THE VERTEBRATE FAUNA OF THE JUDITH RIVER FORMATION, MONTANA

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ABSTRACT

GEOLOGIC INVESTIGATION of the Late Cretaceous Judith River Formation in the area just north of the Judith River on the Missouri River in north-central Montana has resulted in the discovery of varied vertebrate forms. The beds are mainly freshwater continental deposits consisting of crossbedded channel sandstones, gray siltstones, and carbonaceous shales with occasional seams of lignitic coal. The stratigraphic sequence consists of the Marias River Shale overlain by the Eagle, Claggett, Judith River, and Bearpaw formations. The last four constitute the Montana Group. The Judith River Formation is Campanian in age as determined by its position between the fossiliferous marine Claggett and Bearpaw shales.

The fauna was obtained from the upper 50 feet of the formation. The bone concentration in the productive sandstone is the result of size sorting leading to underrepresentation of the larger dinosaurs. Three orders of mammals are represented, the Eutheria by a single genus, the Allotheria by five, and the Metatheria by at least three genera. Teiid and parasaniwid lizards are frequent. Only a fraction of the large number of described dinosaur genera, however, is represented in the collection by isolated teeth. Fish and amphibians form a sizable portion of the fauna.

Vertebrates from the Judith River Formation are more primitive than, but generally similar to, later Maestrichtian species. The mammals differ from their descendants in the Lance Formation at the species level. The community structure and the paleoecology of the fauna of the Judith River Formation resemble those of the Lance Formation. The greatest difference between the two communities is the greater variety of dinosaurs in the earlier formation.

INTRODUCTION

STUDY OF THE VERTEBRATES from the Judith River Formation was undertaken to compare the structure of Campanian mammals and smaller reptiles and their paleoecology with that of their Maestrichtian descendants. Prior to this work, Campanian mammals were very poorly known. There are large collections of Cretaceous mammals from the Maestrichtian (=Lancian) channel sandstones and siltstones of New Mexico, Utah, Wyoming, Montana, and Alberta. Other important, though smaller, collections have been obtained from the Albian of Texas by Patterson (1951, 1955, 1956), and Slaughter (1965, 1968a, 1968b, 1969). From the Albian through the base of the Maestrichtian, a span of some 40 million years (Kulp, 1961), the only mammal remains described from the North American continent consist of three poorly known genera from the Campanian sediments of Montana and Alberta. Current work by M. C. McKenna in the Mesaverde of Wyoming and by R. Fox, from the University of Alberta, in the Oldman Formation, is bound to produce a more comprehensive picture of the Campanian vertebrates over a wide geographical area.

Outside of North America, Cretaceous mammals have been described by Clemens (1963a) and Kermack, Lees, and Mussett (1965) from the Wealden of England, and by Crusafont (1966) from similar sediments in Spain. The classic Cretaceous mammal localities of Djadochta, Mongolia, are believed to be either Cenomanian or Turonian (Kielan-Jaworowska, 1968). Ledoux et al. (1966) recently described a single therian lower molar from the Campanian of France.

The type area of the Judith River Formation has a classic and important position in Cretaceous stratigraphy and paleontology. Early exploration of the Cretaceous stratigraphy of the northern Great Plains was primarily by riverboat and the region around the mouth of the Judith River was the only area on the Missouri River where extensive badlands in terrestrial Cretaceous sediments occurred. Thus Hayden, Leidy, Cope, and Marsh obtained their first Cretaceous nonmarine fossils from this area. These specimens were fragmentary and, with the later abandonment of river navigation in favor of rail transport, no better material was collected from the area for many years. Emphasis shifted to collecting fossils in the equivalent rocks of the Oldman Formation, upper part of the Belly River Group, Alberta. As a result of this geographic shift in emphasis, a different nomenclature, both paleontologic and stratigraphic, arose
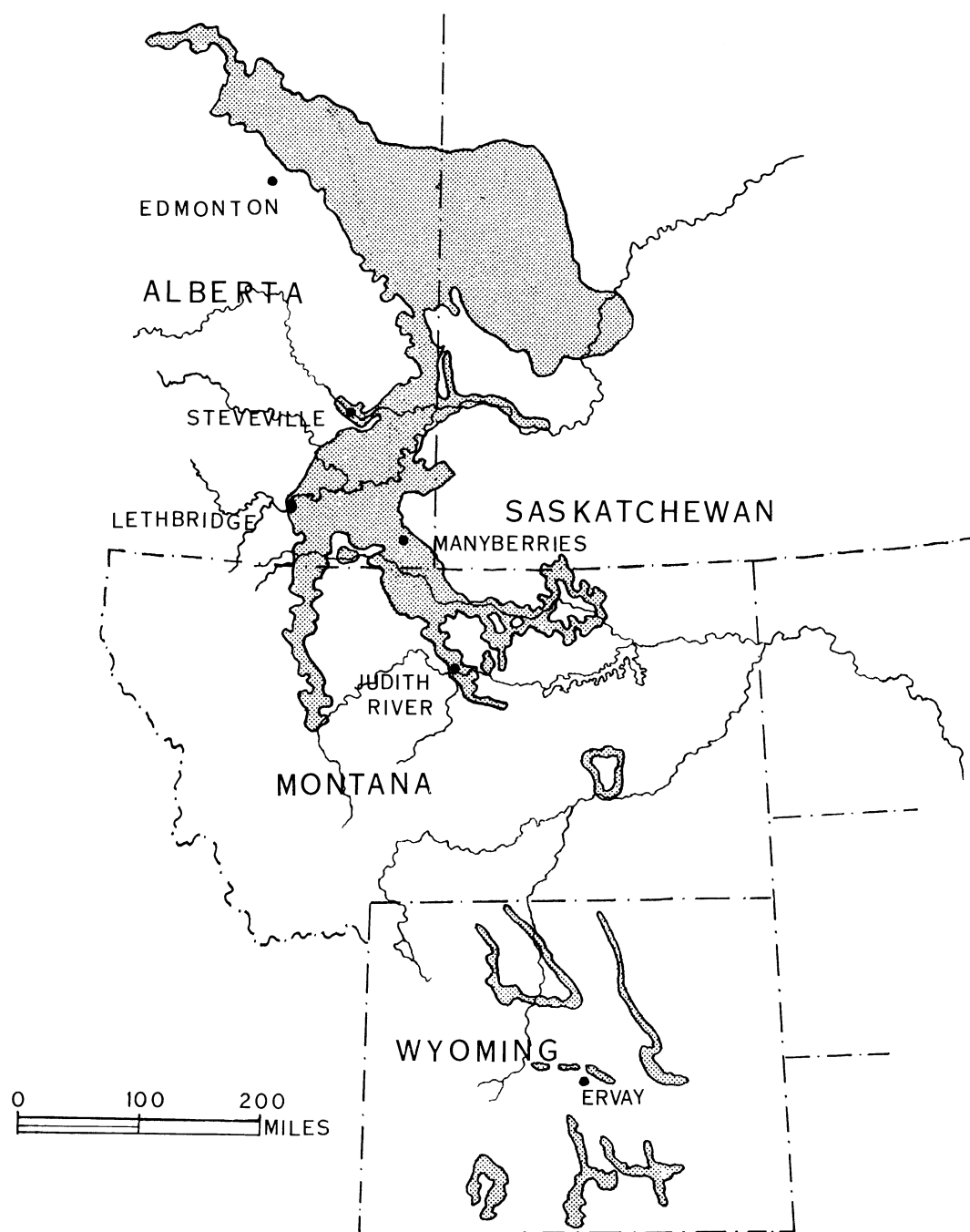
FIG. 1. Index map of the outcrop area of Campanian nonmarine sediments in Alberta, Saskatchewan, Montana, and Wyoming, showing major collecting areas.

on each side of the international boundary. The present study is undertaken to show the relationship between these two sets of terminology. The outcrop of Campanian nonmarine sediments in Alberta, Saskatchewan, Montana, and Wyoming is shown in figure 1.

Three years of exploration (1963–1965) near the mouth of the Judith River in Chouteau and Blaine counties, Montana, produced a collection of mammals and other vertebrates which includes the most complete sample of Campanian mammals in North America to date. The first mammal locality in the type area of the Judith River Formation, Clayball Hill, was discovered in 1963 by Prof. R. E. Sloan and Robert Shoemaker. Clambank Hollow, the most prolific of all Judith River localities, was discovered in 1964, and Ankylosaur Point (very difficult to quarry, but with excellent potential) opened in 1965. Though the bulk of the fish, amphibian, and reptile remains came from mammal localities, some of the lower vertebrates were obtained by surface picking at numerous localities throughout the exposure of the formation.

By the beginning of 1966 processing of the bulk of the material was completed. Recovery of mammals from the treated material was approximately at the rate of 80 teeth per ton of matrix. The original manuscript of the present paper was submitted in March, 1968 in partial fulfillment of the requirements for a Ph.D. at the University of Minnesota. Catalogue numbers for the specimens were allocated by the American Museum of Natural History, and the manuscript was submitted to the Museum for publication shortly after the award of my degree in June, 1968. As a result of the help received from Dr. M. C. McKenna and Dr. R. E. Sloan the thesis was brought to a form suitable for publication.

[Dr. Sahni's paper has been edited with regard to style by Miss Susan Koelle and Mrs. Margaret S. Stevens, under the direction of R. E. Sloan and me.] M. C. McKenna.

ACKNOWLEDGMENTS

ABBREVIATIONS

AMNH, the American Museum of Natural History
BM, British Museum (Natural History)
CM, Carnegie Museum
GSC, Geological Survey of Canada
KU, University of Kansas
NMC, National Museum of Canada
ROM, Royal Ontario Museum
SPSM, St. Paul Science Museum
UAPC, University of Alberta Paleontological Collection
UCMP, University of California (Berkeley) Museum of Paleontology
UMVP, University of Minnesota, Vertebrate Paleontology Collection
USNM, United States National Museum, Smithsonian Institution
YPM, Yale Peabody Museum

HISTORICAL REVIEW

STRATIGRAPHY OF THE JUDITH RIVER FORMATION

ROCKS OF THE JUDITH RIVER AREA were first reported in journals of the Lewis and Clark expedition of 1804, which mentioned the white cliffs formed by what is now called the upper member of the Eagle Sandstone, along the valley of the Missouri River. Meek and Hayden (1856a, 1856b) were the first to collect fossils from the region around the mouth of the Judith River from strata they informally termed the "Judith River beds." They applied this term to the entire stratigraphic interval, consisting of both marine and continental deposits, from what is now known as the Marias River Shale of Santonian age to the Bearpaw Shale of late Campanian age. Hayden (1871) formally named the Judith River Formation and stated that the type area was between the mouths of the Judith River and Little Rocky Mountain Creek, extending 20 miles north and south from the Missouri River. The region is now included in southern Blaine and northern Fergus counties, Montana.

Work on stratigraphy and paleontology of the Judith River Formation can be divided into two periods. The first extended from the time of initial study by Meek and Hayden (1856a, 1856b), to 1905 when Stanton and Hatcher (1905) finally defined and delineated the Judith River and adjacent formations.

The first attempts to determine the age of the Judith River Formation were those of Meek and Hayden (1856b), Hayden (1857, 1858, 1860, 1861, 1871), and Meek and Hayden (1861). These authors vacillated between assigning the Judith River Formation to the Cretaceous (Meek and Hayden, 1856a, 1856b; Hayden, 1858, 1860) or to the Tertiary (Hayden, 1857, 1861, 1871; Meek and Hayden, 1861). Later, Hayden (1876) and Meek (1875, 1876) were convinced that the marine shales (Claggett) underlying the Judith River Formation were equivalent at least in part to the Fox Hills Sandstone. Meek and Hayden, in their reference of the Judith River beds to the Cretaceous, were influenced by the work of Leidy (1856, 1860), who considered the association of vertebrates to be similar to that found in the European Weal-den. Cope (1871) supported this view but maintained that the fossils were Upper Jurassic types. Later, Cope (1874, 1877) considered them to be Upper Cretaceous "with some Tertiary affinities."

During this same period, an indirect contribution to the stratigraphic position of the Judith River Formation was made by Dawson (1875, 1883, 1884a, and 1884b) in connection with his study of the Belly River Series (Oldman Formation) in Canada. Although uncertain about the age of the beds, Dawson (1875) noted the close resemblance of the "Belly River Series" and the Judith River beds. Later Dawson (1883) recognized that the "Belly River Series" occurs below the Pierre Shale, Fox Hills Sandstone, and "Laramie" sequence, and reaffirmed his earlier conviction regarding the correlation of the Judith River beds. The next year Dawson (1884a) was more explicit and correlated the lower part of the "Belly River Series" with the Judith River Formation. Dawson (1884b) made the observation that: "The Belly River series were, in 1875, by me correlated with the Judith River series of the Missouri. Additional and extensive collections of fossils since obtained and now being worked out confirm and strengthen this correlation and lead to the presumption that the so-called Judith River series must also occupy a position well down in the undoubted Cretaceous."

