

**LATE PALEOCENE MAMMALS OF THE TONGUE  
RIVER FORMATION, WESTERN NORTH DAKOTA**

by

**Richard C. Holtzman**

**REPORT OF INVESTIGATION NO. 65**

**NORTH DAKOTA GEOLOGICAL SURVEY**

**Lee C. Gerhard, State Geologist**

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## AUTHOR'S NOTE

Please note the following spelling changes:

<u>As spelled in text</u>	<u>Correct spelling</u>
Paleoryctidae	Palaeoryctidae
<i>Paleoryctes</i>	<i>Palaeoryctes</i>
<i>Propaleosinopa</i>	<i>Propalaeosinopa</i>
<i>Paleosinopa</i>	<i>Palaeosinopa</i>

## ABSTRACT

*On the eastern flank of the Williston basin, North Dakota, the Tongue River Formation contains assemblages of fossil mammals that are Late Paleocene (Tiffanian) in age. The few fossil mammals previously known from the formation in North Dakota led to the general belief that it was of Middle Paleocene (Torrejonian) age. Reexamination of these early-reported occurrences shows that the evidence provided by each is equivocal. New fossil localities near the towns of Riverdale, Judson, and Brisbane have yielded local faunas that are extensive enough to permit accurate age determinations. The Riverdale locality occurs near the upper contact of the Tongue River Formation. The Judson and Brisbane localities occur just above the basal contact with the underlying marine Cannonball Formation. The fossils accumulated in fluvial sands deposited in a fluvio-deltaic environment.*

*The two major localities, Judson and Brisbane, have yielded 27 and 30 species of mammals, respectively. The application of methods developed by means of a Monte Carlo simulation suggests that approximately 80 percent of the potentially recoverable species are now known from both localities. Multituberculates account for slightly more than 50 percent of the number of preserved individuals in both cases. Primates are equally abundant (about 20 percent) at both localities but are more diverse in the Brisbane local fauna. Insectivores are relatively more common at the Brisbane locality, whereas condylarths are relatively more frequent at Judson.*

*In addition to these differences in frequencies, there are taxonomic differences between the local faunas that cannot be accounted for by sampling error. None of the evidence from fossil pollen, mollusks, or non-mammalian vertebrates points to any particular explanation of the differences. The localities are geographically close to each other, and, as far as can be determined, they have identical stratigraphic positions and depositional environments. The Judson and Brisbane localities are, therefore, valuable indicators of the faunal differences that occur on small spatial and temporal scales within the Tongue River Formation.*

## INTRODUCTION

The Fort Union Group of the Williston basin includes nearly half of the North American exposures of continental Paleocene rocks. Despite its large areal distribution, the mammalian paleontology of these beds has remained poorly known. An early recognized scarcity of mammalian fossils in these beds so thoroughly discouraged collectors that by 1960 only five specimens were known from the Paleocene of North Dakota. Since then several productive fossil localities have been discovered and developed. This is the first detailed account of these mammalian local faunas.

In addition to its intrinsic interest an understanding of the mammalian paleontology of the Fort Union Group is important to the geochronology of the Paleocene Epoch. An almost global absence of radiometrically datable rocks of Paleocene age, coupled with the high rates of

mammalian evolution, make fossil mammals the most precise means of dating continental Paleocene rocks. Because of its great areal extent it is desirable to integrate more fully the mammalian paleontology of the Fort Union Group with the existing geochronologic subdivision of the Paleocene.

This work is divided into two parts. The first summarizes the geology, fossil localities, and the mammalian local faunas, their ages and their paleoecology. The second part consists of the systematic description of the mammalian species collected and a summary of the methods used in their study. Itemized conclusions derived from both parts follow Part II.

North Dakota Geological Survey Report of Investigation 59 revised the nomenclature of the Fort Union Group introducing the terms Slope and Bullion Creek Formations and deleting the term Tongue River Formation. This manuscript was prepared prior to publication of the revisions.



To avoid the possibility of misinterpretation, previous stratigraphic terminology is retained for this report.

The systematic collections referred to here have been abbreviated as follows.

- AMNH American Museum of Natural History
- FMNH Field Museum of Natural History
- MCZ Museum of Comparative Zoology, Harvard University
- SMM Science Museum of Minnesota
- PU Princeton University
- UMVP University of Minnesota, Vertebrate Paleontology
- USNM United States National Museum

## **PART I. GEOLOGY, MAMMALIAN FAUNAS, AND PALEOECOLOGY**

### **Geology**

Western North Dakota occupies the center of the Williston basin, a deep structural basin whose deposits range in age from Paleozoic to Cenozoic. Marginal thinning of all formations in the basin suggests a long history of tectonic subsidence and associated sedimentation. The final phase of basinal deposition is represented by a sequence of predominantly terrestrial lignitic sediments that has long been referred to as the "Great Lignite Group" (e.g., Frye, 1969, p. 3).

The exposed bedrock of western North Dakota consists almost entirely of Late Cretaceous to Early Eocene sediments of the "Great Lignite Group." These terrestrial strata are underlain by Cretaceous marine sediments cropping out in eastern and extreme southwestern North Dakota and are interrupted in the eastern part of the basin by a wedge of Paleocene marine sediments. The sequence is terminated by a widespread erosional unconformity over which Oligocene deposits occur as scattered outliers. No widespread unconformities have been found within the sequence, implying that the terrestrial depositional record for this time interval in North Dakota is relatively complete.

The entire "Lignite Group" will probably yield fossil mammals as collecting continues. In order to provide a geologic context for the present study and for future discoveries, a summary of each of the formations in the sequence is included.

Emphasis is placed on the mammalian paleontology and on those aspects of the geologic history most pertinent to the mammalian paleontology.

The stratigraphic nomenclature employed is the usage of the North Dakota Geological Survey (Ting, 1972, p. 4). Other usages have been placed in quotes. The distribution of the Tongue River Formation and its mammal-bearing fossil localities are shown in figure 1. Figure 2, an east-west cross section of the area, shows the major structural relationships in the basin.

### **Hell Creek Formation**

The Hell Creek beds were first named by Barnum Brown (1907) for exposures in Garfield County, Montana, and are correlated with the Lance Formation of Wyoming. These units were considered by Brown (1914) to be lithologically indistinguishable. Roland Brown (1938) indicated that the Hell Creek beds meet the qualifications of a formation and that they represent the latest of the Mesozoic sediments. The long controversy over the placement of the Mesozoic-Cenozoic boundary in the western interior is reviewed by Roland Brown (1962) and is not recapitulated here. The current and long-standing consensus is in agreement with Brown's 1938 interpretation. The Hell Creek Formation in North Dakota has been studied most recently by Frye (1969), who named seven new members in addition to the marine Breien Member of Laird and Mitchell (1942).

The Hell Creek Formation in North Dakota crops out in the valleys of the Missouri and Little Missouri Rivers. The formation reaches its maximum thickness of about 130 meters near Marmarth, thinning westward toward Glendive, Montana, and eastward toward the Missouri valley, where its thickness is about 65 meters. Frye attributes the lateral thinning to loss of beds from the bottom of the formation. The lower contact with the Fox Hills Formation is shown by Dobbin and Reeside (1924) to be gradational and only locally unconformable. The upper contact, as delineated by Frye, is conformable and is marked by a color change to lighter sediments to the west and by a change to bentonite-free sediments to the east.

Lithologically the Hell Creek Formation consists of lignitic and bentonitic terrigenous clastics ranging in size from clay to medium-grained sand. The sediments are usually gray and various

tinges of gray. True lignites are uncommon. The sandstones are unconsolidated and are often crossbedded. The formation on the whole is less well bedded than the overlying Ludlow Formation.

The Hell Creek Formation consists of delta platform sediments terminating a regressional sequence that includes the underlying Fox Hills and Pierre Formations. Detailed studies of the ammonites and datable bentonites of the underlying marine sediments show that the delta prograded northeastward (Gill and Cobban, 1973). Deposition prograding along the axis of a topographic trough can explain the loss of beds from the bottom of the formation observed by Frye.

The age of the Hell Creek Formation is, by the present definition, latest Cretaceous. The problems related to the geochronology of the Cretaceous-Tertiary boundary have therefore become those of identifying and assigning poorly differentiated lithologic units of Cretaceous age to the Hell Creek Formation rather than the more usual problem of determining the age of a well-defined lithologic unit. The traditional method used in the identification of the boundary was first proposed by Calvert (1912) and later modified by Brown (1962). This method can be expressed by the simple rule that the uppermost Cretaceous strata terminate at the lowest persistent lignite above the highest dinosaur bones. By means of these rules the close of the Cretaceous Period (in the geochronologic rather than chronostratigraphic sense) has become identical to the upper boundary of a biostratigraphic zone. The validity of this correspondence depends on the unproved assertion that the extinction of the dinosaurs was isochronous.

Existing evidence of some diachronous aspects of the Hell Creek Formation, in addition to plausible suggestions for the mode of extinction of the dinosaurs suggest that the above rules for finding the Cretaceous-Tertiary geochronologic boundary may not be valid. The Fox Hills Formation (and therefore the base of the Hell Creek Formation) has been shown by Cobban and Reeside (1952) to be younger in central North Dakota than in Wyoming. Continued work by Gill and Cobban (1973), which included both radiometric and paleontologic methods, has resulted not only in the confirmation and measurement of the age differences, but also in the measurement of the actual rates of regression and transgression

within the Montana Group. The rates of regression in most cases are slow with respect to the rates of mammalian evolution. For example, the early part of the Fox Hills regression proceeded at only 55 kilometers per million years. Thus, two lithostratigraphically equivalent local faunas separated by only about 165 kilometers can be expected to differ in age by as much as three million years, an interval that should result in nearly disjoint occurrences of mammalian species.

That the upper contact of the Hell Creek Formation may be diachronous is a possibility that follows logically from the suggestions of Axelrod and Bailey (1968) and Sloan (1970) that the dinosaur extinctions resulted from climatic cooling and an increase in annual temperature ranges. The moderating effect of the nearby sea may have created a coastal sanctuary for the dinosaurs. The lateral movement of the coast as a result of the contemporaneous regression would then have caused a lateral shift in the position of the sanctuary. In this case the upper limit of dinosaur remains would mark the seaward passage of the inland margin of the sanctuary, not the isochronous extinction of the dinosaurs. Because of rapid mammalian evolution in the Late Cretaceous and Early Paleocene, the discovery of productive mammal localities in the Hell Creek Formation of North Dakota would be of great value in sorting out the spatial and temporal relations of the extinctions and the close of the Cretaceous.

The only fossil mammals now known from the Hell Creek Formation of North Dakota consist of three specimens from two localities. They have been identified as *Meniscoessus robustus* (Marsh, 1889) from Morton County, and *Pediomys ?krejci* Clemens (1966) and *Glasbius intracatus* Clemens (1966) from Slope County (Clemens, personal communication, 1977). All these are Cretaceous species, but the sample is inadequate as a basis for conclusions regarding the isochroneity of the upper boundary of the Hell Creek Formation.

### **Ludlow Formation**

Throughout southwestern North Dakota and northwestern South Dakota the Hell Creek Formation is overlain by the Ludlow Formation, which was named by Lloyd and Hares (1915) for exposures near the town of Ludlow, South Dakota. The unit was considered at the time to be a member of the Lance Formation. Later work by Dorf (1940) and Brown (1938, 1948a) resulted in



Figure 1. Generalized distribution map of Tongue River Formation (stipple pattern) and its mammal-bearing fossil localities in western North Dakota (modified from Carlson, 1969). E-W, location of geologic cross section shown in figure 2. Key to localities: B—Brisbane\*, D—Donnybrook\*, J—Judson\*, L—Lloyd and Hares locality, R—Riverdale\*, T—Trenton, WC—Wannagan Creek Quarry. Fossils from localities\* are described in this study.



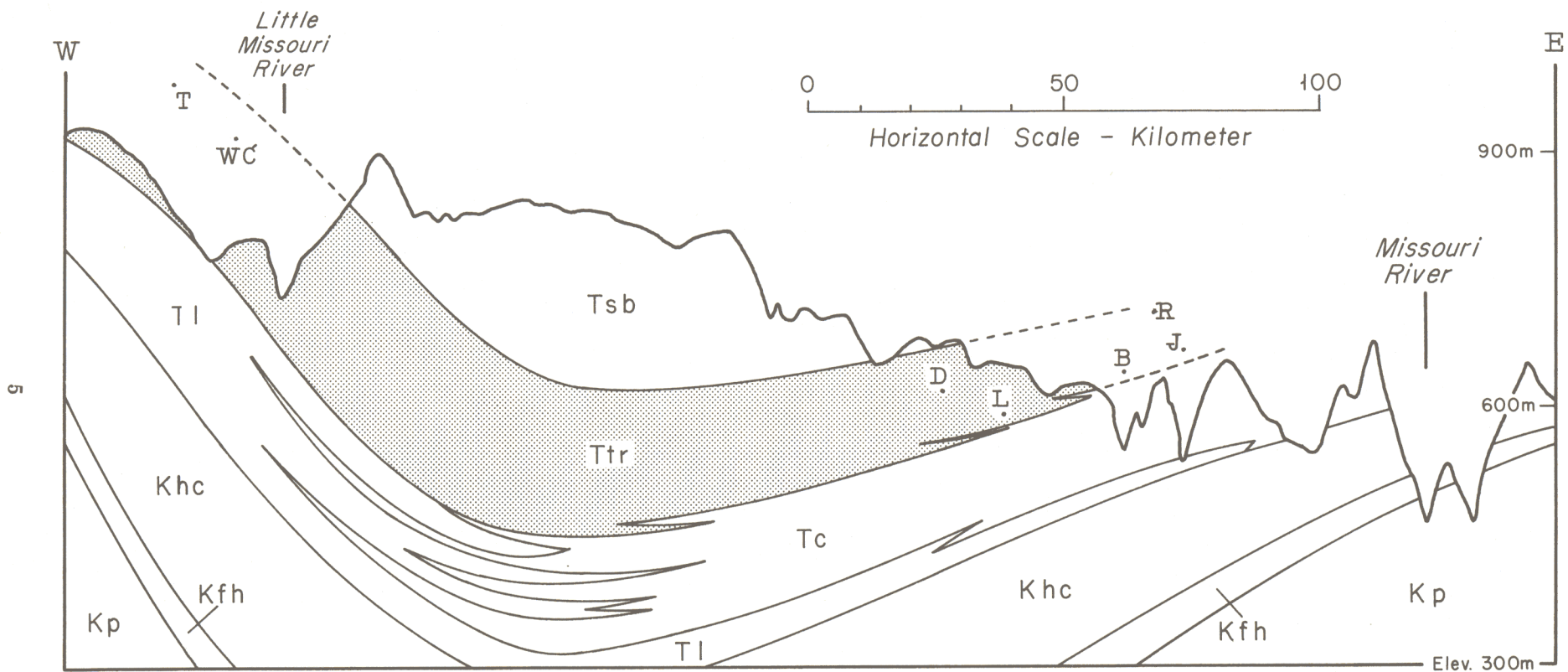


Figure 2. Schematic cross section of western North Dakota showing relative positions of mammal-bearing fossil localities in the Tongue River Formation. See figure 1 for location of cross section and key to fossil localities. Key to formations: Kp—Pierre, Kfh—Fox Hills, Khc—Hell Creek, Tl—Ludlow, Tc—Cannonball, Ttr—Tongue River, Tsb—Sentinel Butte.



the inclusion of the Ludlow Formation as a member of the Fort Union "Formation."

The Ludlow Formation crops out in the Little Missouri valley and in a band encircling the southern margin of the Williston basin and extending into the Missouri valley. Its thickness ranges from 105 meters at the type locality (Hares, 1928) to about 5 meters in the Missouri valley of North Dakota (Laird and Mitchell, 1942; Frye, 1969). The variation in thickness largely reflects the lateral facies transition to marine deposits of the Cannonball Formation. The thin eastern portion of the Ludlow occurs below the Cannonball. The Ludlow and Hell Creek Formations thin northward in central North Dakota, with the result that near Verendrye the Cannonball Formation rests directly on the Fox Hills Formation (Lemke, 1960).

The Ludlow sediments are composed of sandstones, shales, and lignites (Moore, 1976). The abundant lignites serve to differentiate the unit from the underlying Hell Creek Formation and from the basal sands of the overlying Tongue River Formation. The sands in the Ludlow Formation commonly occur as thin crossbedded sheets, and the unit on the whole is much more well bedded than the Hell Creek Formation. The lithology is geographically variable, becoming deficient in lignite in the Missouri valley of North Dakota (Laird and Mitchell, 1942).

The abundant lignites of the Ludlow Formation suggest that the transition from the Hell Creek Formation involved a lowering of the coastal plain close to base level. This interpretation is supported by the extensive intertonguing of the Ludlow and Cannonball Formations in the Little Missouri valley as shown by the presence of beds containing brackish water fossils identified as *Ostrea glabra* (Lloyd and Hares, 1915). Although the absolute sedimentation rates cannot be determined, the Cannonball transgression itself indicates a reduction in the sedimentation rate relative to basinal subsidence. During the transgression the coast probably developed as a linear clastic shoreline with the brackish-water tongues being deposited in lagoons and estuaries.

The age of the Ludlow Formation was shown by Dorf (1940) to be Paleocene. With the exception of correlation with the Cannonball Formation, the age of the Ludlow Formation has not been determined more precisely, either with respect to the North American Land Mammal ages or the European stages. No fossil mammals have been reported from the Ludlow Formation.

## Cannonball Formation

The only true marine sediments of the Fort Union Group are those of the Cannonball Formation, originally named as a member of the Lance Formation by Lloyd (1914; described more completely by Lloyd and Hares, 1915). Type exposures of the formation occur along the bluffs of the Cannonball River in Grant County, North Dakota. The Cannonball Formation has been studied most recently by Cvancara (1966, 1972, 1976).

Outcrops of the Cannonball Formation are restricted to west-central North Dakota along the eastern margin of the Williston basin (Cvancara, 1976). These deposits are separated by many hundreds of kilometers from the nearest contemporary marine sediments. The thickness of the unit ranges from a maximum of 120 meters in Mercer County (Fox and Olsson, 1969) to about 10 meters in the Little Missouri valley, where the Cannonball and Ludlow Formations interfinger. A typical thickness of the formation in central North Dakota is 90 meters. Both the lower contact with the Ludlow Formation and the upper contact with the Tongue River Formation are conformable and gradational, although local unconformities resulting from channel scour occur frequently. Because of poor exposures, tracing the contacts at the surface is difficult. The upper contact is further obscured by the presence of sandy strata on either side of the boundary.

The sediments of the Cannonball Formation are dominated by sandstones and mudstones (Cvancara, 1972, 1976). The fine- to very fine-grained sands consist of quartz, with some mica and glauconite. Crossbedding in the sands is common, with sets up to 10 inches in thickness. The sands are gray-green and weather to yellow or yellow-brown. The muds are dark gray and blocky and contain significant quantities of sand and silt. Both the sands and silts contain abundant carbonate concretions. The sands and muds are often interbedded with gradational contacts.

Cvancara (1976) suggests that the depositional environment of the Cannonball Formation included tidal flats, lagoons, tidal channels, beaches, shorefaces, and shelf bottoms. This combination is in essence a linear clastic shoreline that typically results from a low sediment supply relative to the amount of reworking of sediments by wave action. The extensive brackish-water intertongues of the Cannonball and Ludlow Formations are consistent with Cvancara's interpretation.

In contrast, the contact of the Cannonball and Tongue River Formations lacks major brackish-water intertongues, implying a separation of the marine and fresh-water environments that was more complete than is usual for a linear clastic shoreline. The regression of the Cannonball Sea, the absence of brackish-water facies, and the abundance of sands on either side of the upper contact all suggest a shift in depositional environment to that of a lobate delta. The abundance of sands and absence of brackish-water facies implies that wave action was still active in reworking the sediments into beaches and possibly barriers, which were effective in separating the terrestrial and marine environments.

The onset of the Cannonball regression implies that the rate of sediment supply increased relative to the rate at which it was being reworked by waves. A lowering of sea level by itself would not necessarily produce the observed suite of deltaic features. The thick sequence of non-marine strata overlying the Cannonball Formation and its equivalents in Montana suggest that the regression was caused largely by an increase in the rate of sediment supply initiated by orogenic uplift to the west. Under these conditions, the upper contact of the Cannonball Formation may be far from isochronous, but, unlike the Fox Hills regression, nothing specific is known of the rate of the Cannonball regression.

The age of the Cannonball Formation was first assessed by Stanton (1921; preliminary results reported in Lloyd and Hares, 1915, p. 537). Stanton considered the Cannonball fauna to be a "modified Fox Hills fauna" having closer affinities with the Cretaceous than with the Tertiary. Stanton's opinion was largely responsible for the original inclusion of the Cannonball Formation within the Lance Formation rather than the Fort Union Group. Dorf (1940) determined from fossil leaves that the Ludlow and, therefore, the Cannonball were Paleocene in age. Fox and Ross (1942) studying the Foraminiferida, and Leriche (1942) studying the sharks, confirmed Dorf's conclusion by comparing the Cannonball species to those of the Midway Group of the Gulf coastal plain. Swain (1949) made similar comparisons between the Cannonball and the Midway ostracodes. Cvanara (1966, 1972) concluded from his study of the pelecypods that the Cannonball was "Thanetian (Middle Paleocene)" in age. Further study of the Foraminiferida by Fox and Olsson (1970) resulted in the assignment of a

Danian (Early Paleocene) age. Sloan (1970) assigned a Puercan to Torrejonian (Early to Middle Paleocene) age range to the Cannonball on the basis of fossil mammals found by Lloyd and Hares (1915) in the overlying Tongue River Formation.

The large number of similarities of the Cannonball fauna to that of the Midway Group suggest that the Cannonball Sea was connected to the Gulf of Mexico. The seaway probably was centered in western Texas and probably possessed a bay or estuary extending into central Wyoming that resulted in the deposition of the Early to Middle Paleocene Waltman Shale (Sloan, 1970, p. 441). Most of the evidence against an arctic connection to the Cannonball Sea is equivocal, consisting of the general absence of arctic forms in the Cannonball Formation. Another line of evidence against an arctic connection is the presence of the mammalian genera *Plesiadapis* and *Arctocyon* in the Late Paleocene of Europe (Russell, 1964). Both of these genera have presumed ancestors in the Middle Paleocene of the western interior of North America, i.e., on the western side of the Cannonball Sea. These mammals migrated to Europe through Greenland in the Middle Paleocene or early in the Late Paleocene. Consequently, an arctic connection to the Cannonball Sea could not have been persistent throughout the entire existence of the sea.

### **Tongue River Formation**

Strata now referred to as the Tongue River Formation were first described by Taff (1909) as the "Tongue River coal group" of the Sheridan Coal Field of Wyoming. Hares (1928) extended this nomenclature to North Dakota, where he described the Tongue River "Member" of the Fort Union "Formation" in the Marmarth coal field. Subsequent references to Tongue River sediments in North Dakota were often vague and confusing until Royse (1967) presented a detailed study of the contact between the Tongue River and Sentinel Butte Formations, thereby raising both units to formation rank.

The Tongue River Formation crops out in an elliptical band encircling the North Dakota part of the Williston basin. Its thickness ranges from a maximum of about 185 meters in the Little Missouri valley (Hares, 1928) and the center of the basin (Royse, 1972) to a minimum of 60 to 90 meters on the southern and southeastern flanks of the basin (Royse, 1972). To the east, Carlson



(1972) reported a thickness of 123 meters at a point 16 kilometers north of New Salem. Barclay (1972) reported about 90 meters of Tongue River sediments in the vicinity of Glen Ullin. The Tongue River Formation conformably overlies the Ludlow and Cannonball Formations and is conformably overlain by the Sentinel Butte Formation. Major strata within the formation include a basal sandy unit and the HT Butte lignite at the top.

Fine-grained clastic sediments dominate the Tongue River Formation in which the modal grain size is in the range of silty clay to clayey silt and the color of the sediments ranges from gray to yellow-brown or yellow. Lignites and sand bodies are common and dolomitic limestone lenses are occasionally present.

Jacob (1973) recognizes five major lithologic facies: (1) gray clay and silt, (2) lignite, (3) yellow sand and silt, (4) linear sand bodies, and (5) tabular sand bodies. The first four facies commonly occur in cycles, terminating upward with the linear sand body.

Both the gray clay and silt facies and the lignite facies represent flood basin deposits. The gray clastics are irregularly stratified and are up to 9 meters thick. They grade upward into lignites, which range up to 12 meters thick and show rapid lateral shifts in thickness and elevation. The transition from clay and silt to lignites corresponds to the gradual infilling of the flood basin.

The yellow sand and silt beds are often clayey and very poorly sorted and may reach 15 meters in thickness. They commonly contain iron-stained concretions, limestone lenses, and tree trunks buried in an upright position. These yellow sediments are natural-levee and crevasse-splay deposits whose characteristic color reflects the highly oxidizing environment of deposition.

Both the linear and tabular sand bodies contain fine- to very fine-grained gray to yellow-brown sand that may be up to 40 percent primary carbonate grains. The linear sand bodies are limited to about 300 meters in width, do not consistently fine upward, and are commonly capped with a carbonate concretion. In contrast, the tabular bodies may extend for many hundreds of meters laterally, are upward-fining, and possess sedimentary structures that indicate a decreasing flow regime. The linear sand bodies are typical of near-terminal distributary channels of low sinuosity, whereas the tabular bodies have the characteristics of upstream meanders. Accretion is inferred to be nearly vertical in the

linear bodies and lateral in the tabular bodies.

The depositional environment of the Tongue River Formation is entirely fluvial, although the distribution of sand bodies indicates the presence of two differing fluvial environments. The linear sand bodies are most common in the lower part of the formation, which was deposited closer to the coast. Their position is consistent with their having been the distributary channels of a large prograding delta. Even the lowest parts of the Tongue River Formation are clearly fresh-water, indicating that there existed significant positive landforms such as beach ridges at the coast. The existence of such ridges has not been shown in any detailed studies, but it is consistent with the large amount of sand immediately above and below the Tongue River-Cannonball contact. The upward transition from linear to tabular sand bodies corresponds to a lateral change from a fluvio-deltaic environment of deposition near the coast to a more truly fluvial environment further inland. Rates of deposition in the fluvial environment were probably lower than those of the more deltaic environments because of the reworking of sediments by the lateral movements of meanders. Palynological studies by E. B. Robertson (personal communication, 1973) show that the climate was temperate and that a cedar rain forest prevailed during the time of deposition.

The interpretation of historical events within the time interval represented by the Tongue River Formation depends to a great extent on the environmental interpretation employed. The interpretation presented above implies that most of the formation was deposited under relatively constant conditions, with the basal sand representing coastal deposition and the remainder of the unit representing more inland deposition. The only departure from these constant conditions is the decrease in sediment supply and/or increase in basinal subsidence that resulted in the deposition of the HT Butte lignite at the top of the formation. Except for the top, the entire formation is likely to be highly time transgressive. It is uncertain whether or not the HT Butte lignite, and therefore the contact with the Sentinel Butte Formation, is isochronous over much of the basin.

Small-scale time correlations within the Tongue River Formation are not likely to be reliable because of the nature of the sedimentation. Reworking of sediments by meanders, channel switching in the delta complex, and differential rates of subsidence of distributary channel sands

distort the time record by means of erosion, depositional hiatuses, and locally high sedimentation rates. Thus it is entirely possible to have two closely situated localities in which the stratigraphically higher is actually the older.

Taff (1909), in his original description of the Tongue River beds, considers their age to be basal Tertiary. The first definitive evidence for a more precise age of the Tongue River Formation in North Dakota resulted from the discovery by Lloyd and Hares (1915) of two mammalian fossils from the base of the formation in Grant County. The fossils were identified by Gidley as "*Euprotogonia*" sp. (second lower molar) and *Pantolamda cavirictus* (upper premolar). Simpson (1937a, p. 11) referred the former specimen to *Tetraclaenodon* of the basis of Matthew's (1937) synonymization of the two genera. Simpson was followed by Jepsen (1940, p. 242) and Sloan (1970) in concluding from these fossils that the unit was Torrejonian (Middle Paleocene) in age. In the process of erecting the North American Land Mammal Ages, the Wood Committee (Wood *et al.*, 1941) assigned a Torrejonian age to the Tongue River Formation.

The only other fossil mammal from the Tongue River Formation of North Dakota that was described prior to the present study is the trigonid of a lower molar of an insectivore found by Lemke (1960) near the town of Donnybrook, Ward County. The concept of a Torrejonian age of the Tongue River Formation in North Dakota was perpetuated when Gazin identified the specimen as *Aphronorus*. My examination of the specimen confirms that it is a pantolestoid insectivore, but I do not think that it can be reliably identified at the generic level. Neither this specimen nor those of Lloyd and Hares provide a reasonable basis for the assignment of a Land Mammal Age to the Tongue River Formation of North Dakota.

### **Sentinel Butte Formation**

The earliest reports distinguishing the Sentinel Butte Formation were those of Leonard (1908) and Leonard and Smith (1909). Many informal references to the unit have been made since then, but it was not raised to formational rank until Royse (1967) presented a comprehensive study of its lower contact.

The Sentinel Butte Formation has the largest outcrop area of any of the Paleocene formations in North Dakota. It crops out in an elliptical area extending from the Missouri valley to the Little Missouri valley, and from the Canadian border

southward nearly to the South Dakota border. The thickness of the formation follows very closely the values for the Tongue River Formation described earlier in this study.

The lower contact of the Sentinel Butte Formation is fairly sharp in the Little Missouri valley area of western North Dakota. The HT Butte lignite represents the highest Tongue River sediments and is overlain by a sandy basal unit of the Sentinel Butte Formation (Royse, 1967). Other features distinguishing these two units are given below. The formation is overlain with a gradational contact by the Golden Valley Formation. Locally it is overlain directly by the White River Formation with an unconformable contact.

The Sentinel Butte Formation consists predominantly of somber silts and sand. Lignites, limestones, and linear sand bodies are less common than they are in the Tongue River Formation; whereas bentonites, silicified wood and sediments, and tabular sand bodies are more common (Royse, 1971; Jacob, 1975). Compared to the sediments of the Tongue River Formation, the Sentinel Butte sediments are better sorted, weather to steeper slopes, and have less carbonate cement, less mica, and more montmorillonite. In Folk's (1968) classification, the Sentinel Butte sediments are volcanic, sedimentary litharenites.

The lithology and stratigraphy of the Sentinel Butte Formation imply that it was deposited by meandering rivers. Grain-size analyses by Royse (1972) show that the minimum flood velocity of the rivers was 1.1-1.4 m/sec. (10 m above the channel bottom); comparable values for the Tongue River Formation are 0.9-1.2 m/sec. Paleocurrent directions average southeastward and have a high variance consistent with low slope stability. In conjunction with the rejuvenation of sedimentation following the deposition of the HT Butte lignite and the prominent volcanic component of the sediments, the low slope stability suggests the onset of tectonic activity, both in the source area to the west and in North Dakota.

Because the Sentinel Butte Formation is part of the Fort Union Group, its Tertiary age has long been recognized. Problems with the age determination of the unit have centered around the placement of the Paleocene-Eocene boundary. Thom and Dobbin (1924) assign a Wasatchian (Early Eocene) age to the Sentinel Butte Formation and are followed by Seager *et al.*, (1942) and Hennen (1943). Brown (1948a, 1948b, 1962)



corrected some of the earlier stratigraphic errors and established a Paleocene age for the unit on the basis of fossil plants. The early discovery of the Late Paleocene mammal *Titanoides primaevus* Gidley (1917) was ignored throughout the controversy. With the exception of *Titanoides*, no further mammalian fossils have been found in the Sentinel Butte Formation.

### Golden Valley Formation

The presence of post-Fort Union pre-Oligocene sediments in western North Dakota was first observed by Leonard (1906) in his report on the clays of the State. He noted that these deposits were at one time widespread but exist now only as erosional remnants restricted to high hills. Benson and Laird (1947) formally named the formation for exposures near the town of Golden Valley, North Dakota. Shortly thereafter Benson (1949) indicated the presence of two distinguishable members within the formation.

The lower member of the Golden Valley Formation consists of zero to 20 meters of laterally persistent light-gray sands overlain by white sandy kaolinitic clay, which is in turn overlain by carbonaceous shale grading up to lignite (Freas, 1962; Hickey, 1972). The kaolinitic clay is detrital rather than authigenic or diagenetic, and the sands in the clay are predominantly quartz, with some chert, muscovite, and occasional grains of unaltered orthoclase (Freas, 1962). The clays are resistant, weathering to steep bright-orange slopes. Bedding in the lower member is often lenticular, with crossbedding and rapid lateral changes in lithology and thickness. The lower contact with the Sentinel Butte Formation is conformable and gradational, with only localized areas of scour. The contact between the upper and lower members has been placed by Hickey (1972) at the top of the Alamo Bluff lignite.

The upper member ranges from zero to 45 meters in thickness and is less brightly colored than the lower member. It is typified by illitic and montmorillonitic clays, micaceous sands and silts, and a few thin lignites that are not laterally persistent. Thick, lenticular channel sands occur locally in channels that were eroded through the lower member into the underlying Sentinel Butte Formation. The upper contact of the Golden Valley Formation is a distinct unconformity, the contrast of which is heightened by the development of a paleosol below the erosional surface.

Leonard (1906) first proposed a lacustrine origin for the clays and shales of the lower

member. His interpretation was accepted later by Benson (1954) and Freas (1962). Hickey's thorough study of the formation (Hickey, 1972, 1977) has resulted in a refinement of these interpretations. The variable bedding and lithology of the lower member indicate a fluvial environment that became progressively more paludal or lacustrine through the time during which the Alamo Bluff lignite and carbonaceous zone were deposited. The depositional environment of the upper member is again fluvial. Hickey suggests that the sequence of events began with the uplift of a highly weathered source area. The uplift progressively encroached over western North Dakota, resulting in a return to fluvial conditions. Fossil plants show that the temperatures increased from warm temperate to subtropical during the interval of deposition. The continuation of all of these trends beyond the interval of deposition is indicated by the cessation of deposition, the onset of erosion, and finally the development of an extensive paleosol. Pettyjohn (1966) has shown this paleosol to be a laterite, the development of which requires a hot, wet climate and well-developed drainage.

The first definite evidence for the age of the Golden Valley Formation was presented by Benson and Laird (1947). Their assignment of an Eocene age to the formation was based on the presence of *Salvinia preauriculata* and was later corroborated on the same grounds by Brown (1948a, 1948b, 1962). Jepsen (1963) reported the first fossil mammals from the formation. The mammals occur in the upper member and include typical Eocene genera such as *Pelycodus*, *Lophiparamys*, *Sinopa*, *Miacis*, *Hyopsodus*, *Hyacotherium*, *Homogolax*, and *?Diacodexis*. Jepsen assigned an early Wasatchian age to the fauna. West (1973a) made a small collection nearby that included cf. *Parectypodus*, *Reithroparamys*, and *Phenacolemur praecox*. Hickey (1972) cited unpublished information from Leopold (1970, communication) that the lower member contains a Late Paleocene flora.

