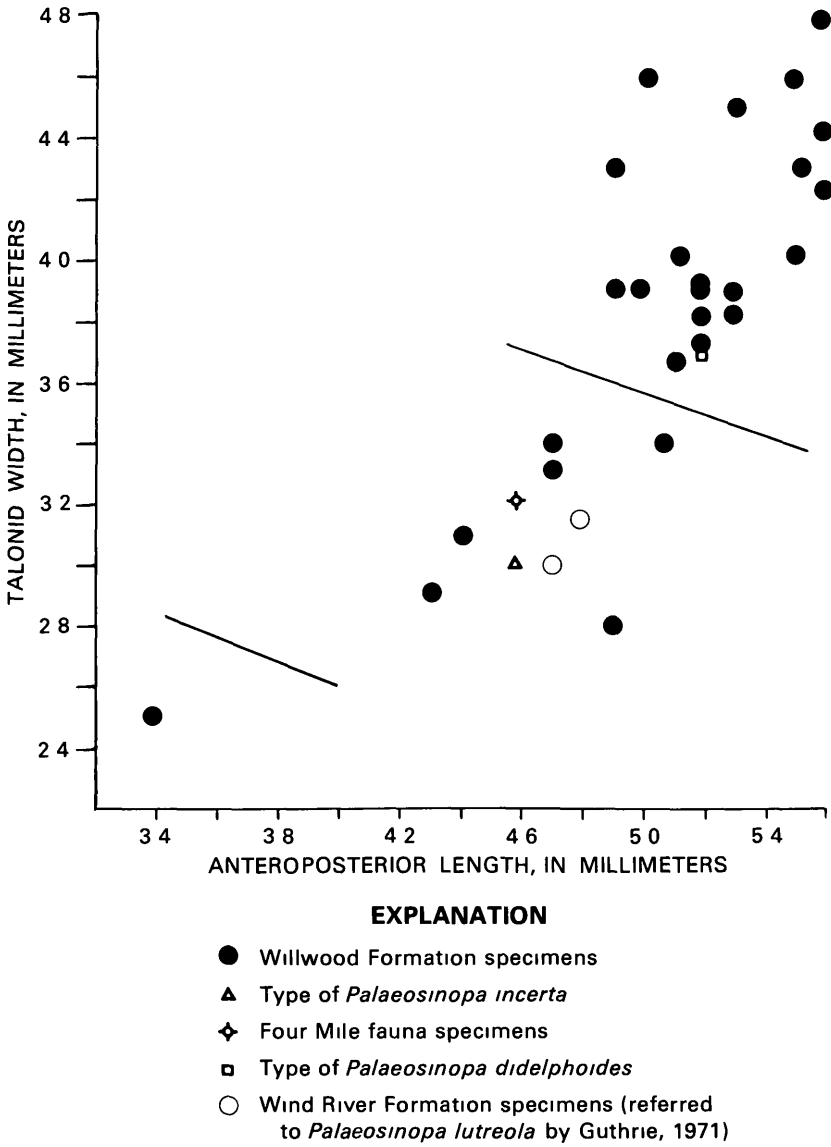


FIGURE 11 —Scatter diagram of measurements in  $M_1$  of early Eocene *Palaeosinopa*. Lines separate *P. lutreola* (bottom), *P. incerta* (middle), and *P. veterrima* (top, excluding type of *P. didelphoides*)

variation for the Willwood Gray Bull zone sample alone is 12.3 for  $M_1W$  and 9.3 for  $M_2W$ . These values are very large for a single species (for example, Gingerich, 1974b). Moreover, a plot of  $\log_e (L \times W)$  of  $M_1$  shows that it would require 0.75 natural log units (fig. 13) to encom-

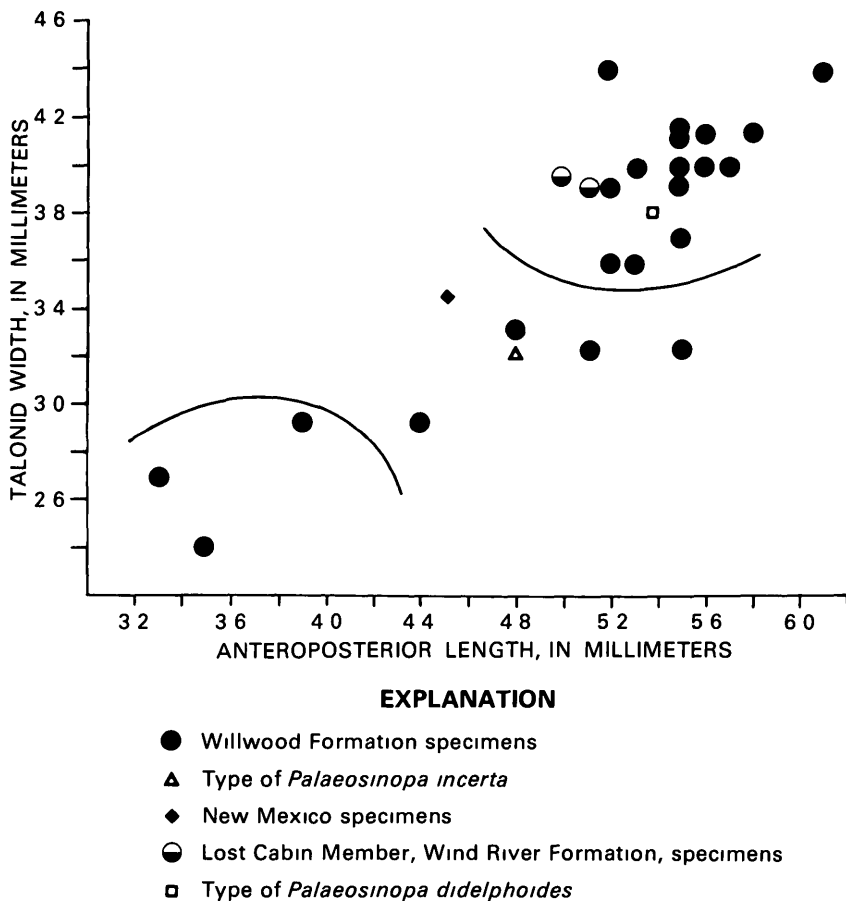


FIGURE 12—Scatter diagram of measurements of  $M_1$  in early Eocene *Palaeosinopa*. Lines separate *P. lutreola* (bottom), *P. incerta* (middle), and *P. veterrima* (top, excluding type of *P. didelphoides*)

pass the entire *P. incerta*-*P. veterrima* complex (*P. didelphoides* was excluded from this histogram). Unpublished data of P. D. Gingerich and D. A. Winkler and of David Schankler shows that the normal range for both extant and fossil species is between 0.35 and 0.45 natural log units. This is approximately the range for each of the two included species, though that of *P. incerta* is somewhat less, possibly due to the small sample size.

All the Wind River Basin specimens (except CM 24042) could be assigned to *P. didelphoides* without increasing the coefficient of variation (6.3 for  $M_1/W$ ) beyond that probable for a single-species. The three smallest specimens have provisionally been referred to *P. in-*

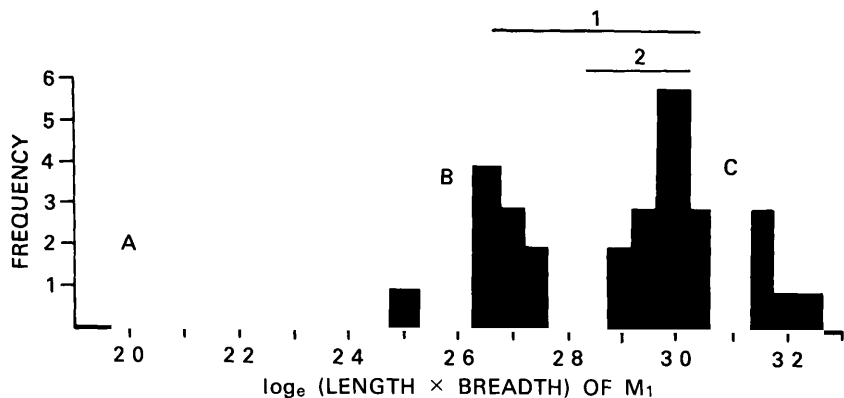


FIGURE 13 —Histogram of  $\log_e (L \times W) M_1$  in early Eocene *Palaeosinopa*. 1 is range of Wind River Formation specimens, including those referred to *P. lutreola* by Guthrie (1971) 2 is range of Wind River Formation specimens, excluding those referred to *P. lutreola* by Guthrie (1971) A, *P. lutreola*, B, *P. incerta*, C, *P. veterrima*.

*certa*. The reinclusion of these specimens in *P. didelphoides* would remove the record of *P. incerta* from the Lost Cabin Member of the Wind River Formation but not from all rocks of Lostcabinian age. The San Jose specimen still falls beyond the range for *P. didelphoides*. Whichever interpretation is correct, *P. didelphoides* is not now known from early or middle Wasatchian faunas, and it is not identified as such in the present scheme because its size range overlaps the upper part of that for *P. incerta* and the lower part of that for *P. veterrima*, without wholly encompassing either.

*Palaeosinopa didelphoides* is probably a descendant of either *P. incerta* or *P. veterrima*. If the three small CM specimens are included in *P. didelphoides*, then that species is probably derived from *P. incerta*; if they are excluded, then derivation from *P. veterrima* is more plausible.

Overall time versus size plots for  $M_2$  and  $M_1$  are presented in figures 14 and 15. The vagueness of these plots is related to the fact that the size measure (a modification of Gingerich, 1974b) discriminates best when changes in size are unaccompanied by changes in shape. In this instance, there is a shape change between *P. incerta* and *P. veterrima*, and the latter also is more robust.

*Palaeosinopa veterrima* Matthew, 1901

Plate 3, figure 1, plate 4, figures 1, 2

*Referred specimens.*—YPM 17032, 22253, 22867, 23469, 23475, 23543, 23569, 23587, 23588, 23738, 23743, 25223, 25849, 26087,

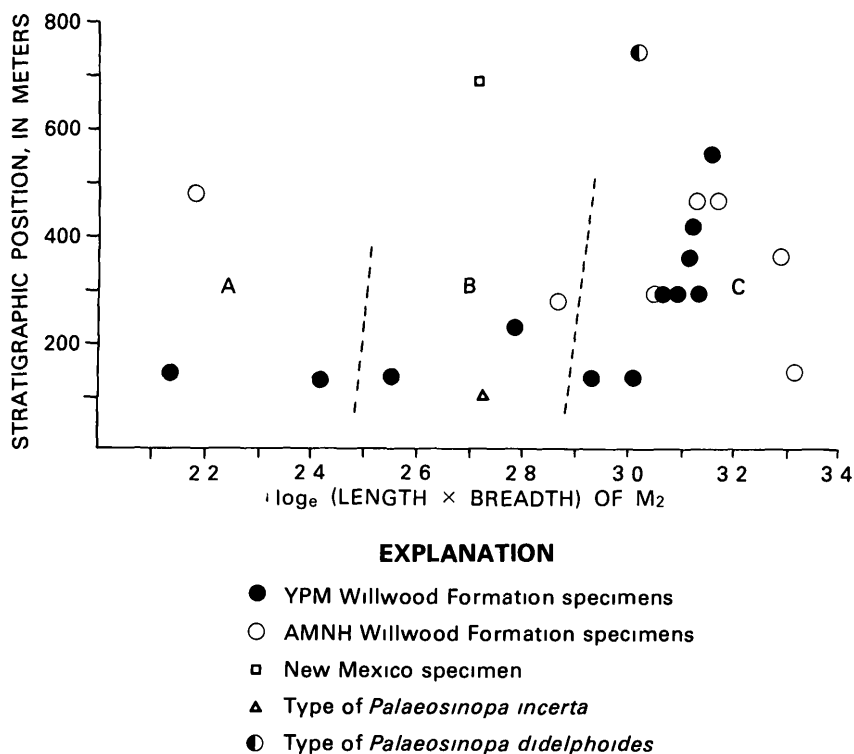
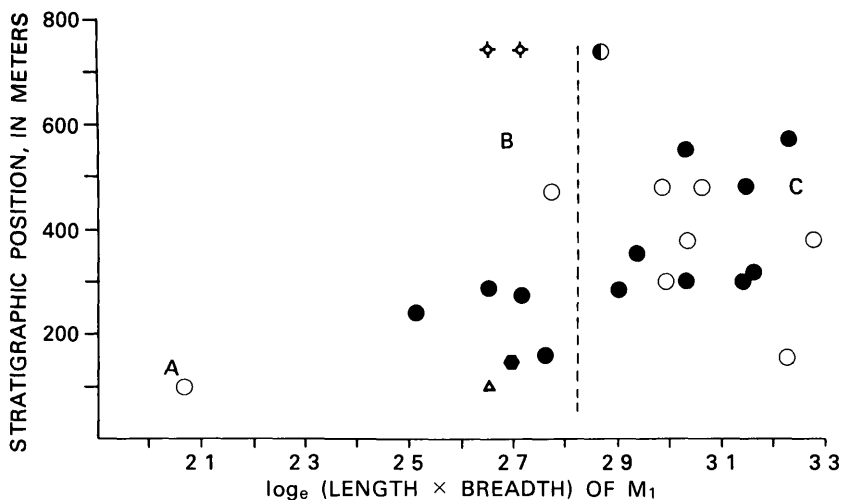


FIGURE 14 —Stratigraphic plots of  $M_2$  in early Eocene *Palaeosinopa*. Measurements of stratigraphic position are from the base of the Willwood Formation. Positions of non-Willwood specimens are hypothesized. Dashed lines separate (A) *Palaeosinopa lutreola*, (B) *Palaeosinopa incerta*, and (C) *Palaeosinopa veterrima* and *P. didelphoides*.

26269, 26674 (pl. 4, fig. 1), 26913, 27063, 27168 (pl. 3, fig. 1), 27216, 28969, 30569, 30576, 30629, 32100, 32173, 33916, 34255 (pl. 4, fig. 2), 35307, 36921, 36925, 37249, YPM field numbers 63-596, 63-891, 65-288, 70-693, 75-415, AMNH 95, 150a, 2849, 2851, 15092, 15095, 15096, 15097, 16822, 16824, 56224, 56225, 94448, 94449, 94450, 94451, possibly AMNH 16943.

**Discussion.**—*Palaeosinopa veterrima* is the most common and temporally wide ranging of Willwood species of this genus. It is known from more than fifty specimens from localities in the lower Gray Bull through Lysite zones. The other two species of Willwood *Palaeosinopa* are, at present, known only from the Gray Bull zone. The absence of *P. veterrima* from the richly fossiliferous level at 645 m probably means that this species became extinct in the Bighorn Basin towards the end of Lysitan time. Its absence in the Lost Cabin biostratigraphic zone of that basin is, therefore, probably real and not merely due to the rarity of the species or to a paucity of fossils. Outside the





## EXPLANATION

- YPM Willwood Formation specimens
- AMNH Willwood Formation specimens
- ▲ Type of *Palaeosinopa incerta*
- Specimens from the Four Mile fauna
- Type of *Palaeosinopa didelphoides*
- ◆ Wind River Formation specimens (referred to *Palaeosinopa lutreola* by Guthrie, 1971)

FIGURE 15 —Stratigraphic plots of  $M_1$  in early Eocene *Palaeosinopa*. Measurements of stratigraphic position are from the base of the Willwood Formation. Positions of non-Willwood specimens are hypothesized: A, *P. lutreola*, B, *P. incerta*, C, *P. veterrima* (excluding type of *P. didelphoides*), dashed line separates B and C

Bighorn Basin, *P. veterrima*, as defined in this paper, is known only from two isolated teeth from the Powder River local fauna (AMNH 56224 and 56225)

As mentioned earlier, *P. veterrima* is considered distinct from *P. didelphoides*, a species shown to occupy only the lower half of the size range of *P. veterrima*. The means of the lengths of  $M_2$  do not differ significantly (5.48 for *P. veterrima*; 5.34 for *P. didelphoides*, from Guthrie, 1971). The mean for the width of  $M_2$  of *P. didelphoides* (3.91) is, however, significantly smaller than that for *P. veterrima* (4.37), with a probability of less than 0.001 ( $t=5.91$ ,  $n=28$ ) that the two samples are from the same statistical population, and that the difference observed is entirely due to stochastic effects. Similar results are obtained from an analysis of  $M_1$ . The difference in tooth lengths is not

significant, whereas the difference in width is ( $p=0.01$ ,  $t=2.76$ ,  $n=24$ ). If the specimens referred to *P. lutreola* by Guthrie (1971) are included in the *P. didelphoides* sample, the results are substantially the same, although the level of significance is more in line with that obtained for  $M_2$ . This level of significance might indicate that the entire Wind River Formation sample belongs to a single species. Which-ever case is correct, *P. didelphoides* has been demonstrated to differ significantly in some measures from *P. veterrima* when the species are considered as populations. *P. didelphoides* has been shown to be slightly less robust than *P. veterrima*, as indicated by Matthew (1918), even though the measurements he gave for individual specimens indicate the reverse (a point noted by Gazin, 1962).

The specimen (CM 24042) referred to *P. veterrima* by Guthrie (1971) is here considered to be representative of a new, larger but less robust species. It falls well outside the boundary of *P. veterrima* in a scatter diagram and is not encompassed in the range of the  $\log_e(L \times W)$  size measure (0.17 natural log units larger than the largest specimen of *P. veterrima*). Although there is considerable variation in the shape of  $M_1$  in *P. veterrima*, the width-to-length ratio of CM 24042 of 0.58 lies more than 3.5 standard deviations from the mean of that for all Willwood specimens of *P. veterrima* ( $\bar{X}=0.75$ ,  $s=0.048$ , range=0.67–0.84).

The upper molars of *P. veterrima* also show considerable variation in shape. This variation can be seen in the condition of the cingulum on  $M^1$  and  $M^2$ . In most specimens, the cingulum is closely appressed to the body of the tooth with the precingula and postcingula being disjunct at the lingual margin. In one specimen (YPM 23475), however, the cingulum is nearly complete, although narrow, and in another (YPM 27216), the postcingulum is expanded with a slight median ridge and the precingula and postcingula are completely confluent on the lingual side of  $M^2$ .

*Palaeosinopa lutreola* Matthew, 1918

Plate 3, figure 2

*Referred specimens.*—YPM 23082, 25843, 26175 (pl. 3, fig. 2), 26604, AMNH 15102, 16170, 56222, 56223, UW 7917, 8995, 9588.

*Discussion*—*Palaeosinopa lutreola* is known from rocks of early Graybullian age in the Powder River Basin, the Clark's Fork Basin, and the Bighorn Basin (both No Water and Elk Creek section faunules). In the fauna of the Elk Creek section, it also occurs in the middle and upper Gray Bull biostratigraphic zones (the type is from the upper Gray Bull zone of the Elk Creek section). *P. lutreola* is the

smallest and least common of *Palaeosinopa* species, and its absence from rocks of the Lysite and Lost Cabin zones in the central Bighorn Basin may be due either to its absence or rarity.

As mentioned earlier, the two specimens from the Lost Cabin Member of the Wind River Formation, referred by Guthrie (1971) to *P. lutreola*, are well outside the range for this species and are more properly assigned to *P. incerta* or possibly *P. didelphoides*. YPM 26604 and specimens referred by Bown (1979) to *P. cf. lutreola* are considerably larger than the type specimen but still are within the possible range for this species and are provisionally referred to it here.

### Family APATEMYIDAE

#### COMMENTS ON *APATEMYS* MARSH, 1872

Analysis of the genus *Apatemys* has been plagued by the paucity of specimens available for study. This shortage of specimens has not, however, precluded the publication of major reviews of *Apatemys* and the Apatemyidae in recent years, one from a principally morphological viewpoint (McKenna, 1963), and another utilizing the biometric approach (West, 1973). The major emphasis in both of these and earlier works on apatemyids has been the attempt to identify consistent and useful characters that allow meaningful separation of this genus into species. McKenna (1960a) recorded two species of *Apatemys* in the early Wasatchian Four Mile fauna and divided the majority of early Eocene apatemyids into two groups. The first of these was believed to be characterized by “\* \* \* a reduced, single-rooted  $P_4$ , a strongly developed fossa beneath  $P_4$ , and two major mental foramina \* \* \*,” and the second group by “\* \* \* an unreduced, semimolariform, double-rooted  $P_4$ , a generally weak or totally absent fossa beneath  $P_4$ , and a single major mental foramen \* \* \*.” Guthrie (1967a), in discussing *Apatemys whitakeri*, demonstrated that the taxonomic utility of the number of mental foramina breaks down within a single species. Robinson (1966), in reviewing the Huerfano fauna, suggested a possible synonymy between the smallest and largest Bridgerian species of *Apatemys*: *A. bellulus* and *A. rodens*.

The most recent and comprehensive review of the apatemyids was published by West (1973). Using the characters cited by McKenna (1960a, 1963) and tooth size distributions, West believed that no correlations could be made and that no unified groups exist within the genus. Consequently, West synonymized all Wasatchian and Bridgerian species of *Apatemys* with the earliest described species, *A. bellus*. The present study is not as exhaustive in terms of the number

of specimens studied as was West's, and so in a few instances West's analytical data was used. In using his data, West's study was examined critically and the following notes were made.

On page 12, West (1973) stated that 95 percent of the measurements of *Apatemys* specimens fall within one standard deviation of the mean, and that this "\* \* \*" confirms the conclusion that all may be assigned to a single species." A recalculation shows that at least 95 percent of the measurements fall within two standard deviations of the mean and that whereas this is consistent with a normal distribution, it does not specify normality nor does it say anything about the number of species contained in the distribution. It should be noted that if it were true that 95 percent of the measurements occurred within one standard deviation, this would be a strong indication of non-normality (that is, a long-tailed distribution, with the specimen or specimens in the tail probably representing a second species). The distribution of Wasatchian M<sub>3</sub> lengths in *Apatemys* (West, 1973, fig. 3) most closely approaches such a situation (82 percent fall within one standard deviation), and it seems clear that the specimen that defines the tail, YPM 23476, represents a distinct species.

After performing t tests on the Wasatchian and Bridgerian samples, West (1973, p. 13) concluded that at "\* \* \*" the 95 percent or higher level of confidence both early and middle Eocene samples could be drawn from the same statistical population." In fact, no probability statement about the populations being the same is justified by the t test. All that can be said is that values of t as large as those obtained would occur at least x percent of the time (where x is determined by t and the degrees of freedom), if the populations were the same. West is correct in noting that the t test is a statement about statistical populations and not about species (that is, two species could be present in both early and middle Eocene samples, but as long as there was no appreciable change in their means and variances, the t test would give the same result).

West (1973) addressed this last point on page 15 where, in discussing the range of variation of the Wasatchian and Bridgerian samples individually, he concluded that only one species is present at each sampled interval. For the Wasatchian sample (including two specimens from the late Tiffanian), West observed that although both small-size and large-size groups exist, the bimodality is not sufficient to warrant recognition of two species and that this conclusion is confirmed by t tests. West did not state if the tested groups were determined by a criterion other than size (for example, number of P<sub>4</sub> roots), but it must be assumed that they were, for it is inconceivable that a distribution solely on the basis of size would not show a significant difference between the two resulting groups if the t test were

used. If one divides the Wasatchian sample in West's (1973) figure 2 at an  $M_1$  length of 2.0 mm (millimeters) and compares the resulting two groups using the  $t$  test, they are shown to be significantly different ( $t=6.37$ ,  $n=18$ ), with a probability of less than 0.001 that this difference is due to chance.