The invertebrates of the Belly River Group were studied by Whiteaves (1885) and the plants by Dawson (1886). Comparisons with "Laramie" types suggested to these authors that the "Laramie" forms could not be distinguished from those from the Belly River Group. White (1877, 1891), working with the invertebrates from the Judith River Formation, came to the same conclusion.

Osborn, in his introduction to Lambe's (1902) contribution to the vertebrate fauna of the "Belly River Series," stated that, whereas the vertebrates were comparable with those described from the Judith River Formation, the stratigraphic record placed the "Judith River beds proper above the Fox Hills and Fort Pierre."

The second period in the investigation of the

Judith River Formation in Montana began with detailed stratigraphic investigations by Stanton (1902) and Hatcher (1903a, 1903b), and culminated in an impressive work by Stanton and Hatcher (1905). For the first time the boundaries of the various formations occurring at the mouth of the Judith River were clearly delineated and characterized by their distinctive suite of fossils. This laid the foundation for future work. Their conclusions are quoted below:

"1. The Judith River beds are distinctly older than the Laramie, being separated from the latter by at least several hundred feet of marine shales, identical in their faunal and lithologic features with the Pierre, to which we have given the local name Bearpaw shales from the Bearpaw Mountains, about which they are well exposed.

"2. The Belly River beds of Canada are identical with the Judith River Beds of Montana. The name Judith River beds, having priority, should be the accepted name for this formation, and the terms Belly River and Fish Creek beds should be dropped.

"3. The marine sandstones and shales immediately underlying the Judith River do not represent either the Benton, as some Canadian geologists have supposed, or the Fox Hills and upper Pierre, as most geologists of the United States who have examined them have believed, but they constitute a distinct horizon within the Montana group which we have called the Claggett Formation, from old Fort Claggett, at the mouth of the Judith River, near which they are well exposed.

"4. The Eagle Formation, from its stratigraphic position and faunal relations, marks the base of the Montana group in this region.

"5. The Bearpaw shales, the Judith River beds, the Claggett, and the Eagle Formation all belong to the Montana Group and together probably form the equivalent of the Pierre as that term is generally understood, though the possibility is recognized that in the typical area the Pierre may have more restricted limits.

"6. Faunas similar to that of the Fox Hills Sandstone have a great vertical range and are likely to be found at any horizon within the Montana Group where a littoral or a shallow water facies is developed. The use of the term Fox Hills as a formation or horizon name outside of the original area in South Dakota is therefore of doubtful priority, as experience has shown."

After Stanton and Hatcher (1905), the only significant contributions to the stratigraphy of the Montana Group and the age of the Judith River Formation were made by Stebinger (1914) and Bowen (1915). The paper by Peale

(1912) suggesting a Tertiary age for the Judith River Formation can be disregarded as it was based on a misconception of the stratigraphy of the area. Stebinger (1914) traced the Montana Group from the type area of the Judith River Formation to northwestern Montana near the Blackfoot Indian Reservation. He pointed out the striking lithologic changes as the beds are followed northward. Similarly, Bowen (1915) made a study of the Montana Group in north-central Montana. Both these authors confirmed the findings of Stanton and Hatcher (1905).

Mention should be made here of the work of Sternberg (1914, 1915). Sternberg's principal contributions were the collection and study of the Campanian vertebrates mostly from the "Belly River Series" of Alberta, but also from the Judith River Formation of Montana. He also presented evidence showing "that the Belly River beds of Alberta are equivalent with the Judith River beds of Montana" (Sternberg, 1915).

Few contributions to the study of the Judith River Formation were made after 1915. The only paper dealing directly with the Judith River Formation is a heavy mineral study by Peterson (MS). The physiographic features of the area were described by Alden (1932) and the structure by Reeves (1946). Indirectly, however, the Judith River Formation has been discussed in a series of articles dealing chiefly with the paleoecology, paleogeographical reconstruction, geologic evolution, and tectonics of the Great Plains region. The most notable among these are by Russell and Landes (1940), Cobban and Reeside (1952), Cobban (1955), Reeside (1957), Weimer (1960), and McMannis (1965).

Recent geologic mapping of the quadrangles extending from the Missouri River north to the Bearpaw Mountains has been carried out by U.S. Geological Survey parties [Bryant, Schmidt, and Pecora (1960); Hearn, Pecora, and Swadley (1964); Kerr et al. (1957); Lindvall (1962); and Pecora, Witkind, and Stewart (1957)].

FAUNA OF THE
JUDITH RIVER FORMATION

The current study of the fauna of the Judith River Formation is part of the general revival of interest in small Cretaceous vertebrates of the American Mesozoic. Studies prior to the use of screening and etching methods were restricted

to surface prospecting and resulted in the dis-
covery of faunas biased in composition and in
size. Early descriptions of the fauna of the
Judith River Formation are no exception. The
first fossils described were four dinosaurian
genera, a crocodile, a turtle, and two nominal
species of Cretaceous garfish (Leidy, 1856).
These fossils were collected by F. V. Hayden
during his preliminary geologic investigation of
the area near the mouth of the Judith River.
During the next 50 years, a number of verte-
brates were obtained from the formation from
scattered locations in north-central Montana.
Most of the localities were unnamed or were
referred to vaguely as "the badlands of the
Judith River Formation." The bulk of the
vertebrates were described in a series of papers
by Leidy (1860, 1868), Cope (1871, 1876b,
1877), Marsh (1888), Stanton and Hatcher
(1905), and Hay (1904, 1908). Study of the
formation and area was then abandoned in
favor of better collecting areas in Alberta.

An attempt has been made herein to relocate
the areas from which some of the type specimens
of Leidy, Cope, Marsh, and others were obtained
(fig. 2). Most of the fossils were described at a
time when neither the stratigraphic position nor
the geographic extent of the formation was
known. Consequently, the stratigraphic horizon
of certain fossils collected by early workers in the
badlands of the Judith River Formation is still
uncertain. Stanton and Hatcher (1905) stated
that *Ornithomimus grandis* Marsh (1890) was
obtained from the Eagle Sandstone, although it
was most likely recovered from the Judith River
Formation. Cope (1876b) reported plesiosaurs
from the Judith River Formation, but as indi-
cated from the present study his specimens were
probably obtained from either the underlying
marine Claggett Shale or from the overlying
Bearpaw Shale. Most taxa known to have been
recovered from the continental Judith River
Formation itself were based on isolated teeth and
vertebrae from unnamed localities. The indis-
criminate naming of genera and species on frag-
mentary and insufficient material has created a
problem in the taxonomy of the taxa involved.

Prior to this investigation, the known fish
fauna of the Judith River Formation consisted
of the following species:

Acipenser albertensis Lambe, 1902
Acipenser eruciferus (Cope, 1876b)
Belonostomus longirostris (Lambe, 1902)

Lepisosteus occidentalis (Leidy, 1856)
Myledephas bipartitus Cope, 1876a

The fish were first described by Leidy (1856)
and Cope (1876a). Later Stanton and Hatcher
(1905) identified Judith River specimens of
Belonostomus longirostris and *Acipenser albertensis*,
which were originally described by Lambe
(1902) from the "Belly River Series" of Alberta.
No serious attempt was made to review the
taxonomy of the genera until the comparative
study by Estes (1964) of the Lance lower verte-
brates. With the possible exception of *Acipenser
albertensis*, all the above species from the Judith
River Formation are specifically indistinguish-
able from those of the Lance Formation. Current
investigation of the Judith River Formation has
resulted in the discovery of *Kindleia* and ?*Paral-
bula* and at least one other genus (here unnamed)
represented by a number of teleost vertebrae.
Kindleia is the best represented genus in the
present collection and the occurrence of ?*Paral-
bula* is the earliest Cretaceous record for the
North American continent.

Before 1964, the only valid species of amphibi-
ans to be reported from the Judith River Forma-
tion was *Scapherpeton tectum*. Originally, Cope
(1876b) had described the genera *Hemitrypus* and
Scapherpeton from the Judith River Formation on
the basis of isolated vertebrae. Estes (1964) con-
sidered all the forms described by Cope (1976b)
to differ from each other in minor, intraspecific
characters, and placed *Hemitrypus jordanianus*,
and the three other species of *Scapherpeton*, *S.
laticolle*, *S. excisum*, and *S. favosum*, in synonymy
with *Scapherpeton tectum*. The anurans, sirenids,
and plethodontids, which are common in the
present collection, were not previously recorded
either from the Judith River or Oldman
formations.

With the exception of lizards, the reptiles of
the Judith River Formation were relatively
better known. Turtles of the formation were dis-
cussed in detail by Hay (1908). The bulk of the
reptiles consisted of different groups of dinosaurs,
known at best from incomplete skeletons and
more often from shed teeth. The Ceratopsidae
were previously reviewed by Hatcher (1907),
Lull (1933), Lull and Hatcher (1907), the
Hadrosauridae by Lull and Wright (1942), and
the Deinodontidae by Matthew and Brown
(1922). The Hypsilophodontidae were not pre-
viously reported from the Campanian sediments
of Montana and Alberta but are represented in
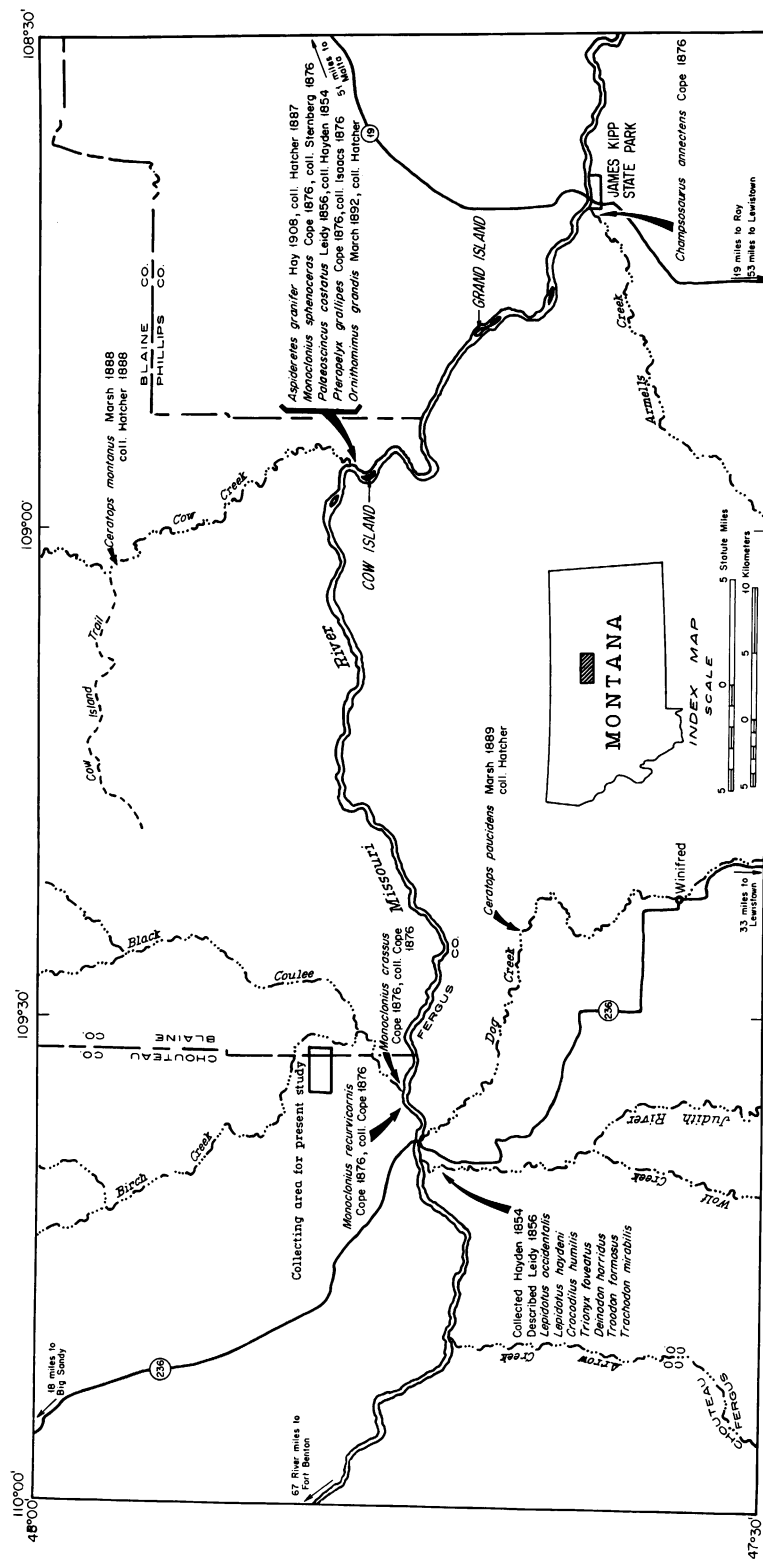
FIG. 2. Index map of the original type area of the Judith River Formation showing localities from which Hayden, Leidy, Cope, and Marsh obtained fossils.

the present collection by the genus *Thescelosaurus*.