### Fossil Mammal Localities

The published references to Paleocene mammals from North Dakota, mentioned above, consist of only five specimens from four localities. As a result of sporadic discoveries in the last 15 years, fossil mammals are now known from an additional seven localities. Six of these localities are in the Tongue River Formation and of them, three (Brisbane, Judson, and Wannagan Creek



Quarry) have produced relatively complete mammalian faunas.

Compiled below are the location, stratigraphy, and history of each of the known Paleocene mammal localities of North Dakota. The localities are treated in the chronologic order of their discovery.

### **Lloyd and Hares Locality**

The geographic position of this locality cannot be established with certainty from published records. The original description of the locality by Lloyd and Hares (1915, p. 538) mentions several channel sand bodies in connection with the discovery of two mammalian teeth. The most precisely located of these occurs on "the north bank of the Heart River in T136N, R88W" (at that time part of Morton County, but now part of Grant County). Similar channels are noted "near Yule and at the mouth of Deep Creek, and also on Sand Creek, in Billings County, North Dakota." Vertebrate remains including two mammalian teeth are then described as coming from "these strata." A succeeding reference to "lenses of conglomerate similar to the one described above" suggests that "these strata" and presumably the teeth were located within a single channel deposit. It is therefore probable that the teeth came from the Heart River locality, since its position was described in the most detail.

Subsequent references to the locality and its fossils have added no new information. Simpson (1937a, p. 11) mentions the fossils as coming from Billings County, a conclusion he drew solely from Lloyd and Hares' published description (Simpson, personal communication, 1975). Jepsen (1940, p. 242) also mentioned the fossils, citing the inconsistent location "in Billings County, North Dakota, T136N, R88W." Simons (1960) lists the locality as Billings County. Sloan (1970, p. 441) cites Jepsen's paper and added that the fossil locality was close to Heart Butte, thereby implying that the Heart River location was correct. It is not known if Jepsen or Simons employed unpublished information in reaching their conclusions, but Sloan (personal communication, 1975) did not.

The Heart River locality was described by Lloyd and Hares as a sand-filled channel at the base of the Tongue River Formation, eroded 30 to 50 feet (9 to 15 meters) into the underlying Cannonball Formation. The Billings County localities are similar channels at the base of the Tongue River Formation (and presumably eroded into the Ludlow Formation), so that there is no

doubt as to the stratigraphic position of the mammal locality.

A channel that matches the Heart River locality of Lloyd and Hares can be found in NW<sup>1</sup>/<sub>4</sub> sec 18, T136N, R88W, Grant County, North Dakota. Although I found no vertebrate fossils at this locality, it is actively eroding and could well be the Lloyd and Hares locality. Erosion may have removed a small fossiliferous pocket from which the original specimens were obtained. The deposit includes two channel bottoms, the deeper of which truncates the shallower. The base of the deeper channel has an elevation of 619 meters and is about 10 meters below the local level of the basal contact of the Tongue River Formation. The basal conglomerate of the channel consists of rounded cobbles and tabular boulders of carbonaceous shale. Both clast types can be interpreted as rip-up clasts from a re-activated abandoned channel. The rounded cobbles may include transported material that was undercut by meanders further upstream. About a meter below the channel is a large lump of lignite (about one meter in diameter) within the sands of the Cannonball Formation. The lump may be either a mass of vegetation or a log rafted into the Cannonball Sea. All of these features indicate a deltaic distributary channel complex as the environment of deposition.

### **Donnybrook Locality**

Discovered by R. W. Lemke and R. W. Brown in 1943, this locality consists of a roadcut on the west side of U.S. Highway 52 in SW<sup>1</sup>/<sub>4</sub> sec 14, T158N, R87W, near the town of Donnybrook, Ward County, North Dakota. In September, 1972, I found it to be completely overgrown.

The stratigraphic position of the locality reported by Lemke (1960) was Tongue River "Member" of the Fort Union "Formation." His usage, however, predates the formal separation of the Tongue River and Sentinel Butte Formations and cannot be assumed to correspond to the Tongue River Formation as it is currently understood. Bedrock outcrops in the area are so limited by a cover of glacial sediments that surface observations cannot be used to establish the stratigraphic level more precisely. Indirect evidence suggests a Tongue River horizon (Holtzman, 1976, p. 28).

### **Riverdale Locality**

Approximately sec 22, T147N, R84W, McLean County, North Dakota; elevation 549 meters. This locality was discovered in 1962 by Bernice A.

Vinje of Hazen, North Dakota. In June of that year, Dr. W. D. Turnbull visited the site and, in the company of Dr. and Mrs. Vinje, collected a number of mammalian fossils. Most of the fossil material came from below a few centimeters of water near the shore of the Garrison Dam Reservoir. The remainder of the fossils was collected from the adjacent beach. The elevation of the locality was established from reservoir water-level measurements supplied by L. J. Geissinger, Army Corps of Engineers (personal communication, 1975). Subsequent filling of the reservoir has submerged the locality beneath an additional 15 meters of water.

Although there is little doubt that the stratigraphic position of this locality is close to the contact between the Tongue River and Sentinel Butte Formations, its precise horizon is uncertain. The lithologic variation in these units renders uncertain the identification of the contact in the eastern part of the Williston basin. Bluemle (1971, p. 13) tentatively places the contact at an elevation of 579 meters in the vicinity of the Garrison Dam. C. G. Carlson (personal communication, 1975) is currently mapping these units for the North Dakota Geological Survey and estimates that the contact is close to the current reservoir water level of 564 meters. In either case it is probable that the fossil locality lies within the upper 30 meters of the Tongue River Formation.

The collection of fossils from this locality was made in two parts. A skull and partial skeleton of *Titanoides* and a number of other relatively large bones were found *in situ* in shallow water. The remaining isolated teeth and small jaws were collected by screening approximately 0.5 metric ton of the sediment from the adjacent beach (Turnbull, personal communication, 1976).

### Judson Locality

This locality consists of four distinct sites, all of which adjoin the western and southern margins of sec 27, T138N, R84W, Morton County, North Dakota. (For individual site locations see Holtzman, 1976, p. 29.) Each site has an elevation of  $639 \pm 2$  meters, with up to 5 meters of relief. The Judson locality lies approximately 24 meters (determined by altimeter survey) stratigraphically above the contact of the Tongue River Formation with the underlying Cannonball Formation. Because of the poor exposures in the area this relationship cannot be shown by the continuous tracing of beds.

Sites 1 and 2 were discovered in 1962 by Joseph

Bell and his father, Dr. Gordon Bell, of Bismarck, North Dakota. Nearly all of the collecting prior to this study was done by Steven P. Lund of Bismarck, North Dakota, who collected from 1963 to 1973. In 1972 I found sites 3 and 4. Sites 1 and 2 were graded and covered with approximately 30 centimeters of soil by the Morton County Highway Department in May, 1973. E. B. Robertson collected a pollen sample from site 2 in 1972. In 1975, J. H. Hartman obtained a large collection of mollusks from site 3.

The fossils collected by Lund were nearly all obtained by surface collecting. This material consisted of 106 identifiable specimens and includes most of the well preserved jaws. Screening operations that I conducted in 1972 and 1973 resulted in the recovery of 185 identifiable mammalian fossils from 8 metric tons of sediment.

One of the major considerations in the choice of collecting methods was the extremely low concentration of fossils. It was necessary to maximize the yield in order to make the acquisition of an adequate sample possible. Sites 1, 2, and 3 consist of completely unconsolidated very fine-grained sand with little or no clay. As a result the matrix passed easily through ordinary brass window screen (1.5 mm by 1.2 mm openings) even when dry. Approximately one ton of sediment was washed under water. Comparison of fossils from this material with fossils from concentrates obtained by dry screening showed no marked difference in the rate of fresh breaks. Furthermore, dry screening preserved a greater number of minute teeth. Therefore, all subsequent collecting was done by dry screening.

The concentrates were roughly sized in the laboratory using minimum necessary exposure in varying sized brass screens, greatly enhancing the rate of recovery of teeth. Site 4 contained numerous granules and pebbles of clay, making it necessary to wash the dry-screened concentrate prior to sizing and picking. This laboratory washing was accomplished by soaking the concentrate in water and then screening it through brass screen having 0.8 mm openings. Most of the concentrate was picked without the use of a microscope. Spot checking by means of re-picking samples showed that virtually all bone material was being removed.

### Brisbane Locality

NW $\frac{1}{4}$ SW $\frac{1}{4}$ SW $\frac{1}{4}$  sec 3, T133N, R86W, Grant County, North Dakota. This locality is a roadcut on the east side of the road leading north from the



abandoned town of Brisbane. It is 1.9 km north of the point where this road crosses a railroad. The elevation determined by altimeter survey is 723 meters.

The stratigraphic horizon of the Brisbane locality is close to that of Judson. In his maps of the Cannonball lignite field, Lloyd (1914) indicates that the upper contact of the Cannonball Formation occurs at approximately 716 meters. Since the strata are more or less flat-lying I conclude that the locality lies about 7 meters above the contact. A slight northward or northwestward dip noted by Lloyd (1914) would place the locality stratigraphically higher, but not higher than 15 meters above the Cannonball Formation.

This locality was discovered by me in 1973. At the same time E. B. Robertson collected a pollen sample from the site. Because of the relatively high concentration of fossils in this sample, collecting was discontinued at Judson and 4.6 metric tons were screened at Brisbane in 1973 and 1974.

The concentrate was processed like that from Judson site 4 because of a similar high clay content. Unlike the Judson locality, the Brisbane locality lacks shell fragments altogether and has an abundance of lithified rock fragments of the same color as the bones and teeth. Thus it became necessary to remove all clay so that surface texture and opacity could be used as cues in picking teeth from the concentrate. The sample was, therefore, soaked in Stoddard solvent before it was washed in water. All samples were picked twice and some three times to ensure that all usable fossils were being removed. A few percent of all mammalian teeth were probably missed, but re-picking showed that nearly all of the specimens obtained on the third pass were useless fragments. Because unbroken teeth are easily recognized by shape, few of them were missed on the first pass. A total of 310 identifiable specimens was recovered.

### **Brisbane West Locality**

W $\frac{1}{2}$ SW $\frac{1}{4}$ NW $\frac{1}{4}$  sec 7, T133N, R86W, Grant County, North Dakota. This locality consists of a roadcut on the east side of a north-south road immediately north of a railroad crossing. Elevation determined by altimeter and Carson SE topographic quadrangle map is 746 meters.

The locality was discovered by me in 1973. A quarter ton sample yielded only half of a mammalian tooth. No further attempts were made to collect vertebrates, but in 1975 J. H. Hartman

obtained a good collection of mollusks by quarrying.

### **Localities Not Studied**

Four other localities in North Dakota have yielded fossil mammals of Paleocene age. These have been excluded from this study for a variety of reasons, but they are discussed briefly below to complete this listing of mammalian fossil localities.

In 1970 B. R. Erickson of the Science Museum of Minnesota began the development of Wannagan Creek Quarry, NW $\frac{1}{4}$ , sec 18, T141N, R102W, Billings County, North Dakota. The biota of this quarry is the subject of an extensive paleoecological study currently in progress (Erickson, personal communication, 1974). The stratigraphic position of the locality is approximately 24 meters below the upper contact of the Tongue River Formation. As a part of its rich fauna and flora, the quarry has yielded a number of well preserved mammalian specimens. The fauna appears to be complete enough to permit an accurate age determination.

Three localities in northwestern North Dakota have yielded isolated finds of *Titanoides*. Two of these occur with some certainty in the Sentinel Butte Formation. The type locality of *T. primaevus* is 5 kilometers northeast of Buford, Williams County, North Dakota (Gidley, 1917). Other specimens presumed to be from the same individual were collected by Jepsen in 1951 (for an account, see Simons, 1960, p. 32). The second locality in the Sentinel Butte Formation occurs in NW $\frac{1}{4}$  sec 30, T148N, R101W, McKenzie County, North Dakota, where McKenna collected parts of three individuals of *Titanoides* in 1963. A third locality has yielded a skull of *T. primaevus*. Its stratigraphic position is in some doubt. The locality, in NW $\frac{1}{4}$  sec 29, T153N, R102W, Williams County, North Dakota, probably occurs in the Tongue River Formation (estimated from Carlson, 1969). The fossils from the first and third localities have been treated by Simons (1960).

### **Mammalian Local Faunas**

The mammalian teeth found by Lloyd and Hares, probably from a locality near the Heart River, were identified by Gidley as an upper premolar of *Pantolambda cavirictus* and a left lower second molar of "*Euprotogonia*" sp. No indication of a collection or of specimen numbers

was given by Lloyd and Hares (1915) when they reported Gidley's findings, nor were the teeth described in any detail. Simpson (1937a) referred to the specimens as *Pantolambda* and *Tetraclaenodon*. The latter change from "*Euprotogonia*" did not result from the examination of the fossils by Simpson (personal communication, 1975), but rather was in accord with Matthew's (1937) synonymization of the two genera. Subsequently Jepsen (1940), Simons (1960), Brown (1962), Russell (1967), and Sloan (1970) have made similar references to the fossils. There is no reason to believe that any of them ever saw the specimens; Sloan (personal communication, 1975) did not.

The identifications made by Gidley are open to question on two grounds. First, the only Paleocene pantodonts known at the time were *Pantolambda cavirictus* and *P. bathmodon*. Since the latter is a very small species, it is probable that any sizable pantodont tooth would have been identified then as *P. cavirictus*. Second, the distinction between *Tetraclaenodon* and *Phenacodus* is based largely on the presence of a mesostyle in the upper molars of *Phenacodus*. Thus the identification of a second lower molar belonging to either of these genera must be regarded as unreliable. Neither of the identifications should be considered more accurate than (1) an indeterminate species of the Pantodonta and (2) an indeterminate phenacodontid condylarth.

Both of these specimens must now be considered lost. As products of United States Geological Survey field work, they should be part of the collections of the National Museum of Natural History; however, attempts by the museum staff and me to locate them have been fruitless.

The single mammalian tooth fragment from the Donnybrook locality is a trigonid of a left lower molar, USNM 205319. It was identified by Gazin as *Aphronorus* (Lemke, 1960) but was not described in detail. Comparisons of the specimen with *Aphronorus fraudator* (USNM 6177 from the type locality, Crazy Mountain Field, Montana) and *Propaleosinopa albertensis* (USNM 33810, type of "*Bessoeceter thomsoni*" from Scarritt Quarry) have convinced me that it cannot be referred with certainty to either of these genera. It may best be identified simply as an indeterminate pantolestoid insectivore.

The Brisbane West locality has also yielded a single mammalian specimen, SMM P77.19.1. It is

the labial portion of P<sup>4</sup> of *Pararyctes pattersoni*. This identification is obviously not highly reliable. The tooth is here collocated with the larger sample of *P. pattersoni* from the Brisbane locality.

The mammalian taxa so far identified from the major localities of Judson, Brisbane, and Riverdale appear in table 1. Each line in the table corresponds to a distinct species, regardless of the level to which the species has been identified. The four occurrences with question marks reflect uncertainty in the identification at the species level. In each case the specific identification of the other occurrences of the species is relatively certain. The following have been identified as new species currently under study, but as yet unpublished, by others: *Mesodma* sp., *Ectypodus* sp., *Neoplagiaulax* sp. (1), and *Parectypodus* sp.

### Age and Correlation of Local Faunas

Four provincial ages are in common use today as a time scale for North American continental Paleocene deposits. From oldest to youngest these are the Puercan, Torrejonian, Tiffanian, and Clarkforkian. This subdivision of the Paleocene is based upon biostratigraphic zones established by the Wood Committee (H. E. Wood *et al.*, 1941). By means of an implicit assumption of the isochroneity of these assemblage zones this subdivision of the Paleocene deposits has been used as a geochronologic subdivision of the Paleocene Epoch. Because of subsequent faunal revisions and numerous taxonomic range extensions, the original definitions of these zones are now largely obsolete. One of the original provincial ages, the Dragonian, has been eliminated. The foundations of the Clarkforkian have recently been questioned by R. C. Wood (1967). Recently Sloan (1970), Gingerich (1975), and Rose (1975) have retained the Clarkforkian, whereas West (1976) has not. The use of the Clarkforkian here is not intended as a statement on its validity, and its meaning is limited to the informal definition given below. The Clarkforkian may still be a useful time division, but it cannot be used with any consistent meaning until it is redefined.

Because of the increasing number of Tiffanian local faunas it should now be possible to subdivide the Tiffanian in order to obtain more precise ages. An informal subdivision into early, middle, and late intervals is used here. It was constructed

TABLE 1. Fossil mammals identified from the Judson, Brisbane, and Riverdale localities, Tongue River Formation, North Dakota.

	Brisbane	Judson	Riverdale
<b>MULTITUBERCULATA</b>			
<i>Ptilodus montanus</i>	X		
<i>Ptilodus wyomingensis</i>		X	
<i>Ptilodus kummae</i>			X
<i>Prochetodon</i> sp.		X	
<i>Mesodma</i> sp.	X	?	
<i>Ectypodus</i> sp.	X	?	
<i>Neoplagiaulax hunteri</i>	X	X	
<i>Neoplagiaulax nanophus</i> , new species		X	
<i>Neoplagiaulax</i> sp. (1)	X	X	
<i>Neoplagiaulax</i> sp. (2)	X		
<i>Neoplagiaulax</i> sp. (3)		X	
<i>Parectypodus</i> sp.	X	X	
<i>Microcosmodon woodi</i>	X		
<b>MARSUPIALIA</b>			
<i>Peradectes elegans</i>	X		
<b>INSECTIVORA</b>			
<i>Paleoryctes</i> sp., cf. <i>P. punctatus</i>	X	X	
<i>Pararyctes pattersoni</i>	X		
<i>Leptacodon tener</i>	X	?	
<i>Litolestes lacunatus</i>	X	X	
<i>Propaleosinopa albertensis</i>	X	X	X
<i>Paleosinopa</i> sp., cf. <i>P. simpsoni</i>	X		
<i>Bisonalveus</i> sp.	X		
<i>Unuchinia dysmathes</i> , new species	X	X	
genus and species indet. (1)	X		
genus and species indet. (2)		X	
<b>PRIMATES</b>			
<i>Plesiadapis rex</i>	X	X	
<i>Plesiadapis</i> sp.			X
<i>Nannodectes</i> sp.	X		
<i>Ignacius frugivorus</i>	X	X	
<i>Carpodaptes hobackensis</i>		X	
<i>Carpodaptes cygneus</i>	X	X	
Picrodontid sp.	X		
<b>CARNIVORA</b>			
<i>Protictis paralus</i> , new species	X	X	
Viverravine sp.		X	
Miacid sp.	X	X	
<b>CONDYLARTHRA</b>			
<i>Thryptacodon australis</i>	X	X	
<i>Arctocyon</i> sp.		X	
Arctocyonid sp.			X
<i>Haplaletes diminutivus</i>	X	X	
<i>Phenacodus primaevus</i>		X	X
<i>Ectocion wyomingensis</i>	X	X	X
genus and species indet. (1)	X		
genus and species indet. (2)		X	
<b>PANTODONTA</b>			
<i>Titanoides primaevus</i>	?	X	X



solely for the purpose of dating the Judson and Brisbane local faunas and therefore is incomplete. Each interval was derived by grouping together reasonably well sampled local faunas that appear on the basis of evolutionary grade to be similar in age. The local faunas employed are largely from the northern Great Plains and Rocky Mountains in order to minimize the effects of geographic variation in faunas. The local faunas used are:

Clarkforkian—Bear Creek, Plateau Valley, Clark Fork.

Late Tiffanian—Princeton Quarry, Badwater Creek locality.

Middle Tiffanian—Scarritt Quarry, Dell Creek, Cypress Hills, Cedar Point.

Early Tiffanian—Shotgun, Bison Saddle, Battle Mountain.

Torrejonian—Gidley Quarry, Rock Bench, Swain Quarry.

Table 2 is a range chart showing the geochronologic ranges of taxa useful in determining the ages of the Judson and Brisbane local faunas. These ranges include only occurrences at the selected typical local faunas in order to express

the most probable ranges in the study area rather than complete ranges.

It is apparent from table 2 that both the Judson and Brisbane localities are of middle Tiffanian age, but that they have more affinities with the early Tiffanian than with the late Tiffanian. These findings contradict the prevailing opinion that the Tongue River Formation in North Dakota is of Torrejonian or Middle Paleocene age. A further implication of these results is that the uppermost part of the Cannonball Formation is probably Late Paleocene (early Tiffanian) in its eastern occurrences.

The remaining localities included in this study cannot be dated with the same precision as Judson and Brisbane because of the much more limited samples. The most that can be said for the locality of Lloyd and Hares and the Donnybrook locality is that they are Torrejonian or younger. As such they contribute essentially nothing to knowledge of the history of the basin.

The Brisbane West locality is probably Tiffanian both on the basis of the probable occurrence of *Pararyctes* and because of its strati-

TABLE 2. Ranges of taxa useful in dating the Brisbane (B) and Judson (J) local faunas based on the occurrence of these taxa at selected localities (see text) used in the informal definition of the time units shown below.

	Torrejonian	Tiffanian			Clarkforkian
		Early	Middle	Late	
<i>Ptilodus montanus</i>	-----	B	-----		
<i>Ptilodus wyomingensis</i>	---- J ----				
<i>Prochetodon</i>				-----	J -----
<i>Mesodma</i> sp.	-----	B	-----		
<i>Ectypodus</i> sp.	---- B ----				
<i>Neoplagiaulax hunteri</i>		-----	BJ	-----	
<i>Neoplagiaulax</i> sp. (1)			--- BJ ---		
<i>Parectypodus</i> sp.		--- BJ ---			
<i>Microcosmodon woodi</i>		---- B ----			
<i>Peradectes elegans</i>		-----	B	-----	
<i>Paleoryctes punctatus</i>					--- BJ ---
<i>Pararyctes pattersoni</i>		-----	B	-----	
<i>Propaleosinopa albertensis</i>	-----	BJ	-----		
<i>Paleosinopa simpsoni</i>			---- B ----		
<i>Leptacodon tener</i>			---- B ----		
<i>Plesiadapis rex</i>		-----	BJ	-----	
<i>Nannodectes</i>		---- B ----			
<i>Ignacius frugivorus</i>			-----	BJ	-----
<i>Carpodaptes hobackensis</i>			---- J ----		
<i>Carpodaptes cygneus</i>			--- BJ ---		
Picrodontidae	-----	B	-----		
<i>Thryptacodon australis</i>			--- BJ ---		
<i>Haplaletes diminutivus</i>			--- BJ ---		
<i>Phenacodus primaevus</i>				-----	J -----
<i>Ectocion wyomingensis</i>		-----	BJ	-----	
<i>Titanoides primaevus</i>				-----	J -----

graphic and geographic proximity to the Brisbane locality.

The Riverdale local fauna is probably younger than either Judson or Brisbane, but it is impossible to say whether it is middle or late Tiffanian. The presence of *Phenacodus*, *Plesiadapis*, *Propaleosinopa*, and *Titanoides* makes a Tiffanian age assignment relatively certain. In addition the specimens of *Ptilodus* from the locality are indistinguishable from a new species, *P. kummae* identified by D. Krause from the Roche Percee local fauna of southeastern Saskatchewan. On this rather thin evidence one may speculate that Riverdale, like Roche Percee, is a little younger than either Judson or Brisbane. This relative age of the Roche Percee local fauna is itself not yet certain, but it is the preliminary estimate of both D. Krause (personal communication, 1975) and me.

### Completeness of Samples

Several of the localities treated in this study are so obviously poorly sampled that their completeness need not be discussed. In spite of its yielding an accurate age, the Riverdale local fauna with seven species must be regarded as poorly sampled in view of the fact that many Tiffanian local faunas include about 25 species. In contrast, the Judson and Brisbane local faunas with 27 and 30 species, respectively, appear on the same basis to be very well sampled. However, the fact that in both local faunas several species are known only from single specimens leaves open the possibility that an appreciable number of uncommon species remain to be discovered. Much of the uncertainty as to the adequacy of these samples can be eliminated by estimating values for their completeness.

Using a method to be described elsewhere (Holtzman, in prep.), the Brisbane local fauna was estimated to be 86 percent complete with 35 available species. The sample was made up of 204 specimens and 30 species. Corresponding values for the Judson local fauna are 77 percent completeness, 35 available species, based on a sample of 231 specimens and 27 species. Because the Judson local fauna is made up of two collections, one primarily screened and one collected from the surface, a second estimate was made, using only the 153 specimens (22 species) of the predominantly screened collection. The resulting values were 77 percent completeness and 29 available species. Because both Judson samples have less evenly distributed species, it is to be

expected that the errors in the estimated number of species are larger than those of the Brisbane sample. A large number of rare species means that small errors in the way the sample represents the distribution of available species result in large errors in the number of species observed when the sample size is not extremely large. Thus, the estimates for the Brisbane local fauna are likely to be much more accurate than those for Judson.

Both the Judson and Brisbane local faunas appear to be reasonably well sampled. There is sound reason to believe that continued collecting will eventually yield perhaps an additional half dozen rare species. As interesting as these species may be biologically, they could not significantly alter the general biostratigraphic results already obtained. The current samples, though not large in comparison to some other comparable local faunas, must be judged adequate for biostratigraphic purposes.

### Composition of Local Faunas

The relative abundance of species in the fossil assemblages are shown in table 3 and were computed by dividing the number of identified teeth (not number of specimens) by the number of identifiable teeth per individual. The Judson local fauna appears twice, once with frequencies based on fossils collected in 1972 and 1973 (omitting the earlier surface collection made by S. P. Lund), and once using the entire sample. Counting the number of teeth rather than specimens eliminates the bias introduced by differences across species in the probabilities of preservation of jaws containing more than one tooth. This estimating procedure compensates for differences in the number of identifiable elements per species, but not for differences in the probabilities of preservation of those parts within a species. Upper teeth are less likely to be preserved than lower teeth, but this difference does not appear to vary greatly across species. Thus the frequency estimates should not be affected by the variable probabilities of preservation of teeth within a species because the effect would be proportional both to the observed number of teeth and the number of identifiable teeth. The advantage of this method is that it does not generate systematic errors that are dependent on sample size.

It is apparent from table 3 that there are major differences between the Judson and Brisbane local faunas, both in the taxa present and in their

TABLE 3. Abundance of mammalian species (in percent) based on estimated numbers of individuals from the Brisbane and Judson local faunas.

	Identi- fiable teeth	Bris- bane	Judson (part)	Judson (total)
<i>Ptilodus montanus</i>	20	7.4	—	—
<i>Ptilodus wyomingensis</i>	20	—	24.2	23.0
<i>Prochetodon</i> sp.	20	—	0.9	0.6
<i>Mesodma</i> sp.	4	3.0	—	—
<i>Ectypodus</i> sp.	4	10.4	2.2	1.5
<i>Neoplagiaulax hunteri</i>	4	5.9	6.7	4.4
<i>Neoplagiaulax nanophus</i>	4	—	9.0	5.8
<i>Neoplagiaulax</i> sp. (1)	4	13.4	4.5	5.8
<i>Neoplagiaulax</i> sp. (2)	4	1.5	—	—
<i>Neoplagiaulax</i> sp. (3)	4	—	2.2	4.4
<i>Parectypodus</i> sp.	4	3.0	6.7	5.8
<i>Microcosmodon woodi</i>	6	5.0	—	—
<i>Peradectes elegans</i>	16	1.1	—	—
<i>Paleoryctes</i> sp., cf. <i>P. punctatus</i>	16	1.9	3.9	2.5
<i>Pararyctes pattersoni</i>	16	2.2	—	—
<i>Leptacodon tener</i>	16	3.3	—	—
<i>Litolestes lacunatus</i>	20	9.2	2.2	1.7
<i>Propaleosinopa albertensis</i>	16	1.9	1.7	1.1
<i>Paleosinopa</i> sp., cf. <i>P. simpsoni</i>	16	0.7	—	—
<i>Bisonalveus</i> sp.	16	0.4	—	—
<i>Unuchinia dysmathes</i>	16	0.4	—	1.1
Insectivore, indet. (1)	16	0.4	—	—
Insectivore, indet. (2)	16	—	0.6	0.4
<i>Plesiadapis rex</i>	24	9.4	13.8	17.7
<i>Nannodectes</i> sp.	24	2.2	—	—
<i>Ignacius frugivorus</i>	18	4.3	4.5	4.2
<i>Carpodaptes hobackensis</i>	18	—	4.5	4.5
<i>Carpodaptes cygneus</i>	18	6.3	—	0.7
Picrodontid, indet.	12	0.5	—	—
<i>Protictis paralus</i>	12	1.5	1.5	2.4
Viverravine, indet.	12	—	0.7	0.5
Miacid, indet.	14	0.8	—	1.2
<i>Thryptacodon australis</i>	16	0.4	2.2	3.6
<i>Arctocyon</i> sp.	16	—	—	0.4
<i>Haplaletes diminutivus</i>	16	1.9	5.0	3.3
<i>Phenacodus primaevus</i>	18	—	2.0	1.3
<i>Ectocion wyomingensis</i>	18	1.0	0.5	1.3
Condylarth, indet. (1)	18	—	—	0.3
Condylarth, indet. (2)	16	0.4	—	—
<i>Titanoides primaevus</i>	20	—	0.4	0.3
? <i>Titanoides</i> sp.	20	0.3	—	0.3
TOTAL		100.1	99.9	100.1
TOTAL TEETH		215	163	262

frequencies. The following faunal differences seem to me to be both real and meaningful:

- 1) The Judson and Brisbane faunas differ in their species of *Ptilodus* and *Carpodaptēs*.
- 2) *Ectypodus*, *Neoplagiaulax* sp. (1), and *Litolestes* are much more abundant at Brisbane than Judson, whereas *Ptilodus*, *Haplaletes* and *Thryptacodon* are much more abundant at Judson.
- 3) *Microcosmodon*, *Peradectes*, *Pararyctes*, *Leptacodon*, and *Nannodectes* are all present and not rare at Brisbane while being absent at Judson. *Neoplagiaulax nanophus* is the only species where the opposite is true, i.e., present and not rare at Judson and absent at Brisbane.

Other apparent differences in the faunas are quite possibly the results of sampling error.

TABLE 4. Abundance of mammalian families (in percent) from the Brisbane and Judson local faunas based on species abundance values of table 3.

	Brisbane	Judson (part)	Judson (total)
Ptilodontidae	7.4	25.1	23.6
Neoplagiaulacidae	37.2	31.3	27.7
Eucosmodontidae	5.0	—	—
Didelphidae	1.1	—	—
Paleoryctidae	4.1	3.9	2.5
Nyctitheriidae	3.3	—	—
Erinaceidae	9.2	2.2	1.7
Pantolestidae	2.6	1.7	1.1
Pentacodontidae	0.4	—	—
Apatemyidae	0.4	—	1.1
Insectivores, indet.	0.4	0.6	0.4
Plesiadapidae	11.6	13.8	17.7
Paromomyidae	4.3	4.5	4.2
Carpolestidae	6.3	4.5	5.2
Picrodontidae	0.5	—	—
Miacidae	2.3	2.2	4.1
Arctocyoniidae	0.4	2.2	4.0
Hyopsodontidae	1.9	5.0	3.3
Phenacodontidae	1.0	2.5	2.6
Condylarths, indet.	0.4	—	0.3
Titanoideidae	0.3	0.4	0.6
TOTAL	100.1	99.9	100.1

Table 4 shows the abundance of mammalian families compiled from the data of table 3. The greater diversity of taxa at the Brisbane locality is apparent from the fact that 18 families are present there, whereas only 14 are present at Judson. Other important differences include the greater abundance of ptilodontids, arctocyonids,

hyopsodontids, and phenacodontids at Judson and the greater abundance of erinaceids and nyctitheriids at Brisbane.

TABLE 5. Abundance of mammalian orders (in percent) from the Brisbane and Judson local faunas from tables 3 and 4.

	Brisbane	Judson (part)	Judson (total)
Multituberculata	49.6	56.4	51.3
Marsupialia	1.1	—	—
Insectivora	20.4	8.4	6.8
Primates	22.7	22.8	27.1
Carnivora	2.3	2.2	4.1
Condylarthra	3.7	9.7	10.2
Pantodonta	0.3	0.4	0.6
TOTAL	100.1	99.9	100.1

Some of these family-level differences are also reflected in the abundance of orders shown in table 5. Condylarths are relatively more frequent at Judson, whereas insectivores are relatively more common at Brisbane. Multituberculates, on the other hand, have similar frequencies in both localities, in each case making up more than half of the once living individuals. The absence of marsupials from the Judson sample may be accidental.

### Paleoecology

The abundances of mammalian taxa preserved at the Judson and Brisbane localities exhibit reasonable ecologic balance. The small herbivores and omnivores far outnumber the carnivores and the larger herbivores and omnivores. It is therefore probable that neither local fauna is severely biased in its representation of the actual fauna that occupied each area at the time of deposition. The true species abundances would, of course, differ from those of table 3 because the remains of longer-lived species accumulate disproportionately slowly in relation to the abundance of shorter-lived species. In both local faunas, however, the species that probably had appreciably longer life spans are so rare that this bias would not be extremely large.

The ecologically balanced composition of the Judson and Brisbane samples probably results from the mode of deposition and the screening process used in collecting. The bones and teeth accumulated in a fluvial environment, either in accreting point bars or in subsiding distributary channels, after having been transported for some



distance. No doubt some of the remains were deposited and reworked by laterally migrating meanders before their final deposition. These processes have resulted in a mixing of species from more than one community. In addition to the inhabitants of the stream banks and natural levees, the inhabitants of the backswamps are probably also present in the sample, albeit in reduced numbers.

The results of palynological studies by E. B. Robertson (personal communication, 1974) have established the major features of the flora associated with the deposition of the Brisbane locality and that associated with the flood basins contiguous with the Judson locality. Pollen was obtained from fine-grained partings rich in organic matter within the sands of the Brisbane locality. The assemblage represents an upland forest habitat and is typical of primary deposits in channel facies. In contrast, the pollen sample from the Judson locality was obtained from the cobbles and pebbles of organic-rich shale deposited in a thin lens having an unconformable base. The area of origin of this pollen sample then is not the channel environment associated with the deposition of the surrounding sands, but probably the adjacent flood basin. Reworking of the flood basin shales by lateral migration of meanders probably accounts for the deposition of these shale clasts. The pollen indicates a backswamp habitat interpreted by Robertson as a temperate cedar rain forest.