For the Bridgerian sample (including a few specimens from rocks of Uintan age), West (1973) observed only that there is less variation than in the Wasatchian sample, a fact he attributed to the smaller geographic and temporal range of this sample. However, a histogram of  $M_2$  lengths in the Bridgerian sample (fig. 16, this paper) shows that the sample separates into three groups. These groups correspond with the three earlier recognized Bridgerian species, *A. bellulus*, *A. bellus*, and *A. rodens*, respectively. To test these two alternative schemes for grouping the samples, a chi-square test and a Bayesian analysis were employed. The only assumption made was that the underlying distributions are approximately normal. For West's (1973) one-species case, the null hypothesis is that the underlying distribution is a normal population with a single mean and standard deviation, as specified by the sample. For the three-species case, the null hypothesis is that there are three normally distributed populations, each having a mean and standard deviation specified by the sample, except for *A. rodens*. The standard deviation for *A. rodens* was made equal to 0.12 and was determined by assuming that *A. rodens* had a coefficient of variation equal to that of *A. bellulus* and *A. bellus*. In the actual sample, *A. rodens* has a standard deviation of zero. This figure is unrealistic and would bias the tests in favor of the three-species hypothesis.

The expected values for the chi-square test (equal to  $np_i$ ) were calculated in the following manner. For the one-species hypothesis,  $n$  equals 27, and for the three-species hypothesis,  $n$  equals 12, 13, or 2, depending on whether the cell is in the subdistribution specified by *A. bellulus*, *A. bellus*, or *A. rodens*, respectively. The probability of being in the cell ( $p_i$ ) is determined from the integral of the Gaussian function defined by the parameters of the hypothesis, that is, the  $i$ th cell (where  $i$  equals a length of  $M_2$  in millimeters) actually represents the interval  $i \pm 0.05$ . This interval specifies an area under the defined normal curve, which, when normalized, equals the probability of being in the  $i$ th cell ( $p_i$ ). The results are given in table 2. As can be seen from this table, the chi-square test could reject the one-species hypothesis at the 0.025 level of significance, but the three-species hypothesis could not be rejected at the 0.70 level of significance. In other words, one would expect to see a deviation as great as that observed in the one-species hypothesis only 2.5 percent of the time, whereas one would expect to see it 70 percent of the time in the three-species hypothesis.

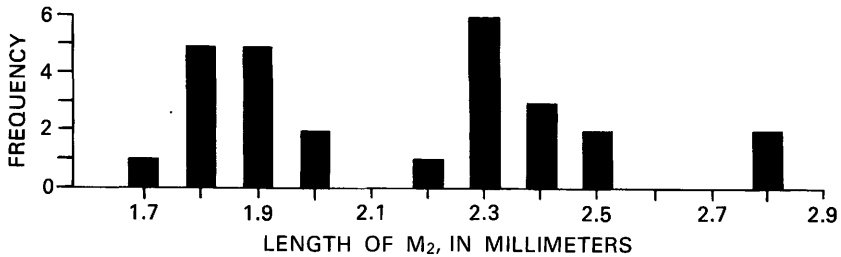


FIGURE 16.—Histogram of length of  $M_2$  for Bridgerian and Uintan sample of *Apatemys* (from West, 1973).

TABLE 2.—*Chi-square analysis of the distribution of length measurements of  $M_2$  for the Bridgerian sample of Apatemys (ungrouped data)*

[Data from West (1973). O, number observed. E, expected]

Length of $M_2$	Number Observed	Expected, 1 species	$\frac{(O-E)^2}{E}$	Expected, 3 species	$\frac{(O-E)^2}{E}$
$\leq 1.7$	1	2.8	1.16	1.30	0.07
1.8	5	1.9	5.06	4.85	.01
1.9	5	2.4	2.82	4.90	.00
2.0	2	3.0	.33	1.75	.04
2.1	0	3.4	3.40	.31	.31
2.2	1	3.4	1.69	1.45	.14
2.3	6	3.0	3.00	4.40	.58
2.4	3	2.4	.15	4.40	.45
2.5	2	1.9	.01	1.48	.18
2.6	0	1.2	1.20	.30	.30
2.7	0	.8	.80	.52	.52
2.8	2	.8	1.80	1.34	.32
Total	27	27.0		27.0	
$\chi^2$			21.42		2.92
p			0.025		0.72

<sup>1</sup>9 degrees of freedom.

<sup>2</sup>5 degrees of freedom.

One of the assumptions of the chi-square test, however, is that  $np_i$  is greater than or equal to 5. This assumption was not met in the analysis, but the data can be grouped (table 3) for the one-species hypothesis such that the expected value is greater than 5. The results are unchanged, and the one-species null hypothesis can still be rejected at the 0.025 level of significance. Because it is impossible to group data for the three-species hypothesis in similar fashion without reducing the degrees of freedom to less than zero, the results of this test are inconclusive, but they are strongly suggestive that the sample contains three species and not only one.

TABLE 3—*Chi-square analysis of the distribution of length measurements of  $M_2$  for the Bridgerian sample of Apatemys (grouped data)*[Data from West (1973) and grouped such that  $np_i$  is greater than or equal to 5 O, number observed E, expected]

Length of $M_1$	Number observed	Expected, 1 species	$\frac{(O-E)^2}{E}$
$\leq 1.8$	6	4.7	0.36
1.9–2.0	7	5.4	.47
2.1–2.2	1	6.8	4.95
2.3–2.4	9	5.4	2.40
$\geq 2.5$	4	4.7	10
Total	27	27.0	
$\chi^2$			0.025
			<sup>1</sup> 8.28
$\leq 1.9$	11	7.1	2.14
2.0–2.1	2	6.4	3.02
2.2–2.3	7	6.4	.06
$\geq 2.4$	7	7.1	.00
Total	27	27.0	
$\chi^2$			0.025
			<sup>2</sup> 5.22

<sup>1</sup>2 degrees of freedom<sup>2</sup>1 degree of freedom

The Bayesian analysis employs the ordinate values of the Gaussian function to determine the relative probability of two or more hypotheses. This method is described in Pilbeam and Vaisnys (1975). This analysis indicates that the three-species hypothesis is 40 times as likely as the one-species hypothesis, given equal a priori probabilities. Because the three-species hypothesis is a priori the more likely on the basis of coefficients of variation (see next page), this test strengthens the original conclusion.

A third alternative is that *A. rodens* is conspecific with *A. bellus* and that only two species were present in the Bridgerian. The Bayesian analysis shows that this hypothesis is one-third as likely as the three-species hypothesis, a relatively inconclusive result.

A fourth alternative, proposed by Robinson (1966), is that the smallest species (*A. bellulus*) and the largest (*A. rodens*) are conspecific. This suggestion was not considered because it is counterintuitive. The union of these species was presumably proposed because of the single-rooted  $P_4$  held in common, but such a union produces a bimodal distribution. Because there is no independent evidence suggesting sexual dimorphism in apatemyids, this synonymy is unfounded. If sexual or size dimorphism were postulated for the *A. bellulus*–*A. rodens* union, it would be expected also in the remainder of the sample with a two-rooted  $P_4$ , and it does not occur there.

One objection that can be raised concerning the preceding analyses is that the pooling of temporally and spatially disjunct samples might invalidate the assumption that the underlying population is normally distributed. The majority of specimens in the Bridgerian sample comes from a relatively restricted geographic area and temporal range in southwestern Wyoming, and the three type specimens from this area span nearly the entire range of size variation. The two or three specimens from other areas (one is from the Huerfano Formation of Colorado, and two are from rocks of Uintan age of California and Wyoming) were not removed from the analyses because it was not possible to distinguish them in West's (1973) scatter diagram. It is not believed that their inclusion appreciably altered the analytical results because they do not represent end points in the size spectra.

West (1973, p. 13) pointed out that the coefficients of variation for his measurements are often greater than 10. In fact, all his coefficients of variation are greater than 10 and most are between 15 and 20. In a list of coefficients of variation for 19 mammalian species compiled by Gingerich (1974b), only two species show coefficients greater than 10, and these species are known to be sexually dimorphic (10.7 for  $M_1W$  in *Papio anubis*, and 10.4 for  $M_2L$  in *Pongo pygmaeus*). West observed that his coefficients of variation are high for single-species populations but attributed it to the "\* \* \* great range of temporal and geographic sources." He believed that "\* \* \* the coefficient of variation is therefore not considered as significant in the statistical interpretation of *Apatemys* as are the comparison of sample means."

It has been seen earlier that a comparison of sample means tells us nothing about how many species are involved within a certain stratigraphic level if one is comparing means between different stratigraphic levels. Known ranges of variation translated into known ranges for coefficients of variation do have interpretive biological significance, and they are, therefore, considered by us to be more significant. Furthermore, West (1973) observed that no significant change had taken place through time in his samples, and nowhere has he demonstrated that populations from different geographic regions differ enough to result in the large coefficients of variation that occur when these samples are pooled. In the absence of this demonstration, it is neither justified nor convincing to assume that large coefficients of variation would result. For the Bridgerian sample of *Apatemys* studied by West, division into three species results in coefficients of variation that are between 4 and 5, well within the range given for several mammals by Gingerich (1974b).

Studies of apatemyids are hampered by the small available



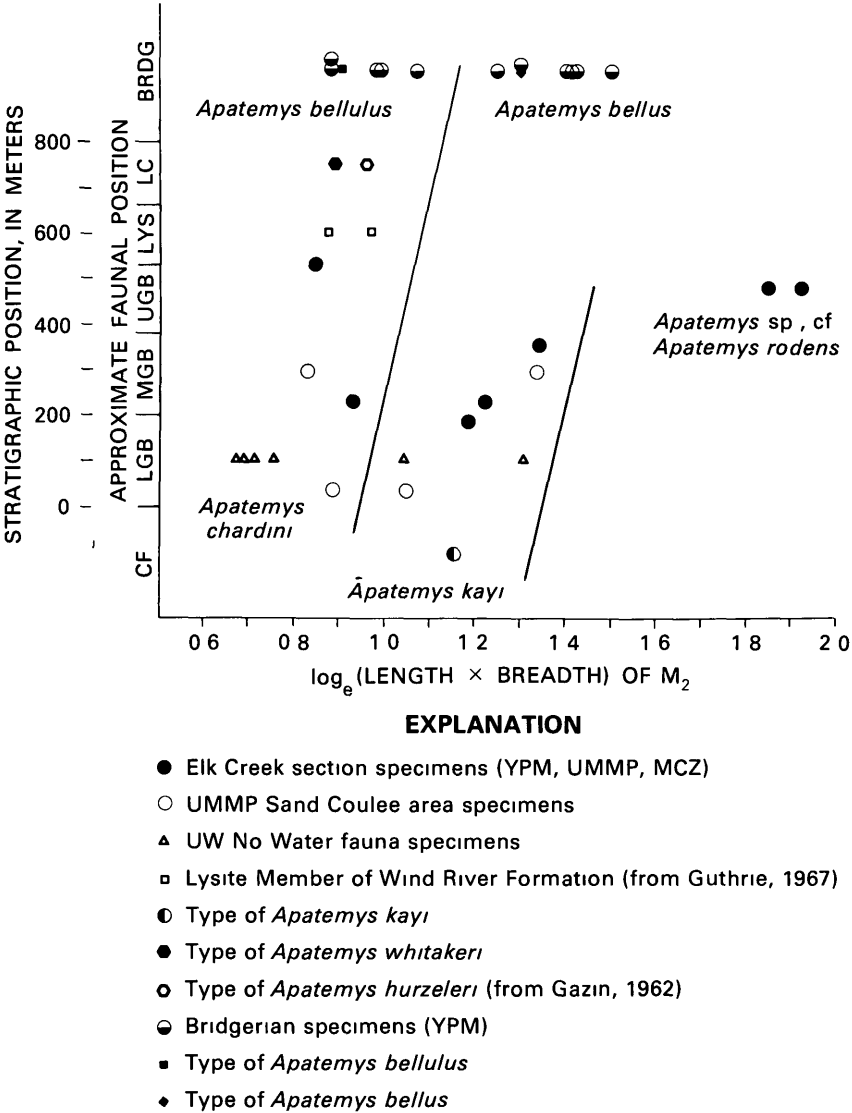


FIGURE 17 —Stratigraphic plot of  $M_2$  in late Paleocene through Bridgerian specimens of *Apatemys*. Measurements of stratigraphic position are from the base of the Willwood Formation CF, Clarkforkian Provincial Age, LGB, MGB, and UGB, lower, middle and upper Gray Bull biostratigraphic zones, LYS, Lysite biostratigraphic zone, LC, Lost Cabin biostratigraphic zone, BRDG, Bridgerian Provincial Age. Lines separate possible lineages.

samples and a lack of good stratigraphic control for these samples. Lumping of samples from stratigraphically disparate localities by earlier workers has, doubtlessly, contributed equally to the problem, because this procedure tends to obfuscate, rather than clarify, complex patterns. As observed by Bown (1979), the pooling of tooth measurements for specimens from different stratigraphic levels in scatter diagrams, histograms, and the like probably gives us no reliable information concerning which and how many species occur in these samples. This lack of information is especially true if tooth sizes have changed significantly through time in the various lineages sampled. Earlier attempts to fit all the *Apatemys* morphologies into one or the other of McKenna's (1963) lineages creates additional problems because, from our study, there appear to be at least three lineages of *Apatemys* in the early Eocene. In figure 17, size measurements for  $M_2$  are plotted against time. The central Bighorn Basin Willwood Formation specimens were plotted according to their positions on a measured section (Schankler, 1980). The remaining specimens were located approximately by faunal comparisons.

As seen in figure 17, two species occur in the lower Gray Bull zone: *Apatemys chardini* and *A. kayi*. *A. chardini* is the smaller of the two and is characterized by a two-rooted  $P_4$ . *A. kayi* is a larger, medium-size species that is typified by a reduced, single-rooted  $P_4$ . Both species exist in the Four Mile and No Water faunas and in the lower Gray Bull zone of the Clark's Fork and central Bighorn Basins. In the Powder River local fauna, only *A. chardini* is known; in the central Bighorn Basin, *A. kayi* does not occur higher than the middle Gray Bull zone; whereas *A. chardini* appears to have given rise to *A. bellulus* (including both *A. whitakeri* and *A. hurzeleri*). The medium-size Bridgerian species *A. bellus* first occurs in rocks of Lostcabinian age (Guthrie, 1971). Because *A. bellus* shows variable conditions of the  $P_4$  roots, it does not seem to be a likely descendant of *A. kayi*.

The fourth and largest lineage of *Apatemys* is represented by three specimens from the central Bighorn Basin. They are all from upper Gray Bull levels, near the boundary of the Gray Bull and Lysite zones, and the specimens are slightly larger than the type specimen of *Apatemys rodens*. From *A. rodens*, they differ in several respects but are here believed to be its Wasatchian precursor.

*Apatemys uintensis* (as defined by West, 1973) probably contains both small and middle-size species, possibly the Uintan descendants of middle Eocene *A. bellulus* and *A. bellus*, respectively.

*Apatemys chardini* (Jepsen, 1930a)

Plate 4, figures 3, 6

*Referred specimens.*—YPM 26468, 30558, 31170, UW 8908, 8997, 9571, 9599, 9630, 9632 (in part), 9633, 9634, 9725, 10243, 10415, 10416, UMMP 64934, 66686 (pl. 4, fig. 3), 67040, 67310, 67380 (pl. 4, fig. 6), 68486, 68565, possibly UMMP 65150, 68592, YPM field numbers 72-1822, 76-132.

*Discussion.*—*Apatemys chardini* is the most common and wide ranging of the Gray Bull zone apatemyids. As mentioned previously, it is known from localities of this age in other basins. The type specimen (PU 13236) is from either a middle or lower Gray Bull zone locality in the central Bighorn Basin. The only other specimens of *A. chardini* from the Elk Creek section of the Willwood Formation occur in middle Gray Bull zone localities.

*A. chardini* is the smallest species of *Apatemys*; the No Water, Powder River, and Four Mile specimens are slightly smaller than the Clark's Fork Basin or central Bighorn Basin specimens. The species differs from coeval *A. kayi* in the possession of a double-rooted  $P_4$  in the majority of specimens. UW 8908, from the No Water fauna, is an edentulous ramus that appears to have a single alveolus for  $P_4$ . The specimen is tentatively referred to *A. chardini* because of its relatively small size. Because *A. chardini* is considered to be ancestral to *A. bellulus*, and assuming only one species is represented in the *A. chardini* sample, it is not unreasonable to expect a small proportion of the *A. chardini* sample to have a single-rooted  $P_4$ .

Referral of the small apatemyid from the Four Mile fauna to *A. whitakeri* (Delson, 1971) seems unwarranted. Delson recommended this name because of the similarity in size and morphology of the  $M_2$  between this specimen and the type of *A. whitakeri*. McKenna (1960a), on the other hand, recorded the similarity between this specimen and the type specimen of *A. chardini* in the size and construction of  $M_3$ . Because comparable elements are not preserved in the types (excluding  $P_4$ , the tooth in which both types differ from each other) and because  $P_4$  is not known in the Four Mile specimen, there is no justification for assigning it to *A. whitakeri*.

*Apatemys bellulus* Marsh, 1872

Plate 4, figure 5

*Synonyms.*—*Teilhardella whitakeri* Simpson, 1954; *Apatemys hurzeleri* Gazin, 1962.

*Referred specimens.*—YPM 27783, YPM field number 71-132; UMMP 66092 (pl. 4, fig. 5), AMNH 48004.

*Discussion.*—*Apatemys bellulus* was first described from Bridgerian rocks, but the species is here taken to include the late Wasatchian *A. whitakeri* and *A. hurzeleri*. Simpson (1954) noted similarities shared by "*Teilhardella whitakeri*" and *A. bellulus*, but he referred his new species to Jepsen's (1930a) *Teilhardella* because of his reluctance to carry a Bridgerian genus into the Wasatchian. A comparison of the two types and other specimens referred to "*T. whitakeri*" and *A. bellulus* has revealed no characters that indicate that they are distinct. The other small late Wasatchian species, *A. hurzeleri*, does have relatively narrower molars than in *A. bellulus*, but, until other specimens are found with this character, Gazin's species is here considered to represent normal variation within *A. bellulus*.

Lysite and Lost Cabin zone *A. bellulus* are intermediate in size between the smaller Graybullian *A. chardini* and the larger *A. bellulus* specimens from Bridgerian rocks. Where this tooth is preserved, all known specimens of *A. bellulus* possess a single-rooted  $P_4$ ; however, this is the only apatemyid now known from deposits of Lysitian age; it occurs in both the Willwood Formation of the central Bighorn Basin and in the Wind River Formation of the Wind River Basin. In Lostcabinian time, it was more widespread (present in the Largo and La Barge faunas and in the type Lost Cabin Member of the Wind River Formation), and it is associated with *A. bellus* in the type Lost Cabin Member (Guthrie, 1971).

*Apatemys kayi* (Simpson, 1929)

Plate 4, figure 4

*Referred specimens.*—YPM 22846, 25990, 26042, 35090, MCZ 19685, UW 8999, 9574, 9622, 9632 (in part), UMMP 65187, 67038, 68588, 68589, 68590, 68591 (pl. 4, fig. 4), 69132, possibly UW 9631.

*Discussion.*—*Apatemys kayi* is the oldest known species of *Apatemys*. The type specimen comes from the Clarkforkian Bear Creek fauna of southern Montana. *A. kayi* persists into the Wasatchian, where it is known from the Four Mile, No Water, Clark's Fork Basin, and central Bighorn Basin faunas. In the Elk Creek section of the Willwood Formation, it is not known higher than the middle Gray Bull zone. Although this species agrees in size with *Apatemys bellus*, it is an unlikely ancestor for that taxon because it is doubtful that the trend for reduction of  $P_4$  was reversed. The  $P_4$  is single rooted in all specimens of *A. kayi* where it is preserved, whereas in *A. bellus* the

condition of the  $P_4$  roots appears to be variable. It is also possible that *A. kayi* is ancestral to the much larger *A. rodens*; however, there is currently no other evidence to suggest this relationship.

*Apatemys* sp., cf. *A. rodens* Troxell, 1923

Plate 2, figure 7

*Referred specimens*.—YPM 23476 (West, 1973, fig. 8), 30582 (pl. 2, fig. 7), AMNH 48999.

*Discussion*.—Three very large specimens of *Apatemys* are known from the Willwood Formation of the central Bighorn Basin. The two YPM specimens are from localities on the eastern side of Red Butte, and the AMNH specimen is from north of Sheep Mountain. None of these localities are tied to measured sections, but other evidence (geographic and topographic positions and associated faunas) indicates a late Graybullian age, near the Graybullian-Lysititan faunal boundary. As demonstrated previously, there is considerable evidence on the basis of  $M_2$  size that *A. rodens* is a valid species, distinct from its penecontemporaries *A. bellus* and *A. bellulus*. It is further distinguished by its very robust mandible and the relatively larger anterior incisor. *A. rodens* is also characterized by a single-rooted  $P_4$ , a weak  $P_4$  fossa, and the presence of a single, large, double mental foramen. The referred specimens agree with the type of *A. rodens* in size and in the single-rooted  $P_4$ , although the alveolus for  $P_4$  in the referred specimens is larger than in the type. In the referred specimens, the two mental foramina are oblique to each other but are clearly distinct, and the size of the  $P_4$  fossa is variable (moderate in YPM 23476, almost absent in YPM 30582). The enamel of the enlarged anterior tooth in the type specimen is confined to the ventral half of the crown, whereas in YPM 23476 the enamel is thin but not well delimited. In the type specimen, the paraconid of  $M_3$  is more prominent and more lingually placed than in the referred specimens. Also, the talonid of  $M_3$  is more elongate and the cusps are more distinct. The basins of the talonids are deeper in the type, and a small ridge connects the entoconid and the hypoconid on  $M_2$ . These differences indicate individual variation but are of doubtful taxonomic significance. The inclusion of the three referred specimens in *A. rodens* extends the known range of this species into early Wasatchian time. The Uintan *Apatemys downsi* may also be referable to *A. rodens*; however, this possibility warrants separate investigation.