Stanton and Hatcher (1905) identified *Mesodma primaevus* and *Boreodon matutinus* as occurring in the Judith River Formation. These are the only mammals previously known from the formation. Both had originally been described from the Oldman Formation of Alberta (Lambe, 1902). No locality was given for the occurrence of *Mesodma primaevus*; *Boreodon matutinus*, represented by the posterior part of a right mandible, was found north of a conspicuously red butte, near the junction of Meili Coulee and the Milk River about 5 miles north of Havre, Montana.

There are some significant differences between the fauna of the Judith River Formation as known before the current investigation and after. These differences result from a change of objectives and methods from those of early workers. The present collection was obtained from an area less than 2 miles in radius and principally from a single locality. The present sample consists of a mixture of size-sorted vertebrate elements from the proximal fluvial community and the more distal, microterrestrial and megaterrestrial communities. The composite picture that emerges from the synthesis of data of earlier workers and the current investigation appears to be a fair representation of the Campanian fauna occupying the lowland coastal plains east of the rising Cordilleras.

GEOLOGY

MONTANA GROUP

THE STRATIGRAPHIC SEQUENCE of beds exposed in the type area of the Judith River Formation and their correlatives in adjacent Alberta is shown in figure 3. The upper part of the Marias River Shale underlies the other Cretaceous formations in the area studied. At places, the exposures are more than 200 feet thick, but it is impossible to estimate the total thickness accurately as the base of the Marias River Shale is not visible. The shale is entirely marine and has numerous bentonitic seams. Fossils recovered from the shales are similar to those obtained from the Colorado Shale and include the molluscs *Scaphites ventricosus, Inoceramus labiatus*, and *I. deformis*.

The Marias River Shale is not part of the Montana Group and is mainly Santonian in age. It was previously referred to as the Benton Shale by Stanton and Hatcher (1905), and as the Colorado Shale by Bowen (1915). The name Marias River Shale was proposed by Cobban et al. (1959) for "900–1200 feet of dark gray shale that lies between the Backleaf and the Telegraph Creek formations on the Sweetgrass Arch and westwards into the Rocky Mountains."

EAGLE SANDSTONE

The Eagle Sandstone was named by Weed (1899) from exposures at the mouth of Eagle Creek on the Missouri River, about 40 river miles below the town of Fort Benton. The exposures occur along the Missouri River as far west as 10 miles below the mouth of the Marias River. The Eagle Sandstone consists of two distinct subdivisions, a lower Virgelle Sandstone and an upper shaly bed. The Virgelle Sandstone was named by Bowen (1915) for the town of Virgelle, near Fort Benton, and consists of a massive white- to buff-colored cross-bedded sandstone, for the most part unfossiliferous. The upper, more shaly subdivision, consists of argillaceous sandstones and carbonaceous shales, and represents a shallowing of the sea. The Eagle Sandstone is overlain conformably by the Claggett Shale.

Lithology of the Eagle Sandstone stratigraphic interval varies greatly from northwest to southeast. The Virgelle Sandstone, which crops out as prominent scarps along the Missouri River, consists of white massive sandstone that becomes gray to buff sandstones farther southeast. The Eagle Sandstone becomes thicker and more continental in a northwesterly direction, and grades into the continental Milk River Formation west of Glacier National Park, near the international boundary.

The Virgelle Sandstone crops out at many places within the area studied and is overlain by alternating beds of shale, carbonaceous shale, and buff-colored consolidated sandstones which comprise the unnamed upper member of the Eagle Sandstone. These sandstones contain an abundant, shallow water, marine, molluscan fauna, including *Cardium speciosum* and *Mactra alta*.

Although Stanton and Hatcher (1905, p. 12) reported that the type of *Ornithomimus grandis* Marsh (1890) was recovered from the Eagle Sandstone near the mouth of Cow Creek, it seems more likely that the fossil was actually collected from the Judith River Formation. The Eagle Sandstone in the area appears to be mostly marine, and prospecting failed to find any trace of terrestrial vertebrates.

CLAGGETT SHALE

The name Claggett Shale was proposed by Stanton and Hatcher (1905) for the marine shales that overlie the Eagle Sandstone and which, in turn, are overlain by the Judith River Formation. The type locality of the Claggett Shale is at old Fort Claggett. The beds here are well exposed and consist of more than 400 feet of dark gray, marine shales with some intercalated beds of sandstone. The molluscs from the Claggett Shale are characteristic of those from the Pierre Shale farther to the east, and consist of forms such as *Baculites compressus, B. ovatus, Inoceramus barabina*, and *Leda evansi* (Bowen, 1915). These species persist into the overlying Bearpaw Shale.

The easily eroded Claggett Shale forms characteristic low, dome-shaped hills with gentle slopes. Abundant selenite crystals up to 2 inches long are found on the slopes. Claggett Shale grades upward into more arenaceous beds.
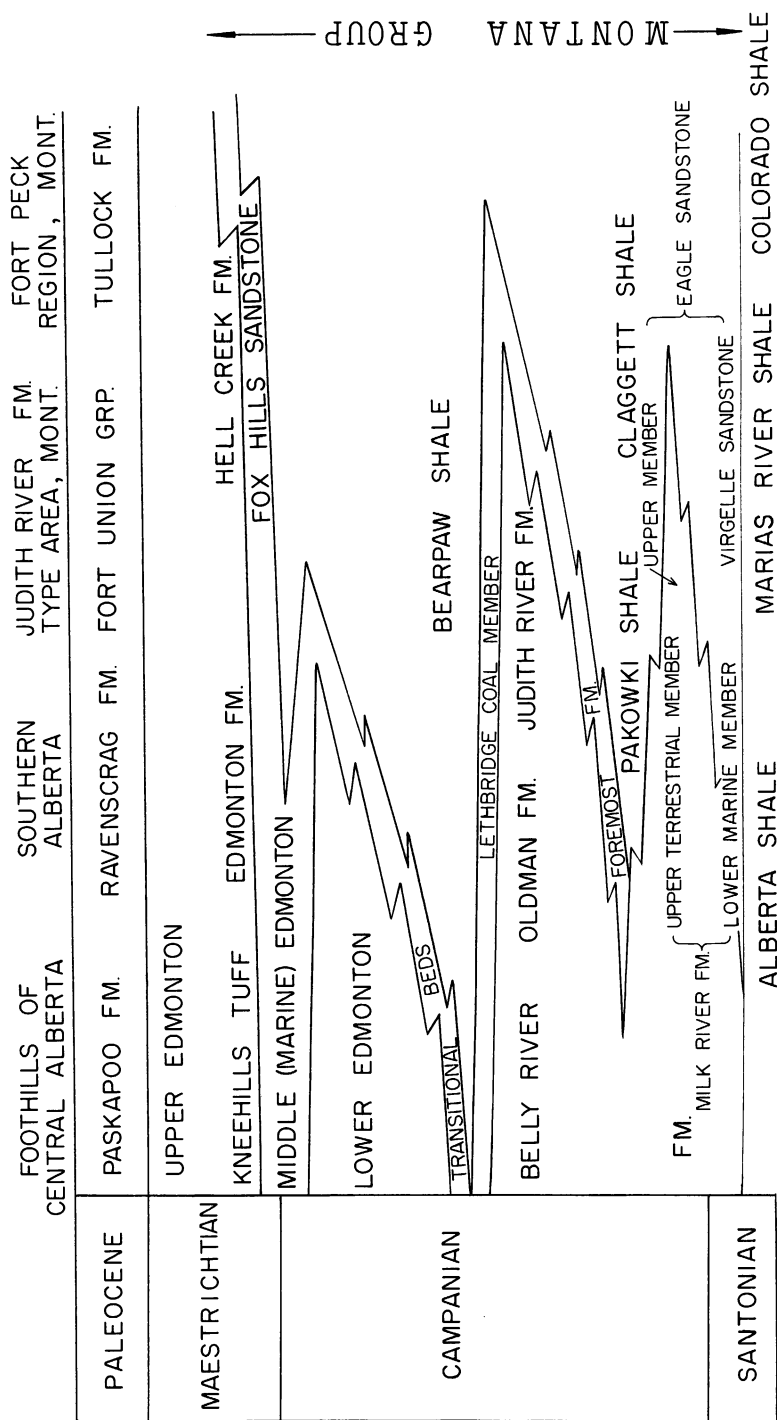
Fig. 3. Diagrammatic cross section of late Cretaceous rocks of Alberta and Montana.

The transition from the underlying Claggett Shale to the Judith River Formation is conformable and has been arbitrarily delineated by several authors. Stanton and Hatcher (1905) studied the area just to the north of the mouth of the Judith River, and included a buff-colored, massive, consolidated sandstone with a thickness of almost 200 feet within the Claggett Shale. Some of the fossils contained in this sandstone, *Tancredia americana*, *Mactra formosa*, and *M. alta*, are also found in the later Fox Hills Sandstone of similar facies. The similarity between the two faunas, however, is merely a result of similar ecologic conditions rather than an equivalency in age. Bowen (1915) suggested that the bed should be included as the base of the Judith River Formation for several reasons. First, the lithologic change between Stanton and Hatcher's upper and lower divisions of the Claggett Shale is more obvious than the change between the upper massive sandstone and the conformable Judith River Formation. Second, farther to the south, the sandstone bed resembles the overlying Judith River Formation more and marine fossils are absent. To the north as well, near the town of Big Sandy, distinctive marine molluscs give way to freshwater and brackish-water forms. Lindvall (1962) followed Bowen (1915) in including the massive sandstone bed (which the former author referred to as the *Tancredia* Sandstone) as the basal part of the Judith River Formation.

JUDITH RIVER FORMATION

The Judith River Formation at the mouth of the Judith River, mainly freshwater deposits, is here defined as that body of rock accruing from the base of the massive ferruginous *Tancredia* Sandstone of Lindvall (apparently equivalent to the Foremost Formation of Alberta) to the twin coal seams (the Lethbridge Coal Member of Alberta). Such a definition appears not only to be stratigraphically sound but is also practical for mapping purposes.

The sediments of the Judith River Formation vary. The basal sandstones are buff-colored, consolidated, shallow-water marine sandstones, representing the transition from the marine Claggett Shale to the continental Judith River Formation. These are overlain by terrestrial beds composed of intercalated siltstones and shales with occasional seams of lignite, coals, and

bentonitic shales. Thin lenses of fragmented freshwater molluscs are found dispersed in the upper part of the formation. The occurrences of these clam beds are significant as they usually indicate the presence of bones. Vertebrate remains are found throughout the formation, although the known mammal localities are restricted to the top 50 feet.

Two coal seams of nearly constant thickness define the top of the Judith River Formation. A coal seam also marks the boundary of the Oldman Formation (Belly River Series), and the Bearpaw Shale in Alberta (Russell and Landes, 1940). Earlier markers included the shaly sandstone immediately overlying the coals and the overlying bed containing *Ostrea subtrigonalis* within the Judith River Formation (Bowen, 1915). I consider the lignitic coal bed as the upper limit of the Judith River Formation because the sandstone overlying the twin coal seams varies laterally in thickness and in lithology, and the oyster bed is not a constant or prominent feature.

BEARPAW SHALE

The Bearpaw Shale was named by Stanton and Hatcher (1905) for exposures of a marine shale that surround all except the western side of the Bearpaw Mountains. The complete thickness of the formation is not exposed, but in the Eskay quadrangle Lindvall (1962) estimated it to be about 700 feet thick. The lower contact of the Bearpaw Shale with the Judith River Formation is conformable and intergradational as is the upper contact of the Bearpaw Shale with the Fox Hills Sandstone.

The Bearpaw Shale bears remarkable similarities to the Claggett Shale in lithology, mode of deposition, type of fossils, weathering surfaces, and in the occurrence of selenite crystals. Some differences exist as summarized by Bowen (1915): "(1) The Bearpaw is much thicker . . . (2) The Bearpaw is more fossiliferous and contains a more diversified fauna. (3) In many places . . . a bed consisting almost wholly of brackish-water shells, largely *Ostrea subtrigonalis*, lies immediately beneath the Bearpaw . . . no shells of this kind are found immediately beneath the Claggett."

The Bearpaw Shale represents the westward continuation of the upper Pierre Shale and is late Campanian in age.

BELLY RIVER GROUP OF
SOUTHERN ALBERTA

The sequence of marine, brackish water, and nonmarine sediments above the Alberta Shale (Alberta Group) and below the Bearpaw Shale has been variously described since its original discussion by Dawson (1884b). Dawson named the deposits between these shales the Belly River Series but failed to distinguish a relatively minor marine transgression represented by the Pakowki Shale. Later, Dowling (1917) redefined the Belly River Series and differentiated four units which, in ascending order, were: the Milk River Formation, the Pakowki Formation, the Foremost Formation, and the Pale Beds. Williams and Dyer (1930), however, chose to restrict the term Belly River Formation to the predominantly nonmarine coastal plain deposits above the Pakowki Shale and below the Bearpaw Shale. They contended, in doing so, that they were following Dawson's original intent. Slipper and Hunter (1931) and Powers (1931) also described the strata on the basis of surface and subsurface samples and were in essential agreement with Dowling's interpretation. Russell (Russell and Landes, 1940), in another major review of the stratigraphy of the plains of southern Alberta, renamed the "Pale Beds" underlying the Bearpaw Shale the Oldman Formation, and distinguished this unit from the older Foremost Formation by the greater occurrence of freshwater fossils and lighter colored sandstones. As generally understood today, the beds between the Alberta Shale and the Bearpaw Shale comprise the Belly River Group of the southern Alberta plains (Lerbekmo, 1961, 1963) and consist in ascending order of the following formations: the Milk River Formation, the Pakowki Shale, the Foremost Sandstone, and the Oldman Formation. The Belly River Group and the overlying Bearpaw Shale represent an interval of time roughly equivalent to that of the Montana Group of north-central Montana.