Fossil mollusks are abundant at the Judson locality, but completely absent at Brisbane. The Judson mollusks, currently under study by J. H. Hartman (1976), include a diverse gastropod fauna suggesting that the immediate environment was a shallow, well-aerated, low-velocity river. These findings are in accord with Royse's (1971) conclusions based on sedimentological studies outlined in the foregoing summary of the Tongue River Formation. *Bicorbula*, a member of the typically marine Corbulidae, is present in the fauna. It is only known from localities geographically and stratigraphically close to the Cannonball Formation, suggesting that it may be ecologically restricted to areas transitional between marine and terrestrial environments.

Non-mammalian vertebrates are common at both the Judson and Brisbane localities but have not been studied in detail. Nevertheless, a few of

the occurrences that have ecologic significance will be mentioned. Unless otherwise noted, the environmental interpretations are those of Estes (1964). A ray, *Myledaphus*, is present in the Judson local fauna. Its nearest living relative, *Hypolophus*, is frequently observed in fresh waters. *Odontaspis* is a galeoid shark found at both Judson and Brisbane. Modern species of this genus are among the few selachians ever observed in fresh water (Gunter, 1942). By analogy to Recent *Amia*, an amiid at Judson suggests a strictly fresh water habitat. *Belonostomus*, present at Judson, occurs primarily in marine deposits, but also in the fresh-water Lance Formation. *Acipenser*, probably present at both localities, and *Lepisosteus*, present at both localities, occur today in fresh to brackish coastal waters, being commonly found in streams and rivers. *Opisthotriton* and *Champsosaurus*, known from both localities, are aquatic. Two other salamanders, one or more small lizards, two crocodylians, turtles, and birds are present but are generally uninformative with respect to the environment.

The available geologic and biologic evidence supports the interpretation of the Judson and Brisbane localities as fresh-water sediments deposited in a fluvial environment in a fluvio-deltaic system. Both localities were relatively close to the shoreline and may, in fact, have been part of the distributary complex. The rivers were probably relatively wide, shallow, and slow-moving, offering a variety of habitats for aquatic and semiaquatic species. The stream banks were almost certainly natural levees backed by shallow swampy areas. Thus there were probably a variety of habitats open to mammals, including (1) the stream bank—natural levee uplands, supporting fossorial and cursorial species, (2) a forest upper story supporting arboreal species, and (3) the backswamp under story supporting a variety of forms, depending largely on the local water depth. Unfortunately, the habits of Paleocene mammals are too poorly known to permit identification of the habitat occupied by each species.



## PART II. SYSTEMATIC PALEONTOLOGY

Nearly all measurements were made with a dissecting microscope and an ocular micrometer whose smallest division was 0.07 mm at the most commonly used magnification. Other magnifications produced smaller lengths per division, but measurements beyond 0.1 mm were found not to be reliably reproducible because of errors produced by variation in orientation of the specimen. Some of the larger specimens were measured with a dial caliper accurate to 0.02 mm. Unless otherwise stated all measurements are in millimeters.

The length of  $P_4$  of multituberculates was measured between the ends of the apical crest, as done by Jepsen (1940), but from the labial side rather than lingual. This length is referred to here as the standard length. In addition to being a measure of gross size it is an important reference line used in the description of shapes. The relative height of the first serration is the ratio of the distance between the first serration and the anterior end of the standard length to the standard length. The notation for cusp formulae follows Simpson (1937a). The ventral projection of the labial enamel of  $P_4$  at the anterior root is here termed the exodaenodont lobe.

Measurements of therian cheek teeth follow Clemens (1966). A few specialized measurements are used and are discussed individually. Nomenclature for metatherian teeth follows Clemens (1966); that for eutherians follows MacIntyre (1966), Van Valen (1966), and Szalay (1969). When applied to teeth, the terms median and medial mean on, near, or toward the longitudinal midline of a tooth; when applied to other anatomical parts these terms are referenced to the longitudinal midline of the animal. Unless otherwise qualified, terms like ascend, descend, above, etc., are referenced to the base of the crown for both upper and lower teeth.

Abbreviations used in the tables are:

N—number of observations

SD—unbiased estimate of standard deviation,  
 $(\sum (x-\bar{x})^2 / (N-1))^{1/2}$

V—coefficient of variation (ratio of SD to mean)

A—anterior

P—posterior

In order to maintain lighting conventions without sacrificing adequate illumination, most

lateral views of the upper teeth in the figures show them in an inverted position.

Specimen numbers of the Science Museum of Minnesota are of the form SMM Py.a.n, where y is the last two digits of the year of accession, a is the sequential accession number for that year, and n is the sequential specimen number within the accession. The specimens described here comprise four accessions:

77.6 specimens collected by S. P. Lund from the Judson locality

77.7 specimens collected by me from the Judson locality

77.8 specimens from the Brisbane locality

77.19 a single specimen from the Brisbane West locality

In the present study a notation of the form SMM P77.8.1-7 is used to denote specimens 1 through 7 of accession 77.8.

Wherever possible, reference is made to adequate dental descriptions already in the literature. In such cases my descriptive comments are limited to peculiarities of the North Dakota samples, comparisons, and expansions of the cited description. Detailed descriptions were prepared for all specimens, however, and can be found in Holtzman (1976).

Class MAMMALIA  
Order MULTITUBERCULATA  
Family PTILODONTIDAE Gregory and  
Simpson, 1926  
*Ptilodus montanus* Douglass, 1908  
Table 6, fig. 3.2

*Referred specimens.*— $P^1$ , SMM P77.8.8-10;  $P^2$ , P77.8.11;  $P^3$ , P77.8.12-13; anterior fragment of  $P^4$ , P77.8.14-15;  $M^1$ , P77.8.16-21;  $M^2$ , P77.8.22-25; partial  $P_4$ , P77.8.26;  $M_1$ , P77.8.27-30;  $M_2$ , P77.8.31-32.

*Locality.*—Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Description.*—These specimens agree in nearly all respects with those described by Simpson (1937, p. 84-94).

There are two specimens consisting of the anterior portion of  $P^4$ . Neither shows any indication of an additional third cusp row on the external margin. The cusp count of the only complete  $M^1$  is 9:10.

$M^2$  has three median cusps and three or four internal cusps. The posterior two median cusps are large. The remaining median cusp and the

TABLE 6. Measurements of *Ptilodus montanus* from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
P <sup>1</sup> Length	3	2.7-3.1	2.83	.23	8.15
Width	3	2.0-2.2	2.10	.10	4.76
P <sup>2</sup> Length	1	—	2.60	—	—
Width	1	—	2.20	—	—
P <sup>3</sup> Length	2	2.5-2.6	2.55	.07	2.77
Width	2	1.8-1.9	1.85	.07	3.82
P <sup>4</sup> Width	2	2.2-2.5	2.35	.21	9.03
M <sup>1</sup> Length	1	—	5.50	—	—
Width	6	2.3-2.6	2.40	.13	5.27
M <sup>2</sup> Length	4	2.5-2.7	2.58	.10	3.72
Width	4	2.3-2.5	2.38	.10	4.03
M <sub>1</sub> Length	4	3.3-3.7	3.53	.21	5.85
Width	4	1.5-1.8	1.60	.14	8.84
M <sub>2</sub> Length	2	—	3.00	—	—
Width	2	2.2-2.5	2.35	.21	9.03

internal cusps are small and nearly equal in size.

The only informative specimen of P<sub>4</sub> is SMM P77.8.26, a partial blade in which all of the serrations are preserved. There are sixteen serrations and the length from the first serration to the posterior margin is 7.2 mm. The length of the complete blade was probably about 9.0 mm, and the width was in excess of 2.5 mm. The labial ridges leading to the first four serrations converge anteriorly. There are no ridges on the lingual side leading to the last four serrations. A wear facet is present on the labial side anteroventral to the last five serrations.

M<sub>1</sub> possesses seven external and five internal cusps (modal value). The first two external cusps are crescentic and concave anterior, the third is bicrescentic, and the remaining cusps are crescentic and concave posterior. The internal cusps have straight transverse margins and a transverse groove on the labial side. The last internal cusp has two such labial grooves.

M<sub>2</sub> bears two internal and four external cusps. These cusps are similar to those of M<sub>1</sub> except that all are concave posterior and have transverse grooves on their median faces.

*Discussion.*—These specimens differ markedly from *P. wyomingensis* as it is known from its type locality and from the Judson locality. The lower blade is longer and has more serrations. Both M<sub>1</sub> and M<sub>2</sub> are longer. The anterior upper premolars are relatively shorter and wider. The internal cusp row of M<sup>1</sup> is shorter. The differences in the length of P<sub>4</sub> and M<sub>2</sub> and the proportions of P<sup>1</sup>-P<sup>3</sup> are features in which the present sample resembles *P. montanus* from Crazy Mountain Field. The only notable differences between these

specimens and the type series of *P. montanus* are the larger serration count of P<sub>4</sub> and the greater length of M<sub>2</sub>. These differences, however, are smaller than those between the Brisbane specimens and other species of *Ptilodus*, and are no more than would be expected due to sampling error resulting from the relatively small size of the Brisbane sample.

#### *Ptilodus wyomingensis* Jepsen, 1940

Table 7, figs. 3.1, 3.4-.5, 3.7

*Referred specimens.*—P<sup>1</sup>, SMM P77.6.1, P77.7.1-4; P<sup>2</sup>, P77.6.2-3, P77.7.5-11; P<sup>3</sup>, P77.6.4-5, P77.7.12-14; P<sup>4</sup>, P77.6.6-8, P77.7.15-27; M<sup>1</sup>, P77.6.9, P77.7.28-32; M<sup>2</sup>, P77.7.33-35; I<sub>1</sub>, P77.6.10-16, P77.7.36-39; P<sub>4</sub>, P77.6.17-24, P77.7.40-49; M<sub>1</sub>, P77.7.50-51; M<sub>2</sub>, P77.7.52-54.

*Locality.*—Judson locality, Tongue River Formation, Morton County, North Dakota.

*Description.*—Except as noted, the specimens referred here are similar to those described by Jepsen (1940; p. 283-289).

P<sup>4</sup> is long and slender with two long cusp rows. The internal row extends the full length of the crown. Each internal cusp bears short anterior and posterior longitudinal crests and a longer transverse crest on the external face. In occlusal view the internal row is gently concave lingually, and in lateral view it is nearly straight. The external cusp row is shorter, lower, and its cusps are better separated. Each cusp has anterior and posterior longitudinal crests and does not usually develop transverse crests. In occlusal view the external row is markedly concave on its lingual side. All of the cusps commonly develop radial ridges and grooves in the enamel. In addition

TABLE 7. Measurements of *Ptilodus wyomingensis* from the Judson locality.

Dimension	N	Range	Mean	SD	V
P <sup>1</sup> Length	5	2.2-2.8	2.44	.25	10.29
Width	5	1.5-2.0	1.74	.19	11.20
P <sup>2</sup> Length	9	2.5-3.2	2.78	.22	7.80
Width	9	1.9-2.8	2.26	.27	11.75
P <sup>3</sup> Length	5	2.5-3.2	2.78	.27	9.65
Width	5	1.7-2.1	1.92	.16	8.56
P <sup>4</sup> Length	12	4.5-5.4	4.88	.27	5.44
Width	12	1.8-2.5	2.14	.21	9.85
M <sup>1</sup> Length	4	4.5-5.2	5.03	.35	6.97
Width	5	2.2-2.5	2.32	.13	5.62
M <sup>2</sup> Length	3	2.4-2.6	2.50	.10	4.00
Width	3	2.3-2.4	2.37	.06	2.44
P <sub>4</sub> Length	9	6.5-8.1	7.23	.45	6.26
Width	11	2.4-3.2	2.67	.23	8.71
M <sub>1</sub> Length	2	3.5-3.7	3.60	.14	3.93
Width	2	1.6-1.7	1.65	.07	4.29
M <sub>2</sub> Length	2	2.0-2.3	2.15	.21	9.87
Width	3	1.9-2.0	1.93	.06	2.99

there is a finer scale sculpture consisting of minute parallel longitudinal ridges that is especially prevalent on the lingual face of the crown.

The wear on P<sup>4</sup> consists of a shear facet on the lingual face and a set of horizontal abrasion craters on the apices of the internal cusps. The shear facet forms first along the base of the crown and later expands ventrally along the posterior margin of the lingual face, eventually encompassing the sides of the posteriormost internal cusps. One set of striae on this facet is directed anteroventrally at a small angle from the horizontal. A second set is oriented approximately perpendicular to the first. The horizontal abrasion craters show considerable variation in the position of maximum wear; it may be either anterior or posterior of the midpoint.

M<sup>1</sup> has a rounded posterior margin and tapers anteriorly. The internal cusp row tapers anteriorly with the individual cusps becoming indistinct. The median cusp row is slightly concave externally. Its cusps are of equal size and are separated by concave-forward crescentic valleys. The external row is essentially straight. Its cusps are about the size of the median cusps but are not crescentic. On the median face of each internal and external cusp, and on both sides of each median cusp, there is a transverse groove. Wear is largely restricted to the longitudinal valleys separating the cusp rows, but there is also a vertical facet on the internal side of the crown.

The latter facet usually involves the removal of the anterior end of the internal cusp row.

M<sup>2</sup> tapers posteriad. Its anterior margin is gently concave, matching the shape of the posterior margin of M<sup>1</sup>. The cusp formula is 3:3, excluding the external cusp row, which consists only of a low cuspidate ridge. The internal cusps are about the size of their posterior counterparts in M<sup>1</sup>, whereas the median cusps are larger. The internal and median cusps bear grooves similar to those of M<sup>1</sup>. The external row continues posteriad to merge smoothly with the last median cusp.

The modal serration count of P<sub>4</sub> is 14. The lateral profile is illustrated in figure 3.1. On the labial side nearly all of the ridges descend ventrally to the level of the standard length. There is no significant branching of the ridges near the posterior end, although on some specimens there are some irregular folds in the enamel above the posterolabial ledge. On the lingual side there are no ridges leading to the last three or four serrations. The posterolabial ledge curves down from the last serration, becoming horizontal at its anterior end. The ledge is narrow and the anterior portion is soon obliterated by wear. The anterior root is grooved and there is a deep anterior basal concavity indicating the presence of P<sub>3</sub>. There are two striae sets on the triangular shear facet above the posterolabial ledge. The two sets are perpendicular and parallel to the standard length. Abrasion occurs on the top of the



apical crest and may eventually remove much of the posterior part of the tooth. In addition, abrasion is in evidence on the side of the exodaenodont lobe.

$M_1$  has two cusp rows, each with six cusps. The transverse valleys separating the cusps are arcuate and concave posteriad, except for the anterior margins of the second and third external cusps which have the opposite curvature. Wear occurs on both sides of all cusps, but the wear on the internal side of the internal row is much less than on the other surfaces.

The cusp formula of  $M_2$  is 4:2. The intercusp valleys are concave posteriad. Wear on the internal side of the internal cusp row is the least, but it is more than the corresponding wear on  $M_1$ .

*Discussion.*—The specimens described above are easily distinguished from *P. mediaevus* Cope (1881) by the smaller size and larger serration count of  $P_4$  and the smaller size and differing cusp formula and structure of  $P^4$ . These specimens are similar to *P. montanus* in the shape and serration count of  $P_4$ , but these  $P_4$ 's are much shorter. The size and cusp formulae of the other parts of the dentition do not differ greatly from *P. montanus*.

The Judson specimens are most similar to *P. wyomingensis* from the Rock Bench level of the Polecat Bench Formation, Wyoming. The only major difference lies in the length of  $P_4$ . The mean length of  $P_4$  in the Judson sample is 7.2 mm and that for *P. wyomingensis* is 7.6 mm. Using a taxonomically conservative estimate of 0.5 mm for the standard deviation in *P. wyomingensis*, this difference in the means is not significant at the  $p=0.1$  level. Although this difference in means between *P. wyomingensis* and *P. montanus* is comparable (0.44 mm), the difference is significant at the  $p=0.01$  level because of the larger size and smaller variance of the latter sample. The difference in the mean lengths of  $P_4$  does not warrant specific separation of the Judson specimens from *P. wyomingensis*. The other differences in the two samples are all minor. Important similarities include the reduced curvature of the lower incisor and the relatively long, narrow proportions of the upper premolars.

***Ptilodus kummae* Krause, 1977**

Fig. 3.3

*Referred specimens.*—Left  $P^1$ , FMNH PM8665; right  $P^3$ , PM8666; left  $P_4$ , PM8667.

*Locality.*—Riverdale locality, Tongue River Formation, McLean County, North Dakota.

*Description.*— $P^1$  is subtriangular with three cusps, one anterior median cusp and two transversely arranged posterior cusps. The anterior margin is rounded, and the posterior margin is oblique with the internal corner being the most posterior point of the crown. There is a diagonal crest on the anterior cusp extending from its anterior margin to its posterolabial margin. The external posterior cusp bears a longitudinal crest. The internal posterior cusp is conical. The length and width are 2.4 mm and 1.8 mm.

$P^3$  is oblong with convex anterior and posterior margins. The cusp formula is 2:2. The antero-external cusp has a diagonal crest oriented as in the anterior cusp of  $P^1$ . The internal cusps bear longitudinal crests. The posteroexternal cusp is conical. The posterior slope of the posterior cusps is shallow. The tooth is 2.8 mm long and 1.9 mm wide.

The apical crest of  $P_4$  is very high (fig. 3.3). The labial side of the crown is markedly concave in anterior view. There are 13 serrations. The ridges on the labial side of the crown all terminate relatively far from the anterior margin of the exodaenodont lobe. The five anteriormost labial ridges converge anteriorly. The posterior two or three labial ridges appear to have been directed more ventrally than anteroventrally, but wear on this part of the crown has obscured their exact orientation. On the lingual side of the crown there are no ridges descending from the last three serrations. The posterolabial ledge descends almost parallel to the posterior root. It may have curved to a more horizontal orientation, but its anterior end has been broken away. Above the ledge there is an oblong wear facet which extends over parts of the last five ridges, but which does not extend ventrad to include the ledge itself. Striae on the facet descend posteriorly at about 15 degrees relative to the standard length. The exodaenodont lobe is robust, but not unusually large in areal extent. The anterior basal concavity is distinct, but not deep. The length is 6.3 mm, the width 2.6 mm.

*Discussion.*—There is little doubt that these specimens represent a newly described species, *P. kummae*, from the Roche Percee local fauna, Ravenscrag Formation, Saskatchewan (Krause, 1977). They are readily distinguishable from all other species of the genus. Although the size of the Riverdale  $P_4$  falls at the lower limit of variation for *P. kummae*, its distinctive

morphology agrees well with the Roche Percee sample.

**Prochetodon sp.**

Figs. 3.6, 3.8-9

*Referred specimen.*—Left P<sup>2</sup>, SMM P77.7.55; left P<sup>4</sup>, P77.7.56.

*Locality.*—Judson locality, Tongue River Formation, Morton County, North Dakota.

*Description.*—There are four cusps on P<sup>2</sup> arranged in two longitudinal rows of two. The posterolingual cusp is subconical and bears anterior, posterior, and labial crests descending radially from its apex. The remaining three cusps are joined together in a quarter-circular ridge composed of diametrically opposed crests radiating from the apex of each cusp. The enamel is smooth. Interdental wear facets are present on both the anterior and posterior ends. The length is 2.4 mm and the width is 1.8 mm. For a comparison of this tooth to P<sup>2</sup> of *Ptilodus*, see figs. 3.5 and 3.8.

The roots of P<sup>4</sup> are bilaterally symmetric except for their oblique central faces, both of which are directed anterolingually. The roots are slender, the anterior being circular and the posterior longitudinally elongate. The anterior and posterior margins of the crown are transverse, the former overhanging the anterior root only slightly. The labial and lingual margins are nearly parallel, converging somewhat posteriad. The labial base of the crown bulges labiad adjacent to the anterior root. In profile the lingual base of the enamel is horizontal, whereas the labial base rises gently at both ends. The crown length is 5.3 mm, the width 1.7 mm.

The internal cusp row of P<sup>4</sup> is slightly concave lingually and extends from the posterolabial corner of the crown to a point just labial to the anterolingual corner. There are 12 internal cusps which are of equal size although their heights above the enamel base increase posteriorly. The anterior internal cusps are three sided and pyramidal, having lingual, anterolabial, and posterolabial faces. Posteriad the internal cusps become more conical and less pointed. There are eight distinct cusps and several minute cuspules in the external row. Of these the second is the highest. Each external cusp is paired transversely with one of the first eight internal cusps, and is a three-sided pyramid arranged as a mirror image of the corresponding internal cusp. P<sup>4</sup> is

shown in figs. 3.6 and 3.9. For a comparison with P<sup>4</sup> of *Ptilodus*, see figs. 3.4 and 3.7.

P<sup>4</sup> bears a large anterior interdental wear facet and a small posterior one. Two additional wear facets occur on the lingual face of the crown, one at the base of the enamel toward the anterior end and one on the near vertical posterior margin of the face.

*Discussion.*—Jepsen (1940) referred a single P<sup>4</sup> to *Prochetodon cavus*. SMM P77.7.56 resembles that specimen in its general features, but differs in having twelve rather than ten external cusps, a longer row of more distinct cusps, and more parallel labial and lingual margins. SMM P77.7.55 differs from Jepsen's only referred specimen of P<sup>2</sup> in having four rather than three cusps. In spite of these differences, the two North Dakota specimens agree so well in structure with a much larger sample of *Prochetodon* from the Roche Percee local fauna now being studied by D. Krause that there can be little doubt of the generic identification.

Family NEOPLAGIAULACIDAE Ameghino,  
1890

**Mesodma sp.**

Figs. 3.10, 3.13, 3.16

*Referred specimens.*—Left P<sup>4</sup>, SMM P77.8.33; right P<sub>4</sub>, P77.8.34.

*Locality.*—Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Description.*—P<sup>4</sup> is minute, measuring 1.8 mm long by 0.7 mm wide. The cusp formula is 2:6. The posterior slope bears a longitudinal groove and descends in a more or less straight line to a basal cuspule. The roots are very slender and are overhung equally by the anterior and posterior ends of the crown.

P<sub>4</sub> is 2.2 mm long and 0.8 mm wide. There are eight or nine serrations; a small portion of the enamel is missing from the anterior end of the tooth, making an exact serration count and measurement of the relative height of the first serration impossible. The apical crest is a smooth, low arc whose highest point is elevated about one-third of the standard length above that length. The ridges on the sides of the crown are all simple arcs that descend anteroventrally with no branching. The exodaenodont lobe is large with anterior and posterior margins that lie about 60 degrees to the standard length. There is an



TABLE 8. Measurements of *Ectypodus* sp. from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
P <sup>4</sup> Length	5	2.2-2.3	2.22	.04	2.01
Width	5	.7- .9	.84	.09	10.65
P <sub>4</sub> Length	2	— —	2.70	—	—
Width	2	.9-1.1	1.00	.14	14.14

anterior basal concavity, indicating the former presence of P<sub>3</sub>.

*Discussion.*—The small size of P<sup>4</sup> and P<sub>4</sub>, the low profile of P<sub>4</sub>, and the cusp and serration counts of these specimens suggest that they represent a small, undescribed species of *Mesodma* that is currently under study by R. E. Sloan. This species is known from a number of Torrejonian and Tiffanian localities, including Gidley Quarry, Rock Bench, the Black Peaks Formation, Swain Quarry, Shotgun, Bison Saddle, and Police Point.

***Ectypodus* sp.**

Table 8, figs. 3.11, 3.14, 3.17

*Referred specimens.*—P<sup>4</sup>, SMM P77.8.35-39; P<sub>4</sub>, P77.8.40-41.

*Localities.*—Brisbane locality, Tongue River Formation, Grant County, North Dakota, and possibly Judson locality, Tongue River Formation, Morton County, North Dakota.

*Description.*—P<sup>4</sup> is relatively narrow, resulting in a trenchant appearance (fig. 3.17). The most common cusp formula is 2:7. The apices of the internal cusps form a nearly straight line with a slight tendency to lingual convexity. The posterior slope is straight in some specimens and concave in others. There is no distinct basal cuspule.

The apical crest of P<sub>4</sub> is moderately low and arcuate (fig. 3.11). There are ten or eleven serrations. The relative height of the first serration is 0.36. The ridges leading to the serrations descend anteroventrally without branching. The central ridges descend below the level of the standard length. The anterior ridges converge and terminate relatively close to the anterior margin of the tooth. The posterolabial ledge is poorly developed. There is a strongly developed anterior basal concavity for the accommodation of P<sub>3</sub>.

*Discussion.*—The steep anterior margin, low first serration, and the relatively low profile of P<sub>4</sub>, and the trenchant shape and nearly straight anterior and posterior slopes of P<sup>4</sup> are characters typical of the genus *Ectypodus*. The specimens

referred here are indistinguishable from an undescribed species of *Ectypodus* known from the Torrejon, Gidley Quarry, and Swain Quarry that is currently under study by R. E. Sloan.

A single specimen of P<sup>4</sup> SMM P77.7.57 from the Judson locality may also belong to this species. It is 2.2 mm long and 0.8 mm wide with a cusp formula of 3:7. Although it is not distinguishable from the P<sup>4</sup>'s referred above, it cannot be identified with certainty beyond its inclusion in *Ectypodus*.

***Neoplagiaulax hunteri* (Simpson, 1936)**

Tables 9-10, figs. 4.1-3

*Referred specimens.*—P<sup>4</sup>, SMM P77.7.58, P77.8.42; P<sub>4</sub>, P77.7.59-60, P77.8.43-45.

*Localities.*—Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, North Dakota.

*Description.*—The crown of P<sup>4</sup> is high and has a distinctive triangular lingual profile. A slight labial projection of the anterior labial margin supports the external cusps. The penultimate serration is the highest on all three specimens. The posterior slope leading to the last serration is somewhat concave. The length, width, and cusp formula for SMM P77.7.58 and P77.8.42 are 3.2 mm, 1.5 mm, 2:9, and 3.7 mm, 1.5 mm, 1:9, respectively.

The apical crest of P<sub>4</sub> rises from its anterior end at an angle of about 60 degrees relative to the standard length. The crest then gradually becomes parallel to the standard length, and at about the eighth serration it takes a sharp bend and descends at an angle of 75 degrees to the posterior end of the crown. There are 15 to 17 closely spaced serrations. The relative height of the first serration is 0.39. The labial ridges are fine but distinct and are nearly parallel to the anterior portion of the apical crest. The labial ridges extend ventrad almost to the level of the interradicular notch. The exodaenodont lobe is large. Its anterior and posterior margins lie at angles of about 50 degrees to the standard length. The labial enamel base above the posterior root



TABLE 9. Measurements of *Neoplagiaulax hunteri* from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
P <sup>4</sup> Length	1	----	3.70	—	—
Width	1	----	1.50	—	—
P <sub>4</sub> Length	3	4.5-4.9	4.67	.21	4.46
Width	3	1.6-1.8	1.70	.10	5.88

TABLE 10. Measurements of *Neoplagiaulax hunteri* from the Judson locality.

Dimension	N	Range	Mean	SD	V
P <sup>4</sup> Length	1	----	3.20	—	—
Width	1	----	1.50	—	—
P <sub>4</sub> Length	2	4.7-5.3	5.00	.42	8.49
Width	1	----	1.90	—	—

extends only a little below the level of the interradicular notch. The posterolabial ledge is short and narrow. Its posterior end curves dorsad to meet the last serration. Above the ledge and perpendicular to it are several ridge-like crenulations in place of a ridge leading to the last serration. There is a well developed anterior basal concavity for the accommodation of P<sub>3</sub>. The anterior root is much more robust than the posterior.

*Discussion.*—Both P<sub>4</sub> and P<sup>4</sup> have distinctive morphologies that are nearly identical to those of the type and referred specimens of *N. hunteri* from Scarritt Quarry of the Crazy Mountain Field, Montana. Notable differences include the greater length of P<sub>4</sub> (difference in means of 0.3 mm is not significant at p=0.01 level) and the presence of an additional serration on P<sub>4</sub> (mean value) in the North Dakota sample. Neither difference warrants specific separation of these specimens from *N. hunteri*.

Molars of this species probably occur in the collections from both localities, but the similar size of *Neoplagiaulax* sp. (1), also present at both localities, precludes their positive identification.

#### *Neoplagiaulax nanophus*, new species

Table 11, fig. 4.4

*Type specimen.*—Right P<sub>4</sub>, SMM P77.7.61.

*Paratypes.*—Right P<sub>4</sub>, SMM P77.7.62; left P<sub>4</sub>, P77.7.63-64.

*Locality.*—Judson locality, Tongue River Formation, Morton County, North Dakota.

*Etymology.*—*nanophos*, Gr., of dwarfish stature.

*Diagnosis.*—Length of P<sub>4</sub> is 3.3 mm, less than all known species of *Neoplagiaulax*; eleven serrations on P<sub>4</sub>, relative height of first serration 0.33, third or fourth serration highest above standard length.

tions on P<sub>4</sub>, relative height of first serration 0.33, third or fourth serration highest above standard length.

*Description.*—Except on SMM P77.7.64, the anterior end of the apical crest of P<sub>4</sub> is nearly straight. There are ten or eleven serrations; the relative height of the first is 0.33. Most of the labial ridges descend below the level of the standard length. The anterior labial ridges terminate in a straight line that parallels and is close to the anterior margin of the exodaenodont lobe. The posterior two or three ridges curve posteriad and descend perpendicular to the posterolabial ledge. The antepenultimate ridge may branch into three parts, one of which parallels the anterior ridges while the others curve posteriad. The posterolabial ledge is perpendicular to the standard length at its posterior end and parallel to it at its anterior end. The ledge is short, terminating below the antepenultimate serration.

Though it is typical in most characters, the type specimen possesses a minute accessory serration at the anterior end of the apical crest. The cuspule is a mere peaking of the enamel and lacks any indication of lateral ridges descending from it. Thus, the profile of the anterior slope of the apical crest (fig. 4.4) appears to be atypically short, steep, and angular.

A moderately deep anterior basal concavity and flattening of the anterior face of the anterior root suggest that P<sub>3</sub> was present in three of the four specimens. A weak concavity and no flattening of the root on SMM P77.7.62 indicate that P<sub>3</sub> may have been absent in this specimen. The anterior and posterior roots of all specimens are parallel. The anterior root is longitudinally elongate,

TABLE 11. Measurements of *Neoplagiaulax nanophus* from the Judson locality.

Dimension	N	Range	Mean	SD	V
P <sub>4</sub> Length	4	3.2-3.4	3.28	.10	2.92
Width	4	1.2-1.3	1.23	.05	4.08

whereas the posterior is slender and cylindrical. There is a small lobe-like keel between the roots.

*Discussion.*—Because of their small size and moderately low profile, these teeth were first thought to represent *Ectypodus powelli* Jepsen (1940). Subsequent discussions with R. E. Sloan revealed that in the context of his revision of the family (study in progress) these specimens would be more appropriately placed in the genus *Neoplagiaulax*. The important traits governing this assignment are (1) the straightened, recumbent anterior end of the apical crest and (2) the branching and reverse inclination of the posterior labial ridges. These characters are absent in *Ectypodus*, except that *E. powelli* exhibits the former. Both of these characters are, however, present in nearly all species of *Neoplagiaulax*.

The small size of this species immediately distinguishes it from all known species of *Neoplagiaulax* (including all undescribed species currently under study by R. E. Sloan). It differs from *Ectypodus powelli* in bearing postero-ventrally inclined posterior labial ridges on P<sub>4</sub> and in having the posterior root of P<sub>4</sub> parallel to the anterior edge of the anterior root.

A number of specimens from the Roche Percee local fauna that were referred to *Ectypodus* cf. *powelli* by Krause (1977) may be referable to *Neoplagiaulax nanophus*. The roots of P<sub>4</sub> in at least one of the Roche Percee specimens (Krause 1977: Plate 6) lie at angles similar to those

observed in *N. nanophus* and differ from *E. powelli* in which the posterior root is inclined toward the anterior root. The same figured specimen from Roche Percee clearly exhibits branching and reverse inclination of the posterior lateral ridges that is typical of *Neoplagiaulax* and is in contrast to *E. powelli* and to *Ectypodus* generally. The differences between the Judson and Roche Percee specimens in the profile of P<sub>4</sub> are slight and do not in themselves warrant specific or generic separation of the two samples.

***Neoplagiaulax* sp. (1)**

Tables 12-13, figs. 4.5-.6, 4.9

*Referred specimens.*—P<sup>4</sup>, SMM P77.7.65-66, P77.8.46-50; left mandible with P<sub>3</sub>-P<sub>4</sub>, P77.8.51; P<sub>4</sub> P77.6.26-27, P77.8.52-54.

*Localities.*—Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, North Dakota.

*Description.*—The upper fourth premolars are long, low, and narrow. There are seven or eight internal cusps and two or three external cusps. The internal cusp row forms a low arc in which the penultimate cusp is usually the highest. The posterior root of most specimens is tapered.

The anteriormost alveolus of the mandible (SMM P77.8.51) shows that the lower incisor was laterally compressed. Maximum and minimum diameters of the alveolus are 1.7 mm and 1.1 mm. The lower third premolar is small and cylindrical

TABLE 12. Measurements of *Neoplagiaulax* sp. (1) from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
P <sup>4</sup> Length	4	2.9-3.5	3.20	.24	7.65
Width	5	1.3-1.5	1.40	.07	5.05
P <sub>4</sub> Length	4	4.2-4.8	4.50	.36	7.91
Width	4	1.7-2.1	1.83	.19	10.37

TABLE 13. Measurements of *Neoplagiaulax* sp. (1) from the Judson locality.

Dimension	N	Range	Mean	SD	V
P <sup>4</sup> Length	2	2.9-3.2	3.05	.21	6.96
Width	2	1.2-1.3	1.25	.07	5.66
P <sub>4</sub> Length	2	4.5-5.1	4.80	.42	8.84
Width	2	— — —	1.80	—	—

with a hemispherical, enamelled crown.  $P_4$  has an apical crest that is nearly circular in lateral profile (see fig. 4.5). The modal serration count is 13. The relative height of the first serration is 0.41. The external ridges of the anterior two or three serrations converge anteriorly but do not actually join. The external ridge of the antepenultimate serration branches ventrally; there is usually a branch parallel to the anterior ridges and one or more branches leading down toward the posterolabial ledge. The external ridges of the last two serrations parallel the posterior branch of the ridge preceding them. The posterolabial ledge is short and simple, terminating below the antepenultimate serration. The anterior margin of the exodaenodont lobe is distinctive, possessing two slight emarginations that result in a gentle sinusoidal curve. The exodaenodont lobe itself is broad. There is a pronounced anterior basal concavity for the accommodation of  $P_3$ . The anterior root of  $P_4$  is anteroposteriorly elongate, whereas the posterior root is slender and cylindrical. The alveolar lengths for  $M_1$  and  $M_2$  are 2.1 mm and 1.2 mm, their estimated crown lengths are 2.5 mm and 1.4 mm.