Order INSECTIVORA  
Suborder ERINACEOMORPHA  
Family DORMAALIIDAE<sup>1</sup>

Krishtalka (1976a) recently reviewed the North American early Tertiary so-called adapisoricid insectivores and concluded, as did Russell, Louis, and Savage (1975), that *Adapisorex* Lemoine (1883) (in Bown, 1979) could not naturally be grouped with the more typical of the so-called adapisoricids. Krishtalka recommended no solution to this abandoned family status, relegating *Adapisorex* to the Erinaceidae, yet continuing use of the name Adapisoricidae for mammals grouped by Quinet (1964) and by Russell, Louis, and Savage (1975) in the Dormaaliinae. We believe that *Adapisorex* and the dormaaliines are distinct at least at the family level, and we elevate the Dormaaliinae to family status. *Adapisorex* appears, in our opinion, to be closest structurally to the erinaceid-like condylarths *Phenacodaptes* and *Apheliscus* (Gazin, 1959), though some specimens of *Adapisorex abundans* (for example, Walbeck 390) are also similar in the lower dentition to Tiffanian *Bisonalveus Dormaalus* is an unfortunate type for this family, partly because of its strong similarity to *Macrocranium nitens* (also noted by Russell and others, 1975) and partly because of the paucity of materials of *Dormaalus*. Both *Macrocranium nitens* and *Dormaalus* share several characters not found in other members of the family, and it may eventually become necessary to create a new subfamily to accommodate *Scenopagus*, *Ankylodon*, *Talpavus*, *Talpavoides* gen. nov. (discussed later), and some of the new later Eocene forms described by Novacek (1976) from California.

Krishtalka (1976a) believed the following insectivores to be valid North American so-called adapisoricid genera:

- Mckennatherium* Van Valen, 1965
- Scenopagus* McKenna and Simpson, 1959
- Ankylodon* Patterson and McGrew, 1937
- Macrocranium* Weitzel, 1949
- Talpavus* Marsh, 1872.

*Mckennatherium ladae* was believed by him to be the earliest as well as the most generalized member of the family, and an enigmatical form, "*Diacodon*" *minutus* Jepsen (1930b), was tentatively transferred to *Adunator*, a middle to late Paleocene European genus

<sup>1</sup>A diagnosis of the Dormaalidae is under investigation by M. J. Novacek, T. M. Bown, and David Schankler (unpub. data, 1981).

(Russell, 1964). "*D.*" *minutus* and *Adunator* were then contrasted with some Paleocene hyopsodontids, with which they certainly share many derived characters. Because of the pivotal position that *Mckennatherium* (as "*Leptacodon*" *ladae*) has played in both recent and early evaluations of the origins of early insectivores and because its status as perceived by Krishtalka (1976a) relegates the genus to either real or supposed plesiomorphy for Eocene dormaaliids, a critical examination of this genus is now necessary.

We have compared most of the best specimens relevant to this problem, including *Mckennatherium* (USNM 9640, type of *Lep-tacodon ladae*; AMNH 35437, type of *Mckennatherium libitum*; AMNH 35954, 35955; PU 17722), and "*Diacodon*" *minutus* (PU 13360, 13360a, 13304, types; PU 19395) with the type specimen of *Adunator lehmani* (Walbeck 368) and conclude, as did Krishtalka, that lower teeth of "*D.*" *minutus* and *Adunator* are virtually identical. Krishtalka (1976a) also recorded similarities of "*D.*" *minutus* to *Mckennatherium* but chose to retain these forms as distinct genera; in his view, the latter genus is the earliest of the so-called adapisoricids, and the former genus is probably a hyopsodontid condylarth. We believe that *Mckennatherium ladae* and "*Diacodon*" *minutus* are very closely related, and that both probably represent North American species of *Adunator*.

Krishtalka (1976a, p. 10) believed that the following are attributes of *Adunator* and "*Diacodon*" *minutus* that are not shared by *Mckennatherium*:

1. The talonids of  $M_{1-2}$  are slightly elongate.
2.  $M_2$  is larger than  $M_1$ .
3. The paraconid on  $M_2$  is extremely compressed and is merged with the anterior part of the metaconid.
4. The metaconid is greatly expanded anteriorly in lingual view so that it is much larger and more bulbous than is the protoconid.
5.  $P_4$  has a well-developed paraconid that is as high (tall) as the metaconid
6. The paraconid is strong on  $P_3$  in "*D.*" *minutus* but is absent in *Mckennatherium*.

These alleged differences led Krishtalka (1976a, p. 10) to remark: "These exceptions to adapisoricid affinities in the lower molars of

*Adunator*—"D." *minutus* are features associated with some Tiffanian hyopsodontid condylarths like *Haplaletes*."

With respect to these differences noted by Krishtalka, we have observed that:

- 1 The talonids of  $M_{1-2}$  in *Adunator lehmani* and "*Diacodon*" *minutus* are not perceptibly longer than in *Mckennatherium*.
2.  $M_2$  is about the same size as  $M_1$  in the type of *Adunator lehmani* (both are approximately 1.7 mm long), as also in *Mckennatherium* (Krishtalka, 1976a, table I).
3. The  $M_2$  paraconid is also compressed and is closely appressed to the metaconid in *Mckennatherium*.
- 4 The  $M_{1-3}$  metaconids are also large and anteriorly expanded in *Mckennatherium*.
5. The  $P_4$  paraconid is shorter (less tall) than the metaconid in *Adunator*, "*Diacodon*" *minutus*, and *Mckennatherium* but does arise at a lower point on the paracristid in the last genus.
6. The  $P_3$  paraconid appears to be absent in some *M. ladae* (for example, PU 17722; this cusp may have been broken off—only a cast of this specimen was examined by us); a strong paraconid is, however, present on  $P_3$  in at least some *Mckennatherium* (for example, AMNH 35954, Krishtalka, 1976a, fig. 2A).

In our opinion, materials of *Adunator*, *Mckennatherium*, and "*Diacodon*" *minutus* are nearly inseparable on the six above criteria, and what slight differences do exist do not argue convincingly for generic distinction. Upper molars referred to *Adunator* and to "*Diacodon*" *minutus* are more distinct (as Krishtalka recognized); however, in both, their association with the lower teeth is uncertain.

*Mckennatherium* is known from lower jaws preserving, in composite,  $P_2$ - $M_3$ , "*Diacodon*" *minutus* is known from nearly the entire



lower dentition, and *Adunator* is known from  $P_2$ - $M_3$ . The comparable parts of these lower dentitions are so similar, even in several trivial respects, that these animals were almost certainly closely related. The dental evidence does not indicate that they are dentally convergent homeomorphs, because there is no good morphologic basis for separation at the generic level. Fairly well established convergent similarities between other groups of well-known early mammals (for example, molars of plesiadapid and nothartine primates) rarely, if ever, pervade both the premolar and molar teeth, and a complex of crossing specialized characters allows the reliable identification of even isolated teeth.

The systematic positions of *Adunator* and its probable North American allies "*Diacodon*" *minutus* and *Mckennatherium ladae* remain in doubt, however, none are dormaaliids. The removal of the last two species leaves this family without any certain described Paleocene representatives but unifies Eocene forms in a more cohesive morphologic group. Even so, the Eocene dormaaliids may not make up a natural grouping. *Macrocranium*, in particular, deviates from *Scenopagus*, *Talpavus*, *Talpavoides*, and *Ankylodon* in several erinaceid features, some of which it shares with *Dormaalius*. In *Macrocranium*, these characters include the reduction in size of  $P_{1-3}$ , the relatively large size of  $P_4$  with respect to  $M_1$ , relatively low molar trigonids, broad molar talonids, relatively tall entoconids, and relatively short (flat) hypoconids.

*Macrocranium nitens* has a close morphologic counterpart in late Paleocene *Litolestes* and differs from that genus principally in having somewhat more shelflike molar paraconids, relatively broader molar talonids, a less compressed  $M_2$  trigonid, and in the greater exaggeration of the tall, lingually deflected molar entoconids.  $P_3$  is variable in *Litolestes*. In AMNH 33936, it is nearly as tall as  $P_4$ , but in PU 19387 (*L. ignotus*) it is short and reduced relative to  $P_4$ .  $P_3$  in *Macrocranium* is, invariably, greatly reduced relative to  $P_4$ . The molars typically decrease in size posteriorly in *Litolestes*, whereas they are more nearly equal in size in *Macrocranium*. None of these characters, however, constitute insurmountable obstacles to the possible familial association of these genera, particularly when one considers our rudimentary knowledge of what are generalized and what are derived characters in early erinaceids. From a cladistic rather than a phylogenetic viewpoint, the association of *Litolestes* and *Macrocranium* is, to us, even more apparent.

An evaluation of the many similarities shared by early erinaceids and certain condylarths is beyond the scope of this paper, and, in itself, warrants a general review.

Perhaps of auxiliary importance to the early history of the dormaaliids is PU 18688, a right  $P_3$ - $M_2$  of dormaaliid-like mammal from the

Torrejonian Rock Bench quarry of the Fort Union Formation (Polecat Bench Formation of Jepsen, 1940). This specimen is now on loan from the Princeton University collections and will, presumably, be described by other workers. However, the teeth appear to be sufficiently generalized to be of potential importance to the origins of the dormaalids, geolabidids, or both.

**Macrocranium nitens (Matthew, 1918)**

Plate 5, figures 1-5, plate 6, figures 1, 2

*Referred specimens.*—YPM 23077 (pl. 5, fig. 1), 23087, 24380 (pl. 5, figs. 2, 5), 27941, 30443, 30533, 30597 (pl. 6, fig. 2), 30622, 30651, 30654, 30655 (pl. 5, figs. 3, 4; pl. 6, fig. 1), 30657, 35159; UW 7057, 8996 (Bown 1979, fig. 42d), 9640, 9641, 9690.

*Discussion.*—As mentioned previously, placement of *Macrocranium* and *Dormaalius* in the same subfamily as *Scenopagus*, *Talpavus*, *Talpavoides*, gen. nov. (p. 50), and *Ankylodon* may not adequately reflect the morphologic disparity between these two groups. The former two genera may even be erinaceids, and their inclusion in the same family as the other four genera is tentative.

Krishtalka (1976a) transferred Matthew's (1918) *Entomolestes nitens* to *Macrocranium* Weitzel (1949), a relationship that was hinted at but not fully endorsed by Russell, Louis, and Savage (1975). The species *nitens* is certainly more aptly placed in *Macrocranium* than in *Entomolestes*, but Krishtalka's (1976a) belief that *nitens* "\* \* \* is virtually identical to *Macrocranium tenerum* (=Messelina) \* \* \*" does not seem compelling to us after we compared a large number of casts, illustrations, and descriptions. What differences do exist, however, seem to be more significant at the specific rather than at the generic level, and we hesitantly accept the synonymy of *Entomolestes nitens* with *Macrocranium*.

Russell, Louis, and Savage (1975) allocated numerous teeth from the French early Eocene to *Entomolestes* cf. *nitens*. Casts of the several specimens of French *E.* cf. *nitens* available to us are also provisionally referable to *Macrocranium*, but we agree with Russell, Louis, and Savage (1975) that the identity of some of this sample is questionable, principally because of the large amount of variation in P<sub>4</sub> and the upper molars. In several respects, the French sample resembles specimens of *M. nitens* from the San Jose Formation of New Mexico more than those from the Willwood or Wind River Formations.

Willwood *Macrocranium nitens* conforms well with the type of the species (also from the Willwood) and with most specimens from the Four Mile fauna (Graybullian) and the Lysite and Lost Cabin

Members of the Wind River Formation. The Almagre and other San Jose Formation specimens, however, show a number of consistent differences that suggest that they may belong to a separate species. The upper molars in AMNH 48177 (from the San Jose Formation) are relatively shorter and less squared, and they appear to have more acute cusps than in either of two upper dentitions from the Willwood Formation (YPM 23077 and 30655). Moreover, the Willwood specimens possess an  $M^1$  that is larger than  $M^2$ , a relatively smaller  $M^1$  mesostyle, a straighter, less V-shaped  $M^2$  ectoflexus, and relatively shorter  $M^{1-2}$  preprotocrista and postprotocrista.

In the lower dentition,  $P_4$  in Willwood *M. nitens* generally has a less well basined talonid than in San Jose or Almagre specimens, though this feature is somewhat variable. This talonid construction is essentially the same as that seen in UCMP 44106 (McKenna, 1960a, fig. 25) from the Four Mile fauna, and TTU-P 4211 from the Lysite Member of the Wind River Formation.

YPM 30655 (pl. 5, figs. 3, 4; pl. 6, fig. 1) is an associated left  $P_4$ - $M_3^2$  (prepared from occlusion) that differs from typical Willwood, Wind River, and Four Mile *M. nitens* in the greatly reduced, nearly absent,  $P_4$  metaconid. The heel of  $P_4$  is short and unbasined (no cristid obliqua) as in the type of the species, TTU-P 4211, AMNH 48174, and most of the other Willwood specimens, and the faint metaconid is probably an individual aberration.

Teeth of *Macrocranium nitens* from low in the Willwood section (for example, YPM 30651, 30553, 30597; at the 145-, 180-, and 240-m levels) are smaller than teeth from higher stratigraphic levels (for example, YPM 23087, 27941, 23077; at the 560-, 590-, and 620-m levels). Measurements are given in table 4.

In the Willwood Formation of the central Bighorn Basin, *M. nitens* is known from the uppermost part of the lower Gray Bull zone to the upper part of the Lysite zone (fig. 18). In the No Water Creek area (Bown, 1979), the species occurs at localities between the 30- and 120-m levels; all are early Graybullian in age. The stratigraphic position of the type specimen is uncertain, but it is probably from the middle or upper Gray Bull zones.

*Scenopagus hewettensis*, sp. nov.

*Etymology*.—For Donnel Foster Hewett, a pioneer geologist of the Bighorn Basin region.

*Holotype*.—UW 8998 (adapisoricid indeterminate of Bown, 1979, fig. 43e), left  $P_4$ - $M_1$ .

*Locality*.—UW locality V-73020, lower part of Willwood Forma-

tion (97-m level of Sand Creek facies), early Graybullian, sec. 9, T. 46 N., R. 91 W., Washakie County, Wyo.

*Hypodigm.*—The type and possibly UW 9738, 10450.

*Diagnosis.*—Size of *Scenopagus edenensis*, larger than *S. curticens*, *S. priscus*, and *Talpavoides dartoni*, gen. et sp. nov. (See p. 53.)  $P_4$  relatively narrower than in *S. edenensis*, and talonid better developed with distinct hypoconid, entoconid, and cristid obliqua.  $P_4$  paraconid arises high on anterior face of trigonid as in *Scenopagus*, not low as in *Leptacodon* (sensu stricto); and talonid of  $M_1$  broader than trigonid in contrast to last genus.

*Discussion.*—Bown (1979) referred the type of *S. hewettensis* and five other specimens to an indeterminate adapisoricid species. Further comparisons convince us that this specimen represents a new, relatively generalized species of *Scenopagus*. Referral of the remainder of the proposed hypodigm is only tentative (especially for the upper teeth) and must be confirmed by the recovery of more com-

TABLE 4—Measurements of teeth of *Macrocranium nitens* from the Willwood Formation

[Values in millimeters x, tooth present but damaged Leaders ( ) indicate no specimen]

Museum Nos	$P_1L$	$P_1W$	$P_2L$	$P_2W$	$M_1L$	$M_1W$	$M_2L$	$M_2W$	$M_3L$	$M_3W$
Peabody Museum, Yale University (YPM)										
23087							x	1 60	1 78	1 24
24380	0 85	0 65	1 63	1 11	1 88	1 60	x	1 68		
27941			1 80	1 20	x	x	1 95	1 65		
30443					x	1 74	1 85	1 76	x	1 47
30553					x	1 32	1 50	1 27		
30622					1 90	1 35				
30651					1 52	1 42	1 59	1 50	1 55	1 12
30654					1 75	1 55	1 75	1 60		
30655			1 68	1 09	2 17	1 60	2 01	1 60	1 95	1 24
30657			1 60	1 05	x	x	x	1 55		
The Geological Museum, University of Wyoming (UW)										
7057							1.75	1 35		
8996	0 85	0 55	1 60	1 00						
9640					1 60	1 30				
9690			1 60	1 05						
Peabody Museum, Yale University (YPM)										
			$P_1L$	$P_1W$	$M_1L$	$M_1W$	$M_2L$	$M_2W$		
23077			1 70	2 40	1 80	2 60	x	2 65		
30597			1 24	1 65	1 42	1 86				
30655			1 52	2 05	2 19	2 49	1 91	2 42		
The Geological Museum, University of Wyoming (UW)										
9641					1 70	2 20				

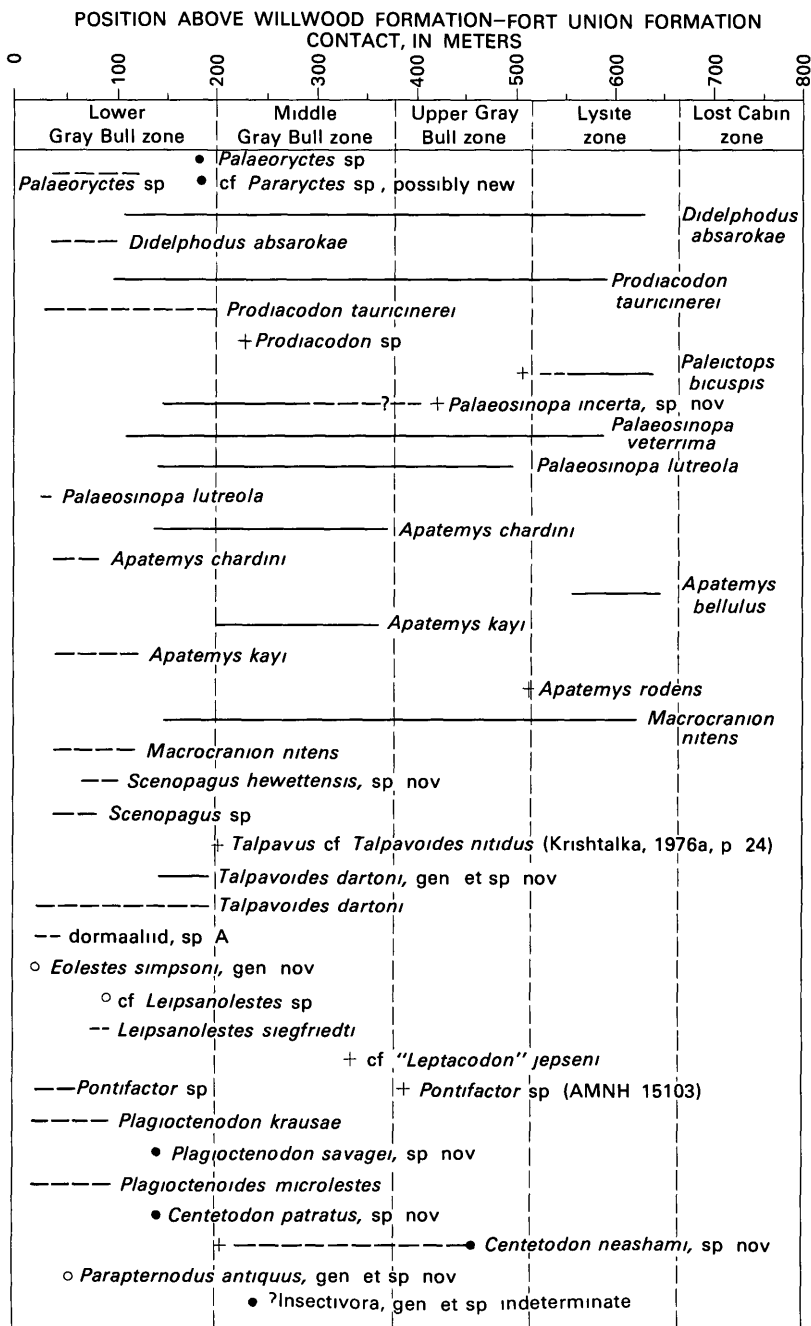


FIGURE 18—Chart showing stratigraphic ranges of insectivores and proteutherians from the Willwood Formation. Solid lines denote ranges for Elk Creek facies, dashed lines denote ranges for Sand Creek facies of Bown (1979)

plete materials and associated upper and lower teeth. The distinctive characters of  $P_4$  in the type specimen of *S. hewettensis* are probably generalized with respect to Bridgerian species.

Krishtalka (1976a) recognized *Scenopagus curticens* as the then-only-known Wasatchian species of *Scenopagus*. *S. hewettensis* differs from *S. curticens* in its much larger size and more molarized  $P_4$ . The only known  $P_4$  of *S. curticens* (Bown, 1981) is premolariform and differs from that in a tentatively referred upper tooth of *S. hewettensis* in the absence of a metacone. Referred specimens of *S. hewettensis* are known only from the early Graybullian Banjo quarry (70-m level, Sand Creek facies).

*Measurements*.—Type specimen (mm):  $P_4L=1.70$ ,  $P_4W=1.06$ ,  $M_1L=2.00$ ,  $M_1WTr=1.35$ ,  $M_1WTal=1.45$ .

#### *Scenopagus* sp.

*Referred specimens*.—YPM 26796, 30614, UW 9595, 9611, 9638 (Bown, 1979, fig. 42c), 9662, 9695, 9699, 9713, 9720, 9729, 10422.

*Discussion*.—This sample contains at least two species of *Scenopagus*, at least one of which is probably new; however, the material is not adequate to name them or to confidently assign them to known species. Two specimens of semimolariform  $P_4$  belong to one of these species, and one of these (UW 9638) is associated with a  $P^3$  and an  $M^2$  of unequivocal *Scenopagus* morphology. Bown (1979) referred UW 9638, among others, to cf. *Scenopagus* sp., probably new, and it is now relatively certain that  $P_4$  (in *S. hewettensis*) and  $P^3$  were semimolariform in at least some early Wasatchian species of *Scenopagus*, in contrast to all known Bridgerian species.

The molars closely resemble their size counterparts in *Scenopagus edenensis* (for example, YPM 26796), *S. curticens* (for example, YPM 30614), and *S. priscus* (for example, UW 9695). *S. edenensis* and *S. priscus* are elsewhere known only from rocks of late Wasatchian and Bridgerian age. However, Krishtalka (1976a) has reported *S. curticens* from the early Wasatchian Four Mile fauna. It is unlikely that any of these species are represented in the sample from the Willwood Formation.

*Scenopagus* sp. is thus far known only from one locality in the central Bighorn Basin Elk Creek section, where it occurs in the lowest sampled level of the middle Gray Bull zone (200-m level). In the Sand Creek facies, *Scenopagus* sp. is known from eight localities, six of which occur between the 30- and 81-m levels; the other two sites are of uncertain stratigraphic position. The Sand Creek localities yield an early Graybullian fauna.

*Measurements*.—Given in table 5.

## 50 PROTEUTHERIA AND INSECTIVORA, WILLWOOD FORMATION, WYO.

TABLE 5.—*Measurements of teeth of Scenopagus sp. from the Willwood Formation*  
[Values in millimeters. Leaders (—) indicate no specimen]

Museum Nos.	M <sub>1</sub> L	M <sub>1</sub> W	M <sub>2</sub> L	M <sub>2</sub> W	M <sub>3</sub> L	M <sub>3</sub> W	P <sub>4</sub> L	P <sub>4</sub> W	M <sub>1</sub> L	M <sub>1</sub> W
The Geological Museum, University of Wyoming (UW)										
9595	...	...	1.60	1.25	1.60	1.10	...	...	...	...
9611	...	...	1.85	1.35	1.80	1.20	...	...	...	...
9638	...	...	...	...	...	...	1.65	1.95	1.55	1.95
9662	...	...	...	...	...	...	...	...	1.50	2.05
9695	...	...	1.40	1.15	...	...	...	...	...	...
9699	...	...	...	...	1.50	1.05	...	...	...	...
9713	...	...	1.55	1.20	...	...	...	...	...	...
9720	...	...	1.50	1.20	...	...	...	...	...	...
9729	...	...	...	...	...	...	1.40	1.50	...	...
10422	1.45	1.05	1.50	1.10	...	...	...	...	...	...
Peabody Museum, Yale University (YPM)										
26796	...	...	2.05	1.45	...	...	...	...	...	...
30614	...	...	...	...	1.65	1.10	...	...	...	...