The Belly River Group when traced westward to the foothills of southern Alberta thickens considerably and becomes an undifferentiated predominantly nonmarine sequence of formational status. According to Lerbekmo (1963), the Belly River Formation of the foothills of southern Alberta consists of 2000 to 2500 feet of deltaic and brackish-water sediments with "thin intraformational mudstones, pebble conglomerates, nodular limestones, coal seams, bentonites,

magnetite-sandstone and pelecypod beds." The Belly River Formation conformably overlies the Wapiabi Formation of the Alberta Group and is overlain by the Bearpaw Shale. Of significance is the stratigraphic position of the major coal seams which are found at various levels within the formation when traced from south to north. Lerbekmo (1963, p. 60) reported the presence of coal in the upper 100 feet of the formation in a section taken at Drywood River. Some 150 miles to the north, however, the prominent coal beds are found at progressively lower levels so that, near the Bow River, the coals occur at the base of the formation. A few fossils have been reported including *Unio*, *Anodonta*, *Sphaerium*, *Viviparus*, *?Campeloma*, and *?Physa*; a dinosaur bone fragment and a part of a turtle carapace were also recovered.

MILK RIVER FORMATION

Dowling (1917) named the Milk River Formation for a sequence of light-colored sandstones and shales exposed along the Milk River. The beds had originally been correlated by Stanton (Stanton and Hatcher, 1905) with the Eagle Sandstone of Montana and consist of a lower arenaceous unit and an upper more argillaceous one. The lower Milk River beds correspond to the Virgelle Sandstone which forms the base of the Montana Group; the upper Milk River beds are more nonmarine than their equivalents from Montana and consist of brackish-water and freshwater deposits with coals and bentonites. The invertebrates include a mixture of brackish-water and freshwater molluscs, whereas the vertebrates are similar to the fauna of the Oldman Formation (Russell, 1935).

The formation is about 300 feet thick and is conformable with the underlying marine Alberta Shale. The base of the formation includes the massive, transitional sandstones which are in part equivalent to the Telegraph Creek Formation of northwestern Montana, and also to the upper 100 to 200 feet of the Warm Creek Shale. Lerbekmo (1961) traced the Milk River Formation westward and came to the conclusion that it interfingers with the lower part of the Belly River Formation of the foothills.

PAKOWKI FORMATION

The Pakowki Formation consists of a sequence of marine shales and sandstones conformably overlying the Milk River Formation. Dowling

(1915) named the formation from exposures in Pakowki Coulee. The outcrop is restricted principally to some areas north and south of the Milk River. The thickness of the formation is usually less than 200 feet but increases toward the northeast to a thickness of 900 feet (Russell and Landes, 1940, p. 44).

The Pakowki Formation is lithologically and faunistically similar to the Claggett Shale of the Montana Group. The fauna of the formation in Alberta was studied by Landes (Russell and Landes, 1940) and is distinct from the marine faunas of the Alberta Shale and the younger Bearpaw Shale.

FOREMOST FORMATION

The name Foremost Formation was applied by Dowling (1915) to a group of beds that had been previously described in ambiguous terms by Dawson (1884b). The type section is exposed along Chin Coulee near the town of Foremost and was estimated by Russell and Landes (1940, p. 54) to be about 490 feet thick. The beds consist of mudstones, silty sandstones, and shales with occasional lignite and coal seams. The invertebrate fauna comprises many brackish-water forms such as *Ostrea* and *Corbula*; the vertebrates have recently been listed by Langston (1965).

Slipper and Hunter (1931) demarcated the base of the formation at a persistent arenaceous horizon (the Verdegris Sandstone). The top of the formation, at its conformable contact with the Oldman Formation, was defined by Dowling (1917) as a "certain coal seam" (the Taber Coal Measures). The definition is only of restricted significance as the coal seams, although wide-spread, are not of uniform thickness and are found at different levels throughout the formation.

The Foremost Formation in eastern Alberta, according to Shaw and Harding (1949), is divisible into nine alternating marine and non-marine deltaic members which thin rapidly to the north and to the east.

OLDMAN FORMATION

The name Oldman Formation was proposed by Russell and Landes (1940, p. 62) for exposures along the Oldman River. The sediments had previously been described as "Pale Beds" by Dawson (1884b). The name was given primarily

to end the confusion resulting from the various interpretations of Dawson's original intent in naming the Belly River Series.

Recently, Lerbekmo (1961), by tracing the Milk River Formation westward, has shown that the Belly River Formation of the foothills is equivalent to all the formations contained in the Belly River Group of the plains.

The Oldman Formation is lithologically similar to the middle and upper beds of the Judith River Formation. The beds consist of cross-bedded consolidated and massive sandstones with lenticular alternating siltstones, lignites, and coals. The thickness of the formation is less than 1000 feet in southeastern Alberta (Russell and Landes, 1940, p. 67) and progressively increases from the southeast to the northwest. The Oldman-Bearpaw contact is considered to be at the top of the Lethbridge Coal Member (Lethbridge Coal Measures).

The Lethbridge Coal Measure, as defined by Link and Childerhose (1931, p. 1227) in the Lethbridge area, includes a single coal seam usually less than 7 feet thick and three other minor coal seams. The total thickness of the member in the Lethbridge area is about 110 feet. The Coal Measures are of wide occurrence and correspond to the 50 feet of carbonaceous shales, lignites, and coal seams at the top of the Judith River Formation.

The faunal list of the vertebrates recovered from the Oldman Formation was most recently compiled by Langston (1965). The fauna is similar to that of the Judith River Formation.

The Upper Cretaceous sequence in Alberta, Montana, and the adjoining states includes numerous bentonitic seams formed as a result of intense and large scale volcanic activity during the close of the Mesozoic. Sanidine and biotite crystals obtained from these bentonites have been extensively used in the radiometric dating of these rocks by the potassium-argon method. The accuracy of the bentonite dates is dependent upon the contemporaneity of volcanic activity and the deposition of the ash to form bentonitic seams. The purity and thickness of the bentonites in the area strongly support the assumption of synchronous vulcanism. Bentonites are more easily discernible in the marine Bearpaw Shale than in the continental deposits underlying them. The lesser frequency of these beds in the Judith River Formation is not so much a result of diminishing volcanic activity at

the time, but rather a result of greater rate of weathering in the nonmarine environment.

Geochronologic dates from the bentonites of the Bearpaw Shale have been the subject of rather detailed studies by Baadsgaard et al. (1964) and Folinsbee and others (1962, 1964, 1965).

Nascimbene (MS) investigated the ages of bentonites of the Bearpaw Shale in order to determine the times of major transgression and regression of the Bearpaw Sea. His data consisted of 17 samples from Alberta, Saskatchewan, and Montana. Some of these samples were obtained close to the contact of the Oldman Formation and the Bearpaw Shale, and consequently are relevant to the present study. Like the contact between the Judith River Formation and the Bearpaw Shale, the contact between the Oldman Formation and the overlying marine shale is taken above a number of coal seams, lignites, and sandy shales, designated in Alberta as the "Lethbridge Member" of the Oldman Formation.

The closest date to the top of the Oldman Formation comes from a sample taken from Bentonite No. 1 in the St. Mary-Lethbridge area of Alberta. The sample was collected 52 feet above the base of the Bearpaw Shale and gives a geochronologic age of 73 million years. Other samples indicating similar ages were obtained from the region around Manyberries, Alberta, from a series of closely spaced bentonites 67 feet above the base of the marine shale. The only radiometric date obtained from the Bearpaw Shale in Montana is from the James Kipp State Park area, 250 feet above the underlying Judith River Formation. The age of this bentonite was 72 million years.

The radiometric dates obtained from Alberta, Saskatchewan, and Montana can be used as good estimates for the time marking the end of deposition of the coastal-plain and deltaic sediments of the Oldman and Judith River formations and the large-scale transgression of the Bearpaw Sea. The transgression of the sea was quite rapid as pointed out by Russell and Landes (1940), who suggested that the base of the Bearpaw Shale is isochronous. Nascimbene (MS, p. 57), however, on the basis of the James Kipp State Park bentonite date from Montana, suggested that the basal beds of the Bearpaw Shale of Alberta are time equivalents of beds higher up in the section in Montana and there-fore "the lower limit of the formation is slightly but definitely diachronous in a northwest-southeast direction." The regression of the Bear-paw Sea, which marked the close of Cretaceous marine sedimentation in this area, was gradual, so that the upper beds of the marine shale become progressively younger from west to east.

Nascimbene (MS) was also able to make an estimate of the rate of sedimentation in the Bearpaw Sea, using as data a large number of radiometric dates of samples collected within a radius of 150 miles in an area where the stratigraphy is well understood. On the basis of Nascimbene's calculated sedimentation rate of 100 to 150 feet per million years, and the dated bentonite from the James Kipp State Park, the upper age limit of the Judith River Formation would be about 74 million years and that of the mammal-bearing beds of the mouth of the Judith River slightly older. As expected, the rate of sedimentation is not constant; it is higher in the marginal areas of the Bearpaw Sea in south-eastern Alberta and slower in the deeper part of the basin in northern and north-central Montana.

UPPER COLORADO GROUP

North of the international boundary, the marine shales of the upper Colorado (Alberta) Group crop out in southern Alberta, central Saskatchewan, and southwestern Manitoba (Williams and Burk, 1964). This marine unit, representing the extension of the Colorado Sea, underlies the Belly River Formation of the foot-hills. The top of the group grades into the over-lying Milk River Formation and represents the shallowing and, in places, the complete with-drawal of the Colorado Sea.

STRATIGRAPHY AND SEDIMENTATION OF THE JUDITH RIVER FORMATION
GEOLOGIC SECTIONS

No complete and continuous section of the Judith River Formation that shows the contacts of the formation with the underlying marine Claggett Shale and with the overlying Bearpaw Shale (fig. 4) could be found in the type area. Section I represents the transition from the underlying marine Claggett Shale through a thick sequence of brackish-water deposits to the more arenaceous freshwater sediments of the Judith River Formation. This section lacks the

Lethbridge Coal Member and the contact with the Bearpaw Shale.

Section II consists of slightly more than 500 feet of the Judith River Formation, and includes sediments which gradually grade into the overlying Bearpaw Shale. Section II begins near the base of the formation, but does not include the contact with the Claggett Shale. Sections I and II overlap to form a composite section for the formation which may be considered the type section. Thickness of the Judith River Formation is estimated to be slightly less than 550 feet in the exposures along the walls of Birch Creek, as based on these two sections.

SECTION I: WEST BIRCH CREEK

The basal part of the Judith River Formation and its contact with the Claggett Shale is exposed in several places in the area. The locality where the section was measured is the SE. $\frac{1}{4}$, sect. 5, T. 24 N., R. 16 E., and the SW. $\frac{1}{4}$, sect. 30, T. 24 N., R. 17 E. (fig. 5). Although the region is severely faulted, the stratigraphic sequence can be measured. The dip of the strata averages 10 to 20 degrees to the east, decreasing eastward and in the upper part of the section. The section was terminated at an unmapped fault of unknown displacement.

The contact between the Claggett Shale and the Judith River Formation is conformable and gradational. A 100-foot thick series of fine-grained unconsolidated sandstones with shallow-water marine fossils comprise the basal part of the Judith River Formation. Although these sediments are not very fossiliferous, forms such as *Mactra alta*, *M. formosa*, and *Tancredia americana* can be found. Ferruginous, cliff-forming sandstones overlie these deposits and their fossil content is similar. These beds are the equivalent of the Foremost Formation of Alberta. The sandstones give way vertically to thin beds of dark chocolate-colored shales, which at places have carbonaceous lenticles. The first definite record of freshwater molluscs is about 200 feet above the base of the Judith River Formation and about 30 feet above the highest shallow-water marine deposits. The only lignitic coal seam in the entire section is present about 40 feet above the occurrence of the freshwater molluscs. Near the top of Section I, dinosaur bone chips, turtle shell fragments, and an assorted association of lower vertebrate elements were found. This horizon represents the upper part of the middle division of the

formation. Earlier workers observed that vertebrates were scarce in the lower part of the formation but became more and more abundant near the top.

SECTION II: BIRCH CREEK

This section includes most of the Judith River Formation and consists of well exposed horizontal strata (fig. 6) on either side of Birch Creek, which flows into the Missouri River 2 miles east of the mouth of the Judith River. The section was measured in the SE. $\frac{1}{4}$ of the NW. $\frac{1}{4}$, sect. 3, T. 23 N., R. 17 E., in Blaine County.