*Discussion.*—The elements of the lower dentition can be referred with some certainty to a new but undescribed species of *Neoplagiaulax* under study by R. E. Sloan and known from Cedar Point Quarry, Polecat Bench Formation, Wyoming. The upper fourth premolars of this species are not known from Cedar Point Quarry. Consequently, the  $P_4$ 's described above were referred only on the basis of frequency, their reasonable size, and their morphology, which is typical of the genus.

**Neoplagiaulax sp. (2)**

Figs. 4.7, 4.10

*Referred specimen.*—Right  $P^4$ , SMM P77.8.55.

*Locality.*—Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Description.*—The upper fourth premolar is 5.0 mm long and 1.8 mm wide. The crown is high and narrow with a moderately arched internal cusp row and a gently concave posterior slope. There is one external cusp and eight internal cusps, of which the antepenultimate is the highest.

*Discussion.*—On the basis of its form, there is little doubt that this tooth represents a species of *Neoplagiaulax*. The only species of the genus that are comparable in size to this specimen are *N. grangeri* (Simpson, 1935b) and *N. douglassi* (Simpson, 1935b). Unfortunately  $P^4$  is unknown in both species, so that direct comparison with this specimen is impossible.

**Neoplagiaulax sp. (3)**

Table 14, figs. 4.8, 4.11

*Referred specimens.*— $P^4$ , SMM P77.6.28-29, P77.7.67.

*Locality.*—Judson locality, Tongue River Formation, Morton County, North Dakota.

*Description.*—The crown of  $P^4$  is long and low. In occlusal view the entire crown is gently concave lingually. In lateral view the internal cusp row rises in a gentle arc. It has eight or nine cusps of which the antepenultimate is the highest. The posterior slope from the ultimate cusp to the base is concave in lateral view.

*Discussion.*—The low relatively broad crowns of these teeth distinguish them from other genera of neoplagiaulacids and from *Anconodon*, whose  $P^4$  has a low narrow crown. The large size of these teeth suggests that they may represent *N. hazeni* (Jepsen, 1940), *N. grangeri*, or *N. douglassi*, but the  $P^4$ 's of these species are too poorly known to permit a specific identification.

**Parectypodus sp.**

Table 15, figs. 3.12, 3.15, 3.18

*Referred specimens.*— $P^4$ , SMM P77.8.56;  $P_4$ , P77.6.30, P77.7.68-70, P77.8.57.

TABLE 14. Measurements of *Neoplagiaulax* sp. (3) from the Judson locality.

Dimension	N	Range	Mean	SD	V
$P^4$ Length	3	3.8-4.0	3.90	.10	2.56
Width	2	— — —	1.50	—	—

TABLE 15. Measurements of *Parectypodus* sp. from the Judson locality.

Dimension	N	Range	Mean	SD	V
$P_4$ Length	4	2.9-3.2	3.03	.13	4.16
Width	3	1.0-1.1	1.07	.06	5.41



*Localities.*—Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, North Dakota.

*Description.*—The upper fourth premolar is 2.5 mm long and 1.1 mm wide. There are seven internal cusps, of which the second is the highest. There are three external cusps, but the anterior-most of these is minute. In side view the posterior slope is gently concave and the primary cusp row is gently convex. In occlusal view the crown is broad, widening smoothly anteriorly with no abrupt lateral swelling near the external cusps.

The apical crest of  $P_4$  is nearly semicircular with a gradual posterior decrease in curvature (fig. 3.12). There are ten to twelve serrations, twelve being the most common number. The relative height of the first serration is 0.36. The labial ridges leading to the posterior serrations descend ventrad to about the level of the standard length. The anterior labial ridges terminate along a line parallel to the anterior margin of the exodaenodont lobe. On the only unworn tooth the labial ridge leading to the antepenultimate serration branches into three parts. The posterolabial ledge is distinct but very short and narrow. A large triangular wear facet develops above the posterolabial ledge. The anterior basal concavity is well developed, indicating the presence of  $P_3$  in this species.

*Discussion.*—The high, arching apical crest with a high first serration, the great labial enamel height, and the large posterior angle of  $P_4$  all indicate that these specimens represent a species of *Parectypodus* (for a revised generic diagnosis, see Sloan, 1966). On some specimens there is a protuberance low on the apical crest that is not fully developed into a serration; this condition is also characteristic of *Parectypodus* (R. E. Sloan, personal communication). The size and structure of the specimens referred here are almost identical to those of a new species of *Parectypodus* from the Shotgun Local Fauna that is currently under study by R. E. Sloan. The generic trend toward vertical elongation of  $P_4$  and the addition of external cusps to  $P_4$  are not accentuated in this species, which is therefore only a moderately progressive member of the genus.

Family EUCOSMODONTIDAE (Jepsen, 1940)

***Microcosmodon woodi***

Holtzman and Wolberg, 1977

Figs. 5.1-4, 5.7

*Type.*—Right  $P_4$ , MCZ 19963.

*Paratype.*—Right  $P_4$ , MCZ 19964.

*Type locality.*—New Anthill locality, anthill L, Shotgun Member, Fort Union Formation, Fremont County, Wyoming. (Precise geographic location on file at the Harvard Museum of Comparative Zoology.)

*Referred specimens.*—Right  $P_4$ , UMVP 5938, SMM P77.8.1-2; right  $M^1$ , SMM P77.8.6; left  $M^1$ , SMM P77.8.7; right  $I_1$ , SMM P77.8.3; left  $P_4$ , SMM P77.8.4-5; right  $P_4$ , UMVP 5001.

*Localities.*—Circle locality, Tongue River Formation, NW $\frac{1}{4}$  sec 7, T18N, R48E, McCone County, Montana; Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Etymology.*—Named for Craig B. Wood, who collected the type and paratype.

*Diagnosis.*—Differs from *M. conus* by the presence of a larger, longer, and lower  $P_4$  that exhibits more distinct serrations, five or six in number, the first of which is set low on the apical crest.

*Description and discussion.*—The specimens referred to *M. woodi* and the affinities of this species are discussed in detail by Holtzman and Wolberg (1977).

The original description of *M. woodi* employed the notation of M in reference to the tooth traditionally denoted P in ptilodontoid and taeniolabidoid multituberculates. I have since concluded that the traditional notation should be retained at least until the premolar homologies between plagiaulacoid and later multituberculates is better understood.

Order MARSUPIALIA

Family DIDELPHIDAE Gray, 1821

***Peradectes elegans*** Matthew and Granger, 1921

Figs. 5.5-6

*Referred specimens.*— $M^3$ , SMM P77.8.58;  $M_1$ , P77.8.59-60.

*Locality.*—Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Description.*—The paracone of  $M^3$  is slightly lower than the metacone. The paraconule is a little larger than the metaconule, but both are minute. There is no lingual cingulum. The stylar cusps are low; cusps B and D are the largest and cusp C, now broken, appears to have been only a little smaller. The crown is 1.6 mm long and 1.9 mm wide.

The protoconid of  $M_1$  is distinctly higher than the metaconid and the paraconid is higher than

the entoconid. There is a short but pronounced anterolabial cingulum. The hypoconulid of SMM P77.8.59 is more lingual and is much further separated from the entoconid than is that of SMM P77.8.60. Both specimens have identical measurements; length, 1.6 mm, anterior and posterior widths, 0.8 mm.

*Comparisons.*—Relative to AMNH 17382 (*P. elegans* from the type locality) this  $M^3$  has reduced styler cusps, centrocrista, and metaconule. The paracone and metacone are more conical and the ectoflexus is deeper. Both teeth have the same proportions, but the Brisbane specimens are a little smaller.

The left  $M_1$  of the type of *P. elegans*, AMNH 17376, has a relatively higher metaconid than either Brisbane specimen. The metaconid of the only known  $M_1$  of *P. pauli* (USNM 20880) was probably about as low as in the Brisbane teeth, but extensive wear on the protoconid makes the metaconid appear quite high. (Cusp heights were compared in posterior view parallel to the trigonid sides.) Of the four available specimens of  $M_1$  the separation between the entoconid and hypoconulid is greatest on SMM P77.8.59 and least on SMM P77.8.60.

*Discussion.*—*P. pauli* Gazin (1956) was separated from *P. elegans* because of the smaller size of the lower molars, "slightly less elevated" protoconids and hypoconids, more closely situated entoconids and hypoconulids, and relatively shorter and narrower talonids. In both the type and paratype of *P. pauli* (the only known specimens) the protoconids, metaconids, and hypoconids are all appreciably worn, making a reliable assessment of their unworn heights impossible. As noted above, the two Brisbane molars (which are identical in all other respects) differ more in the position of the hypoconulid than do *P. elegans* and *P. pauli* as compared by Gazin. It is likely, therefore, that this difference noted by Gazin falls within reasonable limits of intraspecific variation. The remaining characters that distinguish *P. pauli* from *P. elegans* are potentially significant. But in view of the small sample sizes, the differences are too small to warrant specific separation. Consequently, I regard *P. pauli* as a junior synonym of *P. elegans*.

The specimens referred here are distinguishable from *P. protinominatus* McKenna (1960) by the relatively greater length of  $M^3$  and lower metaconid of  $M_1$ . The possibility that SMM

P77.8.58 represents  $M^2$  of *P. protinominatus* is improbable because of its deeper ectoflexus.

Comparison of the Brisbane teeth to the type and other specimens of *P. elegans* reveals no differences that require their specific separation.

#### Order INSECTIVORA

Family PALEORYCTIDAE Winge, 1917

*Paleoryctes* sp., cf. *P. punctatus* Van Valen, 1966

Tables 16-17, figs. 5.8-10

*Referred specimens.*—Partial  $P^4$ , SMM P77.7.71; probable  $M^2$ , P77.7.72, P77.8.61-62, P77.7.73 (partial); P77.8.63 (partial);  $M_1$ , P77.7.74, P77.8.64;  $M_2$ , P77.7.75-76, P77.8.65 (partial); partial  $M_2$  or  $M_3$ , P77.7.77.

*Localities.*—Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, North Dakota.

*Description.*—SMM P77.7.71 consists of the labial portion of  $P^4$ . The paracone is larger than it is on the molars and is centrally located. A distinct metacone is present; it is laterally compressed and is more separate from the paracone than on the molars. Behind the metacone there is a small notch preceding the metastyle. The parastyle is a low but acute cusp joined to the paracone by a low paracrista; it is well separated from the paracone but is joined to its anterior base by a paracingulum, which bears a minute accessory cuspule. The labial margin of the crown is nearly straight. An ectocingulum is present posteriorly and terminates anteriorly in a mesostyle immediately labial to the paracone apex.

The probable second upper molars (fig. 5.8) possess tall, acute, centrally located paracones. The metacone is lower and is connate with the paracone. The parastyle is distinct and pyramidal and projects anteriorly. An indistinct stylocone terminates the paracrista, which bears a small cariniform notch. The styler area is narrow. The metastyle projects labially and is separated from the metacone by a well developed cariniform notch. A small mesostyle is present on the ectocingulum at the deepest point of the moderately well developed ectoflexus. The paracingulum is continuous and well defined from the paraconule to the parastyle. The metacingulum continues labially from the metaconule to a point dorsal to the metacrista notch. The conules and conule wings are well developed but are soon obliterated by wear. A cariniform notch is variably present in the preprotocrista just lingual

TABLE 16. Measurements of *Paleoryctes* sp., cf. *P. punctatus* from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
?M <sup>2</sup> Length	2	1.9-2.3	2.10	.28	13.47
Width(A)	2	2.6-3.2	2.90	.42	14.63
Width(P)	2	3.0-3.6	3.30	.42	12.85
M <sub>1</sub> Length	1	----	2.20	—	—
Width(A)	1	----	1.60	—	—
Width(P)	1	----	1.30	—	—
M <sub>2</sub> Width(A)	1	----	1.50	—	—

TABLE 17. Measurements of *Paleoryctes* sp., cf. *P. punctatus* from the Judson locality.

Dimension	N	Range	Mean	SD	V
P <sup>4</sup> Length	1	----	2.00	—	—
?M <sup>2</sup> Length	2	1.9-2.1	2.00	.14	7.07
Width(A)	1	----	2.80	—	—
Width(P)	1	----	3.20	—	—
M <sub>1</sub> Length	1	----	2.00	—	—
Width(A)	1	----	1.50	—	—
Width(P)	1	----	1.20	—	—
M <sub>2</sub> Length	2	1.9-2.1	2.00	.14	7.07
Width(A)	2	----	1.50	—	—
Width(P)	2	1.1-1.2	1.15	.07	5.89
M <sub>2</sub> or M <sub>3</sub> Width(A)	1	----	1.50	—	—

to the paracone. The protocone is conical except for its flat, vertical labial face. There are no lingual cingula. The best developed shear facet occurs on the postvallum, although there is also a well developed prevallum facet. The protoconid apex of the lower molar wears a transverse groove between the parastyle and stylocone and obliterates the paracingulum anterior to the paracone.

The lower molars (figs. 5.9-.10) have greatly elevated trigonids, deep hypoflexids, and narrow talonids. The anteroexternal cingulum is short and steep. The protoconid is the highest cusp and its central face is flat and faces anterolingually. The metaconid is markedly lower and has a flat central face. The paraconid terminates a low semi-transverse blade-like paracristid; it is sub-internal on M<sub>1</sub> and nearly median on M<sub>2</sub>. The trigonid opens lingually to a vertical groove. The postvallid is slightly oblique. Its surface is not flat, but has the shape of a monocline whose axis runs from the metaconid apex to the labial base of the hypoflexid. Wear striae on the postvallid are parallel to the axis and occur only labiad to it. The talonid basin is shallow and inclined, descending anterolingually. The talonid cusps are all small but distinct. A mesoconid and entoconid are present. The hypoconid is close to the

hypoconid. On both the labial and lingual sides there is a sharp anterior rise in the base of the enamel at the position of the postvallid. The hypoconid is higher relative to the enamel base in M<sub>1</sub> than in M<sub>2</sub>. The cusps of both upper and lower molars are eventually lowered by abrasion.

SMM P77.7.77, an anterior fragment of a lower molar, has a short trigonid and a very transverse paracristid; it may represent M<sub>3</sub>.

*Discussion.* — The allocation of the upper molars as M<sup>2</sup> may be incorrect. Alternatively the first and second molars in this species may not be distinguishable, or the known molars may represent M<sup>1</sup>. Their allocation as probable M<sup>2</sup> is based on the position of the parastyle, which is anterolabial to the paracone and implies a relatively wide trigonid in the corresponding lower molar.

The mode of occlusion shown by these specimens differs from that of *Paleoryctes* described by Van Valen (1966, p. 64-65). In addition to the two modes described by Van Valen, these specimens show clear evidence of prevallum-postvallid shear. Furthermore, this shear stroke, although predominantly vertical, has a lateral component.

These specimens probably represent a new species, but the acquisition of more complete



material (particularly a better representation of the upper dentition) is necessary before this can be determined with certainty. The present sample differs from *P. puercensis* Matthew (1913) primarily in its greater size, weaker stylar area and ectoflexus, shallower talonid basin, and reduced entoconid. So far as can be determined, it differs from *P. punctatus* Van Valen (1966) in its slightly larger size and stronger ectoflexus, and in having the paracrista leading to a stylocone on M<sup>2</sup>. In addition, this sample differs from both species in possessing mesostyles, mesoconids, entoconulids, and more numerous carnassiform notches.

***Pararyctes pattersoni* Van Valen, 1966**

Table 18, figs. 5.11-13

*Referred specimens.*—Partial P<sup>4</sup>, SMM P77.19.1; M<sup>1</sup>, P77.8.66; M<sub>1</sub>, P77.8.67; M<sub>2</sub>, P77.8.68-69; M<sub>3</sub>, P77.8.70, P77.8.71 (partial).

*Localities.*—Brisbane and Brisbane West localities, Tongue River Formation, Grant County, North Dakota.

*Description.*—Only the labial portion of P<sup>4</sup> is preserved. The paracone is large and conical and is connate with the lower, laterally compressed metacone. A small notch separates the metacone and metastyle. The apices of these two cusps and the metastyle have been removed by abrasion. The parastyle projects anterolabially, creating a shallow ectoflexus. An ectocingulum is present on the posterior half of the external margin. A paracingulum may have been present, but if so it was very weak. A remnant of the metacingulum is present below the metacone. The length is 1.7 mm.

The upper first molar (fig. 5.11) is little worn and complete except for the greater part of the

paracone. The paracone and metacone are connate, but demarcated by shallow vertical grooves both internally and externally. The metacrista arcs smoothly to the posteroexternal corner of the crown. There is no distinct metastyle, nor is there a notch in the metacrista. The stylar area is quite narrow, with a complete ectocingulum and a moderate ectoflexus. The paracrista terminates in a weak stylocone just behind the anteriorly projecting parastyle. The conules are small and are located midway between the protocone and paracone. The metacingulum extends labiad beyond the metacone where it curves anteriorly and abutts the base of the metacrista. The only clear wear facet occurs on the preprotocrista and the paracingulum.

The lower molars possess elevated trigonids which are wider than the talonids (figs. 5.12-13). On the labial side there are steep anterior and posterior rises of the enamel base beginning at the midline of each root. On the lingual side there are similar rises, but the anterior rise is less steep and begins at the posterior root. There is a narrow anterolabial cingulum and above it a large shear facet bearing nearly vertical striae. The protoconid is only slightly taller than the metaconid; both are pyramidal cusps with approximately equiangular cross sections. The paraconid is subinternal on M<sub>1</sub> and nearly median on M<sub>3</sub>. On all three molars the paraconid and the lingual portion of the protocristid bear a transverse wear facet. The trigonid basin does not open smoothly to a lingual vertical groove but terminates at a faint metacristid. Notches are present in both the paracristid and the protocristid. The postvallid is nearly transverse on M<sub>1</sub>, becoming fully transverse on M<sub>3</sub>. The postvallid is flat with vertical wear striae distributed evenly over its entire

TABLE 18. Measurements of *Pararyctes pattersoni* from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
M <sup>1</sup> Length	1	----	1.70	—	—
Width(A)	1	----	2.20	—	—
Width(P)	1	----	2.30	—	—
M <sub>1</sub> Length	1	----	1.50	—	—
Width(A)	1	----	1.20	—	—
Width(P)	1	----	1.00	—	—
M <sub>2</sub> Length	2	1.5-1.8	1.65	.21	13.26
Width(A)	2	1.3-1.5	1.40	.14	10.10
Width(P)	2	1.0-1.2	1.10	.14	12.85
M <sub>3</sub> Length	1	----	1.80	—	—
Width(A)	2	----	1.50	—	—
Width(P)	1	----	1.00	—	—

surface. The talonid bears well developed and subequal hypoconid, hypoconulid, and entoconid. There is no mesoconid or entoconulid. On  $M_3$  the hypoconulid projects posteriorly. The apices of all cusps have been lowered by abrasion.

*Comparisons.*—In addition to the structural differences apparent from the above, the lower molars differ from those referred here as *Paleoryctes* sp. in having lower trigonids, both absolutely and relative to the talonids, and in having paraconids that are higher relative to the protoconid but lower relative to the enamel base. The upper molar differs from the type of *P. pattersoni* in having a higher and wider postcingulum and in being less transverse.

*Discussion.*—The size and structure of these specimens agree very well with the type series and other specimens of *P. pattersoni* from Cypress Hills (Krishtalka, 1973). The differences that do exist are consistent with intraspecific variation. As indicated by wear facets, the modes of occlusion consist primarily of vertical pre- and postvallum shear with some transverse motion; this agrees with Van Valen's (1966:65) description of occlusion in *Pararyctes*.

Family NYCTITHERIIDAE Simpson, 1928

***Leptacodon tener*** Matthew and Granger, 1921

Table 19, figs. 6.1-4

*Referred specimens.*—Left  $M^3$ , SMM P77.8.72; left mandible with  $P_4$ - $M_1$ , P77.8.73-74; right  $M_1$ , P77.8.75; right mandible with  $M_1$ - $M_2$ , P77.8.76; right mandible with  $M_2$ , P77.8.77.

*Locality.*—Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Description.*—The upper dentition of *L. tener* has been thoroughly described and illustrated by McKenna (1968) and Krishtalka (1976b).  $M^3$  is relatively longer than the same tooth of AMNH 17179, type specimen of *L. tener*. In addition the ectocingulum and the preparacrista are less

recurved in the parastylar area. The disposition of the cusps and conules and the groove behind the paracingulum are similar in both specimens.

The mandible is slender and elongate. The anterior alveoli include two for a double-rooted  $P_3$ , two small alveoli anterior to  $P_3$  (probably for a double-rooted  $P_2$ ), a larger upright alveolus, and two smaller semiprocumbent alveoli. The large upright alveolus is present and in the same position on three of the four mandibular fragments. A mental foramen is present below the center of  $P_3$  on SMM P77.8.74 and P77.8.77, and between  $P_3$  and  $P_4$  on P77.8.76. Another mental foramen is present on all three specimens just behind the enlarged upright alveolus. The rise of the coronoid is very steep and the external fossa for the insertion of the temporal muscle is deeply excavated.

$P_4$  is submolariform with three trigonid and three talonid cusps. The paraconid is well developed and in a median position; it is conical to blade-like and is joined to the protoconid apex by a sharp, notched crest. The surface below the crest (the prevallid) is cylindrical in the strict sense, being convex labially and flat dorsoventrally. The regularity of the construction of this surface, both in  $P_4$  and the molars, is the most striking feature of the lower dentition. Progressing from  $P_4$  to  $M_2$  the prevallid becomes more transverse and the paraconid becomes more lingual and closer to the metaconid. The metaconid of  $P_4$  is only a little posterior to the level of the protoconid; it is lower than the protoconid and partially connate with it. The hypoflexid is deep and extends to the base of the crown. The hypoconid and hypoconulid are close together and slightly posterior to the entoconid. The talonid basin is small and pit-like and is limited to the lingual half of the crown. The cristid obliqua is nearly longitudinal.

$M_1$  and  $M_2$  taper only slightly anteriorly. The metaconid is lower than the protoconid and tends

TABLE 19. Measurements of *Leptacodon tener* from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
$M^3$ Length	1	---	1.20	—	—
Width	1	---	1.30	—	—
$P_4$ Length	2	1.2-1.3	1.25	.07	5.66
Width	2	---	.70	—	—
$M_1$ Length	4	1.3-1.5	1.38	.10	6.96
Width	4	.8-1.1	.90	.14	15.71
$M_2$ Length	2	1.3-1.4	1.35	.07	5.24
Width	2	.9-1.0	.95	.07	7.44

to be more conical. The paraconid is lower still, but is more blade-like; it is subinternal to internal on both molars. The prevallid of  $M_2$  is less curved and more transverse than that of  $M_1$ . There is an anterolabial cingulum extending almost to the base of the protoconid. The talonid basin is closed and its base is well below the weak talonid notch. The entoconid is the highest talonid cusp. The hypoconulid is the lowest and is a little closer to the entoconid than the hypoconid. The arc of the cristid obliqua is almost identical in shape to that of the prevallid when viewed occlusally. The post-cingulum is absent on  $M_1$  and barely discernible on  $M_2$ . The labial height of the crown exceeds the lingual height as a result of an inclination of the enamel base.

*Discussion.*—The lower teeth closely resemble *L. tener* in size and structure. The estimated length of  $M_1$ - $M_3$  (allowing .15 mm for overhang of the crowns at each end) is 3.7 mm for SMM P77.8.74 and 3.8 mm P77.8.77. The same measurement given by McKenna (1968) for the left jaw of the type is 3.7 mm. The slight posterior concavity of the posterolabial margin of the trigonid is nearly identical to that of the type. The relative heights of the trigonids also match those of the type closely.

The lower teeth are larger than those of *L. mumusculum* Simpson (1937a) and the cusps are lower, less acute, and less recurved than those of *L. packi* Jepsen (1930).

The lower fourth premolar has a more complicated structure than that of "*L.*" *jepseni*

McKenna (1960) from the Wasatchian Four Mile Local Fauna or *L. catulus* Krishtalka (1976b) from the Wasatchian San Jose Formation.

Two upper fourth premolars (SMM P77.7.78 and P77.7.79) from the Judson locality may be referable to this species. They differ, however, from the type of *L. tener* in having a reduced metacone and metastylar area and in having the apex of the protocone closer to the base of the paracone.

Family ERINACEIDAE Fischer von Waldheim,  
1817

***Litolestes lacunatus* Gazin, 1956**

Tables 20-21, figs. 6.5-.14

*Referred specimens.*—Partial right  $P^3$ , SMM P77.8.78-79; right  $P^4$ , P77.8.80; partial right  $P^4$ , P77.7.80, P77.8.81; left maxillary fragment with  $M^1$ - $M^2$ , P77.8.82; left  $M^1$ , P77.8.83; partial left  $M^1$ , P77.7.81; left maxilla with  $M^2$  and alveoli for  $P^3$ - $M^1$ , P77.7.82; left  $M^2$ , P77.8.84; left  $M^3$ , P77.7.83; right  $M^3$ , P77.8.85; right mandible fragment with  $P_3$ - $P_4$  and alveoli for C- $P_2$ , P77.8.86; left  $P_3$ , P77.8.87-89; right  $P_3$ , P77.8.90-91; right  $P_4$ , P77.7.84, P77.8.92-93; partial left  $P_4$ , P77.6.25, P77.8.94; left  $M_1$ , P77.8.95-97; right  $M_1$ , P77.8.98-99; left mandible fragment with  $M_1$ - $M_2$ , P77.8.100; left  $M_2$ , P77.8.101; right  $M_2$ , P77.8.102-104; left  $M_3$ , P77.8.105.

*Localities.*—Brisbane and Judson localities, Tongue River Formation, Grant and Morton

TABLE 20. Measurements of *Litolestes lacunatus* from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
$P^3$ Width	2	----	2.20	—	—
$P^4$ Length	1	----	2.50	—	—
Width	1	----	3.00	—	—
$M^1$ Length	2	2.2-2.3	2.25	.07	3.14
Width	2	2.7-2.9	2.80	.14	5.05
$M^2$ Length	2	----	2.00	—	—
Width	2	2.9-3.0	2.95	.07	2.40
$M^3$ Length	1	----	1.50	—	—
Width	1	----	2.30	—	—
$P_3$ Length	1	----	1.90	—	—
Width	1	----	1.30	—	—
$P_4$ Length	3	2.7-2.8	2.77	.06	2.09
Width	3	1.6-1.8	1.67	.12	6.93
$M_1$ Length	6	2.1-2.5	2.28	.16	7.02
Width	6	1.5-1.8	1.67	.14	8.20
$M_2$ Length	5	2.0-2.2	2.06	.09	4.34
Width	5	1.6-1.8	1.74	.09	5.14
$M_3$ Length	1	----	2.30	—	—
Width	1	----	1.50	—	—



Counties, North Dakota.

*Description.*—The paracone of P<sup>3</sup> is slightly recurved. Its posterior slope forms a longitudinal crest that bears a small metacone and descends to a small metastyle. The protocone is low and crescentic with anterior and posterior cingula originating from it. The posterior cingulum extends from the protocone to the metastyle, creating a small posterointernal basin. There is a short external cingulum extending anteriorly from the metastyle. A parastyle was undoubtedly present, but is now broken off of both specimens. Both referred P<sup>3</sup>'s have a width of 2.2 mm.

TABLE 21. Measurements of *Litolestes lacunatus* from the Judson locality.

	Length	Width
SMM P77.7.80 P <sup>4</sup>	—	3.2
SMM P77.7.81 M <sup>1</sup>	2.5	—
SMM P77.7.82 M <sup>2</sup>	2.3	3.5
SMM P77.7.83 M <sup>3</sup>	1.8	3.0
SMM P77.7.84 P <sup>4</sup>	3.1	1.8
SMM P77.6.25 P <sup>4</sup>	—	1.7

The paracone of P<sup>4</sup> is higher and more recurved than that of P<sup>3</sup>. Again there is a posterior crest bearing a weak metacone, but unlike that of P<sub>3</sub> the crest curves labiad before joining the poorly defined metastyle. The parastyle is well developed and conical. The protocone is much larger than that of P<sup>3</sup>. Distinct pre- and postcingula are present below the protocristae. The postprotocrista is continuous with the meta- cingulum, which terminates posterior and dorsal to the metastyle. There are no definite external cingula. SMM P77.8.80 is 2.5 mm long and 3.0 mm wide.

M<sup>1</sup> and M<sup>2</sup> are very similar, differing primarily in that M<sup>2</sup> is wider and its stylar cusps project labially more than those of M<sup>1</sup> (fig. 6.7). The paracones and metacones of both molars are essentially conical. The paracones are a little larger than the metacones. The protocone has a crescentic shape due to the presence of well developed protocristae. The lingual face of the protocone is fairly steep on both molars, but less so on M<sup>2</sup>. The conules are distinct and pyramidal. The parastyle and metastyle do not form distinct cusps. All crests and cingula are distinct and angular, but not acute. The ectocingulum is moderately inflected and is continuous with the paracingulum and the postmetacrista. The post-

cingulum bears a low conical hypocone and does not join with the precingulum around the lingual side of the protocone.

M<sup>3</sup> is narrower and more transverse than either M<sup>1</sup> or M<sup>2</sup> (fig. 6.8). The metacone is reduced and assumes a more lingual position. The metacingulum abutts the posterolingual margin of the metacone. There is neither a metastyle nor a postmetacrista. The external cingulum narrows posteriorly and terminates adjacent to the metacone apex. The parastylar area is similar to that of the anterior molars. There is no hypocone.

The alveoli of SMM P77.8.86 (fig. 6.13) indicate that this species possessed an enlarged canine, a single-rooted P<sub>1</sub>, and a double-rooted P<sub>2</sub>. The alveolus of P<sub>1</sub> is larger than either of those of P<sub>2</sub>. A longitudinally elongate mental foramen occurs below the alveolus of P<sub>1</sub> and the anterior alveolus of P<sub>2</sub>. A smaller, less elongate foramen is present below the posterior root of P<sub>3</sub>. The mandibular symphysis is restricted to the lower half of the fragment and terminates posteriorly below P<sub>3</sub>.

P<sub>3</sub> is double-rooted and trenchant. It lacks a paraconid. The protoconid is large and acute, bearing a crest on its posterior side. Transverse crests descend from the single talonid cusp.

P<sub>4</sub> shares the general shape of P<sub>3</sub>, but it is larger (figs. 6.11, 6.13). There is a small, sharp, conical paraconid that is positioned lingual to the longitudinal midline. Internal and external cingula extend from the paraconid, terminating at the midpoint of the anterior root. The protoconid is recurved and sharply pointed. Posterolingual to the protoconid, and about halfway down to the base of the tooth, is a small but equally sharp metaconid. The tips of the protoconid and metaconid are quickly removed by wear against the preprotocrista of P<sup>4</sup>. The notch between them, however, remains a functional part of the wear facet until in late stages of wear the anterior part of the facet becomes an abrasion surface. The lingual side of the talonid forms a small basin enclosed by the posterior lingual cingulum. There are two minute cusps on the posterior cingulum.

The lower molars bear subequal, conical metaconids and protoconids (figs. 6.9-10, 6.12, 6.14). The paraconid of M<sub>1</sub> is subinternal and well separated from the other two trigonid cusps. It is also lower and terminates the blade-like paracristid. The trigonid of M<sub>1</sub> opens internally by means of a broad transverse valley. The paraconid of M<sub>2</sub> varies from subinternal to submedian in position. It is much lower than that of M<sub>1</sub> and

the paracristid is likewise reduced. The paraconid of the only specimen of  $M_3$  is submedian and reduced like that of  $M_2$ . On  $M_1$  and  $M_2$  there are usually three cingula; an anterolabial cingulum below the full width of the prevallid, a short external cingulum at the hypoflexid, and a postcingulum rising to the hypoconulid. The third molar has only the anterolabial cingulum. The postvallid of all three molars is slightly oblique and bears a shallow notch in the protocristid. The talonid basins are formed from the intersection of three planar surfaces: the postvallid, the labial face of the entoconid and hypoconulid, and the lingual face of the hypoconid. The basin opens internally through a V-shaped talonid notch. The hypoconid and entoconid are of comparable size. Although distinct, the hypoconulid is smaller and is situated closer to the entoconid than to the hypoconid. The hypoconulid of  $M_3$  is relatively larger than those of  $M_1$  and  $M_2$  and projects posteriorly.

*Discussion.*—The only known specimen of the upper dentition of *L. lacunatus* from the Bison Basin is USNM 20931 from the West End locality. It is a maxillary fragment with  $P^3-M^2$  in which the molars are very worn.  $P^3$  is 2.5 mm long, 2.5 mm wide, and lacks both parastyle and metastyle.  $P^4$  has a parastyle and is 2.8 mm long by 3.5 mm wide. The presence of a metacone on  $P^4$  is indeterminate because of wear. The upper molars have a relatively greater length across the protocone than do the Brisbane specimens. The length and width of  $M^1$  are 2.3 and 3.4 mm. The length and width of  $M^2$  are 2.0 and 3.2 mm.

The Bison Basin specimens show an emphasis on grinding and a reduction in shear and puncturing relative to the North Dakota specimens. This functional difference is manifested in the wider upper molars, the greater lingual length of the upper molars, the absence of the parastyle, metastyle, and metacone on  $P^3$ , and the blunter cusps and greater width of the lower molars in the Bison Basin specimens. These differences suggest that distinct species may be involved. However, most of the morphological differences originate from the single Bison Basin maxillary, which did not come from the type locality and did not occur with any parts of the lower dentition. It is possible, then, that the North Dakota specimens and the type series are conspecific and that the Bison Basin maxillary represents a new species. Because the problem cannot be resolved at the present time, the North

Dakota material is provisionally referred to *L. lacunatus*.

Schwartz and Krishtalka (1976) and Krishtalka (1976a) suggest that the lower dentition of *L. ignotus* Jepsen (1930) consists of  $dP_1P_2-P_5$ , whereas that of *L. notissimus* Simpson (1936) and *L. lacunatus* consists of a true canine and four premolars. Their conclusion, based on greatest parsimony, is reasonable when *L. ignotus* alone is considered, but may not be the most parsimonious interpretation in terms of the genus and its relation to the family.

The similarity in the cheek teeth across all three species suggests a close phylogenetic relationship, rather than convergence. However, so much conservatism in the cheek teeth, while  $C_1$  is lost in one lineage and  $P_1$  is lost in the other, seems improbable. The alternative, that  $P_1$  was lost in a common ancestor and that  $C_1$  became premolariform in one lineage, seems more likely. In either case, additional data on *L. notissimus* and *L. lacunatus* are needed before the genus can be revised satisfactorily.