*Talpavoides*, gen. nov.

*Etymology*.—Greek *eides*; like, having the form of; in allusion to superficial similarities to *Talpavus*.

*Type*.—*Talpavoides dartoni*, sp. nov., and only known species.

*Diagnosis*.—P<sub>4</sub> smaller with respect to M<sub>1</sub> than in *Scenopagus*, *Macrocranium*, or *Plagiostenodon* but semimolariform in contrast to former two genera and *Talpavus*. P<sub>4</sub> talonid basin weak and with poorly formed cristid obliqua in contrast to *Plagiostenodon*, but both structures more strongly developed than in *Talpavus*. M<sub>1</sub> > M<sub>2</sub> > M<sub>3</sub> in contrast to all above genera, and M<sub>1-2</sub> entoconids tall, acute, and slightly displaced linguallly. Molar cristids obliqua join base of metaconid linguallly, and molar entoconids situated at posterolingual talonid margins as in *Plagiostenodon*, not more anteriorly as in most other nyctitheriids.

*Talpavoides dartoni*, sp. nov.

Plate 6, figures 3, 4

*Etymology*.—For Nelson Horatio Darton, a pioneer geologist of the Bighorn Basin region.

*Holotype*.—UW 9624, fragment of right ramus with P<sub>4</sub>–M<sub>2</sub> (pl. 6, fig. 4), UW locality V-73022 (Slick Creek quarry), lower part of Willwood Formation, Sand Creek facies (46-m level), early Graybullian, sec. 1, T. 46 N., R. 92 W., Washakie County, Wyo.

*Hypodigm.*—The type and UW 6974, 6999, 7005, 8586, 8993, 9000, 9597 (pl. 6, fig. 3), 9600, 9610, 9613, 9618, 9623, 9635, 9666, 9674, 9675, 9689, 9697, 9700, 9701, 9704, 9711, 9718, 9722, 9723, 9726, 9728, 9752, 10423, 10448, possibly 9741, 10454, YPM 30544, 30617, 30643, 31168.

*Diagnosis.*—Only known species, same as for genus.

*Discussion* —The more premolariform  $P_4$  (particularly the talonid reduction), the reduction of  $P_4$  relative to  $M_1$  in size, the progressive size decrease of the molars from  $M_1$  to  $M_3$ , and the position of the molar entoconids indicate placement of this form in the Erinaceomorpha. Though the  $M_{1-3}$  size ratio is reminiscent of that in the erinaceids, the remainder of the morphology supports inclusion of *Talpavoides* in the Dormaaliidae.

From Bridgerian and Wasatchian *Talpavus*, *Talpavoides* is distinguished by its better developed  $P_4$  talonid basin, its shorter  $P_4$  metaconid (the  $P_4$  metaconid and protoconid are equal in height in *Talpavus nitidus*), and by the  $M_1$  through  $M_3$  size ratio. The cristid obliqua of  $M_{1-2}$  is also more acute in *Talpavoides*, and the molars, correspondingly, appear to be more exodaenodont than in *Talpavus*.

Krishtalka (1976a) referred several specimens from the Huerfano, Green River, and lower Willwood Formations to *Talpavus* cf. *nitidus*. The Willwood specimens (for example, CM 31180) differ from *Talpavoides* in most *Talpavus*-like features, including the taller  $P_4$  metaconid, a less well defined heel on  $P_4$ , a slightly more compressed  $M_2$  trigonid, and the lack of a well-defined molar size gradient. The former three of these characters are probably derived with respect to the teeth in *Talpavoides*, and the last character is probably generalized.

*Talpavoides* is the most suitable of the generalized dormaaliids for possible inclusion in the ancestry of *Talpavus*. Selection favoring the relative increase in size of  $M_2$  relative to  $M_1$ , or decrease in size of  $M_1$  relative to  $M_2$ , coupled with further reduction of the  $P_4$  talonid and increase in relative size of the  $P_4$  metaconid, would be required to derive *Talpavus nitidus* directly from a population of *Talpavoides dartoni*. Considerable premolarization of  $P_4$  must have taken place at some point in the lineages of *Scenopagus*, *Macrocranium*, and *Talpavus* if PU 18688 (see p. 44) had anything to do with the later Wasatchian and Bridgerian radiation of dormaaliids. As indicated above for *Scenopagus hewettensis* and *Scenopagus* sp.,  $P_4$  premolarization was a characteristic trend in the lineages of that genus.

From *Macrocranium*, *Talpavoides* differs in its much smaller size, its relatively narrower  $P_4$ , taller trigonids and taller, more acute molar cusps, greater exodaenodonty of the molars, and the molar-size gradient. The taller molar entoconids and sharper cusps are probably generalized features relative to *Macrocranium*, whereas the exo-



daenodonty and posteriorly smaller molars are specializations that preclude this genus from a close relationship to *Macrocranium*.

*Talpavoides dartoni* is known from only two localities in the Elk Creek section of the Willwood Formation, where it occurs in the lower Gray Bull zone at the 140- and 180-m levels. In the Sand Creek facies, this taxon is found at 15 localities between the 24- and 180-m levels. The 180-m level in the Sand Creek facies is the lowest occurrence of the adapid primate *Pelycodus trigonodus* in these rocks (Bown, 1979), whereas this animal first appears at the level of locality 355 (240-m level) in the Elk Creek section. *T. dartoni*, therefore, occurs in the lower Gray Bull zone of the Elk Creek section, but in the lower Gray Bull through the lowest part of the middle Gray Bull zones in the Sand Creek facies.

*Measurements*.—Given in table 6.

**dormaaliid, sp. A**

Plate 6, figure 5

*Referred specimens*.—UW 7048, 9627 (pl. 6, fig. 5).

*Diagnostic characters*.—Molars strongly exodaenodont, more so than in *Scenopagus*, *Talpavus*, or *Macrocranium*.  $M_{2-3}$  trigonids strongly compressed anteroposteriorly, and metaconid and entoconid markedly taller than protoconid and hypoconid, respectively. Hypoconulids large, close to entoconids. Entoconids trenchant and deflected lingually and talonid notch acute.  $M_3$  relatively unreduced in comparison to  $M_2$ .

*Discussion*.—This species is known from only two complete teeth, but the characters cited previously appear to be diagnostic. The trigonid structure is reminiscent of that in *Talpavus*; however, the talonids are wholly dissimilar. *Macrocranium*, conversely, has tall, lingual entoconids and large, somewhat lingual hypoconulids, but molars of *M. nitens* are less exodaenodont and have less trenchant cusps and less compressed trigonids. Better material is needed to meaningfully assess the relations and significance of this animal.

*Dormaaliid* sp. A is known only from the early Graybullian Sand Creek facies of the Willwood Formation, where it occurs at two localities at the 30- and 46-m levels.

*Measurements*.—(mm): UW 7048:  $M_2L=1.20$ ,  $M_2W=0.95$ . UW 9627:  $M_3L=1.17$ ,  $M_3W=0.77$ .

**Family ERINACEIDAE**

***Eolestes*, gen. nov.**

*Etymology*.—Greek *eos*; dawn, and Greek *lestes*; robber.

TABLE 6.—Measurements of teeth of *Talpavoides dartoni* from the Willwood Formation  
[Values in millimeters. Leaders (—) indicate no specimen]

Museum Nos.	P <sub>4</sub> L	P <sub>4</sub> W	M <sub>1</sub> L	M <sub>1</sub> W	M <sub>2</sub> L	M <sub>2</sub> W	M <sub>3</sub> L	M <sub>3</sub> W
The Geological Museum, University of Wyoming (UW)								
6974							1.09	0.65
6999	1.05	0.59	1.37	0.90	1.21	0.96		
7005							1.13	.68
8586					1.35	.85	1.10	.55
8993					1.22	.92		
9000							1.15	.71
9597					1.30	1.00	1.14	.70
9600	1.10	.73	1.37	1.00				
9610					1.18	.90		
9613					1.22	.80	1.10	.60
9618					1.10	.90		
9623					1.19	.88	1.12	.66
9635			1.28	.89	1.22	.82		
9666					1.22	.90		
9674					1.20	.75		
9675	1.00	.68						
9689	1.14	.65	1.24	.84				
9697	1.00	.60						
9700			1.21	.81				
9704							1.10	.69
9711					1.21	.94		
9718							1.07	.60
9722					1.15	.87		
9723	1.06	.56						
9726							1.00	.57
9728	1.10	.80						
9752	1.05	.65	1.31	.76				
10423					1.40	.95	1.20	.80
10448					1.35	1.05		
10454								
Peabody Museum, Yale University (YPM)								
30544			1.50	1.05				
30617							1.20	0.95
30643	1.20	0.75						
31168	1.10	.75						

<sup>1</sup>UW number 10454: M<sub>1</sub>L=1.40–1.45 (N=2); M<sub>1</sub>W=1.80–1.90 (N=2).

*Type*.—*Eolestes simpsoni* (Bown, 1979, p. 61), only known species.

*Diagnosis*.—P<sub>4</sub> talonid more reduced than in *Leipsanolestes*, "*Lep-tacodon*" *jepseni*, most *Macrocranium*, and *Talpavus*. P<sub>4</sub> larger with respect to M<sub>1</sub> than in *Entomolestes* or *Talpavus* and with a more lingual paraconid than in these species. P<sub>4</sub> trigonid longer relative to talonid than in *Scenopagus*, developed about as in *Macrocranium* and *Leipsanolestes*. P<sub>4</sub> metaconid smaller relative to protoconid than in *Talpavus* or *Scenopagus*, about same as in *Leipsanolestes*. Molar talonids narrower than in *Macrocranium* or *Scenopagus*, and molar entocristids tall, as in soricids (forming mure) as in *Entomolestes*, taller than in *Talpavus*, *Leipsanolestes*, *Litolestes*, *Scenopagus*, and

"*Leptacodon*" *jepseni*. Molar paraconids more cuspidate (less shelf-like) than in *Macrocranium* or *Leipsanolestes*, and trigonids more anteroposteriorly compressed than in *Macrocranium*.  $M_1$  larger than  $M_2$  in contrast to many dormaalids, and molars more exodaenodont than in *Litolestes*, *Leipsanolestes*, *Macrocranium*, or *Talpavus*. Cristid obliqua joins metaconid and metaconid twinned, in contrast to all above forms.

*Eolestes simpsoni* (Bown, 1979)

Plate 6, figure 6, plate 7, figure 1

*Synonym.*—*Leipsanolestes simpsoni* Bown (1979, p. 61).

*Holotype*—UW 9616, right  $P_4$ - $M_2$  (Bown, 1979, fig. 42b), UW locality V-73041, lower part of Willwood Formation, Sand Creek facies (about 30-m level), early Graybullian, sec. 24, T. 46 N., R. 92 W., Washakie County, Wyo.

*Hypodigm*—The type and YPM 35156 (pl. 6, fig. 6; pl. 7, fig. 1).

*Diagnosis.*—Only known species; same as for genus.

*Measurements.*—(mm): UW 9616 (type):  $P_4L=1.18$ ,  $P_4W=0.81$ ,  $M_1L=1.43$ ,  $M_1W=0.97$ ,  $M_2L=1.19$ ,  $M_2W=0.91$ . YPM 35156:  $P_4L=1.30$ ,  $P_4W=0.80$ ,  $M_1L=1.55$ ,  $M_1W=1.00$ ,  $M_2L=1.38$ ,  $M_2W=1.00$ .

*Discussion.*—Bown (1979) placed the type of *Eolestes* in *Leipsanolestes*, the closest morphologic counterpart of the new genus. Restudy of the type specimen and YPM 35156 and comparisons with new and better materials of *Leipsanolestes siegfriedti* and *Entomolestes grangeri* (Krishtalka, 1976a; Krishtalka and West, 1977) convince us that both Willwood specimens represent a new genus of erinaceid but one that is most closely related to these two mammals. *Eolestes* is retained in the Erinaceidae on the basis of (1) premolar construction, (2) the more cuspidate paraconid on  $M_1$  than on  $M_2$ , (3) the rectangular molars, (4) the high molar entocristids, (5)  $M_1$  larger than  $M_2$ , and (6) very flat hypoconids.

In contrast to *Leipsanolestes siegfriedti*, the molars are strongly exodaenodont, the hypoflexid is deep, the  $P_4$  talonid is more reduced, the molar entocristids are taller, the paraconids are more cuspidate, and the cristids are more oblique and are connected to the metaconid. All these features, except the more cuspidate paraconids, are characters that are probably derived relative to the condition in *Leipsanolestes*, and all, with the exception of the connection of the cristid obliqua and metaconid, parallel the developments in *Entomolestes grangeri*.

From *Entomolestes*, *Eolestes* is distinguished by the last feature, its larger  $P_4$  with respect to  $M_1$ , its less oblique (more anteroposterior)

alinement of the  $P_4$  prevallid (because the paraconid is more anteriorly removed from the metaconid), the less well developed  $M_2$  entocristid, and the deeper hypoflexids. The relative size of the  $P_4$  and the molar entocristid development in *Eolestes* are probably generalized with respect to *Entomolestes*, and the  $P_4$  trigonid construction (similar to that in *Leipsanolestes*) may also be generalized for some early Tertiary erinaceids. The cristid obliqua-metaconid confluence and the resultant deep hypoflexid is unique among the early Tertiary erinaceids and is convergent to some extent with the condition in some talpids (for example, the Desmaninae). This feature is doubtlessly derived with respect to both *Leipsanolestes* and *Entomolestes* and suggests that *Eolestes* is removed from the ancestry of the latter genus.

cf. *Leipsanolestes* sp.

*Referred specimen*.—UW 9672, a left  $M_3$ .

*Discussion*.—This tooth is related to *Leipsanolestes* and the erinaceids in the possession of bulbous cusps in conjunction with a short trigonid, by a shallow hypoflexid, by a strongly developed paraconid shelf without a cuspidate paraconid, by a low, flat hypoconid and taller entoconid, and by its general exodaenodont configuration. The tooth is distinguished from that in *Leipsanolestes siegfriedti* by its 15-percent larger size, a less lingually deflected metaconid, a relatively deeper talonid basin, and a less anteriorly attenuated paraconid shelf. The tooth is less similar to  $M_3$  in *Litolestes* and does not closely resemble molars of *Eolestes*, "*Leptacodon*" *jepseni*, or *Entomolestes grangeri*. It is possible that the specimen represents a large, undescribed species of *Leipsanolestes* that was approximately coeval with Willwood *L. siegfriedti*; however, the material is inadequate to positively ascertain its affinities within the Erinaceidae.

Cf. *Leipsanolestes* sp. is known from only one locality, at the 88-m level of the Sand Creek facies where the only specimen was found in association with an early Graybullian fauna.

*Measurements* —(mm):  $M_3L=1.75$ ,  $M_3W=1.20$ .

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

Plate 7, figure 5

*Referred specimen* —YPM 30559, fragment of left ramus with  $P_4$ – $M_1$  and trigonid of  $M_2$  (pl. 7, fig. 5).

<sup>3</sup>M J Novacek, T M Bown, and David Schankler (unpub. data) include "*Leptacodon*" *jepseni* McKenna (1960a) in a new genus

*Discussion.*—This specimen appears to be a large variant of McKenna's (1960a) "*Leptacodon*" *jepseni*, from which it is nearly inseparable on morphologic grounds (YPM 30559 is larger).  $M_1$  in the Yale specimen has a slightly more anteroposteriorly compressed trigonid than occurs in the type of "*L*" *jepseni*.

"*Leptacodon*" *jepseni* was established on the type lower jaw with  $P_2$ - $M_2$  and two other damaged teeth from the Four Mile Creek area of northwestern Colorado. Delson (1971) referred four additional specimens to this enigmatical species and believed that it is probably more closely related to his concept of the adapisoricids than to *Leptacodon*. This conclusion was later endorsed by Krishtalka (1976a), who did not comment further on its affinities.

Of Delson's referred materials, only AMNH 56313 (an  $M_3$ ) is probably referable to "*L*" *jepseni*. AMNH 56311 and 56312 are nyctitheriids and closely resemble *Leptacodon tener* and small specimens of *Plagiactenodon krausae*.  $M_3$  is not preserved in the type of "*L*" *jepseni*, and the reference of AMNH 56313 to that taxon is provisional and is based on its having a lingual hypoconulid that is not expanded posteriorly as in *Entomolestes grangeri*.

AMNH 56314 and 56315, also from the Powder River local fauna and with labels bearing "*Leptacodon*", most closely resemble *Plagiactenodon savagei*, sp. nov. (see p. 61), differing from it only in the following trivial respects: (1) the teeth are slightly larger, (2) the  $P_4$  talonid is relatively longer and somewhat more squared, (3) the molar talonids are more roundly basined, and (4)  $M_1$  has a more continuous entocristid. The  $M_1$  trigonid is not preserved in the type of *Plagiactenodon savagei*, however, in *P. krausae* the trigonid is more anteroposteriorly compressed than it is in AMNH 56314.

We agree with Delson's (1971) suggestion that "*L*" *jepseni* is in or near the ancestry of Bridgerian *Entomolestes grangeri*. McKenna (1960a, p. 53) also observed that "*Leptacodon*" *jepseni* is "*Entomolestes*-like."  $P_4$  is the most diagnostic tooth in both species and is typified by a very large, anteriorly projecting paraconid that arises very high on the face of the trigonid, in conjunction with a short, poorly basined talonid (pl. 7, fig. 5). The molars of "*L*" *jepseni* differ from those of *E. grangeri* in size (type materials of "*L*" *jepseni* are smaller), in having a smaller  $P_3$  to  $P_4$  size ratio, in the shorter, more curved prevallid, in the slightly larger and more linguolabially compressed entocristids in *Entomolestes*, and in the somewhat more exodaenodont configuration of the molars in the last genus.

"*L*" *jepseni* differs from *Eolestes* in (1) a smaller  $P_4$  with respect to  $M_1$ , (2) the better developed talonid basin in "*L*" *jepseni*, (3) the more poorly developed molar entocristids, (4) the lack of connection of the cristid obliqua to the metaconid, and (5) the presence of a more acute paracristid notch in "*L*." *jepseni*. These observations support our

contention that "*Leptacodon*" *jepseni* is morphologically closer to *Entomolestes grangeri* than to either *Eolestes* or *Leipsanolestes*

Krishtalka and West (1977) described additional specimens of *Entomolestes grangeri* (for 68 years, the type was the only published specimen), and to the hypodigm we add AMNH 98742 (pl. 7, figs. 2, 4) from rocks of late Bridgerian age near Tabernacle Butte. This specimen (identified by James Honey) preserves  $P_4$ - $M_3$ , and, aside from the type, is the most complete undamaged lower dentition. Interestingly, the highly distinctive  $P_4$  construction of both "*L. jepseni*" and *E. grangeri* exists (in modified form) in Aquitanian *Amphechinus*, living *Erinaceus*, and several other advanced erinaceines (see, for example, figures in Rich and Rich, 1971; Rich and Rasmussen, 1973).

*Measurements*.—YPM 30559 (mm):  $P_4L=1.20$ ,  $P_4W=0.80$ ,  $M_1L=1.40$ ,  $M_1W=1.05$ .

Order INSECTIVORA  
Suborder SORICOMORPHA  
Family NYCTITHERIIDAE

In his review of the early Tertiary nyctitheriids of North America, Krishtalka (1975, 1976b) considered the following characters to be diagnostic of the family: (1) the presence of a vespiform constriction between the molar trigonids and talonids, (2) presence of a semimolariform  $P_4$  with a low paraconid projecting out from the anterior part of the base of the protoconid, (3) relatively high (tall) molar hypoconids that did not become flat with wear, (4) unreduced molar hypoconulids, and (5) deep molar hypoflexids. In contrast, the sensu lato adapisoricids (dormaalids of this report) were believed to be characterized by (1) progressive premolarization of  $P_4$ , (2) rectangular molars with low, relatively bunodont cusps, (3) " \* \* \* a compressed, lophid-like paraconid that never joins the metaconid \* \* \* " on  $M_{1-3}$ , (4) wide molar talonids with a high entoconid and lower hypoconid, (5) median, or barely lingual and unreduced molar hypoconulids, and (6) a shallow hypoflexid with the cristid obliqua meeting the postvallid labial to the protocristid notch. In his discussion of "*Leptacodon*" *jepseni*, Krishtalka (1976b, p. 17) also inferred that the position of the  $P_4$  paraconid high on the anterior face of the trigonid was a more typical adapisoricid (sensu Krishtalka) than nyctitheriid character. From our comparisons of early Tertiary dormaalids, erinaceids, and nyctitheriids, we offer the following supplementary notes and qualifications.

First, the  $P_4$  paraconid is relatively as large and arises equally low on the trigonid in *Mckennatherium* (Adapisoricidae, according to Krishtalka, 1976a; for example, AMNH 35955, PU 17722) as it does

in any species of *Leptacodon* or *Nyctitherium*. If *Mckennatherium* is to be retained in the Dormaaliidae (the diminished probability of this association is discussed on p. 42–44), the relative height of the  $P_4$  paraconid is of little diagnostic value. Indeed, the position of this cusp on  $P_4$  in at least some "*Leptacodon*" *munusculum* (for example, PU 20026), *Nyctitherium velox* (for example, YPM 14936), *N. serotinum* (for example, CM 13722), and *Pontifactor* (for example, AMNH 15103) is much higher on the trigonid than it is in *Mckennatherium* and most closely resembles the positions in the dormaaliids *Talpavus* and *Macrocranion*.

Second, other than the deep hypoflexid, we see no particularly overt vespiform constriction between the molar trigonids and talonids in "*Leptacodon*" *munusculum*, "*Leptacodon*" *packi*, or *Nyctitherium velox*. Among known nyctitheriids, this character is perhaps best developed in *Pontifactor*; however, no nyctitheriid has this constriction so explicitly developed as in *Macrocranion* or dormaaliid sp. A. (p. 52). This constriction owes its visual properties to a deep hypoflexid in combination with a lingual leaning of the entoconid. We do not believe that the degree of constriction of the talonid-trigonid juncture is particularly diagnostic for nyctitheriids when compared to its development in both dormaaliids and erinaceids.