At the base of the section in Birch Creek there is a massive consolidated sandstone with steep slopes which is probably equivalent to the upper part of the much thicker ferruginous "*Tancredia*" Sandstone found in Section I. The sandstone is followed by a sequence of silts, shaly sandstones, channel sandstones, chocolate-colored carbonaceous shales, ripple-marked indurated sandstones, banded silts, and other sediments that represent fluvial deposits near the western shore of the Campanian Sea. Pollen samples, being studied by R. Shoemaker at the University of Minnesota, were collected from this measured section.

The top of the Judith River Formation is demarcated by two lignitic coal bands separated by about 5 feet of shaly sandstones. The coal seams form a widely distributed, prominent stratigraphic unit, known in Alberta as the Lethbridge Coal Member.

LOCALITIES
CLAMBANK HOLLOW

Clambank Hollow is the most productive of all the localities discovered during prospecting in the area, and is 40 feet below the top of the Judith River Formation. The quarry (NW. $\frac{1}{4}$, SE. $\frac{1}{4}$, sect. 31, T. 24 N., R. 17 E.) is situated in a small creek running parallel to an east-west dirt road north of the silos of the Halley ranch. The clam/bone bed is exposed on either side of the creek but the north side was worked more extensively than the south. Although not comparable with some of the later Lance and Hell Creek localities in Wyoming and Montana, respectively, the production rate of Clambank Hollow is about 100 mammal teeth to every ton of quarried matrix.

The locality was first noticed by R. Shoemaker and R. Melchior in 1964, who commented

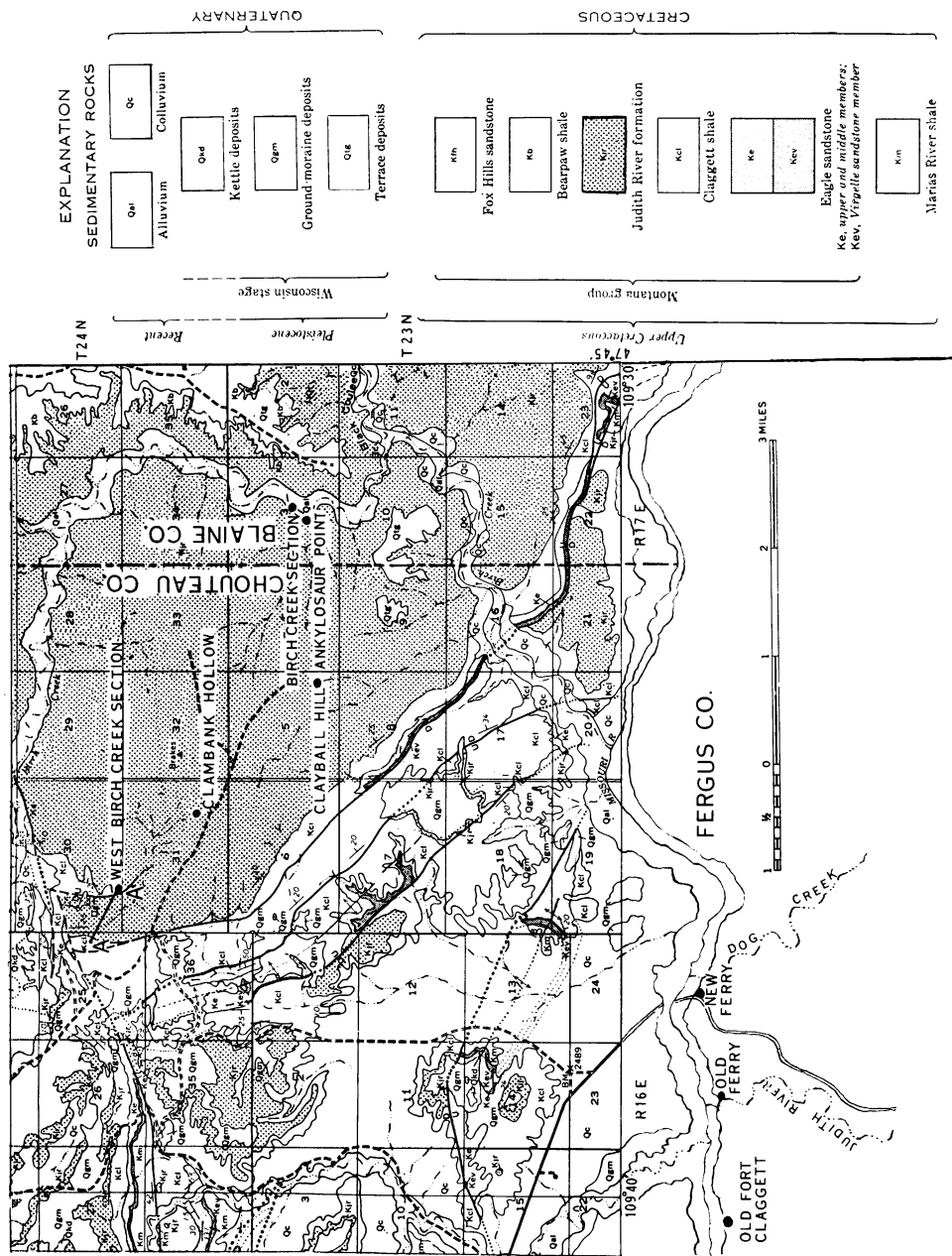FIG. 4. Geologic map of the southeastern part of the Eskay Quadrangle, showing fossil localities and measured sections in the type area of the Judith River Formation (modified from Lindvall, 1962).
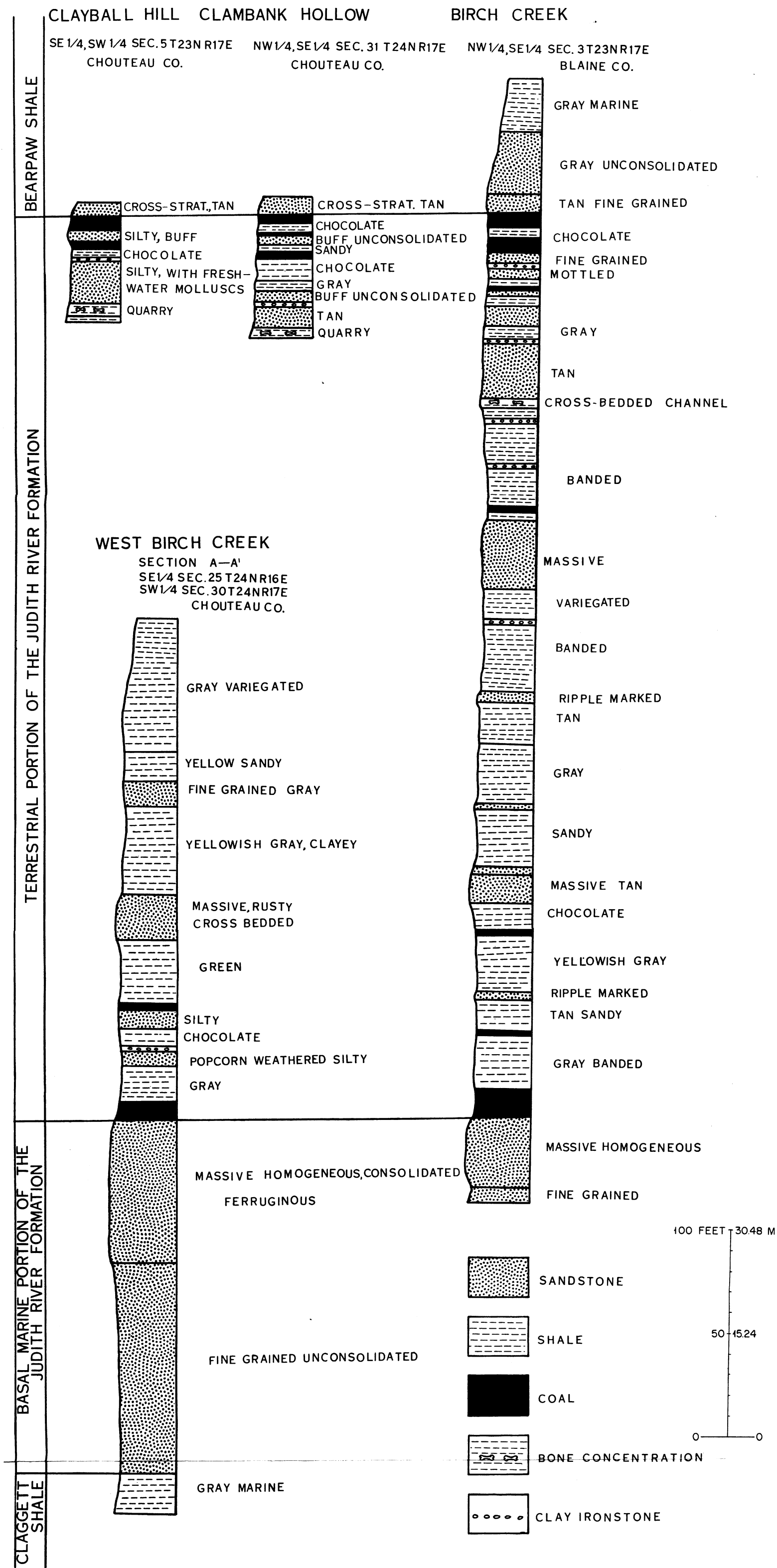
FIG. 5. Columnar sections of the Judith River Formation in the type area, Blaine and Chouteau counties, Montana.
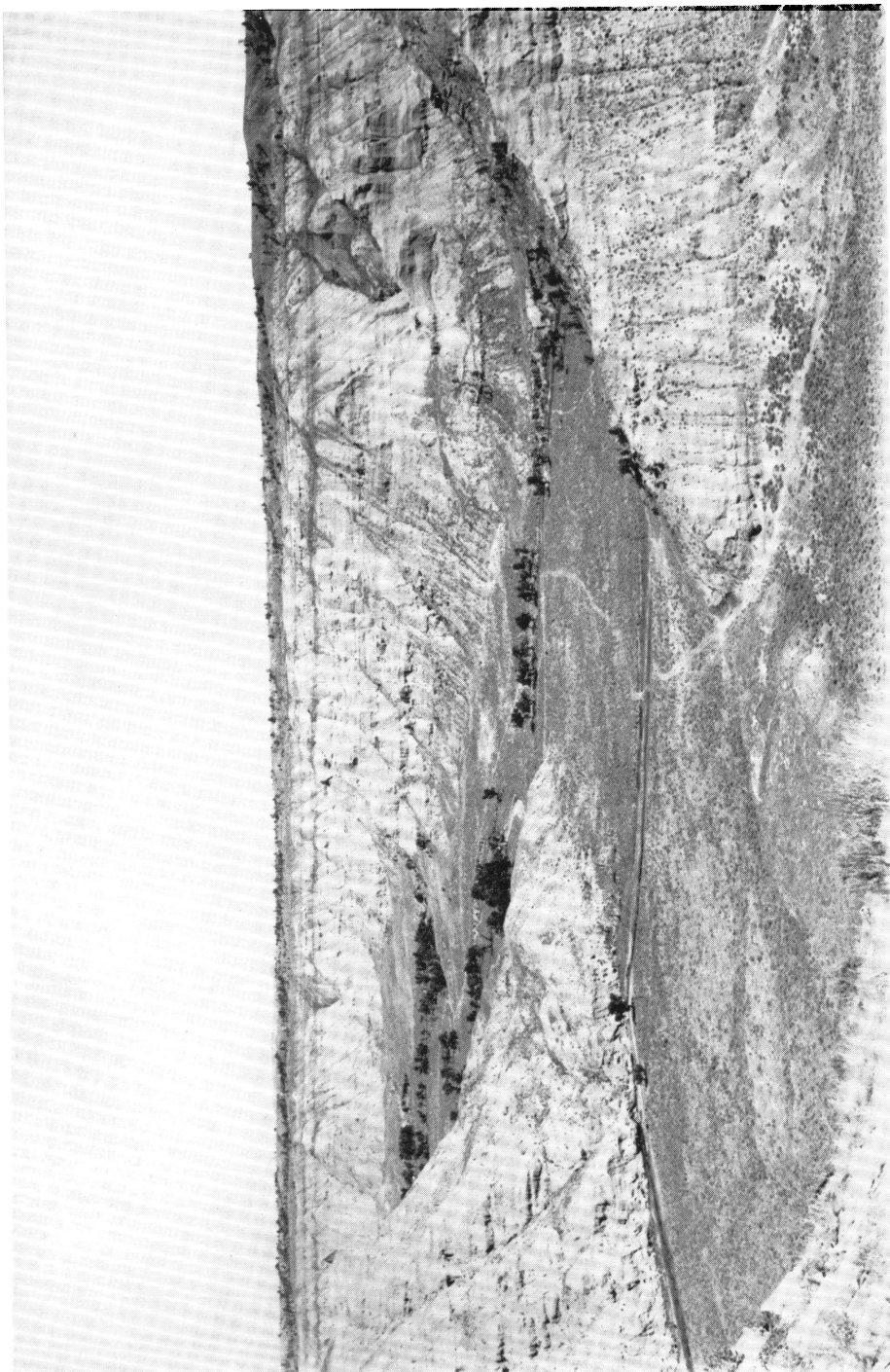
FIG. 6. The type section of the Judith River Formation, Birch Creek, Blaine and Chouteau counties, Montana.

on the richness of the bones on the surface of the bed. Surface picking failed to reveal the presence of any mammals though a number of lower vertebrates were collected.