Family PANTOLESTIDAE Cope, 1884  
*Propaleosinopa albertensis* Simpson, 1927  
 Table 22, figs. 7.1-4

*Referred specimens.*— $M^1$ , SMM P77.7.86, P77.8.106; partial  $M^1$ , P77.8.107;  $P_4$ , P77.8.108; left mandible with  $M_2$ , P77.7.87; FMNH PM8668;  $M_2$ , SMM P77.7.88, P77.8.109; partial  $M_2$ , P77.8.110.

*Localities.*—Brisbane, Judson, and Riverdale localities, Tongue River Formation, Grant, Morton, and McLean Counties, North Dakota.

*Description.*—The paracone of  $M^1$  is slightly taller than the metacone, and both cusps are conical except for the tall postmetacrista that descends in a smooth arc from the apex of the metacone to the metastyle. The labial margin converges anteriorly with a line through the

TABLE 22. Measurements of *Propaleosinopa albertensis* from the Brisbane, Judson, and Riverdale localities.

	Length, mm	Width, mm
SMM P77.7.86 $M^1$	2.7	3.4
SMM P77.8.106 $M^1$	3.0	4.1
SMM P77.8.108 $P_4$	2.3	1.2
SMM P77.7.87 $M_2$	2.7	2.1
SMM P77.7.88 $M_2$	2.5	1.7
SMM P77.8.109 $M_2$	2.6	1.9
FMNH PM8663 $M_2$	3.3	2.4



paracone and metacone and is marked by a weak ectoflexus (fig. 7.1). The parastyle is low and is joined by a low preparacrista to the paracone. The postparacrista and premetacrista are present but weak. The conules are well developed, as are all of the conule cristae except the postparaconule crista. The preparaconule crista and the preprotocrista are continuous and terminate labially by joining the parastyle. A precingulum and postcingulum are present lingually. The postmetaconule crista terminates posterolabial to the metacone below the postmetacrista; it is continuous with the postprotocrista, but does not join the metastyle. The hypocone is relatively large and conical and is positioned posterolingual to the protocone.

P<sub>4</sub> possesses a small, fully internal paraconid from which the paracristid rises to the protoconid apex. There is no trace of a metaconid. The posterior face of the protoconid is marked by a median ridge that has parallel furrows on either side of it. The talonid is shallowly basined and possesses faint swellings which may represent the entoconid and hypoconid. In lateral view the anterior margin of the protoconid is convex, whereas the posterior margin is concave (fig. 7.2).

M<sub>2</sub> is quadrate with large, subequal metaconid and protoconid (figs. 7.3 and 7.4). The paraconid is low, subinternal, and forms a nearly transverse blade, which thickens internally. The protocristid is sharp and possesses a carnassial notch, in contrast to the paracristid. The anteromedial faces of the protoconid and metaconid are slightly convex. A short anterolabial cingulum is present. The postvallid is steeply inclined, planar, and nearly transverse. The talonid portion of the tooth is a little longer than the trigonid and has a closed basin. The entoconid is taller than the hypoconid. The hypoconulid is small but distinct and in a median position. A sharp talonid notch is present. Viewed posteriorly the sides of the trigonid are nearly straight, vertical, and parallel.

The depth of the mandible below M<sub>2</sub> is about 3.3 mm.

*Discussion.*—The dental morphology as well as the wear facets indicate the dominance of prevallum-postvallid shear in mastication. Postvallum-prevallid shear was also present and was combined with occlusion of the anterior face of the metaconid with the posterior face of the hypocone. The postcingulum appears from the available wear states to have functioned as a stop. Two

of the specimens, SMM P77.7.87 (M<sub>2</sub>) and P77.8.106 (M<sup>1</sup>), show large horizontal abrasion surfaces on the paracone, conules, protocone, and hypocone of M<sup>1</sup> and the trigonid cusps of M<sub>2</sub>.

The reference of these specimens to *P. albertensis* follows Van Valen's (1967, p. 226) synonymization of *P. albertensis*, "*Bessoeceter thomsoni*" Simpson (1936), and "*B. diluculi*" (Simpson, 1935b). The present sample resembles the Scarritt Quarry population ("*B. thomsoni*") in the size of P<sub>4</sub> and the hypocone development of M<sup>1</sup>; it resembles the Gidley Quarry population ("*B. diluculi*") in the size and proportions of M<sub>2</sub>. Variation in the specimens referred here is consistent with a single population that should not be separated specifically from either the Scarritt or Gidley Quarry samples.

***Paleosinopa* sp., cf. *P. simpsoni* Van Valen, 1967**

*Referred specimens.*—Left M<sup>2</sup>, SMM P77.8.111; right P<sub>4</sub>, P77.8.112.

*Locality.*—Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Description.*—The referred M<sup>2</sup> is short, wide, and triangular. It measures 4.4 mm long by 6.0 mm wide. The cusps are heavily worn, but their positions are still clear. The protocone is about twice as far from the paracone and metacone as they are from each other. There is a strong metastylar wing curving posterolabially from the metacone and projecting labially at the posterolabial corner of the crown. The ectoflexus is shallow and the parastyle projects anteriorly. The precingulum is narrow, whereas the postcingulum is wide and supports a lingually projecting hypocone.

P<sub>4</sub> is trenchant, having sharp crests on the anterior and posterior sides of the protoconid. In profile the anterior crest is convex. The posterior crest is straight until it turns sharply to extend horizontally to the talonid cusp. A posterior lingual cingulum bears a low cusp, which forms the widest part of the crown. The paraconid is minute. Short, narrow cingula are present at the anterior end of the lingual side and the posterior end of the labial side of the crown. The crown is 4.3 mm long and 2.2 mm wide.

*Discussion.*—The only M<sup>2</sup> of *P. simpsoni* from its type locality, Scarritt Quarry, is AMNH 33828. It is larger than the Brisbane M<sup>2</sup>, measuring 5.0 mm by 8.0 mm (Simpson, 1937b). In addition, it differs in having a narrower post-



cingulum, but in all other respects the two teeth are nearly identical.

Family PENTACODONTIDAE Simpson, 1937

*Bisonalveus* sp.

Figs. 7.5-6, 7.8

*Referred specimen.*—Left probable  $M_1$ , SMM P77.8.113.

*Locality.*—Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Description.*—The trigonid is little elevated above the talonid and bears blunt conical cusps (figs. 7.6 and 7.8). The paraconid is a little lower than the metaconid and is nearly internal. The metaconid is in turn a little lower than the protoconid and is a little posterior to it. The paracristid is L-shaped, extending anteriorly from the protoconid before it turns labial and continues to the paraconid (fig. 7.5). The protocristid consists simply of two perpendicular, straight crests that are worn in a plane that is somewhat oblique to the postvallid. There is no metacristid. A low crest descends lingually from the protoconid into the trigonid basin. The labial and anterior sides of the trigonid are very flattened because of its anterolabial expansion. There is only a vestige of an anterolabial cingulum.

The talonid is dominated by the high, broad hypoconid. Directly lingual to the hypoconid, and shorter than it, is the entoconid, whose apex forms the lingual end of the arcuate postcristid. Two cuspules, now marked by circular abrasion surfaces, occupy the position of the hypoconulid. Similarly, an oblong abrasion surface is present in the position of the mesoconid. The cristid obliqua is curved and rises to the vertex of the protocristid notch.

The base of the enamel on the labial side is expanded into a labially projecting horizontal fold. At the anterolabial corner of the crown the enamel base rises sharply toward the paracristid, resulting in the anterior base being much higher than the labial. The roots are heavy, subequal, and transversely elongate. The crown is 2.9 mm long and 2.0 mm wide.

*Comparisons.*—This tooth differs from  $M_1$  of *Bisonalveus browni* Gazin (1956) (length 2.5 mm, width 1.7 mm) in being 16 percent larger, and in having a more lingual paraconid, a radial crest present on the lingual side of the protoconid, a less elevated trigonid with blunter cusps, more elevated anterior enamel base, and a more

squared trigonid with a flatter labial side. Except for the size difference, it differs from  $M_1$  of *Aphronorus fraudator* Simpson (1935b) in the same ways, except that in each case the difference is greater.

*Discussion.*—The fundamental similarities between this tooth and specimens of *Aphronorus* and *Bisonalveus* leave little doubt that it should be grouped with the Pentacodontidae. Its closest ally in the family is *Bisonalveus browni* and, although the differences in their molars are somewhat large for congeneric species, the Brisbane species can be accommodated within that genus. Similarities of this tooth to apatemyids I believe to be the results of convergence.

Family APATEMYIDAE Matthew, 1909

*Unuchinia dysmathes*, new species

Table 23, figs. 7.7, 7.9-10

*Type specimen.*—Right mandible with  $M_1$ - $M_3$  and six alveoli for five antemolar teeth, including a double-rooted  $P_4$ , SMM P77.6.31.

*Type locality.*—Judson locality, Tongue River Formation, Morton County, North Dakota.

*Referred specimen.*—Left  $M_1$  or  $M_2$ , SMM P77.8.114.

*Locality.*—Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Etymology.*—*Unuchinia* from Mongolian, ünüchin, meaning orphan (G. G. Simpson, personal communication, 1975). Although Mongolian has no genders, the latinized generic name was intended to be feminine. *Dysmathes* from Greek, meaning not easily known, an allusion to the improved but still imperfect understanding of the genus provided by this species.

*Diagnosis.*—Ten to twenty percent larger than *U. asaphes* (Simpson, 1936) with no diastema, and with only one rather than two, unenlarged, single-rooted premolars preceding the first double-rooted tooth. (These are minimum differences that do not depend on the interpretation of

TABLE 23. Measurements of *Unuchinia dysmathes* from the Judson and Brisbane localities.

		Length, mm	Width, mm
SMM P77.6.31	$M_1$	2.8	1.8
	$M_2$	3.0	2.0
	$M_3$	3.4	2.2
SMM P77.8.114	$M_1$ or $M_2$	2.7	1.8

tooth homologies in AMNH 33894, type of *U. asaphes*.)

*Description.*—The mandible is relatively deep, achieving its maximum depth and width at the posterior end of the unsutured mandibular symphysis below  $P_4$ . The mental foramen is simple, exiting anterolabially below the anterior alveolus of the double-rooted  $P_4$ . There is no labial fossa below  $P_4$ , except for that associated with the mental foramen. The rise of the coronoid process is a flattened, labially projecting ledge that bounds anteriorly the deeply excavated mandibular fossa. Situated slightly dorsal to the level of the tops of the molars is the mandibular condyle (fig. 7.10). The angular process is slightly inflected. The dental foramen exits posteriorly at the posterior end of a horizontal ridge that extends anteriorly to a point below  $M_3$ .

The alveoli represent the antemolar dentition completely. The first three are enlarged, elongate, and procumbent. They become progressively longer, deeper, and more elongate anteriorly, and are arranged *en echelon* (see fig. 7.9). The remaining three alveoli are comparable in size to the molar roots. Of these, the first is nearly circular and upright. The last two alveoli appear to have held a double-rooted  $P_4$ ; the wall of bone separating them is thin and their relative sizes are in the same proportion as the molar roots. There is no diastema.

The molars have sharp cusps and elevated trigonids (figs. 7.7 and 7.10). The metaconids and protoconids are of equal height parallel to the sides of the postvallid, but because of the lingual inclination of the crown, the protoconid is the highest cusp relative to the mandible. All of the trigonid cusps are pyramidal with flattened sides facing the trigonid basin. The paraconids are low, blade-like, and submedian to subinternal. There is no anterolabial projection of the trigonid. The postvallid is flat and nearly transverse. The cristid obliqua is straight and abutts the postvallid medially.  $M_2$  and  $M_3$ , but not  $M_1$ , bear mesoconids. On  $M_1$  and  $M_2$  the hypoconid is the highest talonid cusp with the hypoconulid and entoconid descending successively from it. On  $M_3$  the enlarged hypoconulid projects posteriorly and is the highest talonid cusp. The dorsal surface of the talonid is a gently concave surface that is inclined anterolingually. An entocristid extends forward to the postvallid, thus creating a minute closed basin at the anterolingual margin of the talonid. The posterior root of each molar is some-

what elongate and is inclined, diverging from the anterior root. The molar series shows posterior increases in (1) overall size, (2) length of talonid, (3) anteroposterior compression of trigonid, (4) size of paraconid, mesoconid, and hypoconulid, (5) inflection of postcingulum between the hypoconulid and hypoconid, and (6) size of the posterior root and its departure from vertical.

*Comparisons.*—The paraconid of the last molariform tooth of AMNH 33894, type and only specimen of *U. asaphes*, is more internal than the paraconid of any molar of SMM P77.6.31, and is similar to that of SMM P77.8.114. The molariform teeth of AMNH 33894 are ten to twenty percent smaller than the North Dakota specimens and lack mesoconids. The presence of a diastema and two rather than one, unenlarged, single-rooted premolars are the only other features that distinguish AMNH 33894.

*Discussion.*—The molariform teeth of *U. dysmathes* are so similar to those of *U. asaphes*, that had they been found as isolated teeth they would have been referred to the latter species. Differences in the single-rooted premolars, however, suggest that at least a specific separation is warranted.

Simpson (1936) and McKenna (1963) consider the three teeth of AMNH 33894 to be  $P_4$ - $M_2$ , although both admit the possibility that they are  $P_3$ - $M_1$ . Simpson put forth three arguments for his interpretation:

- (1) The mental foramen is usually immediately anterior to  $P_4$ , not  $P_3$ .
- (2) The structural relations and proportions of the molariform teeth are those usual for  $M_1$ - $M_2$  and extraordinary for  $P_4$ - $M_1$ .
- (3) The posterior two alveoli strongly suggest the shape of roots usual for  $M_3$  and very rare for  $M_2$ .

If the teeth of AMNH 33894 are  $P_4$ - $M_2$ , then it differs from SMM P77.6.31 in having a single-rooted rather than double-rooted  $P_4$ . The small anterior alveolus of AMNH 33894 would probably correspond to the somewhat larger single alveolus for  $P_3$  in SMM P77.6.31. Following this interpretation, the mental foramen is positioned near the front of  $P_4$  in both species.

An X-ray photograph of SMM P77.6.31 reveals that the "incisor" alveoli terminate below the anterior alveolus of  $P_4$  and immediately below the mental foramen. There is a rapid shortening of the roots from the anterior root of  $M_1$  forward to the single root of  $P_3$ . Thus the reduction of the



posterior premolars is the result of competition for root space caused by posterior elongation of the "incisor" roots. Continued enlargement of the "incisors" and posterior elongation of their roots could produce the condition seen in *U. asaphes*, in which  $P_3$  is almost eliminated, the anterior root of  $P_4$  is eliminated, and one or more of the "incisor" alveoli extend back below  $M_1$ . Because the reduction of  $P_3$  and  $P_4$  is caused largely by the limited space for the roots rather than the crowns, this trend also accounts for the diastema that is present in *U. asaphes* and absent in *U. dysmathes*. In this case *U. asaphes* must be regarded as the more progressive species.

The alternative interpretation, in which the teeth of AMNH 33894 are considered to be  $P_3$ - $M_1$ , also requires that the major trend in the genus is the enlargement of the "incisors" and consequent reduction of the posterior premolars. The small anterior alveolus of AMNH 33894 (presumably  $P_2$ ) would probably represent a tooth that has been lost in *U. dysmathes*. (It is unlikely that this somewhat vestigial tooth in *U. asaphes* could correspond to one of the enlarged "incisors" of *U. dysmathes*.) In this interpretation the mental foramen occupies an unusual position immediately anterior to  $P_3$ . These relationships can be accounted for by the enlargement of the "incisors" only if *U. asaphes* is the more primitive species. However, that would require the following unlikely primitive conditions within the genus: (1) the mental foramen primitively below  $P_3$ , and (2)  $P_4$  primitively molariform.

The first interpretation is more plausible in that the only improbability required by it is that the molars change very little while the premolars change considerably. On this basis, I agree with Simpson's original assertion that the known teeth of *U. asaphes* are probably  $P_4$ - $M_2$ . *U. dysmathes* is, therefore, probably the more primitive member of the genus.

When the mandible of *U. dysmathes* is compared to the Apatemyinae, the presence of enlarged, procumbent anterior teeth remains as the only possible reason for the including *Unuchinia* within the Apatemyidae. Features distinguishing *Unuchinia* from the remainder of the family now include the presence of three, rather than one or two, enlarged anterior teeth, much more transverse postvallids, absence of an anterolabial projection of the paracristid, the absence of a well developed labial fossa below  $P_4$ , and a much more dorsal position of the mandibular condyle. These

differences do not, however, force the exclusion of *Unuchinia* from the family, where it can best be retained as a matter of taxonomic practicality.

Insectivore, genus and species indeterminate (1)

*Referred specimen.* — Right mandible with worn  $M_2$ , SMM P77.8.115.

*Locality.* — Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Description.* — This species is remarkable only for its small size. The length and width of  $M_2$  are 1.0 mm and 0.8 mm. The depth of the mandible below  $M_2$  is 1.7 mm.

*Discussion.* — Similar edentulous jaws are not infrequent at both Judson and Brisbane. This specimen is, however, too badly worn to permit its identification.

Insectivore, genus and species indeterminate (2)

Fig. 5.14

*Referred specimen.* — Right ? $P^4$ , SMM P77.7.89.

*Locality.* — Judson locality, Tongue River Formation, Morton County, North Dakota.

*Description.* — The labial margin is oblique, directed anterolingually, and bearing a narrow but complete ectocingulum. The anteriorly projecting parastyle is low and conical. The paracone is tall and acute. The metacone is smaller and partially connate, situated on a crest that descends in an arc to the blade-like metastyle. A small notch separates the metacone from the paracone. The protocone is pyramidal. There is no paraconule, and only a vestige of a metaconule. The metacingulum and precingulum are narrow and continuous. A short precingulum continues around the protocone to join the very poorly defined hypocone. There are three roots. The length is 1.5 mm and the width is 1.9 mm.

*Discussion.* — The affinities of this tooth are very unclear. It bears some similarities to *L. tener*, but differs sufficiently to warrant its exclusion from that species. In particular, the much smaller metacone in this specimen leaves even its familial affinities in doubt.

#### Order PRIMATES

Family PLESIADAPIDAE Trouessart, 1897

*Plesiadapis rex* (Gidley, 1923)

Tables 24-25, figs. 8.1-.10

*Referred specimens.* — I<sup>1</sup>, SMM P77.6.32, P77.7.85, P77.7.90-91, P77.8.116-119; P<sup>3</sup>,



P77.7.92-95, P77.8.120; P<sup>4</sup>, P77.6.33-35, P77.7.96-97, P77.8.121-125; M<sup>1</sup>, P77.6.36, P77.7.98-100, P77.6.37 (fragment), P77.8.126-127, P77.8.128 (fragment); M<sup>2</sup>, P77.6.38-39, P77.7.101 (fragment), P77.8.129-130; M<sup>3</sup>, P77.6.40-42, P77.7.102-104, P77.8.131-132; right mandible with I<sub>1</sub>, P<sub>4</sub>-M<sub>3</sub>, P77.6.43; left mandible with P<sub>3</sub>-M<sub>2</sub>, P77.6.44; right mandible with I<sub>1</sub>, P<sub>3</sub>-M<sub>2</sub>, P77.6.45; I<sub>1</sub> (includes numerous broken and worn teeth), P77.6.46-49, P77.7.105-107, P77.8.133-137; P<sub>3</sub>, P77.6.50-51, P77.7.108, P77.8.138; P<sub>4</sub>, P77.7.109, P77.8.139-145; M<sub>1</sub>, P77.6.52-53, P77.7.110-117, P77.8.146-150; M<sub>2</sub>, P77.6.54, P77.7.118-121, P77.8.151-153; M<sub>3</sub>, P77.6.55-58, P77.7.122-124.

*Localities.*—Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, North Dakota.

*Description.*—The anterocone and laterocone of the central upper incisor are large and well differentiated, whereas mediocone and centroconule are greatly reduced (fig. 8.6). On any one specimen the centroconule is consistently a little smaller than the mediocone, but between specimens the pair shows considerable variation in size (absent on one specimen). Two major grooves are present on the posterior face along with other smaller grooves and crenulations, which occur variably.

P<sup>3</sup> bears a small parastyle, a large paracone, a small metacone, an elongate and oblique paraconule, and a large protocone (fig. 8.5). The external margin is oblique and lacks a cingulum. The anterior and posterior margins are weakly

inflected and are bounded by cingula that continue as crests up the anterior and posterior faces of the protocone to its apex. The postcingulum extends lingually beyond the level of the protocone apex before turning anteriorly, thus forming a large inclined posterolingual shelf.

P<sup>4</sup> is similar to P<sup>3</sup> in its basic structure (fig. 8.4). However, it possesses an ectocingulum and its paraconule is less oblique. The precingulum does not rise to the protocone apex, but terminates below and anterior to it. The preprotocrista extends to the base of the paraconule at its anterior end. The anterior margin of the crown is not inflected.

M<sup>1</sup> and M<sup>2</sup> are nearly identical in structure (figs. 8.3 and 8.2) and have been separated here on the basis of the greater width of M<sup>2</sup>. The paracone and metacone are subequal and all but two specimens bear small mesostyles. The conules are equal in size and lack posterior conule cristae. The pre- and postprotocristae are low but distinct. The protocone is the highest and broadest cusp of the crown. The postcingulum extends transversely from the posterior side of the metacone to the posterointernal corner of the crown where it turns sharply anteriorly and rises to the protocone apex. There is no hypocone. The precingulum and ectocingulum are broad and continuous, extending from a point anterior to the protocone around the paracone to the labial side of the metacone. A weak ectoflexus is variably present. Two of the Brisbane specimens bear very narrow lingual cingula.

M<sup>3</sup> differs from M<sup>1</sup> and M<sup>2</sup> in having a reduced

TABLE 24. Measurements of *Plesiadapis rex* from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
P <sup>3</sup> Length	1	—	2.10	—	—
Width	1	—	2.70	—	—
P <sup>4</sup> Length	5	2.3-2.5	2.44	.09	3.67
Width	5	3.4-4.1	3.82	.24	6.25
M <sup>1</sup> Length	2	—	3.30	—	—
Width	2	—	4.90	—	—
M <sup>2</sup> Length	2	3.5-3.7	3.60	.14	3.93
Width	2	5.6-5.7	5.65	.07	1.25
M <sup>3</sup> Length	2	3.0-3.3	3.15	.21	6.73
Width	2	4.4-4.9	4.65	.35	7.60
P <sub>3</sub> Length	1	—	2.40	—	—
Width	1	—	1.80	—	—
P <sub>4</sub> Length	6	2.1-2.8	2.50	.24	9.47
Width	6	2.1-2.5	2.25	.14	6.13
M <sub>1</sub> Length	4	2.9-3.4	3.18	.26	8.28
Width	4	2.7-3.1	2.98	.19	6.36
M <sub>2</sub> Length	3	3.0-3.2	3.10	.10	3.23
Width	2	2.8-3.0	2.90	.14	4.88

TABLE 25. Measurements of *Plesiadapis rex* from the Judson locality.

Dimension	N	Range	Mean	SD	V
P <sup>3</sup> Length	4	2.0-2.2	2.10	.08	3.89
Width	4	2.7-2.8	2.75	.06	2.10
P <sup>4</sup> Length	5	2.3-2.7	2.48	.18	7.21
Width	5	3.6-4.2	3.92	.22	5.53
M <sup>1</sup> Length	4	3.1-3.4	3.23	.13	3.90
Width	4	4.6-4.8	4.70	.08	1.74
M <sup>2</sup> Length	3	3.3-3.4	3.37	.06	1.71
Width	2	5.1-5.3	5.20	.14	2.72
M <sup>3</sup> Length	5	3.1-3.7	3.38	.22	6.41
Width	5	4.7-5.1	4.86	.15	3.12
P <sub>3</sub> Length	5	2.2-2.6	2.38	.18	7.52
Width	5	1.8-2.2	2.00	.16	7.91
P <sub>4</sub> Length	4	2.5-2.8	2.60	.14	5.44
Width	4	2.3-2.8	2.53	.21	8.16
M <sub>1</sub> Length	12	2.9-3.4	3.19	.17	5.27
Width	12	2.7-3.3	2.96	.20	6.69
M <sub>2</sub> Length	8	3.2-3.6	3.44	.14	4.10
Width	8	3.2-3.8	3.44	.23	6.77
M <sub>3</sub> Length	5	4.6-6.1	5.28	.62	11.78
Width	5	2.8-2.0	2.38	.43	13.58

paracone, metacone, and conules. The region of the metacone is areally reduced, resulting in an oblique labial margin and a rounded posterior margin (fig. 8.1). The protocone is expanded longitudinally and its lingual margin is rounded. All specimens lack an ectoflexus, and all but one bear mesostyles. Whereas the enamel of M<sup>1</sup> and M<sup>2</sup> is fairly smooth, that of M<sup>3</sup> is often crenulated.

The three available mandibles are all deep and robust (fig. 8.8). The dental formula is determinable on two specimens and is 1.0.3.3. P<sub>2</sub> is known only from its alveolus, which is minute and is separated from I<sub>1</sub> by a short diastema. Two mental foramina are present, the anterior occurring below the P<sub>2</sub> alveolus, and the posterior occurring below the anterior root of M<sub>1</sub>. On SMM P77.6.45 the posterior foramen is simple, but on the other two jaws there is a minute opening adjacent to the anterior side of the foramen. As shown on X-rays of SMM P77.6.43 and P77.6.45, the incisor root terminates below the anterior end of M<sub>1</sub>.

The lower incisor is laterally compressed and blade-like, with a small, but distinct, margoconid (fig. 8.8).

P<sub>3</sub> and P<sub>4</sub> each consist of an enlarged protoconid and a transverse ledge-like talonid (figs. 8.7 and 8.8). Three weak crests may radiate from the protoconid apex. A short crest that descends anteriorly from the apex is often present. The other two crests descend to the posterointernal and posterioexternal margins of the protoconid. Between the posterior crests is a flattened

surface that may be smooth or crenulated and may bear an additional weak vertical crest. The elevated posterior edge of the talonid ledge usually bears two cuspules, but may have none or as many as three. The fourth premolar differs from the second in being larger and in developing a flattened, overhung surface on its anterior face just above the enamel base. Just above this flattened surface of P<sub>4</sub>, there is often an interdental wear facet. In contrast, the anterior face of P<sub>3</sub> lacks an interdental facet, is nearly vertical, and is gently rounded.

The protoconid of M<sub>1</sub> is its largest trigonid cusp, the paraconid the smallest. The paracristid is a low transverse crest that rises at either end toward the paraconid and protoconid but frequently fails to join the apices of the cusps at either or both ends. The protocristid is straight and only slightly depressed in the position of the protocristid notch. There is no metaacristid. The talonid is broadly basined and is open lingually. The hypoconid is easily the largest talonid cusp. Just anterior to the posterolingual corner of the crown is the entoconid, which is of moderate size. The hypoconulid is not clearly distinguishable, being represented only by a faint swelling of the gently arcuate posterocristid. A short, weak postcingulid is usually present. The cristid obliqua rises in a gentle arc from the hypoconid to the metaconid, forming an inclined ledge on the posterior face of the trigonid. A weak mesoconid, usually absent on M<sub>1</sub>, is present on only one specimen. Metastylid is present on four

specimens. A low ridge and adjacent furrows descend anterolingually from the hypoconid into the talonid basin. Other lower ridges occur variably in the talonid basin. The labial cingulum varies from strong to weak.

M<sub>2</sub> is slightly longer and considerably wider than M<sub>1</sub>. The paraconid is shifted posteriad very close to the metaconid and both cusps are of approximately the same size. A mesoconid is present in all but one specimen. The cristid obliqua does not rise to the metaconid as it does in M<sub>1</sub>, but terminates against the posterior face of the trigonid below and a little lingual to the protoconid apex. A minute entoconulid and metastylid are variably present. Other features of M<sub>2</sub> are essentially identical to those of M<sub>1</sub>.

M<sub>3</sub> is narrower and much longer than M<sub>2</sub>, and its trigonid is more compressed anteroposteriorly (figs. 8.9 and 8.10). The paraconid is larger than the metaconid and is subequal in size to the protoconid. The mesoconid is more prominent than that of M<sub>2</sub>, and the cristid obliqua terminates more labially, below the protoconid apex. The enlarged hypoconulid lobe is divided into three parts by a longitudinal cleft, which exits posteriorly, and a transverse cleft, which exits lingually.

*Discussion.*—Although *Plesiadapis rex* is poorly known from its type locality in the Crazy Mountain Field of Montana, it is now well known from a large collection of jaws from the Cedar Point Quarry of the Big Horn basin, Wyoming. Gingerich's (1975) reference of the latter specimens to *P. rex* seems entirely justified and allows, for the first time, an adequate comparison of other specimens to *P. rex*. The North Dakota specimens referred here are close in nearly all dimensions to those of the Cedar Point sample. The two samples share the following morphologic characters: a distinct centroconule on I<sup>1</sup>, strong paraconules and weak metacones on P<sup>3</sup> and P<sup>4</sup>, weak mesostyles on the upper molars, presence of a short diastema and minute P<sub>2</sub> alveolus on the lower jaw, small talonid heels on P<sub>3</sub> and P<sub>4</sub>, distinct metaconids on M<sub>1</sub> and M<sub>2</sub>, and a broad, squared, and fissured heel on M<sub>3</sub>. The only noteworthy differences are that the North Dakota specimens have a more procumbent lower incisor, slightly longer diastema in the mandible, and more anterior positions of the M<sub>1</sub> and M<sub>2</sub> entoconids.

The only other plesiadapid species of comparable size recognized by Gingerich are *P. fodinatus* Jepsen (1930) and *P. churchilli* Gingerich (1975). The former species is now well

known from its type locality, Princeton Quarry in the Big Horn basin of Wyoming. It differs from *P. rex* and the present specimens in usually lacking P<sub>2</sub>, having much more pronounced crests, stronger mesostyles, and in showing a reduction of the entoconid and the posterolingual portion of the upper molars.

*P. churchilli* is more similar to *P. rex* than to *P. fodinatus*. It differs from *P. rex* in having P<sub>2</sub> variably present, more anterior entoconids, better developed mesostyles, and in being larger. The present sample shows the same differences except for the position of the entoconid. *P. churchilli* is not known from a large sample and its differences from *P. rex* are not large. There is, therefore, reasonable doubt as to the value of its specific separation from *P. rex*.

#### *Plesiadapis* sp.

*Referred specimens.*—I<sub>1</sub>, FMNH PM8668, PM8669; right mandibular fragment with M<sub>2</sub> (partial) and M<sub>3</sub>, FMNH PM8664; left M<sub>3</sub>, FMNH unnumbered specimen.

*Locality.*—Riverdale locality, Tongue River Formation, McLean County, North Dakota.

*Description.*—Both lower incisors bear a posterior basal cuspule, lateral and medial crests, and an interdental facet on the medial face. In addition FMNH PM8668 bears a large abrasion crater at its tip. Width and height of FMNH PM8668 are 3.0 mm and 4.2 mm, of FMNH PM8669, 2.3 mm and 3.8 mm.

The mandibular fragment is uninformative except for the teeth it contains. The anterior and posterior widths of M<sub>2</sub> are nearly equal, the posterior being 3.5 mm, the length 3.6 mm. The trigonid is severely worn. The entoconid is near the posterolingual corner of the crown and is distinct from the postcristid. The length of M<sub>3</sub> is 5.4 mm, posterior width 3.2 mm. A mesoconid is present. The talonid basin is smooth because of wear, but there are several faint crenulations still observable. The hypoconulid heel is wide, roughly squared, and fissured. The unnumbered specimen of M<sub>3</sub> is similar to that of FMNH PM8664, but is more worn. It is 5.7 mm long and 3.5 mm wide at the talonid.

*Discussion.*—These specimens can be referred to *Plesiadapis* with certainty, but the small size and poor condition of the sample makes a specific reference impossible. Although they cannot be distinguished from *P. rex* at the Judson and



Brisbane localities, they might instead represent *P. churchilli*, or (less likely) *P. fodinatus*.

**Nannodectes sp.**

Table 26, figs. 8.11-17

*Referred specimens.*—I<sup>1</sup>, SMM P77.8.154; M<sup>1</sup>, P77.8.155-157; M<sup>2</sup>, P77.8.158-159; P<sub>3</sub>, P77.8.160-161; M<sub>3</sub>, P77.8.162.

*Locality.*—Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Description.*—The anterocone and laterocone of the upper first incisor are prominent and acute (fig. 8.11). The mediocone is small and blunt, and there is no centroconule. The enamel of the posterior face is smooth, bearing no pronounced grooves or ridges. The basal part of the crown, including the posterocone, is missing from the only known I<sup>1</sup>. The crown width is 2.1 mm.

M<sup>1</sup> is subtriangular with a rounded lingual margin and a weak ectoflexus (fig. 8.12). The paracone is a little taller than the metacone, but lower than the protocone. Both conules are small. The centrocrista is straight, low, and sharp, with no mesostyle. The preparacrista and postmetacrista are variable in height, but are always present. The preparaconule crista is pronounced and invariably present. The other conule cristae are variably low or absent. The protocristae are sharply defined and bound the flattened medial face of the protocone. The precingulum originates below and a little lingual to the paracone and terminates anterior to the protocone. The postcingulum originates below the postmetacrista, extends lingually beyond the protocone, and then turns and rises to the protocone apex. Development of the ectocingulum is variable. Its narrowest point (where it may be absent) occurs adjacent to the paracone.

M<sup>2</sup> differs from M<sup>1</sup> in being wider and more quadrate (fig. 8.13). The shelf bounded by the postcingulum is more expanded in the posterior

direction. In the only unworn specimen of M<sup>2</sup>, the protocristae and the preparaconule crista are lower than those of M<sup>1</sup>.

P<sub>3</sub> bears a large protoconid whose sides are smoothly rounded except for the flattened posterior face and a short anterior longitudinal crest (figs. 8.14 and 8.16). The talonid is a simple heel bearing two small cusps.

M<sub>3</sub> possesses a very short trigonid and an elongate talonid (figs. 8.15 and 8.17). Its enamel is smooth. The apices of the trigonid cusps have been removed by abrasion or erosion, but the paraconid and metaconid appear to have been largely connate. The paracristid is a low ridge that descends anteriorly from the paraconid and turns labiad to join the protoconid. There is a short anterior cingulum. The talonid is broad, smooth, and shallowly basined. A well developed mesoconid is present. The hypoconulid lobe is semicircular and is about three quarters as wide as the talonid. The only specimen is 3.5 mm long and 2.3 mm wide.

*Discussion.*—Reference of this species to the genus *Nannodectes* is based on its small size, the absence of a centroconule on I<sup>1</sup>, the narrowness of M<sup>1</sup>, and the simple hypoconulid lobe of M<sub>3</sub>. The small sample size and the relatively large variation makes specific identification impossible. The sample could represent any one of *N. gazini* Gingerich (1975), *N. intermedius* (Gazin, 1971), or *N. simpsoni* (Gazin, 1956).