Third, the relatively high hypoconids considered to be a diagnostic feature of the nyctitheriids by Krishtalka are more evident in *Pontifactor* and some *Nyctitherium* than they are in *Leptacodon*. In some instances, this feature results not from unusually tall hypoconids but from relatively short entoconids. Moreover, in all the forms believed to be nyctitheriids by Krishtalka (1976b), excluding *Saturninia beata* and *Leptacodon tener*, the entoconids are both relatively low and are situated slightly more anteriorly than in adapisoricids. This appears to be a significant shared and derived character uniting "*Leptacodon*" *munusculum* and at least some "*Leptacodon*" *packi* with *Pontifactor* and middle Eocene nyctitheriids. In "*L*" *packi* and in at least some specimens of "*L*" *munusculum* (for example, PU 20026), *Pontifactor* sp. (see p. 59), *Nyctitherium velox*, and *N. serotinum*, the entoconid is also somewhat linguolabially compressed and is connected to the base of the metaconid by a minor entocristid. The development of the entocristid is greater than in any of the dormaaliids and is convergent with that in some erinaceids and in some of the distant nyctitheriid relatives—the shrews.

These differences suggest the division of the Nyctitheriidae into two groups: one containing *Leptacodon tener*, *Plagioctenodon*, *Plagioctenoides*, and *Saturninia beata*; the other with "*Leptacodon*" *munusculum*, "*Leptacodon*" *packi*, *Saturninia gracilis*, *Amphidozotherium*, *Pontifactor*, and *Nyctitherium*. A complex of apparent crossing characters, however, masks the significance of these

shared attributes and indicates that these do not constitute two natural phylogenetic groups.

Krishtalka (1976b) observed that "*Leptacodon*" *munusculum* might belong in *Pontifactor* and that "*L.*" *packi* might more aptly be placed in *Nyctitherium*. This concept independently recognizes the morphologic discrepancies between *Leptacodon tener* and other species referred to this genus; however, we do not recommend these synonymies.

"*Leptacodon*" *packi* Jepsen (1930b) further differs from more typical nyctitheriids in the extremely tall and trenchant  $P_{3-4}$ , and in having a conspicuous labioinferior depression of the enamel beneath the  $P_1$  hypoflexid, and differs from *Nyctitherium* in having the molar trigonids relatively long with respect to the talonids.  $P_{3-4}$  are reminiscent of the general morphology of those teeth in early geolabidids, such as *Centetodon patratius*, sp. nov. (p. 64), or *C. pulcher*. The molars of early *Centetodon*, however, do not particularly resemble those of "*L.*" *packi*, but the premolar similarities suggest that the latter species may have had a more generalized, central position in the ancestry of early Tertiary soricoids, rather than a more specialized position as a possible synonym of *Nyctitherium*.

*Pontifactor* sp. (Krishtalka, 1976b, p. 23)

*Referred specimens.*—UW 8584, 9621, 9649, 9681, 9683, 9710, 9721, 9732, 9733, 10449, 10455, 10456, (see also Bown, 1979).

*Discussion.*—Krishtalka (1976b) transferred Matthew's (1918) referred Willwood specimen of *Nyctitherium celatum* (AMNH 15103) to *Pontifactor* West (1974). Bown (1979) referred additional upper cheek teeth to this animal, under the designation *Pontifactor* cf. *bestiola*. The four additional undescribed specimens at hand (from the original hypodigm of *Plagiostenodon krausae*, see Bown, 1979) are smaller but otherwise closely resemble molars in AMNH 15103 and are here referred to *Pontifactor* sp.

In contrast to both *Plagiostenodon* and *Talpavoides*, these lower molars possess acute, deep talonid basins, a deep hypoflexid, more trenchant cusps, and unreduced hypoconulids, characters that Krishtalka (1976b) cited as diagnostic of nyctitheriids. The molars (only  $M_{1-2}$  are represented) have the anteroposteriorly compressed trigonids, lophid-like and anterolingually flaring paraconids, a large medial hypoconulid, and a tiny mesoconid, all typical of Krishtalka's *Pontifactor* sp. Other than the presence of an eruptive  $M_3$ , we are unable to ascertain by which criteria both Matthew (1918) and Krishtalka (1976b) presumed that  $P_4$  in AMNH 15103 is deciduous. The tooth is broken between the trigonid and talonid, and the talonid



has been rotated posterolabially, but its morphology is consistent with that in permanent  $P_4$  in other nyctitheriids

*Measurements.*—(mm), UW 8584:  $M_2L=1.23$ ,  $M_2W=0.90$ . UW 9649:  $M_2L=1.12$ ,  $M_2W=0.87$ . UW 9683:  $M_1L=1.30$ ,  $M_1W=0.92$ ,  $M_2L=1.19$ ,  $M_2W=0.85$ . UW 9721:  $M_1L=1.30$ ,  $M_1W=0.92$ . UW 9621:  $M_1L=1.60$ ,  $M_1W=1.10$ . UW 9710:  $M_2L=1.35$ ,  $M_2W=0.95$ .

#### COMMENTS ON *PLAGIOCTENODON* BOWN, 1979

Bown (1979) erected the genus *Plagiostenodon* for approximately 40 lower jaws and several individual teeth in the No Water collection from the Sand Creek facies of the Willwood Formation. Owing to the current resurgence of interest in early Eocene faunas in general and early Eocene insectivores in particular, many useful comparative materials were not available for study at the time of the original description of the No Water insectivores, and those observations were based principally on comparisons of published figures, text descriptions, and a few casts. Bown (1979) recognized the large amount of morphologic variation in the sample referred to *Plagiostenodon* and named only the last genus for the most distinctive specimens. Virtually all of the best of the recently published specimens of Paleocene and early Eocene insectivores have now been examined and compared with specimens in the original hypodigm of *Plagiostenodon*, and it is now possible to give a more comprehensive account of the several mammals originally included in the latter genus.

Bown (1979) believed *Plagiostenodon* to be an early adapisoricid (sensu lato), perhaps most closely allied to the enigmatical "*Leptacodon*" *jepseni* but with several crossing specializations that are reminiscent of both early adapisoricids and early nyctitheriids. These conclusions are fundamentally changed by this study; "*Leptacodon*" *jepseni* is an erinaceid mostly closely related to *Entomolestes grangeri* (p. 56), *Plagiostenodon* (sensu stricto) is a nyctitheriid, and the original hypodigms ascribed to *Plagiostenodon krausae* and *P. cf. krausae* contain representatives of five species. Four of these (*Scenopagus* sp., *Talpavoides dartoni*, dormaaliid sp. A., and some specimens of *Pontifactor* sp.) have already been discussed.

#### *Plagiostenodon krausae* Bown, 1979

*Emended hypodigm.*—UW 7047, 9572, 9587, 9592, 9608, 9620, 9653, 9682 (holotype, Bown, 1979, fig. 43a), 9684, 9688, 9692, 9696, 9698, 9709, 9712, 9737, possibly UW 9715, 9716, 9730, 10377, 10451, YPM 31167, 32824.

*Emended diagnosis*.— $P_{2-3}$  anteriorly inclined.  $P_2$  larger than  $P_3$ , and no diastema separates these teeth.  $P_4$  semimolariform, elongated anteroposteriorly, narrow transversely, with paraconid large and anteriorly projecting, and arising higher on the anterior face of the trigonid than in *Leptacodon*.  $P_4$  talonid with two or three well-defined cusps and well-developed basin.  $P_4$  relatively larger with respect to  $M_1$  than in *Talpavoides*.  $M_1$  and  $M_2$  about equal in size;  $M_3$  slightly smaller than  $M_2$ .  $M_{1-2}$  entoconids significantly taller than hypoconids; entoconids do not project lingually and are situated at posterolingual margins of molars, not more anteriorly as in some *Leptacodon* and all *Nyctitherium*. No vespiform constriction between trigonid and talonid of molars.

*Discussion*.—*Plagiectenodon krausae* appears to share some of the characters discussed above with dormaaliids, as suggested by Bown (1979). Particularly relevant here are the shallow molar hypoflexids, tall, posterolingual molar entoconids, open talonid notch, and relatively minor molar hypoconulids. It appears to us more likely, however, that *Plagiectenodon* is a derivative of Paleocene *Leptacodon tener*. The  $P_{2-3}$  construction,  $P_4$  molarization, less compressed  $M_{1-2}$  trigonids, broader molar talonids, and acute molar cusps (especially the metaconid) argue for close affinity to *L. tener* and the earliest nyctitheriids. *L. tener*, *Plagiectenodon*, *Plagiectenoides microlestes* (p. 64), and *Saturninia beata* differ from "*L. munusculum*", *Saturninia gracilis*, *Amphidozotherium*, and *Nyctitherium* in having tall entoconids that are situated at the far posterolingual margins of the molars (see previous discussion of the Nyctitheriidae).

*Plagiectenodon krausae* is known only from the Sand Creek facies of the Willwood Formation where it occurs associated with an early Graybullian fauna between the 34- and 88-m levels, inclusive (fig. 18).

Measurements.—Given in table 7.

*Plagiectenodon savagel*, sp. nov.

Plate 7, figures 3, 6

*Etymology*.—For D. E. Savage, in recognition of his many contributions to Tertiary stratigraphy and paleontology.

*Holotype*.—YPM 34257, right  $P_3$ - $M_2$  (pl. 7, figs. 3, 6); only known specimen.

*Locality*.—YPM locality 104, lower part of Willwood Formation (140-m level of Elk Creek section), early Graybullian, sec. 18, T. 50 N., R. 93 W., Big Horn County, Wyo.

*Diagnosis*.—Teeth 35 percent larger than in *Plagiectenodon krausae* and  $M_2$  paraconid less cuspidate than in that species.

## 62 PROTEUTHERIA AND INSECTIVORA, WILLWOOD FORMATION, WYO.

TABLE 7.—Measurements of teeth of *Plagiostenodon krausae* from the Willwood Formation

[Values in millimeters. x, damaged tooth. Leaders (—) indicate no specimen]

Museum Nos.	P <sub>1</sub> L	P <sub>1</sub> W	P <sub>2</sub> L	P <sub>2</sub> W	M <sub>1</sub> L	M <sub>1</sub> W	M <sub>2</sub> L	M <sub>2</sub> W	M <sub>3</sub> L	M <sub>3</sub> W
The Geological Museum, University of Wyoming (UW)										
7047	...	...	1.35	0.70	1.35	0.85	1.40	0.85	1.30	0.85
9572	...	...	1.20	.80	1.50	.95	...	...	...	...
9587	...	...	1.12	.84	...	...	...	...	...	...
9592	...	...	...	...	1.37	.91	1.31	.89	1.29	.71
9608	...	...	1.50	.90	...	...	...	...	...	...
9620	...	...	1.18	.66	1.28	.87	...	...	...	...
9653	...	...	1.30	.85	...	...	...	...	...	...
9682	0.82	0.48	1.15	.82	...	...	...	...	...	...
9684	...	...	...	...	...	...	...	...	1.14	.75
9688	...	...	...	...	1.23	.97	1.15	.97	...	...
9692	...	...	1.17	.66	1.24	.84	1.21	.86	...	...
9696	...	...	1.40	.75	x	x	1.40	.90	...	...
9698	...	...	1.40	.85	...	...	...	...	...	...
9709	...	...	1.45	.80	...	...	...	...	...	...
9712	...	...	1.45	.85	...	...	...	...	...	...
9737	...	...	1.35	.80	1.50	1.10	1.50	1.10	...	...
10377	...	...	1.25	.75	...	...	...	...	...	...
Peabody Museum, Yale University (YPM)										
31167	...	...	1.35	.85	...	...	...	...	...	...
32824	0.95	0.50	1.35	.80	...	...	...	...	...	...
The Geological Museum, University of Wyoming (UW)										
Museum Nos.			P <sub>1</sub> L	P <sub>1</sub> W	M <sub>1</sub> L	M <sub>1</sub> W	M <sub>2</sub> L	M <sub>2</sub> W		
The Geological Museum, University of Wyoming (UW)										
9715	...	...	...	...	1.40	2.00	...	...		
9716	...	...	2.00	2.30	x	x	1.95	x		
9730	...	...	...	...	1.90	2.60	...	...		

<sup>1</sup>P<sub>2</sub>: L=0.95, W=0.42.

*Discussion.*—The type specimen of *P. savagei*, with the exception of its much larger size, is virtually identical to the specimens previously referred in this report to *Plagiostenodon krausae*. *Plagiostenodon* does not closely resemble *Scenopagus* and the more derived dormaaliids or any erinaceid; and, as observed previously, it is probably most closely related to the *Leptacodon tener* group of nyctitheriids. To clarify the varying degrees of semblance of *P. savagei* to earlier described nyctitheriids, the results of our comparisons are abstracted on the following page.

*Leptacodon tener* Matthew and Granger, 1921:

*P. savagei* P<sub>1</sub> is about 17 percent and M<sub>2</sub> about 38 percent larger than in *L. tener*, and the P<sub>1</sub> paraconid arises higher on the anterior face of the trigonid than in that species. The M<sub>2</sub> paraconid is less cuspidate in *P. savagei*, and the protocristid notch is at the same level as the paracristid notch (higher than in *L. tener*).

*"Leptacodon" munusculum* Simpson, 1935:

*P. savagei* is about 45 percent larger than "*L. munusculum*", and the P<sub>1</sub> paraconid arises higher on the anterior face of the trigonid than in some specimens of the latter species (about as in PU 20026 from Cedar Point Quarry, higher than in AMNH 35943 from Gidley Quarry). The molar entoconids are anterolingual to the hypoconulids in "*L. munusculum*". P<sub>3</sub> is relatively lower with respect to P<sub>1</sub> in both *P. krausae* and *P. savagei*.

*"Leptacodon" packi* Jepsen, 1930b:

*P. savagei* is about 25 percent larger than "*L. packi*". P<sub>3</sub> is tall and trenchant in "*L. packi*", whereas, it is shorter and tilted anteriorly in *Plagiostenodon*. The P<sub>1</sub> paraconid is relatively larger and arises higher on the anterior face of the trigonid in *P. savagei* than in "*L. packi*", and the M<sub>1-2</sub> entocristids are better developed in "*L. packi*". The M<sub>2</sub> paraconid is more cuspidate in "*L. packi*", and the M<sub>1-2</sub> entoconids are anterolingual to the hypoconulids, in contrast to the condition in *Plagiostenodon*.

*Pontifactor* sp. (Krishtalka, 1976b, p. 23-25):

*P. savagei* is about 20 percent larger than *Pontifactor* sp. and has more posterior molar entoconids. The P<sub>1</sub> paraconid is much larger and more anteriorly situated, arising slightly lower on the trigonid in *Plagiostenodon*. The hypoflexid is relatively deeper and the talonid basin is relatively deeper and more acute in *Pontifactor* sp.

*Nyctitherium velox* Marsh, 1872 (pl. 8, figs. 1, 2, this paper):

Teeth of *Plagiostenodon savagei* are about 20 percent larger than in *N. velox*. P<sub>3</sub> has a longer paracristid, a stronger paraconid, and a stronger posterobasal cusp in *P. savagei*, and the P<sub>1</sub> paraconid is much larger and more anteriorly removed from the metaconid than in *N. velox*. The molar hypoconulids appear to be relatively larger and closer to the entoconids in *N. velox*, and the M<sub>1-2</sub> entoconids are anterolingual to the hypoconulids, in contrast to *P. savagei*.

*Saturninia gracilis* Stehlin, 1940, and *S. beata* (Crochet, 1974):

The P<sub>1</sub> paraconid is much stronger in *Plagiostenodon* than in *S. beata* but is developed much as in *S. gracilis*. The talonids of M<sub>1-2</sub> are less reduced with respect to the trigonids than in *S. beata*, and the molars are less elongate than in that species. The M<sub>1-2</sub> entoconids are very small and anteriorly situated in *Saturninia gracilis* (in contrast to both *Plagiostenodon* and *S. beata*), but the internal mure of the entoconid faces buccally in *Plagiostenodon*, not anterobuccally as in *S. beata*.

*Amphidozotherium* Filhol, 1877:

The P<sub>1</sub> paraconid is much stronger and is more anteriorly placed in *Plagiostenodon*. The P<sub>2-3</sub> constructions are dissimilar, the M<sub>1-2</sub> paraconids are less cuspidate and less medial, and the entoconids are larger and less anterior in *Plagiostenodon*.

*Plagioctenodon savagei* is a possible derivative of *P. krausae*. However, the stratigraphic evidence suggests that these two species may have been contemporaries even though they share no localities in common. *Plagioctenodon* is closest to *Leptacodon tener* among known nyctitheriids, as evidenced by the posterior molar entoconids. The less cuspidate  $M_{1-3}$  paraconids and the position of the  $P_4$  paraconid are almost certainly derived characters, relative to *L. tener*.

Cf. *Leptacodon* of Krishtalka (1976b, p. 16) may belong in *P. savagei*, but the referred specimens from the Sand Wash Basin of Colorado are somewhat larger. At any rate,  $M_{1-2}$  in that species appear to have relatively shallow hypoflexids, a highly molarized  $P_4$ , and posteriorly situated entoconids (Krishtalka, 1976b, fig. 4).

*Measurements*.—Type of *P. savagei* (mm):  $P_3L=1.25$ ,  $P_3W=0.70$ ,  $P_4L=1.70$ ,  $P_4W=1.00$ ,  $M_1W=1.50$ ,  $M_2L=1.80$ ,  $M_2W=1.55$ .

#### COMMENTS ON *PLAGIOCTENOIDES* BOWN, 1979

*Plagioctenoides microlestes* was erected by Bown (1979, p. 65) to accommodate six mandibular specimens of a very small insectivore. At the time of its description, *P. microlestes* was believed to be a sensu lato adapisoricid, largely because of the morphology of  $P_4$ . The molar morphology, however, seems more consistent with our revised concept of the nyctitheriids in (1) the trenchant cusps, (2) the deep hypoflexid and long cristid obliqua, (3) the unreduced hypoconulids, and (4) the relatively tall, piercing hypoconids. If this assessment is correct, *Plagioctenoides* is the smallest known nyctitheriid and has an antemolar dentition most like that of late Ludian *Amphidozotherium* in the possession of reduced, single-rooted  $P_{1-3}$  (Crochet, 1974; Sigé, 1977).

#### Family GEOLABIDIDAE McKenna, 1960b *Centetodon patratus*, sp. nov.

Plate 8, figure 3

*Etymology*.—Latin *patratus*, accomplished, the first known early Wasatchian species of *Centetodon*.

*Holotype*.—UCMP 44954, left  $P_4$ – $M_2$  (McKenna, 1960a, p. 61–63, fig. 29); east end of Alheit pocket, Four Mile fauna (early Wasatchian), Sand Wash Basin, Colo.

*Hypodigm*.—The type and YPM 23088 (pl. 8, fig. 3); possibly also UCMP 44957, 44958, 44959 (McKenna, 1960a, p. 61).

*Distribution.*—Early Wasatchian, northwestern Colorado, and Bighorn Basin, Wyo.

*Diagnosis.*—Size of *Centetodon pulcher* and *C. magnus*, much smaller than *C. wolffi* and *C. neashami*, sp. nov. (infra) and larger than other species of *Centetodon*.  $P_4$  with much better developed talonid basin than in *C. pulcher*, *C. new species B* and *C* (of Lillegraven and McKenna, unpublished data, as designated by Krishtalka and Setoguchi, 1977), *C. marginalis*, or *C. magnus*.  $P_4$  paraconid relatively larger than in *C. pulcher* or *C. new species C*, and  $P_4$  without posteriorly flaring protoconid as in *C. magnus*.  $P_4$  longer with respect to  $M_1$  than in *C. pulcher*, *C. marginalis*, and *C. new species B*.

*Discussion.*—*Centetodon patratus* is the oldest known species currently assigned to this genus or to the Geolabididae. The type and other UCMP specimens and the referred Willwood material are all associated with undoubted early Wasatchian faunas and demonstrate that the peculiar morphology of the cheek teeth in *Centetodon* was established early and persisted in its general form for about 15 million years. *C. patratus* is closest in morphology to *C. pulcher*, a species reported from several localities in the Bridger Formation of southwestern Wyoming (J. A. Lillegraven and M. C. McKenna, unpub. data), and possibly from locality VI of the Huerfano Formation (Krishtalka, 1975, p. 98).

YPM 23088 differs from the type of *C. patratus* in having a slightly less exodaenodont  $M_1$  talonid; damage to several cusps gives the impression that the entoconids are not so lingually inflected as in the type. The general sculpture of the teeth in both specimens is quite similar, though, and it is highly probable that they represent the same species.

*C. patratus* differs from *C. pulcher* principally in the structure of  $P_4$  (for example, better developed talonid basin and cristid obliqua, larger  $P_4$  paraconid, and  $P_4$  slightly larger with respect to  $M_1$  in *C. patratus*). All these characters are probably generalized for the genus, if one assumes that there was either a dormaaliiid-like or a *Batodon*-like mammal in the ancestry of *Centetodon* (the latter idea was suggested by M. C. McKenna, oral commun., 1974, and by McKenna in Novacek, 1976, p. 33). The morphology of the cheek teeth in *Centetodon* is remarkably uniform in all species.  $P_4$  is the most diagnostic tooth, with the combination of the very tall, acute protoconid-metacoenid moiety of the trigonid, the lower but distinct and anteriorly projecting paraconid moiety, the steep, flat postvallid, and the labial bulge of enamel beneath the hypoflexid being a unique construction. These characters appear to have been extremely long lived within the *Centetodon* lineage and have persisted with only rela-

tively minor structural changes (ratio of  $P_4/M_1$  size, development of relatively taller, more acute cusps, overall tooth-size changes) from the early Wasatchian through the Chadronian. The occurrence of *C. patratius* is depicted in figure 18.

*Measurements*.—Given below in table 8.

TABLE 8.—*Measurements of teeth of Wasatchian Centetodon*

[Values in millimeters. Leaders (—) indicate no specimen]

Specimen No.	$P_4L$	$P_4W$	$M_1L$	$M_1W$	$M_2L$	$M_2W$
<i>Centetodon patratius</i> , sp. nov.						
UCMP 44954 (type) . . . . .	1.95	1.05	2.00	1.40	1.80	1.25
YPM 23088 . . . . .	...	...	1.91	1.17	1.92	1.25
<i>Centetodon neashami</i> , sp. nov.						
YPM 26626 (type) . . . . .	2.40	1.39	2.52	1.70	...	...
YPM 27011 . . . . .	2.78	1.52	...	...	...	...
YPM 25700 . . . . .	2.20	1.38	2.29	1.60	...	...

*Centetodon neashami*, sp. nov.

Plate 8, figures 4, 5; plate 9, figures 1, 2

*Etymology*.—For J. W. Neasham, in recognition of his contributions to the stratigraphy and sedimentology of the Willwood Formation.

*Holotype*.—YPM 26626, left  $P_4-M_1$  (pl. 8, fig. 4; pl. 9, fig. 2), YPM locality 251, middle part of Willwood Formation (470-m level), late Graybullian, sec. 22, T. 50 N., R. 96 W., Big Horn County, Wyo.

*Hypodigm*.—The type and YPM 27011 (pl. 8, fig. 5); possibly YPM 25700 (pl. 9, fig. 1).

*Distribution*.—Lower middle Gray Bull and upper Gray Bull zones, Willwood Formation, Bighorn Basin, Wyo.