The locality probably represents a river meander or oxbow lake, intermittently connected to the major stream channel. The clam/bone bed is a crescentic lens rapidly pinching out to the east and dipping very steeply to the west, toward what was probably the central part of the ancient river. The exposure of the bed is about 45 to 50 feet from east to west. The clam/bone bed proper is about 2 feet in thickness and can be divided into two parts, a lower subdivision not more than 6 inches thick which is very rich in bones, and an upper extremely well indurated subdivision with less bone concentration. Both lenses contain coal lenticles and plant debris.

CLAYBALL HILL

This locality was discovered by Professor Sloan and Robert Shoemaker on their first trip to the area in the summer of 1963. Although quarried in subsequent years, the yield for Clayball Hill was very low as it produced less than 1 per cent of the mammal fossils obtained from the Judith River Formation. Also, the difficulty in processing the matrix of this locality was excessive. The quarry is situated on the edge of rolling uplands in a deeply eroded region where several creeks drain into a larger unnamed tributary of Birch Creek (SE. $\frac{1}{4}$, SW. $\frac{1}{4}$, sect. 5, T. 23 N., R. 17 E.).

The layer producing mammals and other vertebrates is a buff to gray, fairly homogeneous siltstone. Freshwater molluscs are present but less frequent than at Clambank Hollow. The fossils do not appear to be secondarily concentrated as in Clambank Hollow, but are irregularly dispersed throughout the bed.

Although the top of the formation has been eroded away directly above the quarry face, the contact with the Bearpaw Shale can be traced farther west by following the horizontal beds for a short distance to the prominent coal markers. As in Clambank Hollow, two coal beds are present. The upper one is the thicker of the two and is nearly the same thickness as it is at Clambank Hollow. The locality is about 40 feet below the top of the formation and an estimated 100 feet below the basal Bearpaw Shale oyster bed.

METHODS AND PROCEDURES

The best prospecting in the badlands of the Judith River Formation is in the southeastern part of the Eskay Quadrangle, principally in two areas, one in sect. 31, T. 24 N., R. 17 E., and the other in sect. 5 and 8, T. 23 N., R. 17 E. Prospecting was done at random in selected areas. Although bone fragments abound in most of the upper strata, an effort was made to find concentrations including clam/bone beds which, in eastern Montana, have been found to produce microvertebrate fossils.

Anthills made by species of the red ant *Pogonomyrmex* have frequently produced small vertebrate fossils. No such anthill in this area was found to contain vertebrate material.

Screening has now become a standard practice for the recovery of the smaller fraction of vertebrate faunas. The procedure followed was not very different from that described by Hibbard (1949), McKenna (1965), and Clemens (1965). We used copper screen wire, 14 by 18 meshes to the inch.

The Clambank Hollow locality was quarried and about 9 tons of matrix were removed from the productive siltstone layer. Freshwater molluscs form as much as 30 per cent of the total bulk of the rock at some places, and interfere with sorting. Use of formic acid was initiated to eliminate the calcareous shell fragments. To test the effect of this reagent on bone, small samples of mammal teeth and other delicate bones were treated with dilute formic acid to see if they were subject to solution. No noticeable difference was found between the treated and untreated specimens. The method was consequently employed on a large scale.

FAUNA OF THE JUDITH RIVER FORMATION

FAUNAL LIST OF VERTEBRATES
COLLECTED 1963–1965

Class Elasmobranchii
  Order Rajiformes
    Family Dasyatidae
      Myledaphus bipartitus Cope
Class Osteichthyes
  Order Amiiformes
    Family Amiidae
      Kindleia fragosa Jordan
  Order Aspidorhynchiformes
    Family Aspidorhynchidae
      Belonostomus longirostris (Lambe)
  Order Lepisosteiformes
    Family Lepisosteidae
      Lepisosteus occidentalis (Leidy)
  Order Elopiformes
    Family Albulidae
      ?*Paralbula* sp.
  Infraclass Teleostei, indet.
Class Amphibia
  Order Salientia
    Family Discoglossidae
    Family Pelobatidae
  Order Urodela
    Family Scapherpetonidae
      Scapherpeton tectum Cope
      Lisserpeton bairdi Estes
    Family Sirenidae
      Habrosaurus dilatus Gilmore
    Family Plethodontidae
      Prodesmodon copei Estes
    Family ?Plethodontidae
      Opisthotriton kayi Auffenberg
Class Reptilia
  Order Testudines
    Family Dermatemydidae
      Basilemys sp.
    Family Trionychidae
      Trionyx sp.
    Family ?Baenidae
  Order Eosuchia
    Family Champsosauridae
      Champsosaurus sp.
  Order Crocodilia
    Suborder ?Sebecosuchia
    Suborder Eusuchia
      Family Crocodylidae
        Subfamily Crocodylinae
          Leidyosuchus canadensis Lambe
        Subfamily Alligatorinae
          Brachychampsa montana Gilmore
  Order Sauria
    Family Teiidae

Chamops segnis Marsh
Leptochamops denticulatus (Gilmore)
    Family Anguidae
      Peltosaurus piger Gilmore
    Family Xenosauridae
      Exostinus lancensis Gilmore
    Family ?Xenosauridae
      cf. *Exostinus* sp.
    Family Parasaniwidae
      Parasaniwa wyomingensis Gilmore
      Paraderma bogerti Estes
  Order Saurischia
    Family Deinodontidae
      Deinodon horridus Leidy
      Dromaeosaurus albertensis Matthew and
        Brown
      Troodon formosus Leidy
      Paronychodon lacustris Cope
  Order Ornithischia
    Family Hadrosauridae
      Subfamily Hadrosaurinae
        Kritosaurus cf. *K. breviceps* (Marsh)
      Subfamily Lambeosaurinae
        Procheneosaurus altidens (Lambe)
    Family Pachycephalosauridae
      ?*Stegoceras validus* Lambe
    Family Hypsilophodontidae
      Thescelosaurus cf. *T. neglectus* Gilmore
    Family Ceratopsidae
      Genera and species indet.
    Family Nodosauridae
      Palaeoscincus costatus Leidy
      Edmontonia longiceps Sternberg
Class Mammalia
  Infraclass Allotheria
    Order Multituberculata
      Family Ectypodontidae
        Cimexomys judithae, new species
        Cimexomys magnus, new species
        Mesodma primaevus (Lambe)
      Family Cimolomyidae
        Cimolomys clarki, new species
        Meniscoessus major (Russell), new com-
          bination
      Family Cimolodontidae
        Cimolodon sp.
  Infraclass Metatheria
    Order Marsupicarnivora
      Family Didelphidae
        Alphadon praesagus (Russell), new com-
          bination
        Alphadon halleyi, new species
        Alphadon cf. *A. rhaister* Clemens
      Family Pediomyidae

Pediomys clemensi, new species
Family Stagodontidae
  Boreodon matutinus Lambe
Infraclass Eutheria
  Order Insectivora
    Family Leptictidae
      Subfamily Gypsonictopsinae
        Gypsonictops lewisi, new species

CLASS ELASMOBRANCHII

ORDER RAJIFORMES

FAMILY DASYATIDAE

MYLEDAPHUS COPE, 1876a

Myledaphus bipartitus Cope, 1876a

As recorded by Stanton and Hatcher (1905, p. 68) and Lambe (1902, p. 28) isolated teeth belonging to *Myledaphus bipartitus* are common in late Cretaceous fish faunas of North America. Detached teeth were originally described by Cope (1876a, p. 260) from the Judith River Formation.

The present collection of teeth from the Judith River Formation localities consists of specimens that show not only positional differentiation in a jaw, but also differences between the mandibular and the maxillary dentition. The teeth, probably representing a single species, range in size from 2 mm. to 8 mm., measured in the direction of the long axis of the crown.

Estes (1964) made a detailed study of *Myledaphus bipartitus* and was able to differentiate upper from lower teeth. The criteria that he gave for differentiating between the two sets of teeth are based on his comparison with *Hypolophus sephen*, a Recent dasyatid ray. The upper teeth are asymmetrical and compressed, whereas the lowers are more symmetrical and higher crowned.

An upper tooth, AMNH 10105, has a hexagonal shape and the tooth is dorsoventrally compressed. AMNH 10104 is a large, lower tooth, much larger than the average dimensions of lower teeth, and possesses a robust crown which is heavily striated on the sides as well as on the slightly worn occlusal surface. AMNH 9303, which Estes has tentatively described as a marginal tooth, is similar to AMNH 10106. Both teeth are laterally compressed with a relatively longer bifid root.

Myledaphus bipartitus teeth are fairly common in the Judith River Formation. They are also recorded from the Milk River Formation of southern Alberta by Russell (1935, p. 120) who stated that the Milk River specimens average smaller, but are otherwise similar to those found in the Oldman Formation. The Cretaceous distribution of *Myledaphus* is fairly widespread on the American continent. The genus has also been reported from the Edmonton Formation, Alberta (Sternberg, 1926, p. 14); from the Mesaverde and Lance formations, Wyoming (Estes, 1964, p. 18); from the Kirtland Formation, New Mexico (Gilmore, 1916, p. 280); and from the early Eocene Four Mile Fauna in Colorado (R. Estes, personal commun.).

CLASS OSTEICHTHYES

ORDER AMIIFORMES

FAMILY AMIIDAE

KINDLEIA JORDAN, 1927

Kindleia fragosa Jordan, 1927

Kindleia is a common amiid from the Judith River Formation localities but has not been previously reported from the Campanian of Alberta, Montana, and Wyoming. The species was originally described from the upper Edmonton Formation of Alberta. It is now known from the Judith River Formation from an assortment of skull fragments, dentaries, and vertebrae similar to the material from the later Maestrichtian and Paleocene beds of Montana and Alberta. The cranial and post-cranial anatomy has been dealt with in great detail by Estes (1964, pp. 29–35), who made comparisons with Recent *Amia calva* and found a close resemblance.

A left vomer, AMNH 10109, is referred to *Kindleia fragosa*. The medial edge is relatively straight, whereas the lateral side has a concave outline. The posterior part of the vomer is broken but was probably elongated in the manner illustrated by Estes (1964, p. 37, fig. 17a, right). The Judith River Formation specimen is larger than the figured specimen from the Lance Formation but is otherwise indistinguishable from that of Paleocene material.

The vomer contains about 13 teeth. The anterior teeth, apparently with the enamel missing or imperfectly developed, are slightly more conical in shape than the posterior teeth. The central and the posterior teeth are pillar-like cylindrical pegs.

ORDER LEPISTOSTEIFORMES

FAMILY LEPISTOSTEIDAE

LEPISOSTEUS DE LACEPEDE, 1803

Lepisosteus occidentalis (Leidy, 1856)
Lepidotus occidentalis LEIDY, 1856, p. 73.
Lepidotus haydeni LEIDY, 1856, p. 73.
Lepisosteus occidentalis: COPE, 1877, p. 574.

Scales and vertebrae of *Lepisosteus occidentalis* are some of the more common elements of the Judith River fauna. The widespread occurrence of this gar in most of the localities of the Cretaceous and Paleocene of Montana, Wyoming, and adjoining states makes it an excellent marker for microvertebrate localities (Estes, 1964, p. 43). It closely resembles and probably occupied an ecologic niche similar to that occupied by the large Recent alligator gar, *L. spatula*, which at present is restricted to the large streams and rivers around the Gulf of Mexico.

Originally described as *Lepidotus* by Leidy (1856, p. 73), the material was referred to two species, *L. occidentalis*, on the basis of five scales, and *L. haydeni*, on a single scale. Later, Cope (1877, p. 574) put *L. haydeni* in synonymy with *L. occidentalis*. Reference of other elements of the gar were made from the Hell Creek Formation, Montana, by Brown (1907); Lance Formation, Wyoming, by Williston (1902); and other Upper Cretaceous formations of Colorado by Marsh (1896b).

ORDER ELOPIFORMES

FAMILY ALBULIDAE

?*Paralbula* sp.
Figure 7R–U

Blake (1940) originally reported the genus from the Aquia Formation (lower Eocene) of Maryland. Current investigations, however, have revealed the presence of *Paralbula* not only in the Judith River Formation, Montana, but also in the Oldman Formation, Alberta. The teeth, which are fairly common in both formations, have been tentatively identified as belonging to ?*Paralbula* sp. (Estes, personal commun.).