The upper first molars in this sample are more triangular than in any previously known plesiadapid, although *N. gazini* approaches this condition most closely. The possibility that the specimens referred here as M<sup>1</sup> may in fact be the dP<sup>4</sup> of *Plesiadapis rex* is improbable because of the large number of them relative to the size of the *P. rex* sample from this locality. Furthermore, the enamel is not particularly thin, and the absence of dentine from some of them is

TABLE 26. Measurements of *Nannodectes* sp. from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
M <sup>1</sup> Length	3	2.7-3.0	2.83	.15	5.39
Width	3	—	3.50	—	—
M <sup>2</sup> Length	2	2.8-3.1	2.95	.21	7.19
Width	2	4.2-4.5	4.35	.21	4.88
P <sub>3</sub> Length	2	2.0-2.1	2.05	.07	3.45
Width	2	1.4-1.5	1.45	.07	4.88

uninformative because it occurs commonly at this locality.

Family PAROMOMYIDAE Simpson, 1940  
*Ignacius frugivorus* Matthew and Granger, 1921  
 Tables 27-28, figs. 8.18-27

*Referred specimens.*—dP<sup>4</sup>, SMM P77.7.125; P<sup>4</sup>, P77.6.59, P77.7.126; probable M<sup>1</sup>, P77.8.163; probable M<sup>2</sup>, P77.8.164; M<sup>3</sup>, P77.7.127, P77.8.165-167; left mandible with M<sub>2</sub> and partial M<sub>1</sub>, P77.6.60; M<sub>1</sub>, P77.6.61, P77.8.168; M<sub>2</sub>, P77.7.128-130, P77.8.169-171; M<sub>3</sub>, P77.7.131-132, P77.8.172.

*Localities.*—Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, North Dakota.

*Description.*—The crown of dP<sup>4</sup> is triangular and nearly equilateral (fig. 8.18). The paracone, metacone, and protocone are subequal. A pronounced crest joins the metacone and protocone, showing no trace of a metaconule. The preprotocrista and postparaconule crista are similarly pronounced, but meet in a small para-

conule. A paracingulum joins the paraconule to a well developed parastyle immediately anterior to the paracone. The centrocrista and the posterolabially-directed postmetacrista appear to have been well developed, but are now reduced by wear. The trigon basin is deep. A crest descends posteriad and a little linguad from the apex of the protocone. At the posterolingual corner of the crown this crest turns sharply labiad and becomes the postcingulum. A vestige of a precingulum is present.

P<sup>4</sup> is relatively simple with no external expansion of the paracone region (fig. 8.19). The parastyle projects anteriorly. The paracone is distinctly larger than the metacone and is directly labial to the protocone. There is a small paraconule and both paraconule cristae are present. Preparacristae and postparacristae, as well as a premetacrista, are also present on P<sup>4</sup> and all of the molars.

The referred M<sup>1</sup> and M<sup>2</sup> differ only in size and in the relative reduction of the metacone area of M<sup>2</sup> (fig. 8.23). Both teeth have postmetacristae and on M<sup>2</sup> there is a faint metastyle. The external

TABLE 27. Measurements of *Ignacius frugivorus* from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
M <sup>1</sup> Length	1	----	2.10	—	—
Width	1	----	3.00	—	—
M <sup>2</sup> Length	1	----	1.90	—	—
Width	1	----	3.00	—	—
M <sup>3</sup> Length	3	1.6-1.8	1.67	.12	6.89
Width	3	2.3-2.5	2.43	.12	4.73
M <sub>1</sub> Length	1	----	1.90	—	—
Width	1	----	1.70	—	—
M <sub>2</sub> Length	3	1.8-2.0	1.87	.12	6.15
Width	3	1.5-1.7	1.60	.10	6.25
M <sub>3</sub> Length	1	----	2.80	—	—
Width	1	----	1.20	—	—

TABLE 28. Measurements of *Ignacius frugivorus* from the Judson locality.

Dimension	N	Range	Mean	SD	V
dP <sup>4</sup> Length	1	----	2.20	—	—
Width	1	----	2.00	—	—
P <sup>4</sup> Length	2	----	1.80	—	—
Width	2	----	2.10	—	—
M <sup>3</sup> Length	1	----	1.90	—	—
Width	1	----	2.20	—	—
M <sub>1</sub> Length	1	----	2.00	—	—
Width	1	----	1.80	—	—
M <sub>2</sub> Length	3	1.9-2.1	1.93	.15	7.93
Width	3	1.7-1.8	1.77	.06	3.28
M <sub>3</sub> Length	1	----	2.60	—	—
Width	2	----	1.50	—	—

cingulum terminates on the posterior side of the metacone and on neither tooth is there a mesostylar spur. The paraconule and its cristae are present; there is no metaconule, but there is a low transverse crest in its position. A precingulum is present on about half the width of the tooth. The corner of the posterolingual cingulum is lingual to the protocone.

Four examples of  $M^3$  are present in the collection. The paracone is larger than the metacone. Both conules and all conule cristae except the postmetaconule crista are present. The precingulum is short. The posterolingual part of the tooth projects posteriorly in all specimens, but the degree of expansion is variable. This feature is most developed on the single  $M^3$  referred from the Judson locality, shown in figure 8.24.

The mandible is deep and narrow (depth below  $M_2$  is 5.7 mm). The angle of the ramus projects downward and is not noticeably excavated on its internal side. The rise of the coronoid process is positioned posterior to the alveoli of  $M_3$ . A minute mental foramen is present below the anterior root of  $M_1$ .

The paraconid of  $M_1$  is smaller than the metaconid and is anterointernal to it (fig. 8.27). The protoconid is of intermediate size and is anteroexternal to the metaconid. The paracristid is well developed and the protocristid weak. Although the talonid basin is closed there is a talonid notch at the base of the metaconid. There is no hypoconulid and only a suggestion of an entoconulid. A small posterior extension of the base of the protoconid gives the appearance of a small external cingulum on both  $M_1$  and  $M_2$ .

On  $M_2$  the trigonid is relatively shorter than on  $M_1$  and the protoconid is larger (figs. 8.21 and 8.26). The paraconid and metaconid are subequal as are the development of the paracristid and metacristid. The talonid is less deeply basined and the talonid notch is less acute than on  $M_1$ .

The trigonid of  $M_3$  is very short with the protoconid approaching the size of the other trigonid cusps (figs. 8.20 and 8.25). The paraconid of SMM P77.7.131 is slightly larger than the metaconid, whereas in SMM P77.8.172 these cusps are about equal in size. The talonid is only shallowly basined and the width of the posterior lobe is about 75 percent of the full talonid width.

*Discussion.*—The Judson and Brisbane samples differ somewhat from the Tiffany and Scarritt samples of *I. frugivorus*. The present sample exhibits slightly greater size, slightly greater

relative width of the lower molars, a relatively deeper mandible, and a narrower posterior lobe on  $M_3$ . Of these differences the first two are typical of *Phenacolemur pagei* Jepsen (1930) and *I. graybullianus* Bown and Rose (1976), wherein they are more accentuated.  $M^3$  was previously unknown in *I. frugivorus* and shows expansion of the posterior lobe that is intermediate between the condition of *Paramonys* and *P. pagei*.

Family CARPOLESTIDAE Simpson, 1935

*Carpodaptes hobackensis* Dorr, 1952

Table 29, figs. 9.1-.4

*Referred specimens.*—Left maxilla with  $P^2$ - $M^2$ , SMM P77.7.133; right mandible fragment with  $P_4$ , P77.7.134; partial  $P_4$ , P77.7.135; right mandible with fragments of  $P_4$  and  $M_1$ , P77.7.136; left mandible with  $P_4$ - $M_3$ , P77.6.62;  $M_3$ , P77.7.137-138.

*Locality.*—Judson locality, Tongue River Formation, Morton County, North Dakota.

*Description.*— $P^2$ - $M^2$  are shown in figure 9.4.  $P^2$  is very small and laterally compressed, bearing a single, conical cusp. A basal cingulum originates at the anterior midline and extends around the internal margin to the posteroexternal corner.

$P^3$  has four cusps in the external row, the anteriormost well separated from the other three and forming a marked anterior projection in the crown outline. A median cusp is present midway between the first and second external cusps. It is joined to the anteroexternal cusp by a crest and a second, longer crest extends posterolabial from it, joining the posterior margin of the tooth. Two broad, low cusps are situated on the lingual margin at the internal corners of the crown.

TABLE 29. Measurements of *Carpodaptes hobackensis* from the Judson locality.

	Length, mm	Width, mm
SMM P77.7.133 $P^2$	0.7	0.6
$P^3$	1.8	1.8
$P^4$	1.6	1.9
$M^1$	1.3	1.8
$M^2$	1.2	1.8
SMM P77.7.134 $P_4$	2.3	1.6
SMM P77.6.62 $P_4$	2.4	1.6
$M_1$	1.5	1.4
$M_2$	1.2	1.4
$M_3$	1.8	1.2
SMM P77.7.137 $M_3$	1.7	1.1
SMM P77.7.138 $M_3$	1.7	1.2



These cusps occur on a cingulum that extends from the anteroexternal corner around the internal margin (joining the internal cusps) to a point directly posterior to the median cusp. A weak cingulum is present on the labial margin, but it does not join the other cingulum. A single convolute wear facet bearing transverse striae joins the three posterior external cusps, the posterior median crest, the posterior cingulum, and the posterointernal cusp.

P<sup>4</sup> has five external cusps: two closely joined anterior cusps, a notch, and then three closely joined posterior cusps. Anterior and posterior crests from the median cusp join the anterior and posterior cingula at the margins of the first and last external cusps. There are three internal cusps, of which the center is the highest and least internal. The middle internal cusp is joined to the median cusp by a transverse crest. The cingula of P<sup>4</sup> are similar to those of P<sup>3</sup> except that the anterior and posterior cingula are more deeply inflected. Wear on the external cusp row is discontinuous at the notch between the second and third cusps. These two external wear surfaces are joined to a wear facet on the median cusp and crests, which is in turn connected to wear facets on the anterior and posterior cingula and the anterointernal and posterointernal cusps. The wear surface on the median crest is sculptured into a series of transverse grooves, or scallops. A small isolated wear facet also occurs on the labial side of the central internal cusp. Striae on all of these surfaces are transverse.

On M<sup>1</sup> and M<sup>2</sup>, the paracone is slightly higher than the metacone. The protocristae of M<sup>2</sup> are longer (transversely) than those of M<sup>1</sup>, and the protocone apex has a relatively more forward position. The external cingulum is continuous with both the paracingulum and the meta-cingulum on M<sup>1</sup>. On M<sup>2</sup> the posterior end of the external cingulum terminates labial to the metacone apex. Both molars bear precingula and postcingula that terminate slightly lingual to the protocone apex. The postcingulum widens lingually and bears a low indistinct hypocone. Wear on the molars is similar to that described by Rose (1975, p. 55-60).

The morphology of P<sub>4</sub> has been fully described by Dorr (1952). Two complete and two partial lower fourth premolars of this species are present in the Judson collection. These have either five or six apical cusps in addition to the talonid cusp. When six cusps are present, the anteriormost is

small and is set approximately midway down the anterior face of the crown. The penultimate cusp is set just above the midpoint between the antepenultimate and talonid cusps. The internal ridge leading to the penultimate cusp is weak, and that part of the crown is gently concave. The wear on SMM P77.6.62 occurs as a narrow, continuous facet along the external side of the apical crest. The facet extends from the talonid cusp to the second apical cusp and bears transverse striae. SMM P77.7.134, which is less worn, shows wear only between the antepenultimate cusp and the talonid cusp. Striae on P77.7.134 are also transverse. Abrasion surfaces are present on the internal face near the base of the tooth. On SMM P77.7.136, a very worn specimen, this internal abrasion surface has worn completely through the enamel.

The trigonid of M<sub>1</sub> is elongate with a paraconid-protoconid-metaconid angle of about 105 degrees. The protoconid is slightly higher than the paraconid and metaconid, which are equal in height. The talonid basin is short and relatively narrow. The cristid obliqua is continuous with the metaconid and divides the postvallid into two parallel transverse surfaces; the labial portion is displaced anteriorly with respect to the lingual portion. The hypoconid is not well differentiated. On M<sub>2</sub>, the metaconid is the highest trigonid cusp and the protoconid is the lowest. The trigonid is much shorter and the talonid is much larger than those of M<sub>1</sub>. These differences are accentuated even more in M<sub>3</sub>, which bears in addition a posterior hypoconulid lobe. Wear on the lower molars again agrees with the description by Rose.

*Discussion.*—There are five specimens of P<sub>4</sub> referable to *Carpodaptus* from the Judson locality. Of these, three are similar to *C. hobackensis* Dorr (1952), one is similar to *C. cygneus* (Russell, 1967), and one is so worn as to be indeterminate. *C. hobackensis* may best be distinguished from *C. cygneus* by the presence on P<sub>4</sub> of a posterolingual concavity, weaker ridges in general, and little or no internal ridge leading to the penultimate cusp (Rose, 1975). Using these criteria, three of the four determinable specimens from the Judson locality are referable to *C. hobackensis*. One Judson specimen (SMM P77.6.63) and the three specimens of P<sub>4</sub> from Brisbane are referable to *C. cygneus*. It is important to note that SMM P77.6.63 is heavily water worn, and may have been either reworked or transported a considerable distance before

deposition. Since the upper dentition was not represented in the type series of *C. hobackensis*, the reference of the Judson maxillary to that species may seem speculative because it could simply be a variant of *C. cygneus*. The identification of the maxillary was based, in part, on its marked difference from the corresponding teeth in the Brisbane collection. A more detailed argument for this allocation of the specimens is presented in the discussion of *C. cygneus*.

It is fortuitous that the maxilla and the best preserved mandible (SMM P77.6.62) are from the same side of the dentition so that direct physical manipulation could be used in the study of mastication. Both specimens possess very well developed and well preserved wear facets.

The anteriormost part of the crest of  $P_4$  (including the first cusp when six apical cusps are present) is opposed by that portion of  $P^3$  anterior to the median cusp, but there is no actual contact of the two teeth in this region. The labial side of the antepenultimate cusp and the three cusps preceding it (homologous to the region of molar facet 2 of Kay and Hiiemae, 1974) shear medially across the posterior external cusps (facet 2a), the posterior median crest (facet 2b), the sinuous posterior cingulum, and the posterointernal cusp of  $P^3$ . Wear on the last two surfaces mentioned is roughly equivalent to facet 10 of Kay and Hiiemae, but the motion involved is more strictly intermediate between Phase I and Phase II occlusion. The teeth are aligned so that the cusps of  $P_4$  oppose the gaps between the external cusps of  $P^3$  and  $P^4$ . The remainder of  $P_4$  occludes with the anterior part of  $P^4$  in a manner very similar to its occlusion with  $P^3$ , creating facets homologous to 1a and 1b as well as lingual facets without homologs in the system of Kay and Hiiemae. The antepenultimate cusp moves along the interdental gap between  $P^3$  and  $P^4$ , whereas the penultimate cusp meets the prominent gap in the external cusp row of  $P_4$  and has worn a transverse groove into the anterior median crest adjacent to the gap. The notch between the penultimate and talonid cusps of  $P_4$  occludes with the middle external cusp, the median cusp, and the middle internal cusp of  $P^4$ . The striae directions and the position of the wear facets on the labial side of the crest of  $P_4$  indicate that the lower premolar was drawn lingually across  $P^3$  and  $P^4$  as a prominent component of Phase I shear. In this respect I disagree with Rose (1975, p. 60) who concludes that " $P_4$  was not very important in Phase I" and

that " $P_4$  probably functioned in a saw-like manner." The lingually decreasing slope of the facets of the upper premolars shows that the lower jaw must have rotated as  $P_4$  was drawn across  $P^3$  and  $P^4$ .

The mode of occlusion of the trigonid of  $M_1$  with  $P^4$  and  $M^1$  is similar to that of  $P_4$ . The elongate trigonid of  $M_1$  functions like a smaller and simplified version of  $P_4$ , producing analogous facets and transverse grooves.

In addition to the shearing mode of occlusion, a limited amount of grinding between the molars was possible. Due to the posterior decrease in the relief of the talonid basins and the protocones, there is a posterior increase in the horizontal displacements permissible during grinding. The first molar pair could do little more than crush and shear, but the last molar is capable of a moderate amount of grinding. The maximum horizontal displacements of the molars can be achieved near the end of the transverse shear stroke when the top of the lower jaw is rotated inward so as to allow clearance between  $P_4$  and the upper premolars. In this position the molars can perform both longitudinal and transverse grinding motions.

The degree of rotation of the lower jaw, both in the shear stroke and in the attainment of the grinding position, required several adaptations in the jaw mechanics of *Carpodaptus*. The musculature of the occluding jaw would have been required to produce effective lateral translation and rotation as well as the more normal adduction. The fossa for the insertion of *M. zygomaticomandibularis* on SMM P77.6.62 is expanded anteroventrally and posterodorsally at the expense of the insertion area of *M. temporalis*. The angular process projects posteroventrally and is slightly inflected. The insertion area of the *M. pterygoideus internus* includes the internal face of the process and extends dorsad to the dental foramen, which is just a little below the level of  $M_3$ . The combined action of these two muscles as well as *M. temporalis* would produce the lower jaw motion that has been inferred from the dentition, and the relative increase in the size of the former muscles and the reduction of the latter may be regarded as adaptations that complement the dentition.

The most probable diet of *C. hobackensis* appears to have been plant tissue that was both fibrous and succulent. The lower blade functions much like a complexly shaped chisel. Its ridges



operated in a tongue-in-groove fashion with the transverse troughs and intercuspal gaps of the upper premolars. The structure is ideally suited to cutting fibers because the grooves and ridges would prevent the fibers from sliding along the crests and thereby escaping being cut. The food being sheared in this manner could not have been very thick; otherwise  $P_4$  would cease its close interaction with the upper premolars and would begin to function simply as a wedge. Larger food and a wedge-like function of  $P_4$  may have been important in some carpolestids, accounting for the rapid abrasion in some species noted by Rose (1975). The limited grinding capability in this species suggests that if the food was plant tissue it was probably succulent; turgid plant cells can be burst simply by crushing, whereas flaccid cells must be ground or cut in order to be opened.

***Carpodectes cygneus* (Russell, 1967)**

Table 30, figs. 9.5-15

*Referred specimens.*— $P^3$ , SMM P77.8.173-176; right maxilla with  $P^4$ - $M^3$ , P77.8.177;  $M^2$ , P77.8.178;  $P_4$ , P77.8.179-180; right mandible with  $P_4$ , P77.8.181; left mandible with  $P_4$ - $M_1$ , P77.6.63;  $M_1$ , P77.8.182-183;  $M_2$ , P77.8.184; left mandible with partial  $M_1$  and  $M_2$ - $M_3$ , P77.8.185;  $M_3$ , P77.8.186.

*Localities.*—Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, North Dakota.

*Description.*—The dental morphology of *C. cygneus* is close to that of *C. hobackensis*. Des-

cription will be largely limited to differences between the species and to features not previously known in *C. cygneus*.

The anterior external cusp of  $P^3$  does not form a distinct anterior projection (fig. 9.5). The posterior median crest bears no cuspules and is gently sinuous. The anterior crest emanating from the median cusp is variable: on two specimens it is absent, on one specimen it leads to the anterior cingulum, and on the remaining specimen it leads to the anteroexternal cusp. The posterior internal cusp is not situated on the posterointernal corner of the crown, but is distinctly anterior to it.

On  $P^4$  the central transverse crest joining the median cusp and the central internal cusp is indistinct and the basins anterior and posterior to it are poorly developed. The wear facets are not particularly informative in any of the specimens of the upper dentition.

Two of the mandibles possess alveoli anterior to  $P_4$ . The alveolus for the incisor is large, laterally compressed, and semi-procumbent. Posterior to it are three small circular alveoli. The anterior-most of the three is minute and is displaced labially. The posterior two alveoli are directly anterior to  $P_4$ .

$P_4$  has five distinct apical cusps in addition to the talonid cusp. In no case is there a tendency to develop an additional anterior cusp low on the anterior slope. Both the anterior and posterior slopes of the apical crest are steep. The vertical ridges leading to the apical cusps are very weak on the external side and stronger on the internal

TABLE 30. Measurements of *Carpodectes cygneus* from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
$P^3$ Length	4	1.6-1.8	1.68	.10	5.72
Width	4	1.8-2.1	1.95	.13	6.62
$P^4$ Length	1	----	1.70	—	—
Width	1	----	2.20	—	—
$M^1$ Length	1	----	1.40	—	—
Width	1	----	2.20	—	—
$M^2$ Length	2	----	1.30	—	—
Width	2	2.0-2.1	2.05	.07	3.45
$M^3$ Length	1	----	1.20	—	—
Width	1	----	1.80	—	—
$P_4$ Length	3	2.0-2.2	2.13	.12	5.41
Width	3	1.5-1.8	1.60	.17	10.83
$M_1$ Length	2	----	1.50	—	—
Width	2	1.3-1.4	1.35	.07	5.24
$M_2$ Length	2	----	1.30	—	—
Width	2	1.3-1.4	1.35	.07	5.24
$M_3$ Length	2	----	1.80	—	—
Width	2	1.2-1.3	1.25	.07	5.66



side. The internal ridge leading to the penultimate cusp is strong, and there is no marked overall concavity of that area. The penultimate cusp is high on the posterior slope, close to the antepenultimate cusp. The apical crest is nearly straight in occlusal view with only a slight tendency to form an S-shaped curve. Wear is similar to *C. hobackensis*.

The trigonid of  $M_1$  is long and blade-like with a paraconid-protoconid-metaconid angle of about 105 degrees. The cristid obliqua is continuous with the metaconid, forming two parallel surfaces, which together comprise the postvallid. The entoconid and hypoconid are well developed, whereas the hypoconulid is indistinct. The talonid basin is relatively wide and deep and is open on its lingual side. The second and third lower molars show a progressive lowering and shortening of the trigonid, a reduction in the relief of the talonid, and a relative widening of the talonid basin. The lower third molar possesses a posterior hypoconulid lobe that is narrow and bulbous on one specimen and broad on the other.

The measurements of SMM P77.6.63, the only specimen referred to this species from the Judson locality, are:  $P_4$ , length 2.0 mm, width 1.4 mm;  $M_1$ , length 1.5 mm, width 1.3 mm.

*Comparisons.*—The following are features of *C. cygneus* that differ from the corresponding features of *C. hobackensis*.  $P^3$  is shorter and wider, with less inflected transverse margins and cingula and a more forward position of the posterior internal cusp.  $P^4$  is more transverse, with a reduced notch in the external cusp row, a weaker central transverse crest, less inflected anterior and posterior margins and cingula, and reduced anterointernal and posterointernal basins. The upper molars are also more transverse and have better developed pre- and postcingula and hypocones.  $P_4$  has steeper anterior and posterior slopes, a higher penultimate cusp with a stronger internal ridge, no posterointernal concavity, and more distinct talonid cusp and crests. The widths of the talonid basins of all the lower molars are relatively greater.

*Discussion.*—With the exception of one mandible, SMM P77.6.63, all of the elements of the lower dentition from Judson exhibit the *C. hobackensis* variety of  $P_4$  and lower molars with narrow talonids. All of the elements of the lower dentition from Brisbane and SMM P77.6.63 have the *C. cygneus* variety of  $P_4$  and lower molars with wide talonids. The absence of intergradation

in the structure of either  $P_4$  or the molars and the absence of any mixing of characters with respect to  $P_4$  and the molars strongly suggest the presence of two distinct morphologic forms in the samples. The uneven distribution of the two morphologic forms between the two localities makes it highly improbable that the two forms represent sexual dimorphism. It is therefore likely that both *C. cygneus* and *C. hobackensis* are present in the samples, rather than a single, variable population.

The allocation of elements of the upper dentition is complicated by the fact that the upper dentition of *C. hobackensis* is entirely unknown from its type area, and  $P^3$  is the only element of the upper dentition of *C. cygneus* that is known from its type area. All of the elements of the upper dentition from Brisbane either have  $P^3$ 's like *C. cygneus* or have wide molars and are therefore consistent with the elements of the lower dentition from Brisbane and can be referred with relative certainty to *C. cygneus*. Although direct comparison of the Judson maxilla with known specimens of *C. hobackensis* is impossible, it is markedly different from all of the Brisbane specimens and the differences are consistent with their allocation to *C. hobackensis*.

All of the structural differences between *C. cygneus* and *C. hobackensis* indicate more emphasis on molar grinding and less emphasis on premolar shear in the former species. This difference in function is readily apparent in the structure of the molars. Whereas in most dimensions the two species are of identical size, the wide talonid basins and wide upper molars of *C. cygneus* provide an areally greater grinding surface. The relative emphasis of premolar shear in *C. hobackensis* is less obvious, but equally certain. The posterointernal concavity of  $P_4$  provides a sharper cutting edge. The S-shapes of the apical crest of  $P_4$  provides a closer conformation to the shapes of  $P^3$  and  $P^4$ . The marked inflections of the postcingulum of  $P^3$  and both the anterior and posterior cingula of  $P^4$  provide a greater effective anteroposterior length to these crests as they are sheared transversely by the cutting edges of  $P_4$  and  $M_1$ . The more posterior penultimate cusp of  $P_4$  and the better developed external notch of  $P^4$  improve the shearing efficiency by inhibiting the longitudinal movement of food that might otherwise not be cut during the shearing stroke. The more posterior position of the posterior internal cusp of  $P^3$

increases the inflection of the posterior cingulum and lengthens it lingually where it is occluding with the notch anterior to the antepenultimate cusp of P<sub>4</sub>; in both effects the available length of shear crests is increased. These differences in function indicate that the food of *C. cygneus* was probably less fibrous or less succulent than that of *C. hobackensis* (see discussion of diet in the discussion section of *C. hobackensis*).

The biological relationship between these species remains uncertain. The presence of a single, water-worn specimen of *C. cygneus* at the Judson locality does not constitute good evidence for sympatry of the two species since it may differ in provenance from the other Judson specimens. It is possible that an ancestor-descendant relationship exists between the species. If that is true, then in the context of the evolution of the family, *C. cygneus* would most likely be the ancestral species because it is less specialized with respect to premolar shear.

Family PICRODONTIDAE Simpson, 1937

Genus and species indeterminate

Fig. 9.16

*Referred specimen.*—Partial right M<sup>1</sup>, SMM P77.8.187.

*Locality.*—Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Description.*—UMVP 6821 (fig. 9.16) probably consists of the anterior portion of M<sup>1</sup>. The anterolingual corner is slightly expanded. The pre-

cingulum is truncated by the preprotocrista, which extends from the protocone to a point anterior and dorsal to the paracone. The included angle between the postcingulum and a line joining the paracone to the protocone is less than 90 degrees. A postprotocrista cannot be distinguished. The enamel of the crown has many fine ridges that roughly parallel the postcingulum. The anterior width is 2.4 mm. The anterior surface of the precingulum below the apex of the protocone shows evidence of interdental wear.

*Discussion.*—The specimen resembles M<sup>1</sup> in the form of the anterior margin, but resembles M<sup>2</sup> in the absence of a postprotocrista and the presence of interdental wear on the anterior margin of the crown. The fragmentary nature of the specimen makes generic identification impossible.

Order CARNIVORA

Family MIACIDAE Cope, 1880

*Protictis (Protictis) paralus*, new species

Table 31, figs. 10.1-3

*Type specimen.*—Right mandible with C, P<sub>4</sub>-M<sub>2</sub>, alveoli for P<sub>1</sub>-P<sub>3</sub>, SMM P77.6.64.

*Paratypes.*—Left M<sup>1</sup>, SMM P77.7.139; right M<sub>1</sub> trigonid, P77.7.140.

*Type locality.*—Judson locality, Tongue River Formation, Morton County, North Dakota.

*Referred specimens.*—P<sub>4</sub>, SMM P77.8.188-189; M<sub>1</sub>, P77.8.190.

TABLE 31. Measurements of *Protictis paralus*, new species, from the Judson and Brisbane localities. All dimensions are those of MacIntyre (1966).

Dimension	SMM P77.7.139	SMM P77.6.64	SMM P77.7.140	SMM P77.8.188	SMM P77.8.190	SMM P77.8.189
M <sup>1</sup> Length	3.9					
Width, ant.	5.6					
Width, post.	5.0					
Grind width	4.5					
P <sub>4</sub> Length		4.0		3.8		—
Width		1.8		1.8		1.7
M <sub>1</sub> Length		4.5	—		4.5	
Width, ant.		3.0	2.7		3.0	
Width, post.		2.3	—		2.2	
Grind width		2.2	—		2.1	
Length, talonid		1.7	—		1.8	
Length, trigonid		2.8	2.6		2.6	
Length, paraconid		1.5	—		1.7	
Length, metaconid		1.2	1.1		1.4	
M <sub>2</sub> Length		3.9				
Width, ant.		2.0				
Width, post.		1.8				
Grind width		1.8				

*Locality.*—Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Etymology.*—*paralos*, Gr. near the sea, in reference to the former proximity of the type locality to the Cannonball Sea.

*Diagnosis.*—Differs from *P. (Protictis) haydenianus* in being smaller and having a relatively longer talonid and higher trigonid on  $M_2$ . Differs from *P. (Simpsonictis) tenuis* in being larger, having a large hypoconid and hypoconulid on  $P_4$ , and in having relatively lower trigonids, but higher paraconids on  $M_1$  and  $M_2$ . Differs from *P. (Bryanictis) microlestes* as follows:  $P_4$  narrower with reduced paraconid and cingula, large hypoconulid (not separable from posthypoconid), and minute entoconid;  $M_1$  having a higher trigonid, higher and more anterior paraconid, more distinct hypoconulid, and minute entoconid;  $M_2$  longer with higher trigonid, more erect protoconid, higher paraconid;  $M^1$  relatively wider with reduced cingula and labially projecting metastylar shelf. Differs from *P. vanvaleni* in lacking a metaconid on  $P_4$  and in having a more anterior paraconid on  $M_1$ .

*Description.*—The outline of  $M^1$  is shown in figure 10.3. The paracone is the highest cusp and is an erect, acute cone. The metacone is a lower, slightly recumbent cone. The preparacrista extends labially toward (but does not join) the small stylocone. Although it has been removed by wear, the centrocrista appears to have been straight. The postmetacrista is a symmetric counterpart of the preparacrista except that it extends to the labial margin of the crown and is continuous with the weak, but complete ectocingulum. A parastyle was probably present, but has been removed by wear. The preprotocrista is straight and is separated from the paraconule by a carnassiform notch. The postprotocrista lacks a notch and is continuous with the postmetaconule crista, which terminates below the postmetacrista and posterior to the metacone apex. The precingula and postcingula are short and lingually discontinuous. The hypocone has been obliterated by wear. All crests and cingula except the ectocingulum have wear facets. Of these, all of the facets are well developed except that on the postmetacrista. Nearly all of the enamel in the trigon basin has been removed by wear. The only effects of abrasion are the removal of the paracone and metacone apices.

The mandible is slender and bears a shallow longitudinal depression on its lingual side that

follows the ventral margin. Four small mental foramina are present, occurring below the alveolus of  $P_1$ , the posterior alveolus of  $P_2$ , the midpoint of  $P_3$ , and the anterior root of  $P_4$ . The alveoli of  $P_1$ - $P_3$  are closely spaced and of nearly equal size, that of  $P_1$  being the largest.

The lower canine is broken so that very little of its crown remains. Its base measures 2.0 mm long by 1.5 mm wide.

$P_4$  bears a small, essentially conical paraconid. The protoconid is tall and slightly recurved, and bears anterior and posterior crests (fig. 10.1). Halfway down the posterior crest of the protoconid is a large hypoconid, set off from both protoconid and hypoconulid by well developed carnassiform notches. The hypoconulid is high, acute and blade-like, and on two of three specimens it is joined by a low lingual crest to a minute entoconid. The talonid is not basined, but opens lingually. The only cingulum occurs on the labial side and extends from the hypoconulid down to a point below the hypoconid. In occlusal view (fig. 10.2), the posterior margin is rounded and the four largest cusps are arranged in an arc that is concave lingually. There is a small wear facet on the labial side of the paraconid and three much larger ones on the labial side of the hypoconid, hypoconulid, and the labial cingulum. The apices of the paraconid and protoconid bear abrasion craters.

$M_1$  has a relatively high and open trigonid. The paraconid-protoconid-metaconid angle is about 60 degrees. The protoconid is much higher than the metaconid, which is a little higher than the paraconid. Well developed carnassial notches are present in both the paracristid and protocristid. The postvallid is essentially transverse and a little wider than the talonid. There is a weak anterolabial cingulum, and a weak labial cingulum was evidently present at the hypoflexid, but has been largely removed by contact with the paracone of  $M^1$ . The hypoconid is broader and larger than the entoconid. Projecting a little posteriorly, the hypoconulid is a little smaller than the entoconid. A very small entoconulid is present anteroventral to the entoconid. The posterior cingulum extends from the hypoconulid to the labial enamel base adjacent to the hypoconid. As in  $P_4$  the talonid does not form a closed basin and the lingual talonid crest is weak. Large shear facets cover both the prevallid and postvallid. In addition, there is a vertical groove below the posterior carnassial notch that is apparently



caused by contact with the paraconule of  $M^1$ . The anterior and posterior faces of the hypoconid show extensive wear resulting from occlusion with the paracone and metacone respectively. The cristid obliqua and the lingual face of the hypoconid show extensive wear and abrasion resulting from occlusion of a grinding nature. All cusps but the protoconid, entoconid, and entoconulid have apical abrasion craters.

$M_2$  differs from  $M_1$  in having a lower trigonid and a longer talonid. The paraconid-protoconid-metaconid angle is about 50 degrees. The metaconid is higher than the protoconid, but the latter is quite worn. The sides of the postvallid are parallel. The hypoconulid is the tallest talonid cusp and it projects posteriorly. Wear is similar to  $M_1$  except that there is more abrasion of the paraconid, no abrasion of the metaconid, some abrasion of the protoconid, and the entire dorsal surface of the talonid is extensively worn by grinding.

*Discussion.*—Although the number of known specimens of *P. paralus* is small, they are sufficiently numerous and regular to indicate that the type is reasonably accurate in its representation of the species. The distinction of this species from *P. haydenianus* (Cope, 1882b), *P. tenuis* (Simpson, 1935b), and *P. vanvaleni* MacIntyre (1966) is obvious and easily diagnosed. Its distinction from *P. microlestes* (Simpson, 1935b) is less obvious.