*Diagnosis*.—Largest Eocene species of genus; approximate size of *Centetodon wolffi* (J. A. Lillegraven and M. C. McKenna, unpub. data).  $P_4$  larger with respect to  $M_1$  than in *C. pulcher*, *C. new species B* (mentioned in "*C. patratius*" section), and *C. marginalis*.  $P_4$  with good talonid basin, both basin and cristid obliqua better developed than in *C. pulcher* and all later species, about as in *C. patratius*.  $P_4$  paraconid relatively larger than in *C. pulcher* and with more obliquely oriented (less longitudinal) cristid obliqua than in *C. patratius*.  $P_4$  cusps less acute than in *C. marginalis*, *C. new species B* and *C*, and with more erect trigonid than in either *C. marginalis* or *C. magnus*.  $M_1$  prevallid

more transverse (less oblique) than in *C magnus*.  $P_4$  relatively broader and  $M_1$  trigonid less compressed anteroposteriorly than in *C* new species *C*.

*Discussion.*—*Centetodon neashami* is closest in its known morphology to Graybullian *C. patratius* and might be included in that species were it not for the profound discrepancy in size (*C. neashami* is 13–42 percent larger in  $P_4$ , 15–26 percent larger in  $M_1$ ). The type specimen and YPM 27011 are the largest specimens, and YPM 27500 is approximately intermediate in size and stratigraphic position between the types of *C. patratius* and *C. neashami*. If YPM 27500 were eliminated from the hypodigm of *C. neashami* (its referral is provisional), the size discrepancy is even more marked (23–42 percent for  $P_4$ , 20–26 percent for  $M_1$ ). Both the type of *C. neashami* and YPM 27011 are from relatively high levels of the Willwood Formation (470-m level and indeterminate upper Gray Bull zone level, respectively); whereas, YPM 23088 (*C. patratius*) is from considerably lower (140-m level), and YPM locality 290N (provenance of YPM 25700) is almost certainly intermediate (indeterminate level, probably in lower part of middle Gray Bull zone).

*Centetodon neashami* is clearly distinct from other samples of Eocene and Oligocene *Centetodon*. Only the unique specimen of Brule Formation (middle Oligocene) *C. wolffi* approaches the new species in size, and the  $P_4$ – $M_1$  morphology of *C. neashami* is, like that of *C. patratius*, more generalized than in known Bridgerian, Uintan, or Chadronian species.

*Measurements.*—Given in table 8.

Family APTERNODONTIDAE (Matthew, 1910) Simpson, 1931

*Parapternodus*, gen. nov.

*Etymology.*—Greek *para*: near, beside; in allusion to similarities to *Apternodus*.

*Type.*—*Parapternodus antiquus*, sp. nov., and only known species.

*Diagnosis.*—Small apternodontid, size of *Oligoryctes cameronensis*.  $M_2$  paracristid and postvallid relatively narrower transversely than in *Oligoryctes* or *Apternodus* and developed about as in  $P_4$  of *Apternodus* and  $M_2$  of “*Eoryctes*” nomen nudum.  $M_2$  trigonid less compressed anteroposteriorly than in *Oligoryctes* and *Apternodus*, developed about as in “*Eoryctes*.” Postvallid oriented transversely on  $M_2$ , not more anterolingually-posterolabially as in latter three forms.  $M_3$  postvallid oriented anterolabially-posterolingually, not transversely as in *Oligoryctes* and *Apternodus*, or more anterolingually-posterolabially as in “*Eoryctes*.”  $M_2$  talonid ex-



panded ventrolabially as in "*Eoryctes*" and in contrast to condition in *Oligoryctes* and *Apternodus*.  $M_{2-3}$  lack precingulids, and  $M_3$  short, apparently without talonid cusp as occurs in *Oligoryctes*, *Apternodus*, and "*Eoryctes*."  $M_{2-3}$  crowns tall and hypertrophied as in *Oligoryctes* and *Apternodus*, not relatively low as in "*Eoryctes*." Prevallid shearing surface (number 2) more extensive than in "*Eoryctes*," less extensive than in *Oligoryctes* or *Apternodus*.

*Parapternodus antiquus*, sp. nov.

Plate 9, figures 3, 4

*Etymology*.—Latin *antiquus*. old; this species is the oldest described member of the Apternodontidae

*Holotype*.—YPM 31169, fragment of left ramus with  $M_{2-3}$  (pl. 9, figs. 3, 4), only known specimen.

*Locality*.—YPM locality 370a (Banjo quarry, equals UW locality V-73016A of Bown, 1979), lower part of Willwood Formation (Sand Creek facies, 70-m level), early Graybullian, sec. 33, T. 47 N., R. 91 W., Washakie County, Wyo.

*Diagnosis*.—Only known species; same as for genus.

*Discussion*.—Most of the significant descriptive characters appear in the diagnosis. The talonid of  $M_3$  is damaged; however, the contour and length of the tooth suggest that the  $M_3$  talonid was relatively short and did not possess a prominent posterobasal cusp. The buccal margin of the  $M_2$  talonid is slightly more expanded posteriorly than in *Apternodus* and *Oligoryctes*; but, as in these genera, the talonid shelf is relatively unbasined and has no distinct cusps.

*Parapternodus*, in addition to *Apternodus* and *Oligoryctes*, is only the third apternodontid to be described; all are from lower Tertiary rocks. Hough (1956) reviewed the then-known apternodontids and recommended the resurrection of Simpson's (1931) family. G. G. Simpson (in McGrew and others, 1959, p. 151), West (1969, p. 88), and West and Atkins (1970, p. 20) have recorded the presence of a fourth, as yet undescribed apternodontid genus from rocks of late Bridgerian age at Tabernacle Butte, Sublette County, Wyo. (for example, AMNH 55689). AMNH 55689, CM 13627 (also from Tabernacle Butte, McKenna and others, 1962), and several other teeth of this animal from the Green River Formation of Utah (Powder Wash locality, early Bridgerian) are being studied by M. C. McKenna (oral commun., 1979). Romer (1966, p. 381) and Novacek (1976, p. 34) have published McKenna's manuscript name for this animal as a nomen nudum (*Eoryctes*). Though *Parapternodus* is considerably older than materials of "*Eoryctes*," the latter animal is much more generalized in the known parts of the dentition.

*Parapternodus* is clearly referable to the Apternodontidae by virtue of its transverse molar trigonids and greatly reduced talonids. The generic ties of the new genus are less clear, but the hypertrophied molars link it more closely to *Oligoryctes* and *Apternodus* than to "*Eoryctes*", a form typified by its relatively short molar trigonids. Although *Parapternodus* is the oldest documented representative of its family (but see Sloan, 1969, fig. 6), the possession of a relatively short  $M_3$  that lacks a talonid cusp is almost certainly derived relative to this tooth in all other apternodontids. The hypertrophied molar trigonids of *Apternodus*, *Parapternodus*, and *Oligoryctes* may be either generalized or derived, depending on whether one favors a palaeoryctid or dormaaliid (or other) antecedent for this family (Van Valen, 1967). The narrow trigonids with small prevallid and postvallid surfaces, the less anteroposteriorly compressed trigonids, and the expanded ventrolabial margin of the  $M_2$  talonid are characters shared by *Parapternodus* and "*Eoryctes*" that are probably generalized with respect to *Oligoryctes* and *Apternodus*.

Aside from the apparently reduced  $M_3$  talonid in *Parapternodus*, this early Wasatchian insectivore appears to be suitably generalized for inclusion in the ancestry of known Oligocene apternodontids. Unfortunately, the ascending ramus of the mandible is unknown for the new genus, and it is uncertain whether or not this insectivore possessed a soricid-like mandible like that in "*Eoryctes*" (AMNH 55689; G. G. Simpson, in McGrew and others, 1959) and *Oligoryctes* (for example, slender jaw with shallow external temporal fossa, deep triangular posterointernal ramal fossa, large angular process, condyle placement and configuration, deep inferior pterygoid fossa), or a more robust, divergently specialized mandible as in *Apternodus*.

*Measurements*.—(mm):  $M_2L=1.15$ ,  $M_2WTri=0.90$ ,  $M_2WTal=0.55$ ,  $M_3L=1.20$  (estimated),  $M_3WTri=0.75$ ,  $M_3WTal=0.30$  (estimated).

Order INSECTIVORA(?), incertae sedis  
Insectivora, gen et sp indeterminate

Plate 9, figure 5

*Referred specimen*.—YPM 30860, fragment of right ramus with  $M_1(?)$  and trigonid of  $M_2(?)$  (pl. 9, fig. 5), YPM locality 355

*Discussion*.—This specimen may be of an unusual insectivore or a microchiropteran; however, these two teeth do not closely resemble molars of any mammal known to us. At first glance, the teeth appear to have been distorted by linguolabial crushing of the trigonids. The trigonid of  $M_1(?)$  has, indeed, been damaged on the labial side. However, examination of the anterior and lingual borders of the tooth and comparison with  $M_2(?)$  indicate that the peculiar mor-

phology probably does not result from postmortem damage. It is also conceivable that the teeth represent the deciduous  $P_{3-4}$  of a dormaaliid-like *Macrocranium*, dormaaliid sp. A, or the erinaceid *Eolestes*. There is, however, no indication of an unerupted permanent dentition on the excavated labial side of the jaw, and the preserved parts of the two teeth are identical—a feature that is unusual in  $dP_{3-4}$  of most primitive mammals.

? $M_{1-2}$  are characterized by extremely narrow trigonids, and ? $M_1$  has a very broad, acute talonid. The paraconid is a large shelf that projects anterolingually from the trigonid, and the protoconid is situated well anterior to the metaconid, resulting in a trigonid basin that is oriented anterolingually-posterolabially. Judging from ? $M_2$ , the metaconid appears to have been considerably taller than the protoconid. The cristid obliqua joins the base of the metaconid, and the labial part of the postcristid is of equal length as the cristid obliqua and is nearly straight, imparting a symmetrical, V-shaped configuration to the talonid. The hypoconid is very low, the hypoconulid is large and medial, and the entoconid is tall, trenchant, and lingually deflected as it is in *Macrocranium* and dormaaliid sp. A.

YPM 30860 was recovered from a locality in the lower part of the middle Gray Bull zone (240-m level)

*Measurements*.—(mm): ? $M_1$ ,  $L = 1.75$ , ? $M_1$ ,  $W_{Tri} = 0.95$ , ? $M_1$ ,  $W_{Tal} = 1.25$ , ? $M_2$ ,  $W_{Tri} = 1.00$ .

#### *Creotarsus lepidus* Matthew and Granger, 1918

*Type specimen*.—AMNH 16169, left ramus with  $P_4$ – $M_2$ , and associated tarsal bones.

*Locality*.—"lower Gray Bull beds, Coon Creek, Garland Road, Big Horn Basin, Wyoming."

*Discussion*.—Originally compared with the Artiodactyla, Creodonta, Condylarthra, and Insectivora by Matthew and Granger (1918), *Creotarsus* remains an animal of enigmatic affinities. Van Valen (1967) placed the genus in the sensu lato Adapisoricidae, along with such morphologically disparate forms as *Litolestes*, *Amphilemur*, *Amphidozotherium*, and *Ictopidium*, but *Creotarsus* does not closely resemble any of the sensu stricto dormaaliids.  $P_4$  is similar to that in the didelphodontine palaeoryctid *Didelphodus*, but the molars are wholly dissimilar.  $P_4$  also resembles that in several condylarths, for example, *Bisonalveus*, but again the molars are different, and are closer to *Palaeosinopa*. It seems likely that *Creotarsus* is most closely related to the Pantolestidae, but its affinities will remain uncertain until better material is available.

## SUMMARY

The lower Eocene Willwood Formation of the Bighorn Basin in northwest Wyoming has the largest and most diverse representation of proteutherian and insectivore mammals in the Western Hemisphere. A new sample of about 330 specimens, collected from several different stratigraphic levels of the Willwood Formation, clarifies evolutionary patterns and variation in these animals when compared with specimens of similar age from elsewhere.

The Willwood fauna (including several new taxa) indicates that the radiation of the lipotyphian insectivores was well underway by Wasatchian time and probably began much earlier. Two groups much better represented in younger rocks, the Apternodontidae and the Geolabididae, were already clearly differentiated by early Eocene time. They are represented by new taxa that record the earliest known occurrences of these families.

The Dormaaliidae, originally described from the Sparnacian of Europe, are abundantly represented in the North American Wasatchian, and North American and European nyctitheriids show several similarities. These similarities indicate that the well-documented Clarkforkian through Wasatchian faunal interchange with Europe also included a variety of small lipotyphlan insectivores. Stratigraphic ranges of some of these animals in the Willwood Formation suggest that proteutherians and insectivores have potential value as guide fossils when they are better known. Figure 18 on page 48 depicts the known stratigraphic ranges of Willwood proteutherians and insectivores with reference to the biostratigraphic zones discussed in the text and illustrated in figure 1. The proteutherians and insectivores now known from the Willwood Formation are summarized as follows:

## Order Proteutheria

## Family Palaeoryctidae

## Subfamily Palaeoryctinae

*Palaeoryctes* spcf *Pararyctes* sp

## Subfamily Didelphodontinae

*Didelphodus absarokae*

## Family Leptictidae

## Subfamily Leptictinae

*Prodiacodon tauricinerei**Prodiacodon* sp*Palaeictops bicuspis*

## 72 PROTEUTHERIA AND INSECTIVORA, WILLWOOD FORMATION, WYO

### Family Pantolestidae

*Palaeosinopa incerta*, sp nov

*Palaeosinopa veterrima*

*Palaeosinopa lutreola*

### Family Apatemyidae

*Apatemys chardini*

*Apatemys bellulus*

*Apatemys kayi*

*Apatemys* sp, cf *A rodens*

## Order Insectivora (=Lipotyphla, as used here)

### Suborder Erinaceomorpha

#### Family Dormaalidae

*Macrocranion nitens*

*Scenopagus hewettensis*, sp nov

*Scenopagus* sp

*Talpavoides dartoni*, gen et sp nov

*dormaalud*, sp A

#### Family Erinaceidae

*Eolestes simpsoni*, gen nov

*Leipsanolestes siegfriedti*<sup>3</sup>

cf *Leipsanolestes* sp

cf "*Leptacodon*" *jepseni* New genus of M J Novacek, T M Bown, and David Schankler, unpub data, 1981)

### Suborder Soricomorpha

#### Superfamily Sorcoidea

##### Family Nyctitheriidae

*Pontifactor* sp

*Plagioctenodon krausae*

*Plagioctenodon savagei*, sp nov

*Plagioctenoides microlestes*

cf *Leptacodon packi*,<sup>4</sup>

#### Family Geolabididae

*Centetodon patratius*, sp nov

*Centetodon neashami*, sp nov

#### Family Apternodontidae

*Parapternodus antiquus*, gen et sp nov

## Order Insectivora, incertae sedis

?*Insectivora*, gen et sp indeterminate

*Creotarsus lepidus*

<sup>3</sup>Discussed by Rose (1981) See also Bown (1979, p 60)

<sup>4</sup>Discussed by Rose (1981)

# REFERENCES CITED

- Bown, T M , 1975, Paleocene and lower Eocene rocks in the Sand Creek-No Water Creek area, Washakie County, Wyoming Wyoming Geological Association, 27th Annual Field Conference, Guidebook, p 55-61
- \_\_\_\_\_, 1979, Geology and mammalian paleontology of the Sand Creek facies, lower Willwood Formation (lower Eocene), Washakie County, Wyoming Wyoming Geological Survey Memoir 2, 151 p
- \_\_\_\_\_, 1980, The Willwood Formation (lower Eocene) of the southern Bighorn Basin, Wyoming, and its mammalian fauna. Michigan University Papers on Paleontology, no 24, p 127-138
- \_\_\_\_\_, 1982, Geology, paleontology, and correlation of Eocene volcanoclastic rocks, southeast Absaroka Range, Hot Springs County, Wyoming US Geological Survey Professional Paper 1201-A, 75 p
- Cope, E D , 1880, Geology and paleontology American Naturalist, v 14, p 745-748
- \_\_\_\_\_, 1881, The temporary dentition of a new creodont American Naturalist, v 15, p 667-669
- \_\_\_\_\_, 1882, Notes on Eocene Mammalia. American Naturalist, v 16, p 522
- Crochet, J -Y , 1974, Les insectivores des Phosphorites du Quercy Palaeovertebrata, Montpellier, v 6, no 1-2, p 109-159 (Includes English and German summaries )
- Delson, Eric, 1971, Fossil mammals of the early Wasatchian Powder River local fauna, Eocene of northeast Wyoming American Museum of Natural History Bulletin, v 146, p 309-364
- Filhol, H , 1877, Considération sur la découverte de quelques mammifères fossiles appartenant à l'Eocène supérieur Societe Philosophique de Paris Bulletin, v 1, p 51-54
- Gazin, C L , 1959, Early Tertiary *Apheliscus* and *Phenacodaptes* as pantolestid insectivores Smithsonian Miscellaneous Collection, v 139, no 7, p 1-7
- \_\_\_\_\_, 1962, A further study of the lower Eocene mammalian faunas of southwestern Wyoming Smithsonian Miscellaneous Collection, v 144, no 1, 98 p
- Gingerich, P D , 1974a, Stratigraphic record of early Eocene *Hyopsodus* and the geometry of mammalian phylogeny Nature, v 248, no 5444, p 107-109
- \_\_\_\_\_, 1974b, Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species Journal of Paleontology, v 48, no 5, p 895-903
- \_\_\_\_\_, 1976, Paleontology and phylogeny—patterns of evolution at the species level in Early Tertiary mammals American Journal of Science, v 276, no 1, p 1-28
- \_\_\_\_\_, 1977, Patterns of evolution in the mammalian fossil record, in A H Hallam, ed , Patterns of evolution Amsterdam, Elsevier, p 469-500
- Gingerich, P D , and Rose, K D , 1977, Preliminary report on the American Clark Fork mammal fauna, and its correlation with similar faunas in Europe and Asia Geobios—Paléontologie, Stratigraphie, Paléoecologie Mémoir Spécial 1, p 39-45
- Gingerich, P D , and Simons, E L , 1977, Systematics, phylogeny, and evolution of early Eocene Adapidae (Mammalia, Primates) in North America. Michigan University, Contributions from the Museum of Paleontology, v 24, p 245-279
- Guthrie, D A , 1967a, The mammalian fauna of the Lysite Member, Wind River Formation (early Eocene) of Wyoming Southern California Academy of Science Memoirs, v 5, 53 p
- \_\_\_\_\_, 1967b, *Paenoprolimnocyon*, a new genus of early Eocene limnocyonid (Mammalia, Creodonts) Journal of Paleontology, v 41, no 5, p 1285-1287
- \_\_\_\_\_, 1971, The mammalian fauna of the Lost Cabin Member, Wind River Formation (lower Eocene) of Wyoming Carnegie Museum Annals, v 43, no 4, p 47-113

- Hough, M J , 1956, A new insectivore from the Oligocene of the Wind River Basin, Wyoming, with notes on the taxonomy of the Oligocene Tenrecoidea. *Journal of Paleontology*, v 30, no 3, p 531-541
- Jepsen, G L , 1930a, New vertebrate fossils from the lower Eocene of the Bighorn Basin, Wyoming American Philosophical Society Proceedings, v 69, no 4, p 117-131
- 1930b, Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming American Philosophical Society Proceedings, v 69, no 7, p 463-528
- 1940, Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming, Part 1 American Philosophical Society Proceedings, v 83, no 2, p 217-340
- Krishtalka, L B , 1975, Systematics and relationships of Early Tertiary Lipotyphla (Mammalia, Insectivora) of North America. Lubbock, Texas Tech University, Ph D thesis, 121 p
- 1976a, Early Tertiary Adapisonicidae and Erinaceidae (Mammalia, Insectivora) of North America. *Carnegie Museum Bulletin*, no 1, 40 p
- 1976b, North American Nyctitheriidae (Mammalia, Insectivora) *Carnegie Museum Annals*, v 46, p 7-28
- Krishtalka, L B , and Setoguchi, Takeshi, 1977, Paleontology and geology of the Badwater Creek area, central Wyoming, part 13 The late Eocene Insectivora and Dermoptera. *Carnegie Museum Annals*, v 46, p 71-99
- Krishtalka, L B , and West, R M , 1977, Paleontology and geology of the Bridger Formation, southern Green River Basin, southwestern Wyoming Part 2, The Bridgerian insectivore *Entomolestes grangeri* Milwaukee Public Museum Contributions in Biology and Geology, no 14, 11 p
- McGrew, P O , Berman, J E , Hecht, M K , Hummell, J M , Simpson, G G , and Wood, A E , 1959, The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming American Museum of Natural History Bulletin, v 117, art 3, p 117-176
- McKenna, M C , 1960a, Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene, of northwest Colorado California University Publications in Geological Sciences, v 37, no 1, 130 p
- 1960b, The Geolabidinae—A new subfamily of Early Cenozoic erinaceoid insectivores California University Publications in Geological Sciences, v 37, no 2, p 131-164
- 1963, Primitive Paleocene and Eocene Apatemyidae (Mammalia, Insectivora) and the primate-insectivore boundary American Museum Novitates, no 2160, 39 p
- McKenna, M C , Robinson, Peter, and Taylor, D W , 1962, Notes on Eocene Mammalia and Mollusca from Tabernacle Butte, Wyoming American Museum Novitates, no 2102, 33 p
- McKenna, M C , and Simpson, G G , 1959, A new insectivore from the middle Eocene of Tabernacle Butte, Wyoming American Museum Novitates, no 1952, 12 p
- Marsh, O C , 1872, Preliminary description of new Tertiary mammals American Journal of Science, v 4, ser 3, p 122-128, 202-224
- Matthew, W D , 1901, Additional observations on the Creodonta. American Museum of Natural History Bulletin, v 14, p 1-38
- 1910, On the skull of *Apternodus* and the skeleton of a new artiodactyl [*Eotylopus reedi*] American Museum of Natural History, Bulletin 28, p 33-42
- 1918, Part V—Insectivora (continued), Glres, Edentata, in W D Matthew, and Walter Granger, A revision of the lower Eocene Wasatch and Wind River faunas American Museum of Natural History Bulletin, v 38, art 16, p 565-657
- Matthew, W D , and Granger, Walter, 1921, New genera of Paleocene mammals American Museum Novitates, no 13, 7 p