The Judith River Formation specimens from Clambank Hollow are similar to those obtained from the Oldman Formation and consist of a mixture of thoroughly eroded to well-preserved teeth. The teeth vary in size and shape. Some are round, most are slightly convex, and a few

are elongate or rectangular. AMNH 10100 has an average diameter of 2.5 mm. and AMNH 10101 has a length of 3.5 mm. (fig. 7R–U). The attachment surface of the teeth is slightly concave and is characterized by a few concentric layers. The larger teeth comprise the central part of the pharyngeal plate, whereas the smaller, more rounded ones form the peripheral areas. The isolated occurrence of the teeth makes it impossible to decipher the arrangement in which the teeth were stacked, and hence makes comment on their affinity to phyllodonts inadvisable at this time. The affinities and relationships of the Alberta and Montana occurrences of *Paralbula* are currently under study by Estes, at Boston University.

ORDER ASPIDORHYNCHIFORMES

FAMILY ASPIDORHYNCHIDAE

BELONOSTOMUS AGASSIZ, 1834
Belonostomus AGASSIZ, 1834, p. 388.
Diphyodus LAMBE, 1902, p. 30.

Belonostomus longirostris (Lambe, 1902)

Diphyodus longirostris LAMBE, 1902, p. 30.
Belonostomus longirostris: ESTES, 1964, p. 25.

A broken rostrum and a few scales that are referable to *Belonostomus longirostris* have been recovered during the present investigation. Although the genus does not occur commonly in the formation, it was first reported by Lambe (1902) from the Oldman Formation as *Diphyodus longirostris*. It was identified three years later (Stanton and Hatcher, 1905, p. 57) from the Judith River Formation of Montana. The genus *Diphyodus* was put in synonymy with *Belonostomus* by Estes (1964, p. 25) on the basis of the similarity of the rostrum and the fragmentary scales of the lateral line system. The fragment of the rostrum (AMNH 10111) from Clambank Hollow shows the presence of two rows of teeth along the outer margin. The width of the rostrum is about 3.6 mm. The dimensions compare closely with those of the type specimen described by Lambe (1902, p. 30) in which the anterior end of the dentary is 3.5 mm. wide and the posterior width is slightly larger (4.0 mm.).

The occurrence of this marine fish in these coastal plain deposits can only be attributed to the proximity of the sediments to the sea.
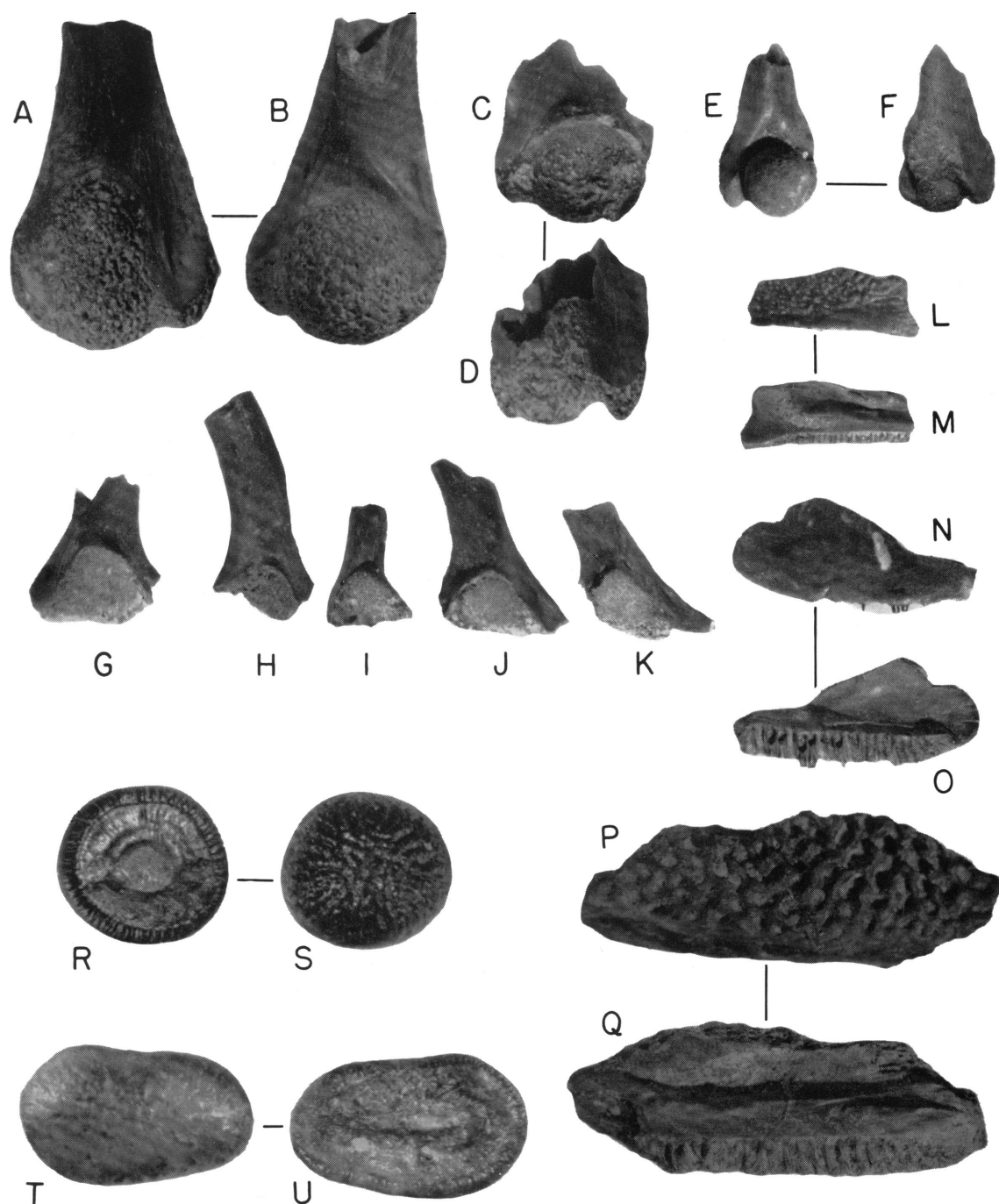
Fig. 7. A. AMNH 8446, ventral view of left discoglossid (A) humerus. B. Dorsal view. Both × 5. C. AMNH 8449, ventral view of left discoglossid (B) humerus. D. Dorsal view. Both × 5. E. AMNH 8450, ventral view of left discoglossid (C) humerus. F. Dorsal view. Both × 5. G. AMNH 8456, lateral view of distal portion of right discoglossid ilium, × 5. H. AMNH 8457, lateral view of distal portion of left discoglossid ilium, × 5. I. AMNH 8459, lateral view of distal portion of left discoglossid ilium, × 5. J. AMNH 8452, lateral view of distal portion of left pelobatid ilium, × 5. K. AMNH 8453, lateral view of distal portion of pelobatid ilium, × 5. L. AMNH 8460, external view of left discoglossid (C) maxilla. M. Internal view. Both × 5. N. AMNH 8462, external view of right discoglossid (B) maxilla. O. Internal view. Both × 5. P. AMNH 8461, external view of left discoglossid (A) maxilla. Q. Internal view. Both × 5. R. AMNH 10100, occlusal view of ?*Paralbula* sp. S. Basal view. Both × 10. T. AMNH 10101, occlusal view of ?*Paralbula* sp. U. Basal view. Both × 10.

CLASS AMPHIBIA

ORDER SALIENTIA

Four species of frogs can be recognized in the Judith River materials based on different types of ilia, humeri, and maxillae. Associations are not possible and none of the specimens is adequate for describing new taxa.

FAMILY DISCOGLOSSIDAE
Figure 7A–I, L–Q

MAXILLAE: The maxillary elements have been grouped informally into three divisions: (1) Large frog with sculptured maxilla (discoglossid A). (2) Large frog with smooth maxilla (discoglossid B). (3) Small frog with sculptured maxilla (discoglossid C).

Discoglossid A

The external sculpturing in AMNH 8461 (fig. 7P, Q) is basically of the pattern found in the smaller group of frogs represented by AMNH 8460, and can be distinguished from them by the greater depth of the pits and the greater prominence of the surrounding ridges, which occasionally become isolated into tubercle-like projections. As in the smaller specimens, the external sculpturing is not present at the ventral border of the maxilla. On the maxilla about 20 teeth are present in a distance of 8 mm.

Discoglossid B

These are much larger than the small frogs with sculptured maxillae and only slightly smaller than the larger forms with sculptured maxillae. The maxilla in AMNH 8462 is essentially smooth. A few faint anteroposteriorly elongate grooves are present in some specimens. The height of the teeth is the same as in AMNH 8461 and 20 teeth occupy a distance of 5.6 mm. on the maxilla (fig. 7N, O).

Discoglossid C

A number of maxillary fragments have been recovered which are dimensionally and morphologically distinct from other anuran maxillae. AMNH 8460 is a slender maxilla containing a number of teeth, the crowns of which have been broken (fig. 7L, M). The teeth are about 0.25 mm. in height and 20 teeth are present in a distance of 3.6 mm. The external sculpturing is quite distinctive and consists of shallow pitted depressions bounded by ridges. The ventral edge of the maxilla is free of sculpturing.

HUMERI: The criteria for differentiating distal ends of frog humeri were discussed by Hecht and Estes (1960) in their study of the amphibians from the Jurassic Como Bluff localities in Wyoming. Some of these features are: the distance from the lateral to the medial epicondyle; the diameter of the distal ball; the relative development of the fossa cubitus ventralis; the development of the crests originating from the condyles, and the shape and size of the olecranon scar including the position of its dorsal termination.

Discoglossid A

A distinct group of humeri is represented by AMNH 8446 (fig. 7A, B). These humeral fragments are easily differentiated from other humeri on the basis of size and other criteria. These robust humeri measure 6.4 mm. from the lateral epicondyle to the medial epicondyle, and the diameter of the head ball is 4.4 mm. Apart from their large size, these humeri can be distinguished by better development of the lateral epicondyle than in either AMNH 8450 or 8449. The medial crest does not originate from the medial epicondyle but usually from a point between the medial epicondyle and the ball. The crest is distinct and a small foramen lies medial to it. The lateral crest is much smaller and less distinct, and originates slightly lateral to the ball. The two crests do not meet although the medial crest continues dorsally along with humeral shaft. The olecranon scar is well developed and the dorsal apex is not so pointed as in AMNH 8450 and 8449 nor is it situated so far laterally.

Discoglossid B

A fragment of a humerus, AMNH 8449, is distinct from the other humeri in the collection (fig. 7C, D). It is dissimilar from AMNH 8450 in the development of the epicondyles, particularly in the position and degree of separation of the lateral epicondyle from the ball, and also in size. The diameter of the ball is 3.2 mm. and the distance between the epicondyles is 4.5 mm. The crests are developed as in AMNH 8450, and the medial crest is distinctly more prominent than the lateral crest. The crests do not join dorsal to the fossa cubitus ventralis and gradually become indistinct. The fossa cubitus ventralis is a fairly deep crescentic depression. Most of the olecranon scar is broken away but its dorsal termination appears to be also close to the lateral

border. Just dorsal to the fossa cubitus ventralis, the shaft is dorsoventrally compressed.

Discoglossid C

The distal part of a humerus, AMNH 8450 (fig. 7E, F), is referable to this category. Its humeral ball is spherical with a diameter of 2 mm. The lateral epicondyle is closely approximated to the ball and not well formed, but the medial condyle is strongly developed and well separated from the ball. A prominent crest originates at the ventral edge of the medial epicondyle and extends dorsally. The medial crest is much better developed than the lateral crest, the latter originating at the dorsal limit of the lateral epicondyle. The fossa cubitus ventralis is shallow. Neither of the crests is very distinct. The area dorsal to the lateral epicondyle is laterally expanded and flattened.

The olecranon scar is relatively large and sub-triangular; the dorsal apex of the scar is situated close to the lateral border. The shaft narrows considerably at the point of dorsal termination of the olecranon scar and the cross section of the shaft becomes rounded.

ILIA: Six specimens are referred to the Discoglossidae on the basis of characters listed by Estes (1964, p. 56). AMNH 8456 is a partially complete right ilium (fig. 7G). The acetabulum is relatively larger and more rounded than in the pelobatid specimens. The pubic process is short and the shaft relatively straight, as can be seen in AMNH 8457 (fig. 7H). The dorsal crest is not well developed but an elongate prominent groove is present ventral to it.

A single specimen, AMNH 8459, is different from ilia represented by AMNH 8452 and 8453, and has been referred to the Discoglossidae (fig. 7I). The most obvious difference is in the expansion of the acetabulum anteriorly. The acetabulum is shallowly depressed and well separated from the rest of the bone by a prominent raised rim. The anterior edge of the acetabulum is pointed and projects anteriorly. The pubic process of the ilium is greatly reduced and the ischial process is shorter than in the other anuran ilia recovered.