Important functional differences between *P. paralus* and *P. microlestes* are obscured in a casual comparison by the similar size of the species, and by the absence of simple diagnostic structural differences. These functional differences are a generally greater shearing capacity in *P. paralus*, particularly that involving  $M_2$ . The general difference is manifested in the more trenchant talonid of  $P_4$  and the elevated trigonids and higher, more anterior paraconids of  $M_1$  and  $M_2$  in *P. paralus*. The relatively greater shear against  $M_2$  in *P. paralus* is shown by the much greater trigonid height and by its more labial protoconid compared to *P. microlestes*. When viewed posteriorly the postvallid of  $M_2$  in *P. paralus* has parallel sides, whereas that of *P. microlestes* has sides that converge dorsally. The labially projecting metastylar shelf of  $M^1$  in *P. paralus* is undoubtedly related to the more labial and more erect protoconid of  $M_2$ .

Additional specimens from Cedar Point Quarry, Wyoming, are apparently referable to

*P. paralus* (Gingerich, personal communication, 1977).

The present subgeneric classification of *Protictis* as formulated by MacIntyre (1966) consists of three subgenera: *P. (Protictis)*, including *P. haydenianus*; *P. (Simpsonictis)*, including *P. tenuis*; and *P. (Bryanictis)*, including *P. microlestes* and *P. vanvaleni*. Although these species fall into three corresponding size groups, gross size does not enter into MacIntyre's subgeneric diagnoses. Instead, the subgenera are diagnosed on the basis of morphologic differences that correspond to three distinct modes of dental function. Both of the subgenera *Protictis* and *Simpsonictis* have relatively greater shear capabilities than does *Bryanictis*. This is accomplished in *Protictis* by increasing shear involving  $P_4$  and  $M_1$ . In *Simpsonictis* shear involving  $M_1$  and  $M_2$  is increased. Inasmuch as *P. paralus* differs from *Bryanictis* in having greater shear involving  $P_4$ ,  $M_1$ , and  $M_2$ , a case could be made for the creation of yet another subgenus. To do so, however, would result in the genus having five species distributed among four subgenera. The limited value of such a classification needs no further comment.

*Protictis paralus* is here referred to the subgenus *P. (Protictis)*. This assignment entails the fewest discrepancies and maintains the complexity of  $P_4$  and trigonid height of  $M_1$  as the two major criteria of classification. The discrepancies are the relatively higher trigonid and longer talonid of  $M_2$  in *P. paralus*.

Viverravine, genus and species indeterminate  
Fig. 10.8

*Referred specimen.*—Partial left  $P^4$ , SMM P77.7.141.

*Locality.*—Judson locality, Tongue River Formation, Morton County, North Dakota.

*Description.*—SMM P77.7.141 is a complete  $P^4$  except for the protocone. The paracone bears anterolabial and posterior crests and a rounded anteromedial face. The parastyle is small and conical rather than pyramidal. The presence or absence of a crest and notch on the posterior side of the parastyle cannot be determined due to abrasion of the parastyle apex and combined abrasion and wear of the saddle between the parastyle and paracone. A narrow posterolingual cingulum is present and slopes dorsad for the entire length of the posterior root. The stylar

cingulum is also narrow; it begins near the center of the labial emargination and narrows as it rises to the summit of the metastyle crest at the posterior corner of the tooth. The metastyle blade and carnassial notch are well developed (fig. 10.8). A large shear facet covers most of the posterolingual face of the metastyle blade and the cingulum below it as well as the posterolingual face of the paracone. There is a vertical groove on the anterior face of the paracone caused by occlusion of the tip of the protoconid of P<sub>4</sub>. The labial length is 8.8 mm and the metastyle length is 3.5 mm.

*Discussion.*—This tooth undoubtedly represents a viverravine miacid, but generic or specific allocation is not possible. Compared to *Protictis haydenianus* this tooth is larger and has reduced cingula, more inflated cusps, and a relatively longer metastyle blade. It is unlikely that SMM P77.7.141 is referable to *P. haydenianus* although it may represent a later species of the same genus. It is also possible that it pertains to an early species of *Didymictis* such as *D. dellensis* Dorr (1952), but direct comparison is impossible since P<sup>4</sup> is unknown in that species.

Miacid, genus and species indeterminate  
Figs. 10.4-7

*Referred specimens.*—P<sup>3</sup>, SMM P77.8.191; partial P<sup>4</sup>, P77.6.65, P77.8.192; partial M<sub>1</sub>, P77.6.66-67.

*Localities.*—Judson and Brisbane localities, Tongue River Formation, Morton and Grant Counties, North Dakota.

*Description.*—The inferred P<sup>3</sup> is a simple tooth bearing a minute parastyle, high blade-like paracone, and a metastyle blade that is separated from the paracone by a carnassiform notch (fig. 10.4). There is no protocone. The length of P<sup>3</sup> is 3.1 mm, the width 1.2 mm.

SMM P77.8.192, a left P<sup>4</sup>, is complete except for the protocone. The parastyle is low and conical and is joined to a paracone apex by a sharp crest. Both the posterior crest of the paracone and the metastyle blade are thin and sharp; they are separated by a deep carnassiform notch (fig. 10.6). The labial cingulum extends from the posterior corner of the tooth to a point below the notch. The posterolingual cingulum appears to terminate below the paracone apex. The labial

length is 3.3 mm, length of metastyle blade 0.9 mm.

SMM P77.6.65, also a P<sup>4</sup>, is lacking enamel and the parastyle. The protocone is low and conical. This tooth differs from SMM P77.8.192 in having a more inflected labial margin, longer metastyle blade, and longer posterolingual cingulum extending to protocone. The lingual length is 3.5 mm, the length of metastyle blade 1.3 mm.

One of the lower molars, SMM P77.6.66, is complete except for the paraconid. The trigonid is quite elevated, having the protoconid as its highest cusp (fig. 10.5). The postvallid is slightly oblique and bears a well developed carnassiform notch in the protocristid. There was apparently an even deeper notch in the paracristid, as the anterior crest of the protoconid can be traced down about half the height of the trigonid before intersecting the broken edge of the crown. The talonid is wider than the trigonid (anterior width 1.9 mm, posterior width 2.1 mm). The talonid is trenchant, having an elevated hypoconid, and hypoconulid, inclined central surface, and little or no entoconid. There is a large, deep talonid notch. The length of the crown was greater than 4.1 mm. Another fragment, SMM P77.6.67, consists of a molar trigonid in which the paraconid is preserved. The paraconid is lower than the metaconid, is separated from the protoconid by a deep carnassiform notch, and is set far forward. The paraconid-protoconid-metaconid angle is about 75 degrees. In all other respects, including size, the fragment resembles SMM P77.6.66.

*Discussion.*—The collocation of these specimens is the result of their similarity in size and their hypercarnivorous, miacid-like appearance. If the assigned tooth positions are correct, this group of specimens is suggestive of late viverravines, such as *Viverravus*, or some of the early miacines.

Order CONDYLARTHRA

Family ARCTOCYONIDAE Murray, 1866

*Thryptacodon australis* Simpson, 1935a

Table 32, figs. 11.1-.3, 11.5-.10

*Referred specimens.*—dP<sup>4</sup>, SMM P77.6.68; M<sup>1</sup>, P77.6.69-70; M<sup>2</sup>, P77.6.71; left mandible with M<sub>1</sub>, P77.6.72; M<sub>1</sub>, P77.7.142-143; M<sub>2</sub>, P77.6.73, P77.7.144; M<sub>3</sub>, P77.6.74, P77.7.145, P77.8.193.

*Localities.*—Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, North Dakota.

*Description.*—The referred dP<sup>4</sup> bears subequal



paracone, metacone, and protocone, a smaller and lingually-displaced hypocone, and a prominent parastyle and metastyle (fig. 11.1). The trigon basin is deep. There is a distinct metaconule, but no paraconule. The paracristae and metacristae are sharply defined and the postprotocrista is arcuate and continuous with the metacingulum. The precingula and postcingula are greatly reduced. There are two large wear facets, one on the preparacrista and parastyle, and the other on the postvallum adjacent to the metaconule. The enamel is thin.

M<sup>1</sup> is nearly quadrate with a narrow but continuous cingulum encircling the tooth (fig. 11.2). The metaconule is well developed and has a premetaconule crista. A small paraconule is present, but its conule cristae are indistinct. The postprotocrista forms an arcuate loph, whereas the preprotocrista is less elevated, shorter, and nearly transverse. The hypocone is relatively large. All of the cusps have been lowered by abrasion.

The structure of M<sup>2</sup> is similar to that of M<sup>1</sup> (fig. 11.3), but the crown is a little longer and considerably wider. The ectoflexus is shallower than in M<sup>1</sup>.

The alveoli of the lower premolars are preserved on the mandible, SMM P77.6.72. All of the premolars had two roots, except for P<sub>1</sub>, which had but one. There is a short diastema separating P<sub>1</sub> from P<sub>2</sub>, and another of equal length separating P<sub>2</sub> from P<sub>3</sub>. Mental foramina are present below the anterior diastema and below the anterior root of P<sub>3</sub>. There is a marked longitudinal groove occupying the ventral half (or a little more) of the lingual side of the mandible. The depth of the mandible below the posterior root of M<sub>1</sub> is 7.6 mm.

M<sub>1</sub> is elongate and narrows anteriorly (fig. 11.8). The trigonid is moderately elevated and

bears distinct cusps that are in the form of blunt cones (fig. 11.5). The paraconid is fully internal and is well differentiated, although it is much lower than either the metaconid or protoconid. The paracristid is loph-like and the protocristid is weakly notched. The ectocingulid originates on the posterior face of the protoconid and is continuous with the postcingulid, which rises to join the hypoconulid. The cristid obliqua is arcuate and loph-like. The talonid basin is closed and its depth is variable between specimens. The hypoconulid is small and close to the entoconid. There is a small entoconulid.

M<sub>2</sub> is a little shorter and markedly wider than M<sub>1</sub> (figs. 11.6 and 11.9). The trigonid is less elevated and its cusps are blunter and less well differentiated. The paraconid is subinternal, and the trigonid bears a metacristid. The precingulid, ectocingulid, and postcingulid are continuous and very narrow adjacent to the protoconid and hypoconid.

M<sub>3</sub> narrows posteriorly to such a degree that it is almost triangular (fig. 11.10). Relief on the entire crown is very low (fig. 11.7). The paracristid and metacristid are arcuate and about equally long. The paraconid is fully median. The postcristid joins the hypoconid and entoconid, excluding the hypoconulid from the rim of the talonid basin. The hypoconulid is quite large and projects posteriorly. The precingulid, ectocingulid, and postcingulid are all short and discontinuous.

*Comparison.*—Compared to the type of *T. australis* from Mason Pocket (Simpson, 1935a), the Judson specimens show (1) a weaker ectoflexus on M<sup>2</sup>, (2) a similarly shallow mandible, (3) a shorter diastema between P<sub>1</sub> and P<sub>2</sub>, (4) a diastema present behind P<sub>2</sub>, (5) a more forward posterior mental foramen, (6) shorter M<sub>2</sub> and M<sup>2</sup>, (7) similarly developed basal cingula, but weaker

TABLE 32. Measurements of *Thryptacodon australis* from the Judson locality.

Dimension	N	Range	Mean	SD	V
M <sup>1</sup> Length	2	5.8-5.9	5.85	.07	1.20
Width	2	6.6-6.8	6.70	.14	2.09
M <sup>2</sup> Length	1	—	6.20	—	—
Width	1	—	7.80	—	—
M <sub>1</sub> Length	3	6.2-6.6	6.37	.22	3.49
Width	2	4.3-4.5	4.40	.14	3.18
M <sub>2</sub> Length	2	5.9-6.5	6.20	.42	6.77
Width	2	4.8-5.8	5.30	.71	13.40
M <sub>3</sub> Length	2	6.3-6.6	6.45	.21	3.26
Width	2	—	4.80	—	—



entoconulids on the lower molars, (8) similar proportions of the trigonids and talonids, and (9) similar elongation of the entoconid-hypoconulid region but lower entoconid and paraconid of  $M_3$ .

The Judson specimens differ from *T. demari* Gazin (1956) in possessing (1) a shallower mandible, (2) a more forward posterior mental foramen, (3) more developed basal cingula on the lower molars, (4) less developed cingula on the upper molars, (5) less pyramidal and more conical cusps on the upper molars, and (6) a more elongate entoconid-hypoconulid region of  $M_3$ . The significant similarities between the Judson material and *T. demari* are the shortness of  $M_2$  and  $M^2$  and the presence of diastemata.

The Judson specimens differ from *T. antiquus* Matthew (1915) in much the same way that they differ from *T. demari* except that in addition  $M_2$  is relatively smaller and the diastemata are much shorter. *T. belli* is considerably smaller than the Judson specimens.

*Discussion.* — The similarity between the Judson specimens and *T. demari* in the relative size of the second molar and the corresponding difference from *T. australis* may be the result of sampling error, inasmuch as the Judson sample is small and consists entirely of isolated teeth. Except for the anterior diastemata, the remaining morphologic features of the Judson specimens are much more similar to *T. australis* than to *T. demari* and the specimens have, therefore, been referred to the former species.

#### Arctocyon sp.

Fig. 11.11

*Referred specimen.* — Labial fragment of left  $P^4$ , SMM P77.6.75.

*Locality.* — Judson locality, Tongue River Formation, Morton County, North Dakota.

*Description.* — All but the protocone of SMM P77.6.75 is preserved. The paracone is large and bears three crests that radiate from its apex (fig. 11.11). Two of the crests are longitudinal, descending anteriorly and posteriorly. The third descends anterolingually, presumably toward the protocone. There is no trace of a metacone. The parastyle and metastyle are formed as elevated portions of the precingula and postcingula. These cingula are broad and crenulated and both extend around the labial corners of the crown onto its labial margin. The labial expansion of the base of the crown adjacent to the metastyle, and the

absence of a complete ectocingulum result in a weak emargination of the labial border. The crown length is 13.6 mm.

*Discussion.* — The proportions of the paracone and the positions of its crests make the reference of this tooth to *Arctocyon* reasonably certain. Its large size is comparable with *A. primaevus* Blainville (1841), *A. ferox* (Cope, 1883) and *A. acrogenius* (Gazin, 1956), but the specimen is inadequate to permit a specific identification.

#### Arctocyonid, genus and species indeterminate

Fig. 11.4

*Referred specimen.* — Partial  $M^1$ , FMNH PM8660.

*Locality.* — Riverdale locality, Tongue River Formation, McLean County, North Dakota.

*Description.* — The ectocingulum of  $M^1$  is indistinct (fig. 11.4). The paracone and metacone are subequal, blunt, and conical. The paraconule is small, the metaconule large. The parastyle projects anteriorly, and there is no distinct metastyle. The hypocone is lingual to, and a little smaller than, the metaconule. The trigon basin is broad. The protocone is lingual to the paracone so that the preprotocrista is almost transverse and the postprotocrista is nearly longitudinal. The length is 8.2 mm.

*Discussion.* — This tooth is surely an arctocyonid closely related to, if not referable to, *Thryptacodon*. It is, however, relatively narrower than, and absolutely larger than, any known species of the genus.

#### Family HYOPSODONTIDAE Lydekker, 1889

##### *Haplaletes diminutivus* Dorr, 1952

Tables 33-34, figs. 10.9-13

*Referred specimens.* —  $M^1$  or  $M^2$ , SMM P77.8.194-195;  $M_1$ , P77.7.146, partial  $M_2$ , P77.7.147-148;  $M_2$ , P77.7.149-150, P77.8.196-197; left mandible with  $M_2$  and alveoli for  $M_3$ , P77.7.151; right mandible with  $M_2$ , P77.8.198; right mandible with  $M_2$ - $M_3$ , P77.7.152;  $M_3$ , P77.7.153.

*Localities.* — Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, North Dakota.

*Description.* — The anterior upper molars have been described by Dorr (1952) and require little additional comment. The paracone is a little broader and higher than the metacone. The

hypocone and pericone are slightly lingual to the protocone apex. Wear facets resulting from transverse motion are present on the paracristae and metacristae, the paracingulum, the precingulum, the posterior side of the postparaconule crista, the anterior side of the premetaconule crista, and on both the preprotocristae and post-protocristae.

The lower molars are characterized by reduced paraconids and large metaconids and protoconids (figs. 10.9, 10.11-13). The metaconid is the highest cusp on  $M_2$  and  $M_3$ ; its unworn height on  $M_1$  is unknown. Both the metaconid and protoconid are blunt cones that are moderately elevated and well separated. Only  $M_1$  has the paraconid present as a distinct cusp; it is submedian to median and is joined to the protoconid by a weak, curving paracristid. On  $M_2$  and  $M_3$  the paracristid is nearly transverse, terminating just labial to the level of the metaconid. A weak anterior cingulum is present on  $M_1$ ; the  $M_2$  and  $M_3$  this cingulum continues around the protoconid and terminates variably between the level of the protoconid apex and the hypoflexid. The talonid basins are simple, having enlarged hypoconids that are more massive and a little higher than the entoconids. The hypoconulid on  $M_1$  and  $M_2$  is small and median with a postcingulum extending from it down to the posterolabial base of the crown. The hypoconulid of  $M_3$  is relatively larger and projects posteriorly. The deepest part of the talonid basins is below the level of the V-shaped talonid notch. The anterior molars are of approximately equal size, whereas the third is considerably smaller.

*Discussion.*—*H. diminutivus* was described by Dorr (1952) from the Dell Creek Local Fauna of the Hoback Formation, Wyoming. The type and only known specimen is a maxillary fragment in which  $P_4$ - $M_2$  are preserved. The anterior upper molars from the Brisbane locality are smaller than those of the type, but are morphologically similar to them. The generic reference of the lower

molars is based on comparison with USNM 9500, the type specimen of *H. disceptatrix* Simpson (1935b), type species of the genus. The lower molars from the North Dakota localities are structurally similar to *H. disceptatrix* and are referred to *H. diminutivus* solely on the basis of size.

Another group of similar-sized hyposodontid condylarths is present at the Olive Local Fauna, which is currently being studied by Donald L. Wolberg. When compared to the Olive specimens the upper molars referred here have slightly sharper cusps and crests, deeper trigon basins, a steeper lingual slope of the protocone, shorter lingual lengths, and are smaller in overall size. When the lower molars are compared, the Olive specimens have blunter and less well separated metaconids and protoconids than do the North Dakota specimens. Although the North Dakota and Olive specimens are readily distinguishable, neither population appears to be distinctly separable from *H. diminutivus*.

Family PHENACODONTIDAE Cope, 1881

*Phenacodus primaevus* Cope, 1873

Fig. 11.20

*Referred specimens.*—Left maxilla with  $P^3$ - $M^2$  and alveoli for C- $P^2$ , SMM P77.7.154; right  $dP^4$ , FMNH PM8661; ? $M^1$ , FMNH PM 8662.

*Localities.*—Judson and Riverdale localities, Tongue River Formation, Morton and McLean Counties, North Dakota.

*Description.*—The  $dP^4$  bears subequal paracone, metacone, and protocone. The hypocone, parastyle, and mesostyle are subequal and lower than the primary cusps. Both conules are well developed. The anterior margin is oblique, giving the crown a nearly triangular trapezoidal shape. The length is 14.1 mm and the width is 13.6 mm.

The alveolus for the canine is laterally compressed with a width equal to about half its length. Behind it are a single alveolus for  $P^1$  and alveoli for a double rooted  $P^2$ . There is no ap-

TABLE 33. Measurements of *Haplaletes diminutivus* from the Judson locality.

Dimension	N	Range	Mean	SD	V
$M^1$ Length	1	----	2.30	—	—
Width	1	----	1.70	—	—
$M_2$ Length	4	1.8-2.2	2.03	.21	10.18
Width	4	1.4-1.8	1.55	.17	11.17
$M_3$ Length	1	----	1.80	—	—
Width	1	----	1.20	—	—

preciable diastema between P<sup>2</sup> and P<sup>3</sup> or between any of the alveoli that are present.

All of the teeth in the maxilla are heavily worn (fig. 11.20), particularly on their lingual sides where no structures can be distinguished. A slight indentation of the enamel of P<sup>3</sup> suggests a former presence of a separate paracone and metacone. The external cingulum continues posteriad from the parastyle, thinning rapidly to a minimum below the paracone and then slowly thickening as it rises to the metastyle. The labial slopes of the paracone and metacone of both P<sup>3</sup> and P<sup>4</sup> are crenulate. The length and width of P<sup>3</sup> are 10.4 mm and 10.3 mm.

P<sup>4</sup> has a squared labial margin and a rounded lingual margin. The parastyle is large and the configuration of the external cingulum is as in P<sup>3</sup> except that it is absent below the paracone. The metastyle is distinct, but smaller than that of P<sup>3</sup>. A broad postcingulum is present. The paracone and metacone are close, but well differentiated. The length of P<sup>4</sup> is 10.8 mm, the width 13.3 mm.

M<sup>1</sup> of SMM P77.7.154 bears a parastyle that is smaller than that of P<sup>4</sup>. The paracone and metacone are large, low and rounded. There is a large mesostyle that forms an external projection of the labial margin. The external cingulum is continuous, thins posteriad, and is joined to the much thicker postcingulum by a very small metastyle. A vestige of the metaconule suggests it was immediately lingual to the metacone. M<sup>1</sup> of SMM P77.7.154 is 12.1 mm long and about 15.4 mm wide.

M<sup>2</sup> is incomplete, consisting of the labial half of the tooth. The styler area is almost identical to M<sup>1</sup>. The metacone is not greatly reduced relative to the paracone. The conules are quite large, but very low. The metaconule is lingual to the metacone. The length of M<sup>2</sup> is 11.4 mm.

*Discussion.*—The partial M<sup>2</sup> of SMM P77.7.154 was collected almost a year after the discovery of the maxilla but from exactly the same site. Interdental wear in this specimen is pronounced and the fit between M<sup>1</sup> and M<sup>2</sup> is perfect. Additional evidence of the probable association of these teeth

is the continuation of a white etched area on M<sup>2</sup> across the interdental wear surface and onto M<sup>1</sup>.

The deciduous P<sup>4</sup> was so identified because of its large parastyle, its shape, and its dimensions, all of which agree with known characters of dP<sup>4</sup> of *Phenacodus* (West, 1971).

The size and proportions of these teeth make them surely referable to the latest Paleocene to Middle Eocene species *Phenacodus primaevus* as it is currently understood by West (1976).

#### *Ectocion wyomingensis* (Gazin, 1956)

Figs. 11.12-18

*Referred specimens.*—P<sup>3</sup>, SMM P77.8.199; partial ?P<sup>4</sup>, P77.6.76; partial M<sup>1</sup> or M<sup>2</sup>, P77.8.200; M<sup>2</sup>, P77.6.77; M<sup>3</sup>, P77.7.155; M<sub>3</sub>, P77.6.78; trigonid of M<sub>3</sub>, P77.8.201.

*Localities.*—Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, North Dakota.

*Description.*—The paracone of P<sup>3</sup> is the largest cusp. The metacone is closely joined to the paracone, but is easily distinguishable (fig. 11.12). These cusps are joined together and joined to the styles by a continuous longitudinal crest. The metastyle is small and positioned halfway up the side of the metacone. The parastyle is low and projects anteriorly. A cingulum completely encircles the crown, rising to the protocone apex on the lingual side. Dimensions of SMM P77.8.199 are length 5.5 mm and width 5.2 mm.

SMM P77.6.76 consists of the labial half of either P<sup>3</sup> or P<sup>4</sup>. This tooth differs from SMM P77.8.199 primarily in the presence of a well developed paraconule. In addition, the metacone and paracone are more separate, and the parastyle is less projecting and a little smaller. The length of SMM P77.6.76 is 4.8 mm.

M<sup>2</sup> is bunodont, the low bulky cusps having only weakly developed lophs (fig. 11.15). The parastyle, mesostyle, and hypocone are all quite large. The basal cingulum is discontinuous around the base of the mesostyle and the lingual margin of the protocone. The metaconule lies anterior to

TABLE 34. Measurements of *Haplaletes diminutivus* from the Brisbane locality.

Dimension	N	Range	Mean	SD	V
M <sup>1</sup> or M <sup>2</sup>					
Length	2	1.6-1.8	1.70	.14	8.23
Width	2	2.3-2.5	2.40	.14	5.83
M <sub>2</sub> Length	3	1.7-2.0	1.87	.15	8.18
Width	3	1.4-1.5	1.43	.06	4.06



a line joining the metacone and hypocone. The paracristae, metacristae, and protocristae are all relatively weak. The tooth has a length of 7.2 mm and a width of 10.5 mm. SMM P77.8.200 (fig. 11.14), referred here as an anterior upper molar, is a little smaller than SMM P77.6.77 (length 6.7 mm). It differs from SMM P77.6.77 in having much smaller stylar cusps, larger and more lophodont paracone and metacone, and a complete external cingulum.

On  $M^3$  the paracone, its crests, and the preprotocrista are well developed and the metacone is small (fig. 11.16). A continuous cingulum encircles the tooth. The parastyle and mesostyle are like those of SMM P77.8.200. The length of SMM P77.7.155 is 4.9 mm; the width is 7.5 mm.

The lower third molar has a low trigonid which is considerably shorter than the talonid (figs. 11.17-18). The protoconid and metaconid are prominent and somewhat pyramidal. The paraconid is a low median shelf joined to the protoconid by a bulky crest. The hypoconid is much larger than the entoconid. The hypoconulid is about the size of the hypoconid and projects posteriorly. The talonid basin is deep, but not closed. Basal cingula are present below the paracristid, hypoflexid, and below and between the hypoconid and hypoconulid. SMM P77.6.78 is 7.7 mm long and 5.0 mm wide; the width of SMM P77.8.201 is 5.4 mm.

*Comparisons.* —  $P^3$  is laterally compressed and small relative to the molars. In these respects it differs from *E. montanensis* (Gidley in Simpson, 1935b). The lateral compression of  $P^3$  is a similarity to "*E. ralstonensis*" Granger (1915). Although  $P^3$  is unknown in *E. wyomingensis*, the small size of  $P_3$  in that species is comparable with the present sample.

The referred partial upper molar and  $M^3$  are consistent with *E. wyomingensis*, differing only in having narrower cingula and reduced parastyles. SMM P77.6.77, referred as  $M^2$ , differs from *E. wyomingensis* in having a much larger mesostyle, larger and more separated parastyle, narrower cingula, and in being less lophodont. The large mesostyle and state of lophodonty are similar to *E. osbornianum* Cope (1882a), whereas the large size of both styles is similar to *Phenacodus*.

*Discussion.* — All of these specimens, with the exception of SMM P77.6.77, agree well in size and structure with *E. wyomingensis*. SMM P77.6.77 is atypically bunodont, resembling *E. osborn-*

*ianum*, and possibly even representing a second species of *Phenacodus* at the Judson locality.

Condylarth, genus and species indeterminate (1)  
Fig. 11.19

*Referred specimen.* — Left ? $P^4$ , SMM P77.8.202.

*Locality.* — Brisbane locality, Tongue River Formation, Grant County, North Dakota.

*Description.* — The paracone and protocone are large, blunt, and conical (fig. 11.19). The parastyle is also conical, but very much smaller than the protocone. The posterior crest of the paracone is low and distinct. The corresponding anterior crest extends only a short way up the paracone from the parastyle. A complete, narrow ecto-cingulum joins the precingula and postcingula, both of which end lingually at the level of the protocone apex. There is a minute wear facet on the anterolingual side of the parastyle, an interdental facet on the anterolingual side of the parastyle, and an interdental facet on the posterior margin. The length is 3.5 mm; the width is 4.6 mm.

*Discussion.* — In outline this tooth is somewhat like  $P^4$  of *Thryptacodon*, but it is smaller and has much lower, more rounded cusps.

Condylarth, genus and species indeterminate (2)  
Fig. 11.21

*Referred specimen.* — Left ? $P^4$ , SMM P77.6.79.

*Locality.* — Judson locality, Tongue River Formation, Morton County, North Dakota.

*Description.* — There is a large paracone and slightly smaller, subconical protocone. The styles are small and arranged longitudinally about the paracone apex at the ends of the precingula and postcingula. These cingula do not connect around the protocone and there is no ecto-cingulum. There is an interdental wear facet on the posterior side only. The length is 7.9 mm; width is 8.8 mm.

*Discussion.* — This tooth resembles  $P^4$  of *Mioclaenus*, but its affinities are otherwise unclear.

Order PANTODONTA  
Family TITANOIDEIDAE Simons, 1960  
*Titanoides primaevus* Gidley, 1917  
Figs. 12.1-2

*Referred specimens.* — Skull with right  $P^1$ - $M^1$ ,  $M^3$ , and alveoli for right C,  $M^2$ , and left C- $M^3$ ,

right scapula, distal end of left humerus, several fragmentary vertebrae and one metapodial, FMNH PM8655; right M<sup>2</sup>, FMNH PM8656; lingual fragment of left P<sup>4</sup>, SMM P77.6.80.

*Localities.*—Riverdale and Judson localities, Tongue River Formation, McLean and Morton Counties, North Dakota.

*Description.*—The referred skull, shown in figures 12.1-2, is well preserved and exhibits many anatomical features previously unknown or poorly known in Paleocene pantodonts. It will be described in a separate paper. The description below is limited largely to the dentition, which is adequate to establish specific identity.

The canines are absent, but their alveoli are nearly circular with transverse with longitudinal diameters of 15 mm. There is no evidence of a permanent tooth in the alveolus.

The premolars are three-rooted and triangular. The paracone is prominent and occurs at the vertex of the V-shaped preparacristae and postparacristae. This arrangement of the primary cusps and their precristae and postcristae holds also for each primary cusp of the molars. On P<sup>2</sup>.P<sup>4</sup> there is a well developed protocone; it is anteroposteriorly compressed and displaced anteriorly. The anterior, posterior, and external cingula are weak, the first two not being continuous. The ectoflexus is deep.

The lengths and widths of the premolars are: P<sup>1</sup>, 12.6 mm, 9.8 mm; P<sup>2</sup>, 15.0 mm, 17.6 mm; P<sup>3</sup>, 16.4 mm, 22.8 mm. The approximate width of P<sup>4</sup> is 24.8 mm.

Only the protocone of M<sup>1</sup> is preserved. It is smaller, but identical in form to that of M<sup>3</sup>.

M<sup>2</sup> (PM 8656) bears subequal paracone and metacone. The metacone is slightly more lingual than the paracone. The protocone is low and broad. There is no metaconule and the paraconule is barely distinguishable. The precingulum and postcingulum are discontinuous. The ecto-tingulum is weak. The posterior width is 29.2 mm.

M<sup>3</sup> is constructed like M<sup>2</sup>, but is larger and appears to have had a reduced metacone area (although this part of the tooth is missing, the root below the metacone is reduced). It differs from M<sup>2</sup> in having a more definite paraconule and continuous precingula and postcingula. The anterior width is 34.3 mm.

The supraspinous and infraspinous fossae of the scapula are areally subequal. The coracoid process is missing, but was evidently massive.

There is a very gradual posterior expansion of the acromion and the acromion process extends only a little beyond the glenoid.

The entepicondyle of the humerus is massive, but not greatly projecting. It bears a large entepicondylar foramen enclosed by a delicate bridge of bone.

*Discussion.*—In addition to the material described above two other relevant tooth fragments of pantodonts have been collected. One of these is a very worn ?dP<sup>4</sup> (SMM P77.6.81) from Judson, questionably referable to this species. It is distinctive because of its laterally projecting parastylar region. It is, however, markedly smaller than P<sup>4</sup> or M<sup>1</sup> of the type. An uncatalogued tooth fragment from Brisbane probably represents this species, but more certainly represents some very large pantodont.

The biostratigraphic implications of these occurrences of *T. primaevus* are not definitive. All previous records of the species can be interpreted as Clarkforkian, or at least late Tiffanian in age. The Riverdale skull falls in the same range due to ambiguity in the age of the local fauna. The fragmentary P<sup>4</sup> from Judson agrees well with P<sup>4</sup> of *T. primaevus* and, furthermore, differs from all other known pantodont species. It could, of course, represent a new species, differing in other characters. It is, however, probable that *T. primaevus* existed in the mid-Tiffanian and therefore cannot be considered as a guide fossil to the Clarkforkian.

The possibility of sexual dimorphism in *T. primaevus* is suggested by the reduced sagittal and lambdoidal crests and the small upper canines exhibited in the Riverdale skull. The length of the canine alveolus is only half the length of the canine in the presumed type, PU 16490, and the only other known specimen, FMNH PM15520.

## CONCLUSION

The preceding detailed studies of the Judson and Brisbane mammalian local faunas, located near the base of the Tongue River Formation in west central North Dakota, indicate a middle Late Paleocene (middle Tiffanian) age for these strata. It is therefore likely that at least the uppermost part of the Cannonball Formation in that area is also Late Paleocene in age. These results differ from the long-held consensus that



the Tongue River Formation is Middle Paleocene in age.

Of the Late Cretaceous and Early Tertiary non-marine deposits of western North Dakota, the only units whose vertebrate faunas are reasonably well known are the Tongue River Formation (Late Paleocene) and the upper member of the Golden Valley Formation (Early Eocene). The discovery of productive fossil mammal sites in the remaining units would provide major contributions to the history of the basin and to the history of mammalian evolution in this critical time span. Mammals from the Hell Creek Formation would help in determining the extent to which the upper boundary is diachronous. The Ludlow Formation probably records all of the Early, Middle, and possibly early Late Paleocene. The Sentinel Butte Formation and the lower member of the Golden Valley Formation, on the other hand, span primarily only the latest Paleocene and may provide a valuable comparison to the Clarkforkian of the Bighorn basin, Wyoming.

Three mammalian local faunas from the Paleocene of North Dakota are described in this paper. They are the Judson and Brisbane faunas from the basal Tongue River Formation in Morton and Grant Counties, and the Riverdale local fauna from the uppermost part of the formation in McLean County. The Judson and Brisbane faunas contain 27 and 30 species, respectively, consisting primarily of multituberculates and primates, but also including a marsupial, insectivores, carnivores, condylarths, and a pantodont. In contrast, the Riverdale local fauna is poorly known, providing neither a precise age nor an adequate faunal sample.

The major systematic paleontology results are:

1. *Ptilodus wyomingensis*, previously known only from the Torrejonian, persisted into mid-Tiffanian times in western North Dakota where it occurs in the Judson local fauna.  $P_4$  in this sample is uniformly smaller than in the type series, possibly indicating a form transitional to an even smaller undescribed species, *Ptilodus kummae*, occurring in the Riverdale and Roche Percee local faunas. Interestingly, the species of *Ptilodus* at the nearby Brisbane local fauna is more similar to *P. montanus*, although the poorer sample renders the identification less satisfactory.
2. *Neoplagiaulax nanophus*, a new neoplagiaulacid multituberculate, is the smallest

known member of the genus. It is known only from the Judson local fauna.