- Neasham, J W , and Vondra, C F , 1972, Stratigraphy and petrology of the lower Eocene Willwood Formation, Bighorn Basin, Wyoming Geological Society of America Bulletin, v 83, no 7, p 2167-2180
- Novacek, M J , 1976, Insectivora and Proteuthera of the later Eocene (Uintan) of San Diego County, California. Los Angeles County Natural History Museum Contributions in Science, no 283, 52 p
- 1977, A review of Paleocene and Eocene Leptictidae (Eutheria. Mammalia) from North America. Paleobios, no 24, 42 p
- Patterson, Bryan, and McGrew, P O , 1937, A soricid and two erinaceids from the White River Oligocene Field Museum of Natural History Publication 401, Geological Series, v 6, no 18, p 245-272
- Pulbeam, D R , and Vasnys, J R , 1975, Hypothesis testing in paleoanthropology, in R H Tuttle, ed , Paleoanthropology, morphology, and paleoecology Paris, Mouton, p 3-14
- Quinet, G E , 1964, Morphologie dentaire des mammifères éocènes de Dormaal Groupement Internationale pour la Recherche Scientifique en Stomatologie, v 7, p 272-294
- Rich, T H V , and Rasmussen, D L , 1973, New North American Erinaceine hedgehogs (Mammalia. Insectivora) Kansas University Museum of Natural History Occasional Papers, no 21, 54 p
- Rich, T H V , and Rich, P V , 1971, *Brachyerix*, a Miocene hedgehog from western North America, with a description of the tympanic regions of *Paraechinus* and *Podogymnura* American Museum Novitates, no 2477, 58 p
- Robinson, Peter, 1966, Fossil Mammalia of the Huerfano Formation, Eocene, of Colorado Peabody Museum of Natural History (Yale) Bulletin 21, 95 p
- Romer, A S , 1966, Vertebrate paleontology (3rd ed ) Chicago, University of Chicago Press, 468 p
- Rose, K D , 1978, Clarkforkian mammal fauna of the northern Bighorn Basin, Wyoming Geological Society of America Abstracts with Programs, v 10, no 6, p 283
- 1981, The Clarkforkian land-mammal "age" and mammalian faunal composition across the Paleocene-Eocene boundary Michigan University Museum of Paleontology, Papers on Paleontology, in press
- Russell, D E , 1964, Les Mammifères Paléocènes d'Europe Mémoires Muséum National d'Histoire Naturelle, v 13, (sér C), 324 p
- Russell, D E , Louis, Pierre, and Savage, D E , 1975, Les Adapisoricidae de l'Eocène inférieur de France Réévaluation des formes considérées affines Muséum National d'Histoire Naturelle Bulletin, v 327, p 129-193
- Schankler, David, 1980, Faunal zonation of the Willwood Formation in the central Bighorn Basin, Wyoming Michigan University Papers on Paleontology, no 24, p 99-114
- Sigé, Bernard, 1977, Insectivores primitifs de l'Eocène supérieur et Oligocene inférieur d'Europe occidentale, Nyctithéridés Muséum National d'Histoire Naturelle Mémoires, ser C , v 34, 140 p
- Simpson, G G , 1929, A collection of Paleocene mammals from Bear Creek, Montana. Carnegie Museum Annals, v 19, no 2, p 115-122
- 1931, A new classification of mammals American Museum of Natural History Bulletin, v 59, art 5, p 259-293
- 1935, New Paleocene mammals from the Fort Union of Montana. US National Museum Proceedings, v 83, no 2981, p 221-244
- 1954, An apatemyid from the early Eocene of New Mexico American Museum Novitates, no 1654, 4 p



## 76 PROTEUTHERIA AND INSECTIVORA, WILLWOOD FORMATION, WYO

- Sloan, R E , 1970, Cretaceous and Paleocene terrestrial communities of western North America, *in* Evolution of communities North American Paleontological Convention, Chicago, 1969, Proceedings, pt E, p 427-453
- Stehlin, H G , 1940, Zur Stammesgeschichte der Soriciden *Eclogia Geologica Helvetica*, v 33, p 298-306
- Troxell, E L , 1923, The Apatemyidae *American Journal of Science*, 5th ser , v 5, p 503-506
- Van Houten, F B , 1945, Review of latest Paleocene and early Eocene mammalian faunas *Journal of Paleontology*, v 19, no 5, p 421-461
- Van Valen, Leigh, 1965, A middle Palaeocene primate *Nature*, v 207, no 4995, p 435-436
- \_\_\_\_\_, 1966, Deltatheridia, a new order of mammals *American Museum of Natural History Bulletin*, v 132, art 1, p 1-126
- \_\_\_\_\_, 1967, New Paleocene insectivores and insectivore classification *American Museum of Natural History Bulletin*, v 135, art 5, p 219-284
- Weitzel, Karl, 1949, Neue Wirbeltiere (Rodentia, Insectivora, Testudinata) aus dem Mitteleozan von Messel bei Darmstadt *Senckenbergische Naturforschende Gesellschaft Abhandlungen*, no 480, 24 p
- West, R M , 1969, Geology and vertebrate paleontology of the northeastern Green River Basin, Wyoming, *in* Symposium on Tertiary rocks of Wyoming Wyoming Geological Association, 21st Annual Field Conference, Guidebook, p 77-92
- \_\_\_\_\_, 1973, Review of North American Eocene and Oligocene Apatemyidae (Mammalia, Insectivora) *Texas Tech University Museum Special Publication* 3, 42 p
- \_\_\_\_\_, 1974, New North American middle Eocene nyctitheres (Mammalia, Insectivora) *Journal of Paleontology*, v 48, no 5, p 983-987
- West, R M , and Atkins, E G , 1970, Additional middle Eocene (Bridgerian) mammals from Tabernacle Butte, Wyoming *American Museum Novitates*, no 2404, 26 p
- Wood, H E , 2nd, Chaney, R W , Clark, John, Colbert, E H , Jepsen, G L , Reeside, J B , Jr , and Stock, Chester, 1941, Nomenclature and correlation of the North American continental Tertiary *Geological Society of America Bulletin*, v 52, no 1, p 1-48

	E
early Graybullian	4, 46, 47, 49, 50, 52, 54
Elk Creek section	4, 6, 29, 38, 39, 49, 52
<i>Entomolestes</i>	53
<i>grangeri</i>	54, 55, 56, 60, pl 7
<i>nitens</i>	45
<i>Eolestes</i> , gen nov	52, 55, 70
<i>simpsoni</i>	53, 54, 72, pls 6, 7
" <i>Eoryctes</i> "	67, 68
Ernaceidae	52, 55, 72
Ernaceomorpha	41, 51, 72

	F, G	Page		Page
Fort Union Formation		45	lower Gray Bull zone	4, 7, 21, 27, 29, 37, 46, 49, 52, 54, 55, 61, 67, 68, 70
Four Mile fauna	2, 16, 21, 22, 30, 37, 38, 39, 45, 46, 49, 56, 64		Ludian age	64
Garland Road		70	<i>lutreola</i> , <i>Palaeosinopa</i>	20, 21, 29, 30, 72, pl 3
Geolabididae	64, 71, 72		Lysite Member, Wind River Formation	7, 16, 45, 46
Gidley Quarry		63	Lysite biostratigraphic zone	4, 7, 11, 16, 19, 27, 39, 46
Graybullian age	2, 3, 29		"Lysite equivalent"	3
"Gray Bull Member"		3	Lysitan age	2
Gray Bull zone		16		
See also lower, middle, and upper Gray Bull zone			M	
Green River Basin		20	<i>Macrocranion</i>	44, 51, 52, 53, 58, 70
Green River Formation		51, 68	<i>nitens</i>	41, 44, 45, 72, pls 5, 6
			<i>tenerum</i>	45
H			Mammala	6
<i>Heptodon</i>		3	<i>Mckennatherrum</i>	41, 43, 57, 58
Hewett, Donnel Foster		46	<i>ladae</i>	41, 43
<i>hewettensis</i> , <i>Scenopagus</i>	46, 72		<i>libitum</i>	42
History		2	<i>Messelina</i>	45
<i>Homogalax</i>		3	Microchropteran	69
<i>prolapirinus</i>		3	middle Gray Bull zone	4, 7, 16, 19, 21, 27, 29, 38, 39, 46, 49, 52, 66, 70
Huerfano Formation	30, 35, 51, 65			
			N	
I, J, K			Neasham, J W	66
<i>Ictopidium</i>		70	<i>neashami</i> , <i>Centetodon</i>	65, 66, 72, pls 8, 9
<i>incerta</i> , <i>Palaeosinopa</i>	20, 72, pls 3, 10		<i>nitens</i> , <i>Macrocranion</i>	41, 44, 45, 72, pls 5, 6
Insectivora	2, 5, 41, 57, 69, 70, 72		No Water Creek area	46
Insectivora, gen et sp indeterminate		69	No Water fauna	2, 29, 37, 38, 39, 60
<i>jepseni</i> , "Leptacodon"	53, 55, 57, 60, 72, pl 7		Nyctitheridae	57, 60, 71, 72
<i>kayn</i> , <i>Apatemys</i>	37, 39, 72, pl 4		<i>Nyctitherium</i>	58, 61
<i>krausae</i> , <i>Plagioctenodon</i>	56, 59, 60, 64, 72		<i>celatum</i>	59
			<i>serotinum</i>	58
			<i>velox</i>	58, 63, pl 8
L			O, P	
La Barge fauna	16, 20, 39		<i>Ohgoryctes</i>	68
<i>Lambdaotherium</i>		2, 3	<i>cameronensis</i>	67
Largo fauna		39	<i>Palaeictops</i>	10
late Graybullian fauna		4	<i>bicusps</i>	10, 11, 16, 17, 19, 71, pl 2
<i>Leipsanolestes</i>		53	<i>bridgeri</i>	20
<i>sieffriedti</i>	54, 72		<i>matthewi</i>	11
<i>simpsoni</i>	2, 54		<i>multicusps</i>	10
sp	55, 72		<i>pinneyensis</i>	16
<i>lepidus</i> , <i>Creotarsus</i>	70, 72		"pinneyensis"	20
<i>Leptacodon</i>	58, 61		sp, characteristics	10
<i>munusculum</i>		61	<i>Palaeoryctes</i> sp	6, 71
<i>packi</i>		72	Palaeoryctidae	6, 71
<i>tener</i>	56, 58, 61, 62, 63, 64		Palaeoryctinae	6, 71
"Leptacodon" <i>jepseni</i>	53, 55, 57, 60, 72, pl 7		<i>Palaeosinopa</i>	70
<i>ladae</i>		42	<i>didelphoides</i>	20, 21, 25, 28
<i>munusculum</i>	58, 63		<i>incerta</i> , sp nov	20, 72, pls 3, 10
<i>packi</i>	58, 63		<i>lutreola</i>	20, 21, 29, 30, 72, pl 3
Leptictidae	10, 71		<i>veterrima</i>	21, 26, 72, pls 3, 4
<i>Lipotyphla</i>		72	sp	20
<i>Litolestes</i>	44, 53, 55, 70		sp E	21, 22
<i>ignotus</i>		44	Pantolestidae	20, 70, 72
Lost Cabin Member	7, 19, 21, 39, 45		<i>Papio anubis</i>	35
"Lost Cabin equivalent"		3	<i>Parapternodus</i> , gen nov	67
Lost Cabin biostratigraphic zone		4, 39	<i>antiquus</i> , sp nov	67, 68, 72, pl 9
Lostcabinian age	2, 4, 18, 37		<i>Pararyctes</i> sp	6, 71

## 79

R. S

**T**

**U, V**

W. Y



---

---

## PLATES 1-10

Contact photographs of the plates in this report are available at cost, from the U S  
Geological Survey Photographic Library, Federal Center, Denver, Colorado 80225

---

---

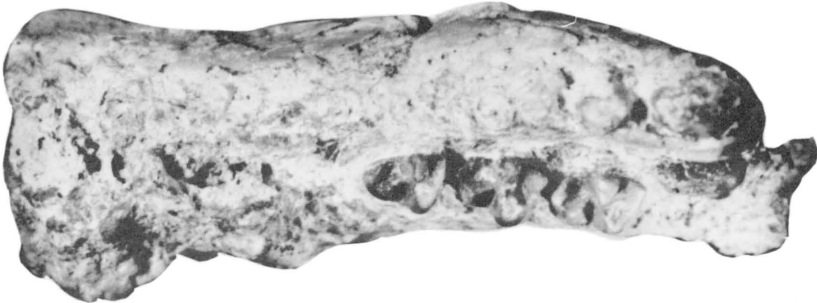
## PLATE 1

FIGURES 1, 2. *Didelphodus absarokae* (Cope, 1881) (p. 6.)

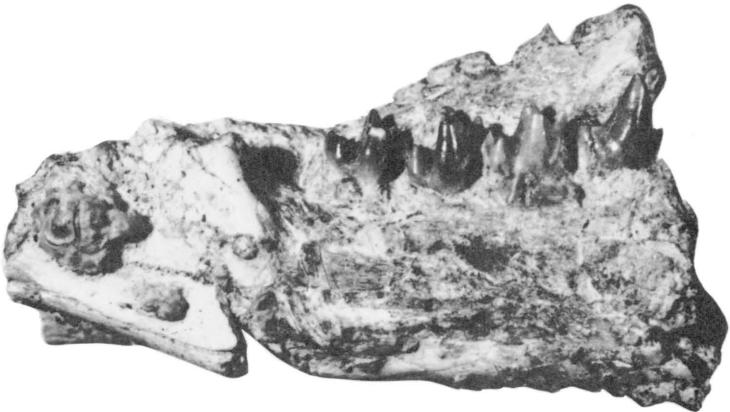
Right P<sub>4</sub>-M<sub>3</sub>, USGS 303, × 4.2. Both views are  
stereophotographs

1 Occlusal view.

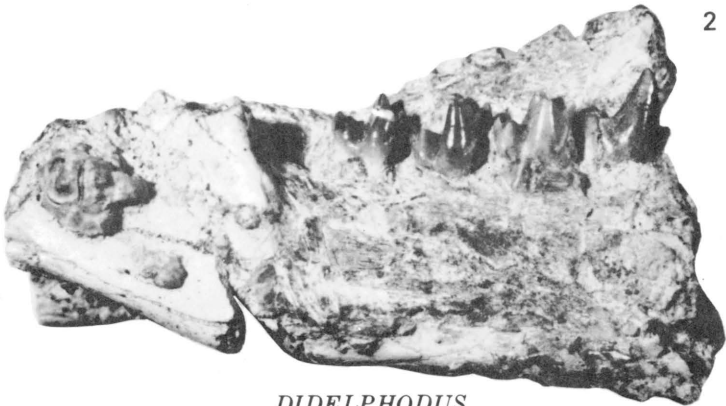
2. Labial view.



1



2



*DIDELPHODUS*



## PLATE 2

### FIGURES 1-7. Proteutherians from the Willwood Formation.

1, 2, 4. *Didelphodus absarokae*. (Cope, 1881) (p. 6.)

1. Labial aspect of YPM 18971, right  $M_{1-2}$ ,  
 $\times 2.2$ .

2. Occlusal view of YPM 25361, left  $P^4-M^1$ ,  
 $\times 3$  1. Stereophotograph.

4. Occlusal view of YPM 18971, right  $M_{1-2}$ ,  
 $\times 3.6$ .

3, 5. *Palaeictops bicuspis* (Cope, 1880) (p. 19.)

3. Occlusal view of YPM 23723, left  $P^{4-5}$ ,  
 $M^{1-3}$ ,  $\times 3.0$ . Stereophotograph.

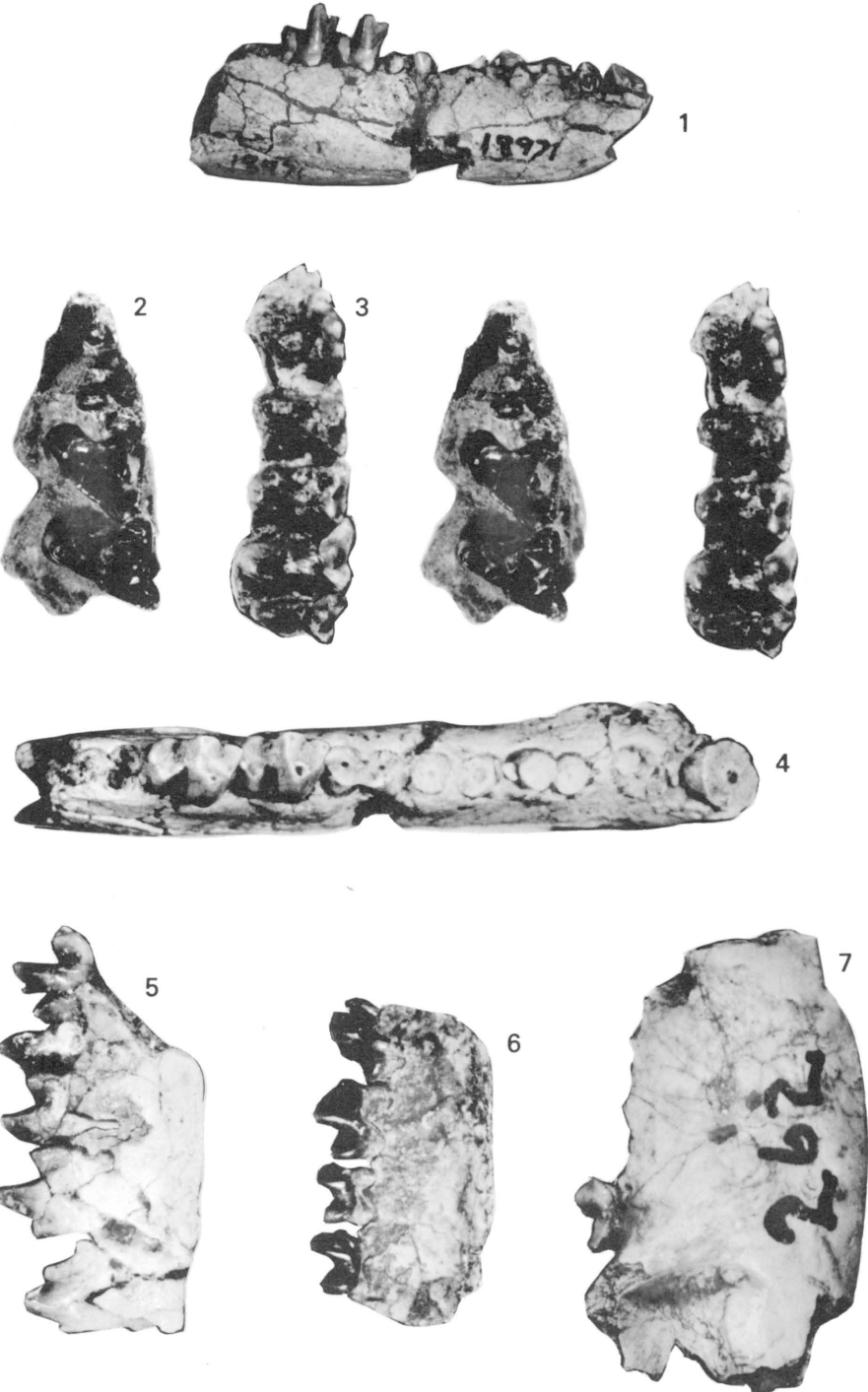
5. Labial view of YPM 23723, left  $P_{4-5}$ ,  
 $M_{1-3}$ ,  $\times 3.5$ .

6. *Prodiacodon* sp. (p. 18.)

Labial aspect of YPM 26040, right  $P_{4-5}$ ,  
 $M_{1-2}$ ,  $\times 3.4$ .

7. *Apatemys* sp., cf *A. rodens* Troxell, 1923  
(p 40 )

Labial view of YPM 30582, right ramus  
with /C and  $M_3$ ,  $\times 3.6$ .



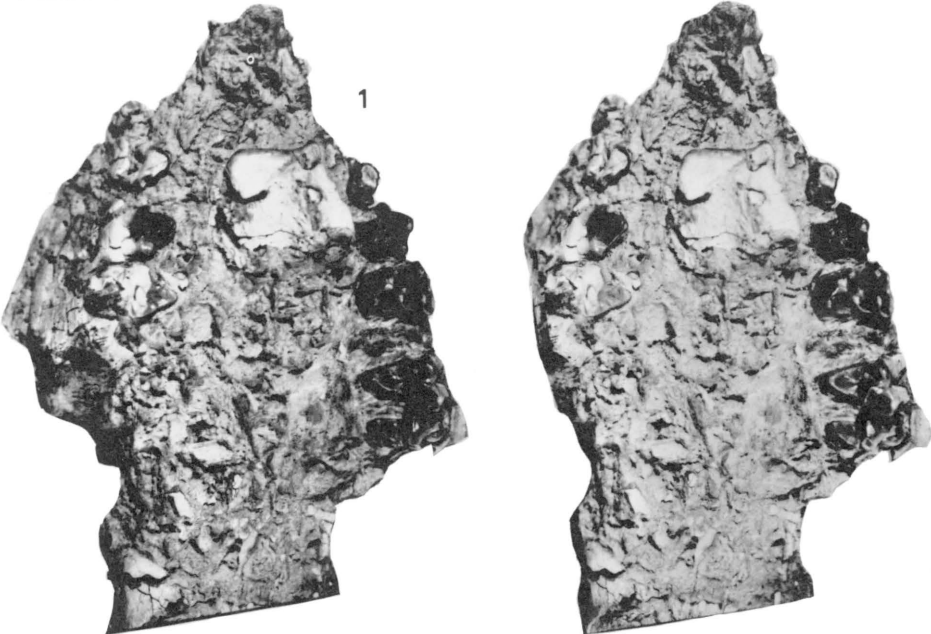
*DIDELPHODUS, PALAEICTOPS, PRODIACODON, AND APATEMYS*

## PLATE 3

### FIGURES 1-4. *Palaeosinopa*

#### Early Eocene

1. *P. veterrima* Matthew, 1901 (p. 26.)  
Occlusal aspect of YPM 27168, right  $P^3$ - $M^2$  and left  $P^3$ - $M^3$ ,  $\times 1.6$ , lower jaws unfigured. Stereophotograph
2. *P. lutreola* Matthew, 1918 (p. 29.)  
Occlusal view of YPM 26175, right  $M_1$  (damaged),  $M_{2-3}$ ,  $\times 4.8$ . Stereophotograph
- 3, 4. *P. incerta*, sp. nov. (p. 20.)
  3. Occlusal aspect of YPM 30613, right  $M^{2-3}$ ,  $\times 3.2$ . Stereophotograph
  4. Labial aspect of AMNH 39565, left  $M_{1-3}$ ,  $\times 2.7$ . Other broken teeth are unfigured.



*PALAEOSINOPA*

## PLATE 4

FIGURES 1, 2. *Palaeosinopa veterrima* Matthew, 1901 (p. 26.)

From the Willwood Formation. Stereophotographs.

1. Occlusal aspect of YPM 26674, right  $M_{1-3}$ ,  
 $\times 19$ .
2. Occlusal view of YPM 34255, right  $M_{1-3}$ ,  
 $\times 16$ .

3-6. *Apatemys*

From the Willwood Formation. Stereophotographs.

3, 6. *A. chardini* (Jepsen, 1930a) (p. 38.)

3. Occlusal aspect of UMMP 66686,  
right  $M^{2-3}$ ,  $\times 6.4$ .

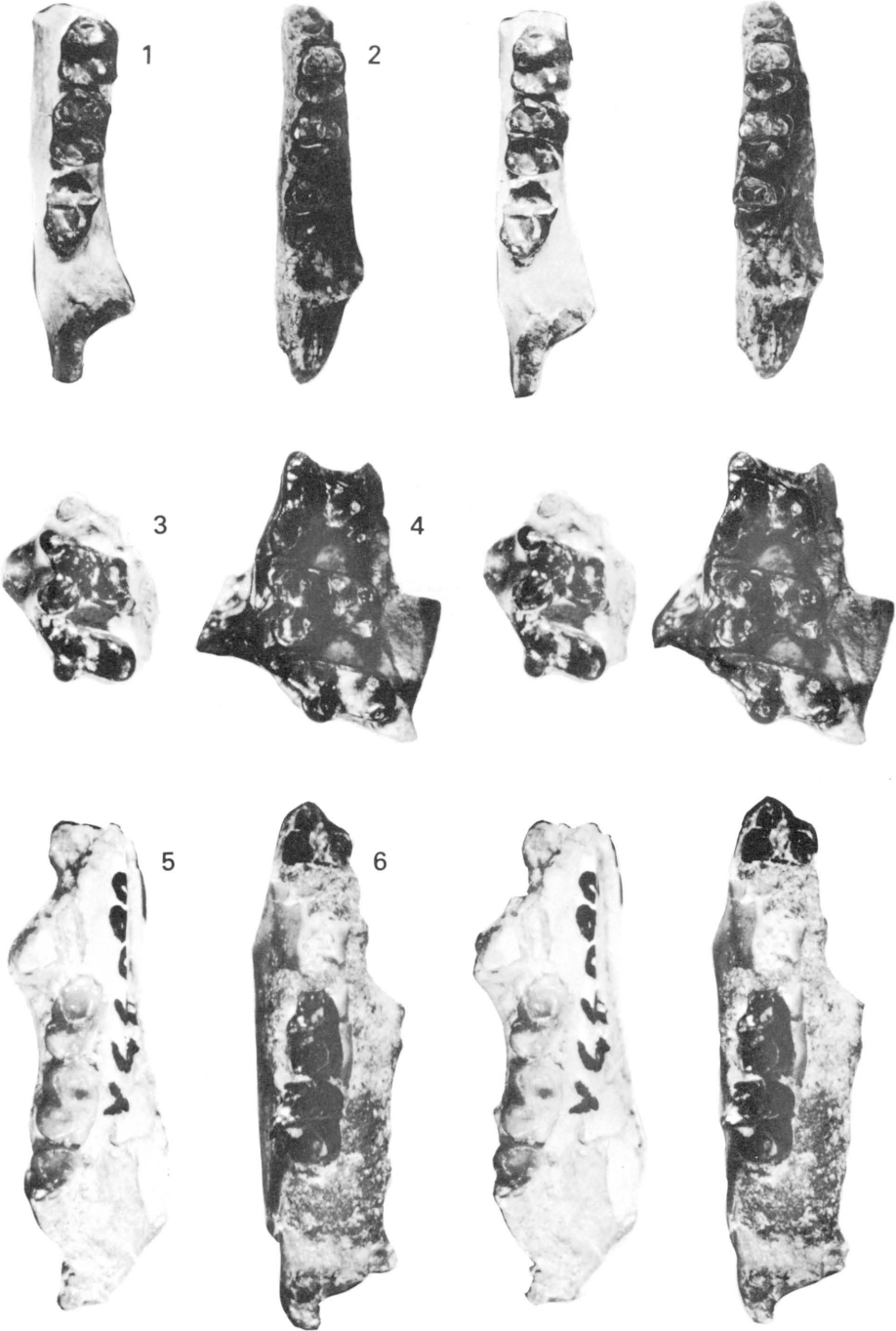
6. Occlusal aspect of UMMP 67380,  
right  $M_{1-2}$ ,  $\times 6.3$ .

4. *A. kayi* (Simpson, 1929) (p. 38.)

Occlusal aspect of UMMP 68591, right  
 $M^{1-3}$ ,  $\times 6.4$ .

5. *A. bellulus* Marsh, 1872 (p. 38.)

Occlusal aspect of UMMP 66092, left  
 $M_{1-3}$ ,  $\times 6.3$ .



*PALAEOSINOPA AND APATEMYS*

## PLATE 5

FIGURES 1-5. *Macrocranium nitens* (Matthew, 1918) (p. 45 )

From the Willwood Formation

1. Occlusal aspect of YPM 23077, right  $P^4-M^2$ ,  
× 10.0 Stereophotograph.
2. Occlusal aspect of YPM 24380, right  $P_3-M_2$ ,  
× 10.0. Stereophotograph
3. Occlusal view of YPM 30655, left  $P_4-M_3$ ,  
× 6.8 Stereophotograph
4. Occlusal view of YPM 30655, left  $P^4-M^2$ ,  
× 6.3. Stereophotograph
5. Labial view of YPM 24380, right  $P_3-M_2$ ,  
× 10.0



*MACROCRANION*



## PLATE 6

FIGURES 1, 2 *Macrocranium nitens* (p. 45.)

1. Labial aspect of YPM 30655, left  $P_4-M_3$ ,  $\times 7.7$

2. Occlusal view of YPM 30597, right  $P^4-M^1$ ,  $\times 12.3$ .  
Stereophotograph.

3, 4 *Talpavoides dartoni*, gen. et sp. nov. (p. 50)

Stereophotographs

3. Occlusal aspect of UW 9597, right  $M_{2-3}$ ,  
 $\times 13.0$ .

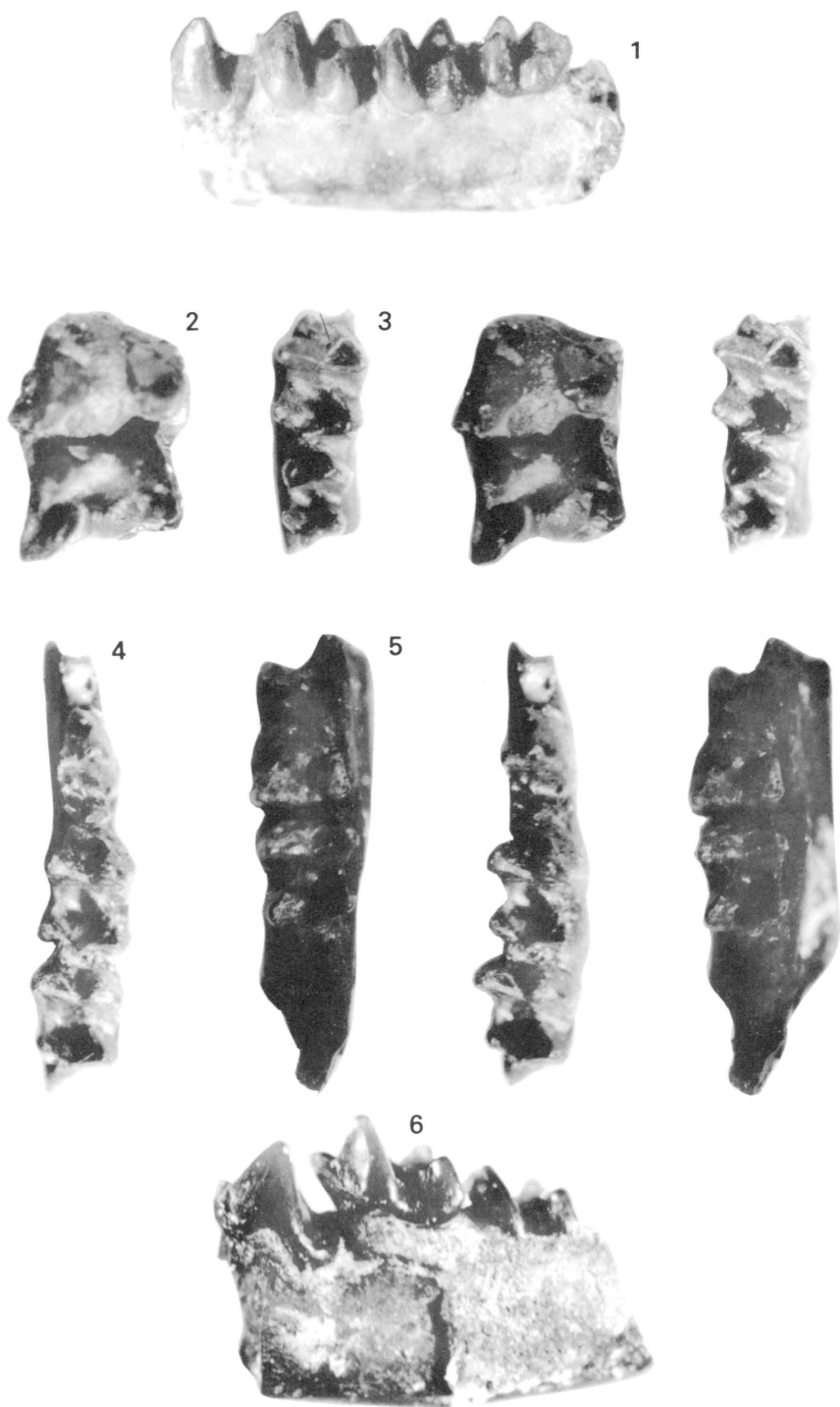
4. Occlusal aspect of UW 9624 (type specimen),  
right  $P_4-M_2$ ,  $\times 14.5$ .

5. *Dormaalid*, sp. A (p. 52.)

Occlusal aspect of UW 9627, left  $M_2$  (damaged),  
 $M_3$ ,  $\times 14.3$

6 *Eolestes simpsoni*, gen. nov. (Bown, 1979) (p. 54)

Labial view of YPM 35156, left  $P_4-M_2$ ,  $\times 13.5$

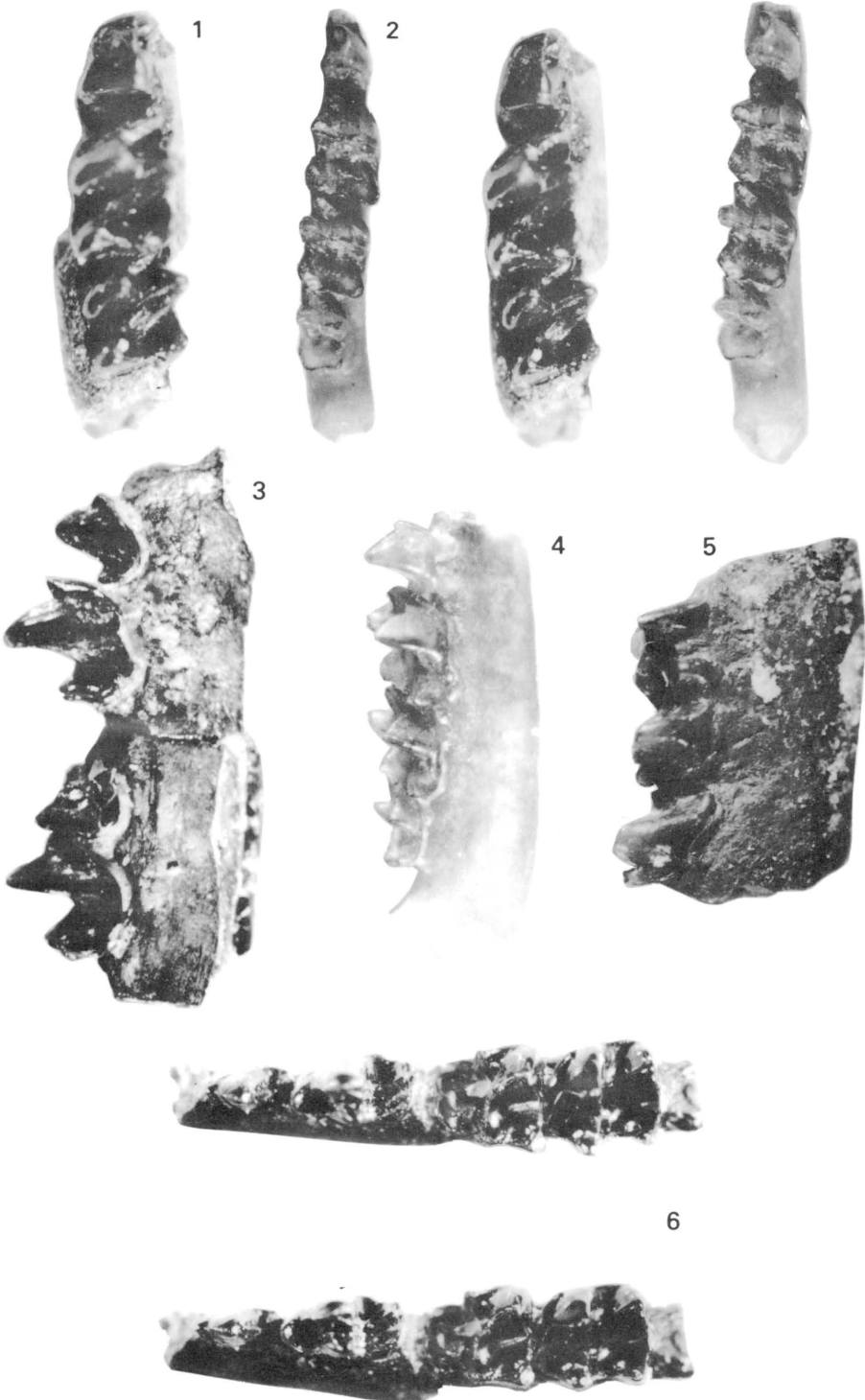


*MACROCRANION, TALPAVOIDES, DORMAALIID, AND EOlestES*

## PLATE 7

[All from the Eocene of Wyoming]

- FIGURE      1. *Eolestes simpsoni*, gen. nov (Bown, 1979) (p. 54.)  
                    Occlusal aspect of YPM 35156, left  $P_4-M_2$ ,  $\times 12.5$ .  
                    Stereophotograph.
- 2, 4. *Entomolestes grangeri* (p. 56.)  
                    2. Occlusal aspect of AMNH 98742,  $P_4-M_3$ ,  $\times 9.6$ .  
                    Stereophotograph.  
                    4. Labial view of AMNH 98742, right  $P_4-M_3$ ,  $\times 10.0$ .
- 3, 6. *Plagioctenodon savagei*, sp. nov. (p. 61.)  
                    3 Labial aspect of YPM 34257 (type), right  $P_3-M_2$ ,  
                     $\times 10.4$ .  $M_1$  damaged.  
                    6. Occlusal aspect of YPM 34257 (type),  
                    right  $P_3-M_2$ ,  $\times 9.9$   
                     $M_1$  damaged Stereophotograph.
5. "*Leptacodon*" *jepseni* (p. 55.)  
                    Labial view of YPM 30559, right  $P_4-M_2$ ,  $\times 11.5$



*Eolestes, Entomolestes, PlagiocTENodon, and "Leptacodon"*

## PLATE 8

FIGURES 1,2. *Nyctitherium velox* Marsh, 1872 (p. 63 )

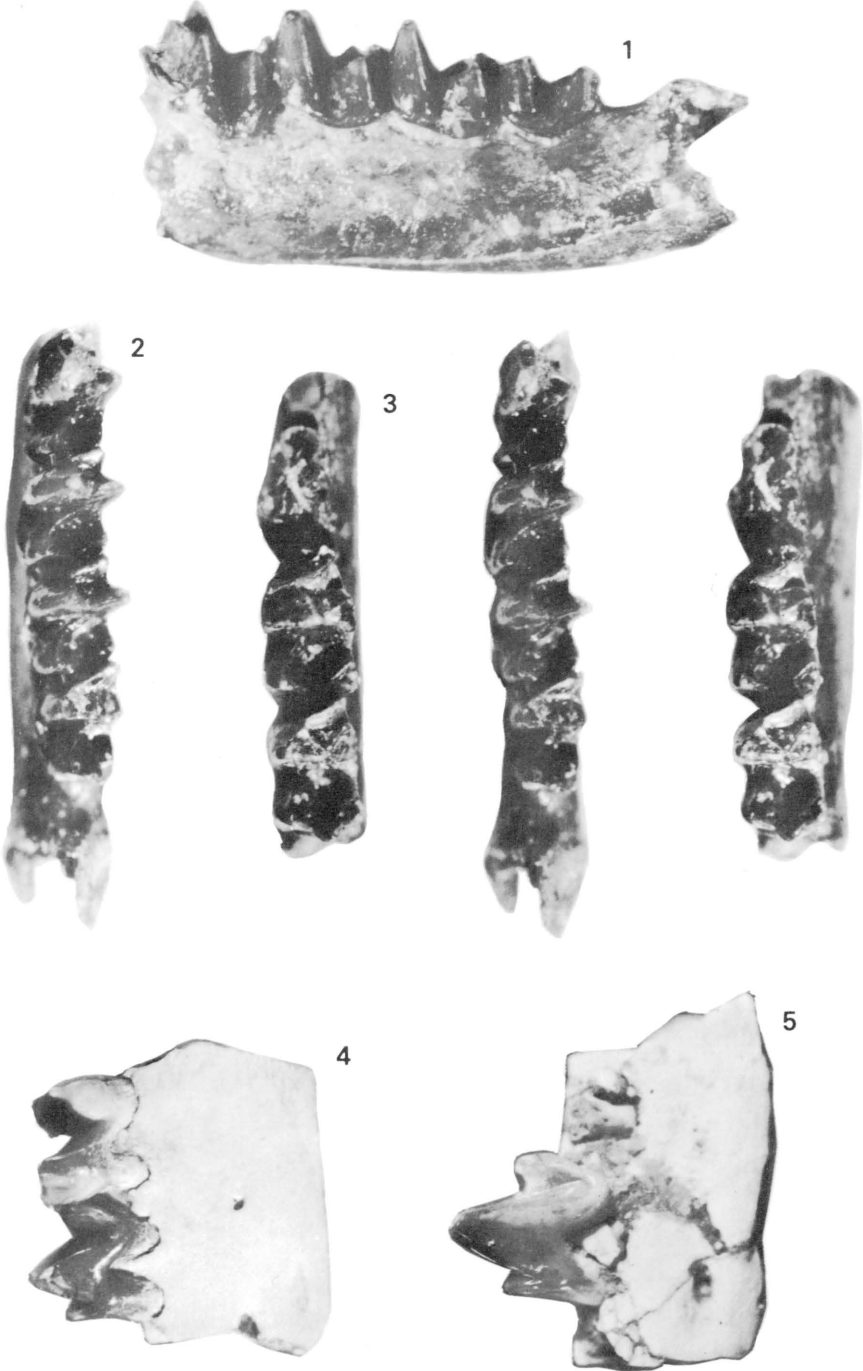
From the middle Eocene of Wyoming.

1. Labial aspect of UW 11386, left  $P_4$ - $M_3$ ,  
 $\times 9.2$ .
2. Occlusal view of UW 11386, left  $P_4$ - $M_3$ ,  
 $\times 9.2$  Stereophotograph.

3-5. *Centetodon*

From the early Eocene of Wyoming.

3. *C. patratius*, sp. nov. (p. 64.)  
Occlusal aspect of YPM 23088, left  $P_4$   
(damaged),  $M_{1-2}$ ,  $\times 8.9$ . Stereophotograph
- 4, 5. *C. neashami*, sp. nov. (p. 66.)
  4. Labial view of YPM 26626 (type), left  
 $P_4$ - $M_1$ ,  $\times 6.4$ .
  5. Labial view of YPM 27011, left  $P_4$ ,  
 $\times 6.8$ .



*NYCTITHERIUM AND CENTETODON*

## PLATE 9

FIGURES 1, 2 *Centetodon neashami*, sp. nov. (p. 66)

From the Willwood Formation

Labial view of YPM 25700, right  $P_4-M_1$ ,  
 $\times 7.7$

2. Occlusal aspect of YPM 26626 (type), left  
 $P_4-M_1$ ,  $\times 6.4$

3, 4. *Parapternodus antiquus*, gen. et sp. nov. (p. 68.)

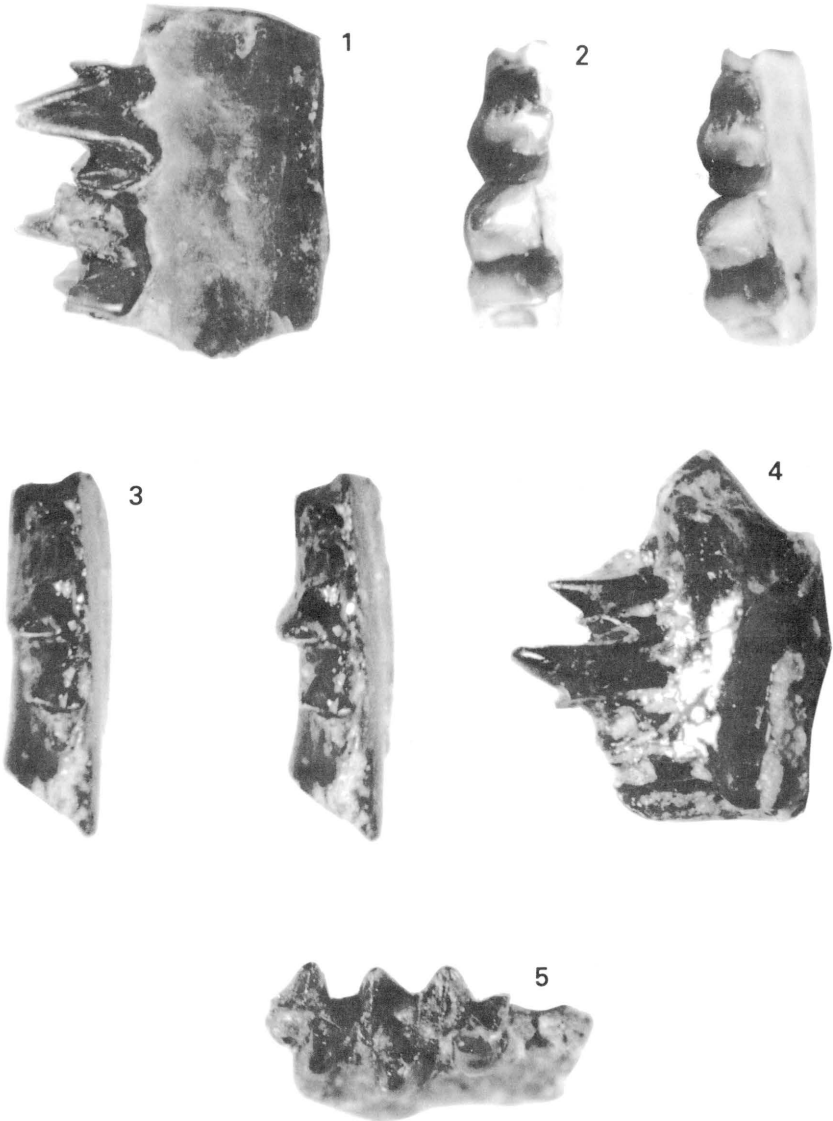
From the Willwood Formation.

3. Occlusal aspect of YPM 31169 (type), left  
 $M_{2-3}$ ,  $\times 10.7$ . Stereophotograph

4. Labial view of YPM 31169 (type), left  $M_{2-3}$ ,  
 $\times 10.7$

5. ?*Insectivora*, gen. et sp. indeterminate (p. 69)

Occlusal view of YPM 30860, right ? $M_{1-2}$ ,  $\times 11.6$ .  
From the Willwood Formation



*CENTETODON*, *PARAPTERNODUS*, AND ?INSECTIVORE



## PLATE 10

[Bar is 10.0 mm long]

FIGURES 1, 2. *Palaeosinopa incerta*, sp. nov. (p. 20.)

From the Willwood Formation UMMP 69722, type specimen preserving upper and lower cheek teeth and fragments of the cranium and rostrum. Courtesy of P. D. Gingerich; photograph by K. Steelquist

1. Left aspect.
2. Right aspect.



*PALAEOSINOPA*