3. Specimens of *Microcosmodon woodi* from the Brisbane local fauna illustrate the primitive character of this species and indicate that *M. woodi*, *M. conus*, and *Pentacosmodon pronus*, now united as the *Microcosmodontinae*, had a long history independent from the remainder of the *Encosmodontidae*.
4. *Peradectes pauli* cannot be reasonably separated from *P. elegans*, and is here regarded as a junior synonym of the latter.
5. An unnamed but probably new species of *Paleoryctes* (cf. *P. punctatus*) is known from both the Judson and Brisbane local faunas.
6. A large number of specimens tentatively referred to *Litolestes lacunatus* exemplify most of the post canine dentition ( $P^3$ - $M^3$  and  $P_3$ - $M_3$ ).
7. A new but unnamed pentacodontid insectivore from the Brisbane local fauna is very progressive and has been tentatively referred to the genus *Bisonalveus*.
8. A well preserved jaw of *Unuchinia dysmathes*, new species, exhibits alveoli for three enlarged "incisors," similar in form but not in number to the "incisors" of apatemyine insectivores. A double-rooted  $P_4$  in *U. dysmathes* suggests that it is more primitive than *U. asaphes*.
9. Nearly complete upper dentitions of *Carpodaptes hobackensis* and *C. cygneus* are now known from the Judson and Brisbane local faunas respectively. An analysis of dental function reveals that the enlarged, blade-like  $P_4$  sheared against  $P^3$  and  $P^4$  in an exaggerated form of the Phase I shear normally found in early primates.
10.  $dP^4$  and  $M^3$  of *Ignacius frugivorus* have been identified and described.
11. A large and possibly new picrodontid primate is present in the Brisbane local fauna.
12. *Protictis paralus*, a new medium-sized viverravine carnivore that exhibits pronounced shearing capacity of  $P_4$ ,  $M_1$ , and  $M_2$ , is present in both the Judson and Brisbane local faunas.
13. Five specimens identified only as miacid carnivores may represent early miacine carnivores.
14. A number of upper and lower molars from both the Judson and Brisbane local faunas have been identified as *Haplaletes dimin-*

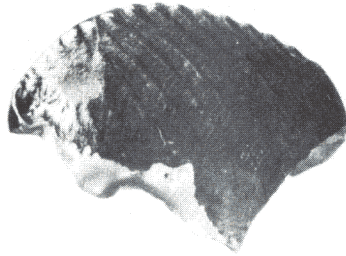


*utivus*, previously known only from the Dell Creek local fauna. Specimens from the Olive local fauna identified as the same species by D. L. Wolberg differ markedly from the North Dakota material. The entire assemblage almost certainly includes more than one species, but the data is too scant to permit a resolution of the problem at this time.

15. An extraordinarily well preserved skull of *Titanoides primaevus* from the Riverdale locality exhibits structural features not previously observed in Paleocene members of the Pantodonta. Comparison with other specimens of *T. primaevus* suggests that variation in the canines, zygomatic arches, and cranial crests may be due to sexual dimorphism.



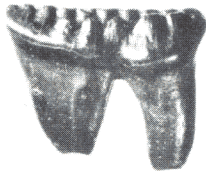
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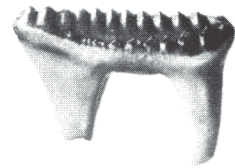
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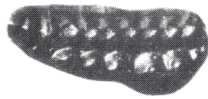
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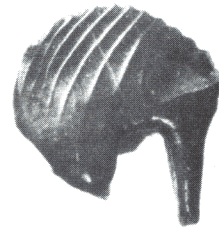
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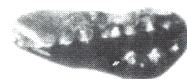
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Figure 3. Ptilodontid and neoplagiaulacid multituberculates from the Brisbane, Judson, and Riverdale localities.

*Ptilodus wyomingensis*, Judson, all X5.5.

1. SMM P77.6.20, right  $P_4$ , labial view.

4,7. SMM P77.6.8, left  $P^4$ , labial and occlusal views.

5. SMM P77.7.6, left  $P^2$ , occlusal view.

*Ptilodus montanus*, Brisbane, X5.5.

2. SMM P77.8.26, right  $P_4$ , labial view.

*Ptilodus kummae*, Riverdale, X5.5.

3. FMNH PM8667, left  $P_4$ , labial view.

*Prochetodon* sp., Judson, all X5.5.

6,9. SMM P77.7.56, left  $P^4$ , labial and occlusal views.

8. SMM P77.7.55, left  $P^2$ , occlusal view.

*Mesodma* sp., Brisbane, all X9.5.

10. SMM P77.8.34, right  $P_4$ , labial view.

13,16. SMM P77.8.33, left  $P^4$ , labial and occlusal views.

*Ectypodus* sp., Brisbane, all X9.5.

11. SMM P77.8.41, right  $P_4$ , labial view.

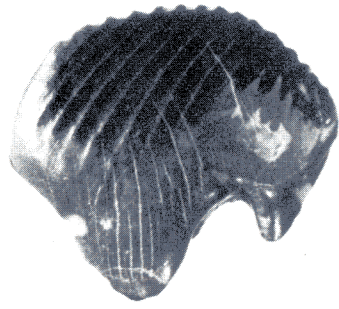
14,17. SMM P77.8.38, right  $P^4$ , labial and occlusal views.

*Parectypodus* sp., Judson and Brisbane, all X9.5.

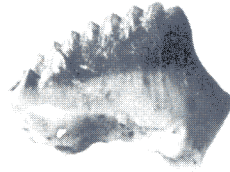
12. SMM P77.6.30, left  $P_4$ , labial view.

15,18. SMM P77.8.56, left  $P^4$ , labial and occlusal views.

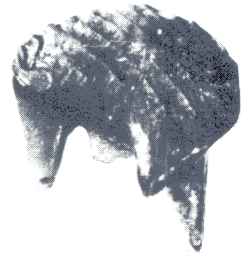




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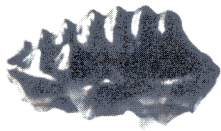
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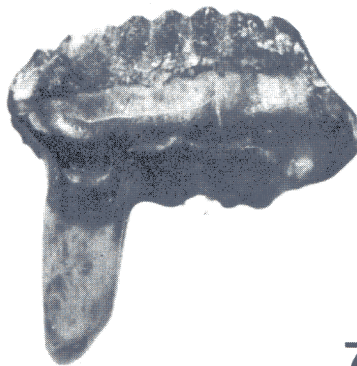
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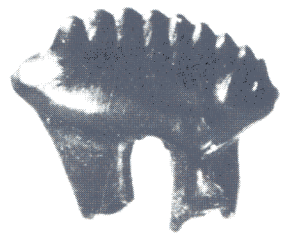
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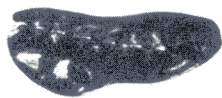
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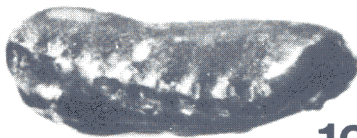
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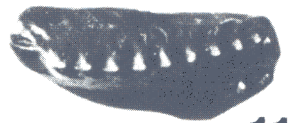
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Figure 4. Neoplagiaulacid multituberculates from the Brisbane and Judson localities, all X9.3.

*Neoplagiaulax hunteri*, Judson.

1. SMM P77.7.60, left P<sub>4</sub>, labial view.
- 2,3. SMM P77.7.58, right P<sup>4</sup>, labial and occlusal views.

*Neoplagiaulax nanophus*, Judson.

4. SMM P77.7.61, type, right P<sub>4</sub>, labial view.

*Neoplagiaulax* sp. (1), Brisbane.

5. SMM P77.8.51, left mandible with P<sub>3</sub>-P<sub>4</sub>, labial view.
- 6,9. SMM P77.8.49, right P<sup>4</sup>, labial and occlusal views.

*Neoplagiaulax* sp. (2), Brisbane.

- 7,10. SMM P77.8.55, right P<sup>4</sup>, labial and occlusal views.

*Neoplagiaulax* sp. (3), Judson.

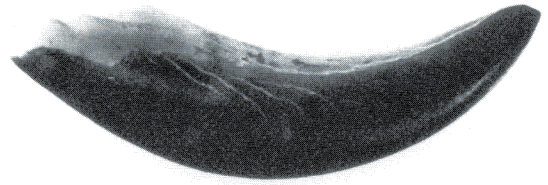
- 8,11. SMM P77.6.28, left P<sup>4</sup>, labial and occlusal views.



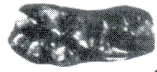
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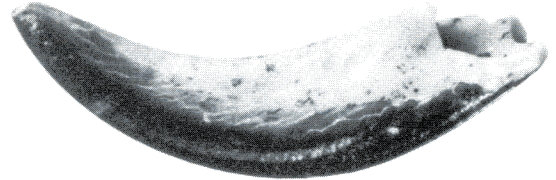
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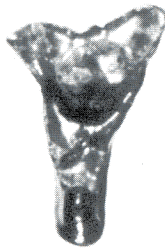
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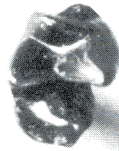
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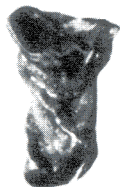
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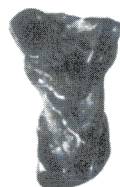
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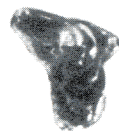
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Figure 5. Multituberculates, marsupials, and insectivores from the Brisbane and Judson localities, all X9.2.

*Microcosmodon woodi*, Brisbane.

1. SMM P77.8.4, left P<sub>4</sub>, labial view.
- 2,3. SMM P77.8.2, right P<sup>4</sup>, labial and occlusal views.
- 4,7. SMM P77.8.3, right I<sub>1</sub>, labial and lingual views.

*Peradectes elegans*, Brisbane.

5. SMM P77.8.58, left M<sup>3</sup>, occlusal view.
6. SMM P77.8.60, left M<sub>1</sub>, occlusal view.

*Paleoryctes* sp., cf. *P. punctatus*, Brisbane and Judson.

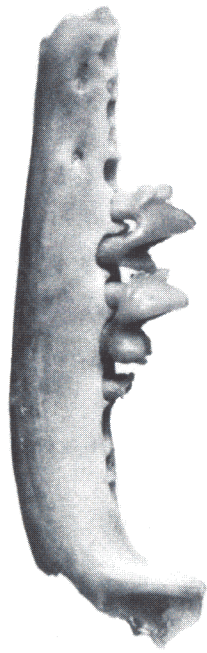
8. SMM P77.8.62, left M<sup>2</sup>, stereo occlusal views.
- 9,10. SMM P77.7.76, right M<sub>2</sub>, stereo occlusal and labial views.

*Pararyctes pattersoni*, Brisbane.

11. SMM P77.8.66, right M<sup>1</sup>, stereo occlusal views.
- 12,13. SMM P77.8.67, right M<sub>1</sub>, stereo occlusal and labial views.

Insectivore, indet. (2), Judson.

14. SMM P77.7.89, right ?P<sup>4</sup>, stereo occlusal views.



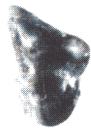
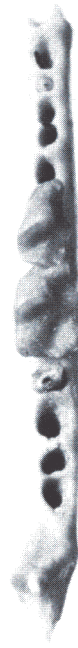
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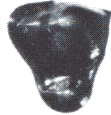
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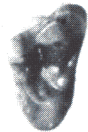
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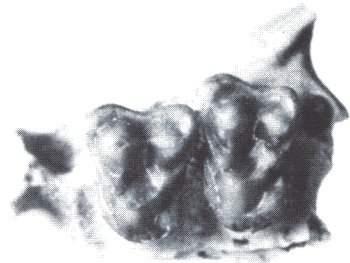
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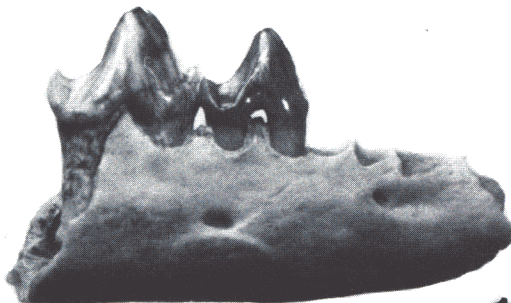
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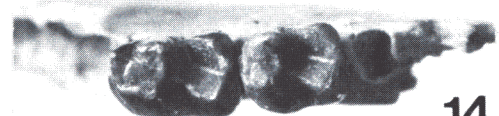
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Figure 6. Nyctitheriid and erinaceid insectivores from the Brisbane locality.

*Leptacodon tener*, all X9.4.

- 1,2,3. SMM P77.8.74, left mandible with P<sub>4</sub>-M<sub>1</sub>, labial, stereo occlusal, and lingual views.
4. SMM P77.8.72, left M<sup>3</sup>, occlusal view.

*Litolestes lacunatus*, all X6.8.

5. SMM P77.8.78, right P<sup>3</sup>, occlusal view.
6. SMM P77.8.80, right P<sup>4</sup>, occlusal view.
7. SMM P77.8.82, left maxilla with M<sup>1</sup>-M<sup>2</sup>, occlusal view.
- 9,10. SMM P77.8.105, left M<sub>3</sub>, labial and occlusal views.
- 11,13. SMM P77.8.86, right mandible with P<sub>3</sub>-P<sub>4</sub>, labial and occlusal views.
- 12,14. SMM P77.8.100, left mandible with M<sub>1</sub>-M<sub>2</sub>, labial and occlusal views.





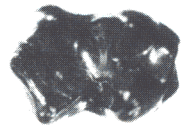
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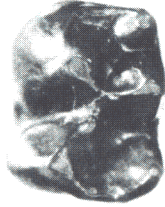
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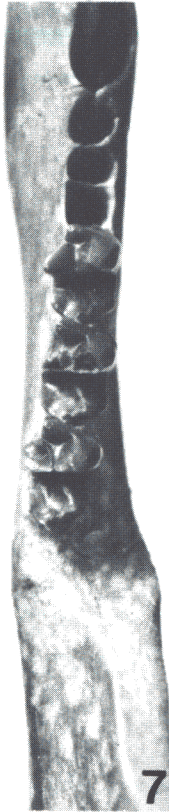
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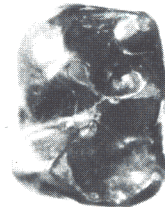
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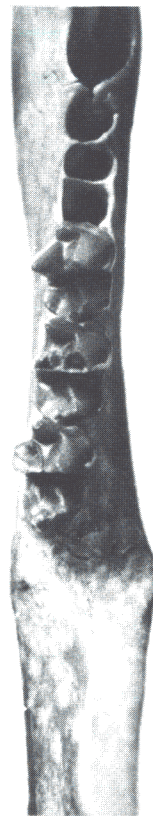
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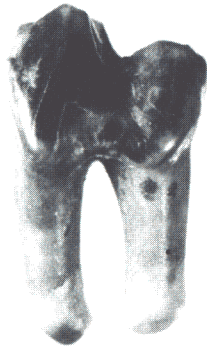
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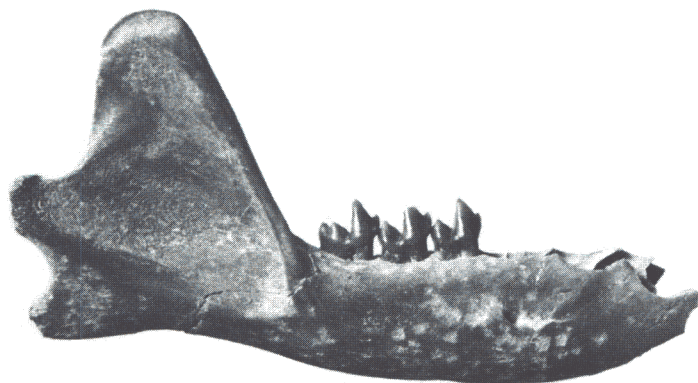
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Figure 7. Pantolestid, pentacodontid, and apatemyid insectivores from the Brisbane and Judson localities.

*Propaleosinopa albertensis*, Judson and Brisbane, all X9.0.

1. SMM P77.7.86, right M<sup>1</sup>, occlusal view.
2. SMM P77.8.108, right P<sub>4</sub>, labial view.
- 3,4. SMM P77.7.88, right M<sub>2</sub>, labial and occlusal views.

*Bisonalveus* sp., Brisbane, all X9.0.

- 5,6,8. SMM P77.8.113, left ?M<sub>1</sub>, stereo occlusal, labial, and lingual views.

*Unuchinia dysmathes*, Judson.

- 7,9,10. SMM P77.6.31, type, right mandible with M<sub>1</sub>-M<sub>3</sub>, stereo occlusal, oblique anterior (showing three enlarged "incisor" alveoli), and labial views, X4.6, X2.0, X2.0.

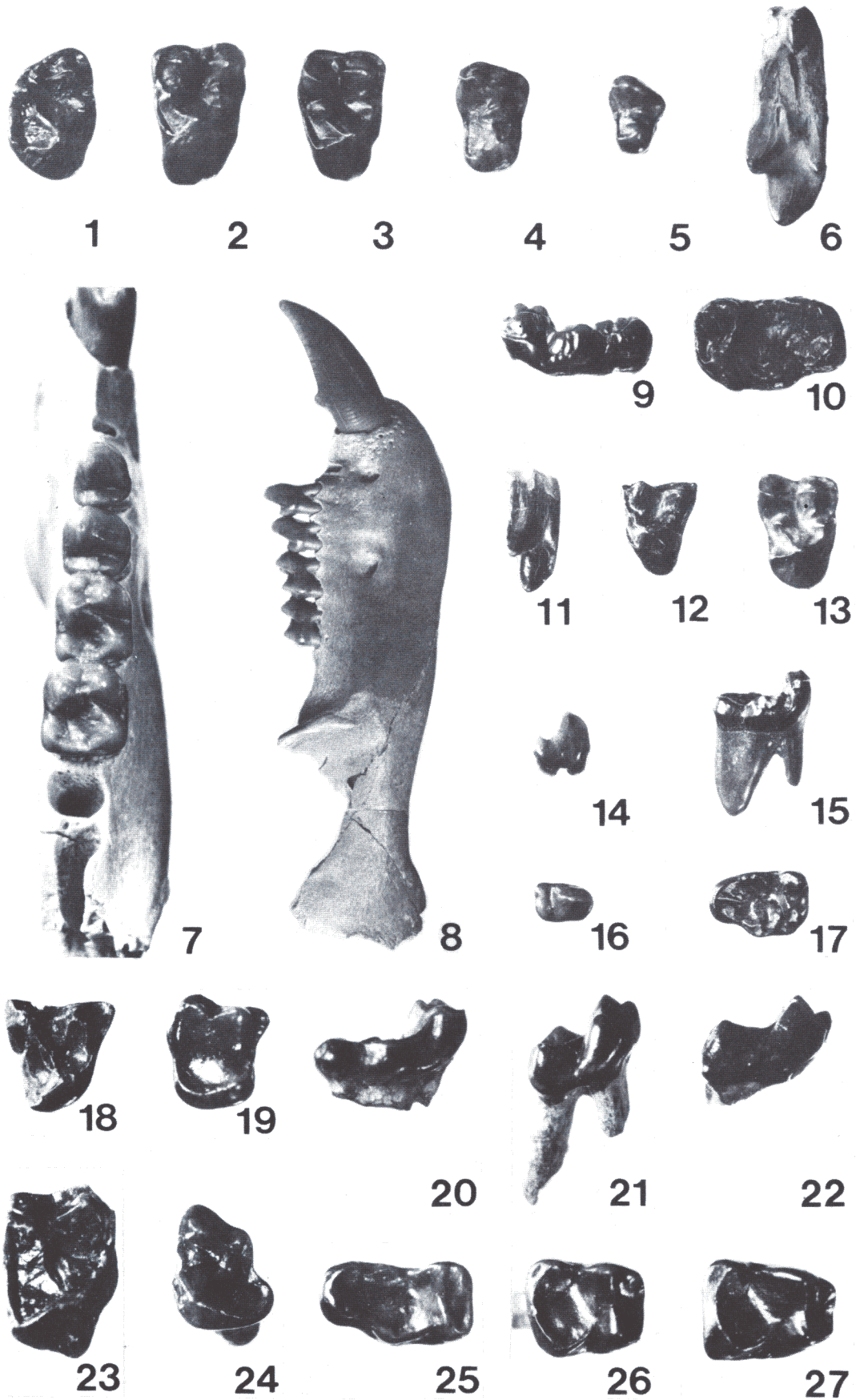




Figure 8. Plesiadapid and paromomyid primates from the Brisbane and Judson localities.

*Plesiadapis rex*, Judson.

1. SMM P77.7.103, right M<sup>3</sup>, occlusal view, X4.5.
2. SMM P77.6.39, right M<sup>2</sup>, occlusal view, X4.5.
3. SMM P77.6.36, right M<sup>1</sup>, occlusal view, X4.5.
4. SMM P77.7.96, right P<sup>4</sup>, occlusal view, X4.5.
5. SMM P77.7.95, right P<sup>3</sup>, occlusal view, X4.5.
6. SMM P77.7.90, left I<sup>1</sup>, posterior view, X4.5.
- 7,8. SMM P77.6.45, right mandible with I<sub>1</sub>, P<sub>3</sub>-M<sub>2</sub>, occlusal view, X4.5, labial view, X2.4.
- 9,10. SMM P77.6.56, left M<sub>3</sub>, labial and occlusal views, X4.5.

*Nannodectes* sp., all X4.5.

11. SMM P77.8.154, left I<sup>1</sup>, posterior view.
12. SMM P77.8.156, left M<sup>1</sup>, occlusal view.
13. SMM P77.8.159, right M<sup>2</sup>, occlusal view.
- 14,16. SMM P77.8.160, right P<sub>3</sub>, labial and occlusal views.
- 15,17. SMM P77.8.162, right M<sub>3</sub>, labial and occlusal views.

*Ignacius frugivorus*, Judson and Brisbane, all X9.5.

18. SMM P77.7.125, right dP<sup>4</sup>, occlusal view.
19. SMM P77.7.126, right P<sup>4</sup>, occlusal view.
- 20,25. SMM P77.7.131, right M<sub>3</sub>, labial and occlusal views.
- 21,26. SMM P77.7.128, right M<sub>2</sub>, labial and occlusal views.
- 22,27. SMM P77.6.61, right M<sub>1</sub>, labial and occlusal views.
23. SMM P77.8.163, right ?M<sup>1</sup>, occlusal view.
24. SMM P77.7.127, left M<sup>3</sup>, occlusal view.



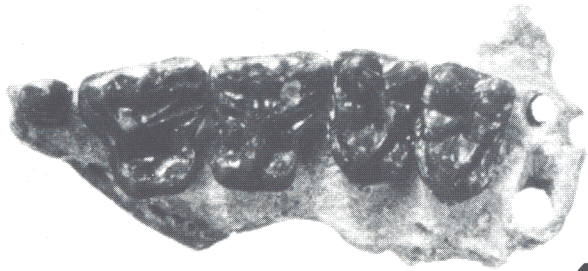
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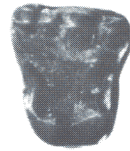
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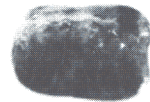
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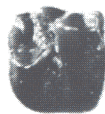
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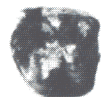
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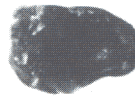
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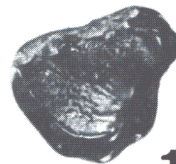
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Figure 9. Carpolestid and picodontid primates from the Brisbane and Judson localities.

*Carpodaptes hobackensis*, Judson.

- 1,2,3. SMM P77.6.62, left mandible with P<sub>4</sub>-M<sub>3</sub>, labial, stereo occlusal, and lingual views, all X4.8.
4. SMM P77.7.133, left maxilla with P<sup>2</sup>-M<sup>2</sup>, occlusal view, X9.5.

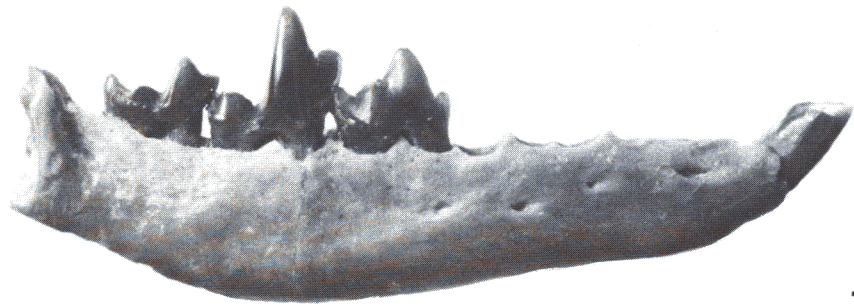
*Carpodaptes cygneus*, Brisbane, all X9.5.

5. SMM P77.8.174, right P<sup>3</sup>, occlusal view.
6. SMM P77.8.177, right maxilla with P<sup>4</sup>-M<sup>3</sup>, occlusal view.
- 7,8,12. SMM P77.8.179, left P<sub>4</sub>, lingual, labial, and occlusal views.
- 9,13. SMM P77.8.183, right M<sub>1</sub>, labial and occlusal views.
- 10,14. SMM P77.8.184, right M<sub>2</sub>, labial and occlusal views.
- 11,15. SMM P77.8.186, left M<sub>3</sub>, labial and occlusal views.

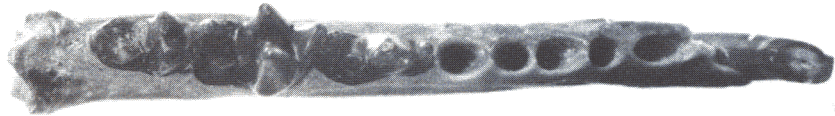
Picodontid sp., Brisbane, X9.5.

16. SMM P77.8.187, right M<sup>1</sup>, occlusal view.

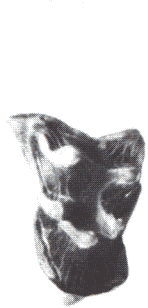




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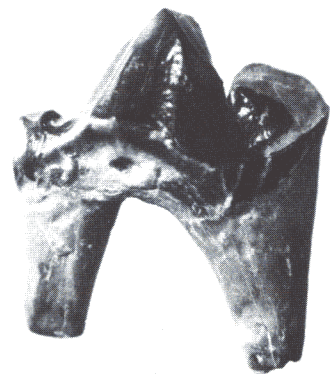
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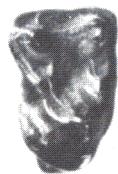
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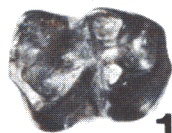
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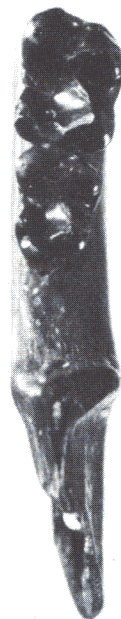
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Figure 10. Miacid carnivores and a hyopsodontid condylarth from the Brisbane and Judson localities.

*Protictis paralus*, Judson.

- 1,2. SMM P77.6.64, type, right mandible with C, P<sub>4</sub>-M<sub>2</sub>, labial and occlusal views, X3.8.
3. SMM P77.7.139, paratype, left M<sup>1</sup>, occlusal view, X4.7.

Miacid sp., Brisbane and Judson, all X4.7.

4. SMM P77.8.191, left P<sup>3</sup>, lingual view.
- 5,7. SMM P77.6.66, left M<sub>1</sub>, labial and occlusal views.
6. SMM P77.8.192, left P<sup>4</sup>, lingual view.

Viverravine sp., Judson, X4.7.

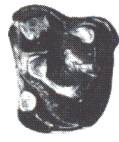
8. SMM P77.7.141, left P<sup>4</sup>, lingual view.

*Haplaletes diminutivus*, Judson and Brisbane, all X9.4.

- 9,13. SMM P77.7.152, right mandible with M<sub>2</sub>-M<sub>3</sub>, stereo occlusal and labial views.
10. SMM P77.8.195, right M<sup>1</sup> or M<sup>2</sup>, occlusal view.
- 11,12. SMM P77.7.146, right M<sub>1</sub>, labial and occlusal views.



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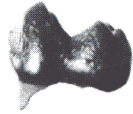
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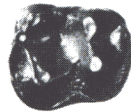
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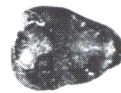
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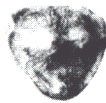
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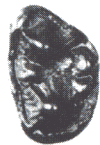
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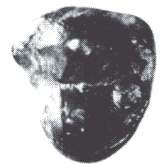
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Figure 11. Arctocyonid and phenacodontid condylarths from the Brisbane, Judson, and Riverdale localities.

*Thryptacodon australis*, Judson, all X2.5.

1. SMM P77.6.68, right dP<sup>4</sup>, occlusal view.
2. SMM P77.6.69, right M<sup>1</sup>, occlusal view.
3. SMM P77.6.71, right M<sup>2</sup>, occlusal view.
- 5,8. SMM P77.7.143, left M<sub>1</sub>, labial and occlusal views.
- 6,9. SMM P77.7.144, right M<sub>2</sub>, labial and occlusal views.
- 7,10. SMM P77.7.145, left M<sub>3</sub>, labial and occlusal views.

Arctocyonid sp., Riverdale, X2.5.

4. FMNH PM8660, left M<sup>1</sup>, occlusal view.

*Arctocyon* sp., Judson, X2.5.

11. SMM P77.6.75, left P<sup>4</sup>, labial view.

*Ectocion wyomingensis*, Brisbane and Judson, all X2.5.

12. SMM P77.8.199, left P<sup>3</sup>, occlusal view.
13. SMM P77.6.76, right ?P<sup>4</sup>, occlusal view.
14. SMM P77.8.200, right M<sup>1</sup> or M<sup>2</sup>, occlusal view.
15. SMM P77.6.77, right M<sup>2</sup>, occlusal view.
16. SMM P77.7.155, left M<sup>3</sup>, occlusal view.
- 17,18. SMM P77.6.78, right M<sub>3</sub>, labial and occlusal views.

Condylarth, indet. (1), Brisbane, X5.0.

19. SMM P77.8.202, left ?P<sup>4</sup>, occlusal view.

*Phenacodus primaevus*, Judson, X1.25.

20. SMM P77.7.154, left maxilla with P<sup>3</sup>-M<sup>2</sup>, occlusal view.

Condylarth, indet. (2), Judson, X2.5.

21. SMM P77.6.79, left P<sup>4</sup>, occlusal view.

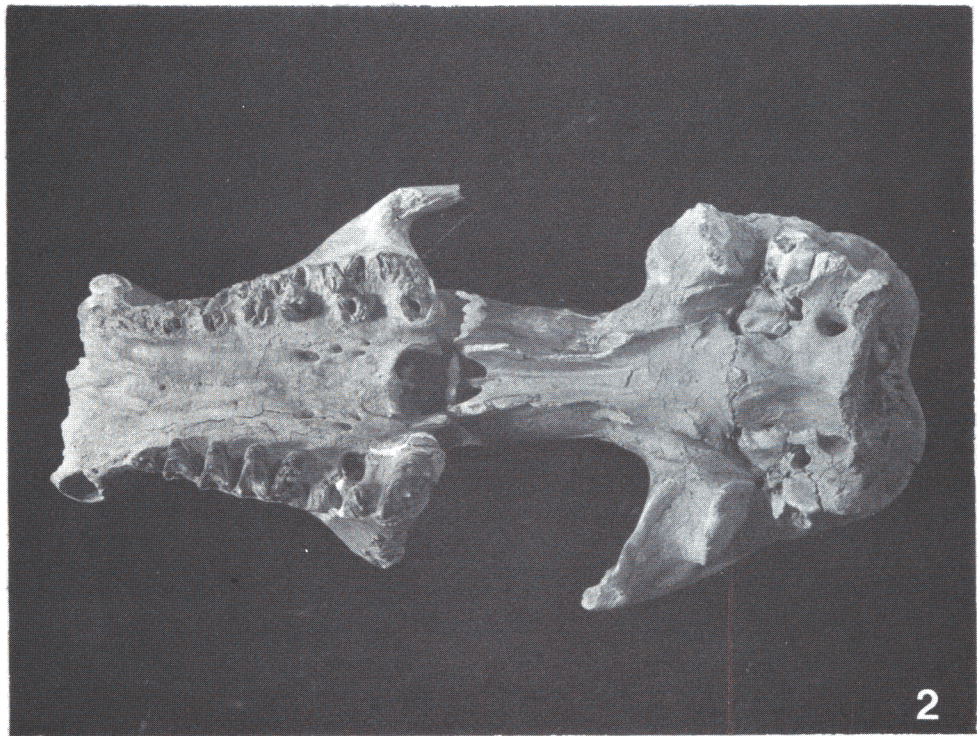
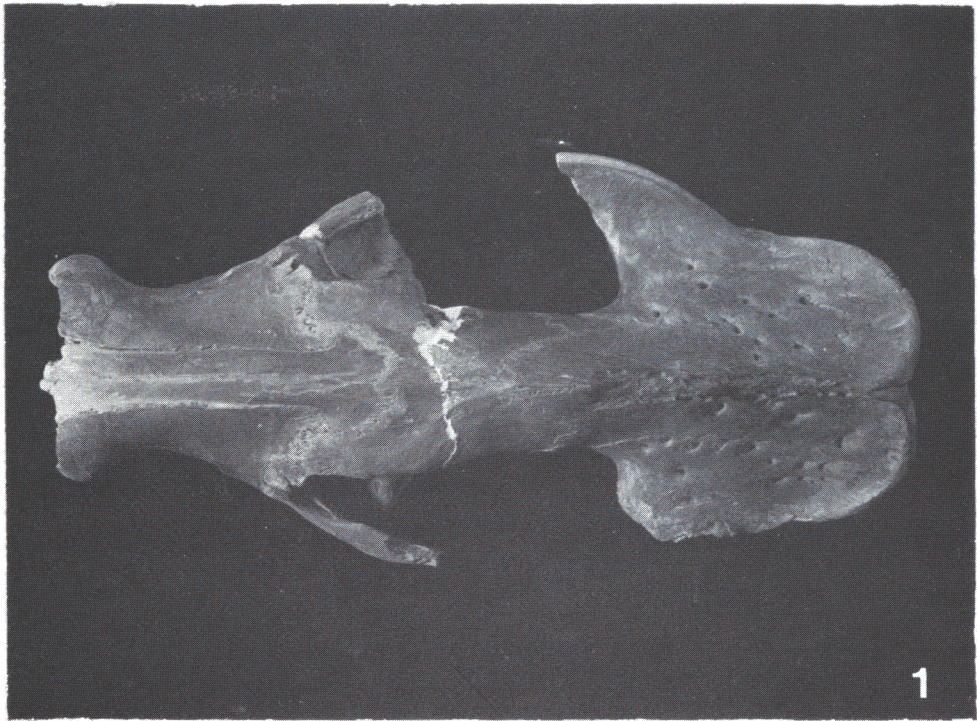


Figure 12. The pantodont *Titanoides primaevus*, FMNH PM8655, from the Riverdale locality, dorsal and ventral views of skull, X0.3.



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