FAMILY PELOBATIDAE
Figure 7J, K

Two ilia, AMNH 8452 and 8453, are tentatively referred to the Pelobatidae (fig. 7J, K). The identification is uncertain as the specimens are broken and consist only of the acetabular region. AMNH 8452 and 8453 are easily distinguished from other anuran ilia in the collection by the shape of the acetabulum and the relatively greater elongation of the posterior ischial process. In size AMNH 8452 most closely resembles UCMP 49524, a left pelobatid ilium, tentatively identified by Estes (1964, p. 59). The acetabulum of AMNH 8452 is more triangular than semicircular, with a raised and pointed dorsal apex. The posterior part of the acetabulum is at the same level as the ischial process, although anteriorly it develops a prominent rim near the pubic process. This process is broken in both specimens but was probably developed to the same extent as in UCMP 49524 from the Lance Formation. The medial view shows no features of diagnostic value except for an ornamentation consisting of parallel striations along the contact with the ischium and the pubis.

ANURAN VERTEBRA

A well-preserved, procoelous, anuran vertebra, AMNH 8424, has a dorsoventrally compressed centrum (fig. 11O, P). The neural arch is incomplete and tapers dorsally, and the transverse processes are short and robust. The length of the vertebra, the only one of its kind in the collection, is 1.6 mm.

ORDER URODELA

SUBORDER CRYPTOBRANCHOIDEA

FAMILY SCAPHERPETONIDAE

SCAPHERPETON COPE, 1876b

Scapherpeton tectum Cope, 1876b

Scapherpeton tectum COPE, 1876b, p. 355.
Scapherpeton laticolle COPE, 1876b, p. 356.
Scapherpeton excisum COPE, 1876b, p. 357.
Scapherpeton favosum COPE, 1876b, p. 357.
Hemitrypus jordanianus COPE, 1876b, p. 358.
Hedronchus sternbergi COPE, 1876b, p. 359.

Cope originally described this species and others now regarded as synonyms from materials collected near the mouth of the Judith River in the Judith River Formation. The present collection contains many specimens of Scapherpeton tectum. The morphology and description of this form have been adequately discussed by Auffenberg and Goin (1959) and by Estes (1964);

further discussion would be repetitive. The collection includes isolated dentaries, maxillae, and vertebrae of which the atlas is the most common element recovered and the most readily identifiable.

Two genera, *Scapherpeton* and *Hemitrypus*, were described by Cope (1876b) from the Judith River Formation of Montana. Originally four species of *Scapherpeton* were distinguished: *S. laticolle*, founded on an atlas and dorsal vertebrae; *S. excisum*, on a cervical vertebra; and *S. favosum* and *S. tectum*, on single vertebrae. Auffenberg and Goin (1959) placed the other three species of *Scapherpeton* in synonymy with *S. tectum* and erected a new family Scapherpetonidae for its inclusion. Estes (1964) also put *Hemitrypus jordanianus* Cope (1876b) and *Hedronchus sternbergi* Cope (1876b) in synonymy with the single species of *Scapherpeton*.

LISSERPETON ESTES, 1965

Lisserpeton bairdi Estes, 1965

The material collected from the Judith River Formation and referable to *Lisserpeton* consists of a number of atlas and dorsal vertebrae and a fragmentary exoccipital. The Campanian specimens are indistinguishable from those of the Maestrichtian recovered from the Lance Formation, Wyoming, and the Hell Creek Formation, Montana.

DISCUSSION: The genera *Scapherpeton* and *Lisserpeton* are common in the fauna, although the former is more frequent. The *Schapherpeton* material from the Judith River Formation is identical to that from the large collections obtained from the Lance and Hell Creek formations of Wyoming and Montana. The presence of *Lisserpeton* in the Judith River Formation extends its geologic range downward and increases its geographic distribution. To date it has been reported from the Lance Formation of Wyoming; from a number of localities near the Fort Peck Reservoir, eastern Montana; and from the late Paleocene of the same region.

SUBORDER MEANTES

FAMILY SIRENIDAE

HABROSAURUS GILMORE, 1928

Habrosaurus dilatus Gilmore, 1928

A fragmentary, edentulous, right dentary of *Habrosaurus*, AMNH 8477, has been recovered from the Clambank Hollow locality. The dentary does not seem to be so curved in the medial direction as some of the later Lance specimens. Anteriorly the jaw is broken, but as in the Lance specimens the teeth reach close to the ventral border. The pleurodont teeth are in a tooth border which is wide anteriorly and narrows considerably posteriorly. Externally, there is a long, narrow groove leading into a foramen at the position of the third or fourth tooth from the posterior.

DISCUSSION: Fossil sirens are reported in the Cretaceous of North America from the Albian of Texas, from the Maestrichtian of Montana and Wyoming, and now from the Campanian of Montana. Originally described by Gilmore (1928, p. 161), *Habrosaurus dilatus* was placed, "Amphibia *incertae sedis*."

Recent members of the family Sirenidae are restricted to the southern coast of North America. The family contains two genera, *Pseudobranchus* and *Siren*, the latter having two species, *S. lacertina* and *S. intermedia*. Phylogeny of the sirenids has been reviewed by Goin and Auffenberg (1955, 1957) and Estes (1964). The oldest known form is *Prosiren elinorae* from the Albian Trinity Sandstone of Texas (Goin and Auffenberg, 1958). It probably gave rise to the Upper Cretaceous *Habrosaurus dilatus*. Both Recent forms share a number of common features with the Cretaceous *Habrosaurus*.

SUBORDER SALAMANDROIDEA

FAMILY PLETHODONTIDAE

SUBFAMILY DESMOGNATHINAE

PRODESMODON ESTES, 1964

Prodesmodon copei Estes, 1964

Prodesmodon copei is represented in the Judith River Formation by a number of dentaries and maxillae from Clambank Hollow. Although all the specimens are distinctly smaller than those from the Lance Formation figured by Estes (1964, pp. 90, 91), they are included in the same species. Morphology of the dentary and the form of the teeth is exceedingly similar in specimens from the two formations. As the present dentaries are incomplete, it is impossible to count the teeth on the lower jaw but the number appears to be less in the Campanian specimens.

The teeth are pleurodont and vary considerably in size. The front teeth in AMNH 8479, except for the anteriormost two or three, are quite large (height 0.8 mm.) as compared with the teeth in the posterior part of the dentary. Enlargement of the anterior teeth is accompanied by a corresponding deepening of the jaw. A small foramen is present at the base of each tooth. Externally, the dentary is smooth and is strongly curved in dorsal view.

?FAMILY PLETHODONTIDAE

?SUBFAMILY DESMOGNATHINAE

OPISTHOTRITON AUFFENBERG, 1961

Opisthotriton kayi Auffenberg, 1961

ATLAS: The cotyles of a partial atlas, AMNH 8481, are round in shape and are separated by a short intercotyle process. The posterior cotyle is round and is incompletely filled in with bone. The ventral side of the vertebra is marked by a depression, which is deeper on the anterior side and bounded by two ridges that meet along the midline. The atlas of *Opisthotriton* can be distinguished from that of *Prodesmodon* by its larger size, rounded cotyles, and more prominent intercotylar process.

DORSAL VERTEBRAE: A dorsal vertebra of *Opisthotriton kayi* has been described in great detail by Estes (1964, pp. 82–83). The Judith River Formation specimens are of the same size or slightly smaller than AMNH 8112 from the Lance Formation, but are otherwise morphologically indistinguishable.

DENTARY: Unfortunately, specimen AMNH 8485 is fragmentary and without teeth. The tooth bases indicate that the teeth are pleurodont and extend close to the lingual edge of the tooth-bearing border. The anterior part of Meckel's fossa has been broken and the divergence between the dorsal and ventral border of the fossa is not so great as in *Habrosaurus*.

CLASS REPTILIA

ORDER TESTUDINES

The present collection of turtles from the Judith River Formation consists of isolated and fragmentary carapace and plastron plates. These are in most instances inadequate for generic identification and only two genera have

been distinguished, namely *Trionyx* and *Basilemys*. Baenid turtles may also be present but the material is too fragmentary for identification. The chelonians previously reported from the Judith River Formation are *Baena, Polythorax, Plastomenus*, and possibly *Adocus* (see Hay, 1908).

SUBORDER CRYPTODIRA

SUPERFAMILY TESTUDINOIDEA

FAMILY DERMATEMYDIDAE

Basilemys sp.

Basilemys is common in most upper Cretaceous formations of Wyoming, Montana, and Alberta. It has also been reported from the Milk River Formation of Alberta by Russell (1935, p. 121).

The genus can be identified by its sculpturing, which consists of a patterned arrangement of pits, and by the considerable thickness of the fragments.

SUPERFAMILY TRIONYCHOIDEA

FAMILY TRIONYCHIDAE

TRIONYX GEOFFROY SAINT-HILAIRE, 1809

Trionyx sp.

Together with *Basilemys*, *Trionyx* forms the bulk of the identifiable turtle fragments. The abundance of the trionychids is another indication of the freshwater environment in which the deposits of the Judith River Formation were laid down.

FAMILY ?BAENIDAE

Some fragments from Clambank Hollow, unassociated but given the group catalogue number AMNH 8437, cannot be distinguished from parts of baenid shells. However, the sculpture pattern is not unique to this family and a definitive identification cannot be made.

ORDER EOSUCHIA

SUBORDER CHORISTODERA

FAMILY CHAMPSOSAURIDAE

CHAMPSOSAURUS COPE, 1876b

Champsosaurus sp.

Four species of *Champsosaurus* were described by Cope (1876b) on the basis of isolated

vertebrae from the Judith River Formation. As it is impossible to specifically distinguish among any of Cope's species, the material recently collected from the formation will be identified only to genus. Specimens from the Oldman Formation are more complete and have been referred to three species, *C. natator, C. inelegans,* and *C. inflatus* (Russell, 1964, p. 12).

ORDER CROCODILIA

SUBORDER ?SEBECOSUCHIA
Figure 8Y, Z

AMNH 8549 represents another rare group which is tentatively assigned to the Sebecosuchia (fig. 8Y, Z). Sebecosuchian teeth resemble theropod teeth as pointed out by Simpson (1937a, 1937b) and Colbert (1946), and were consistently confused as such by earlier workers. Such teeth differ from contemporary theropod teeth in that the blade is usually straighter, the serrations on the anterior and the posterior sides are finer, and a more prominent groove is present along the midline of the tooth on the lingual and labial side.

Similar teeth have been reported from the Milk River Formation of Alberta (Russell, 1935, p. 123, fig. 9) and from the Lance Formation of Wyoming (Estes, 1964, p. 143). They have yet to be reported, however, from the Judith River Formation or from its equivalent formation in Alberta.

Russell (1935) suggested that the teeth may have come from the premaxilla of a deinodont. Considering the known skulls of these large carnivores, this seems unlikely. Estes (1964, p. 143), on the other hand, believed it probable that the teeth represent a juvenile theropod. At present, there is no conclusive evidence that the teeth belong to the theropods, or, for that matter, to the Saurischia.

Langston (1956) reviewed criteria useful in distinguishing between sebecid teeth and carnosaur teeth.

SUBORDER EUSUCHIA

FAMILY CROCODYLIDAE

SUBFAMILY CROCODYLINAE

LEIDYOSUCHUS LAMBE, 1907

Leidyosuchus canadensis Lambe, 1907

Many unnumbered isolated teeth, vertebrae, and scutes can be referred to *Leidyosuchus canaden-* *sis,* described by Lambe (1907) on the basis of an almost complete skull and jaws from the Oldman Formation of Alberta. Teeth similar to those of this genus had originally been described by Leidy (1856, p. 73) from the Judith River Formation as *Crocodylus humilis,* but the term was abandoned by Lambe (1907) on the discovery of much better material. Gilmore (1910) described another skull from the type area of the Lance Formation, *Leidyosuchus sternbergi. Leidyosuchus canadensis* has priority in the event that species prove to be synonymous. Yet another genus, *Deinosuchus,* was described by Holland (1909) from the Judith River Formation at Willow Creek, Fergus County. *Deinosuchus hatcheri* is a very large crocodile known from vertebrae, ribs, and scutes and has not yet been identified in the present collection.

SUBFAMILY ALLIGATORINAE

BRACHYCHAMPSA GILMORE, 1911

Brachychampsa montana Gilmore, 1911

The species is represented by isolated teeth. The genus has not been reported from the Judith River Formation, although teeth similar to those from this formation occur in the Oldman Formation and have been identified by Lambe (1902, p. 48) as *Bottosaurus perrugosus* Cope (1874, p. 26).

ORDER SAURIA

With the greater collecting efficiency achieved by the use of screening methods, not only has the taxonomy of small mammals become clearer but so has that of other small vertebrates, notably lizards.

The lizards are represented by a fragmentary assortment of dentaries, maxillae, and vertebrae. Most of the jaw pieces reveal the presence of well-worn or digested teeth. Some of the better preserved specimens come from Clayball Hill, where the productive layer is a silty shale in which the delicate bones are less fragmented than in the bone concentrate from Clambank Hollow. There are no differences among the identifiable lizards of the Judith River Formation, Montana, and the Lance Formation, Wyoming, at the species level.

Gilmore (1928, 1938) was the pioneer in the study of Cretaceous lizards and snakes. Gilmore

(1943) also discussed the lizards obtained from the Djadochta Formation of Mongolia and described nine genera representing the families Agamidae, Chamaeleontidae, Ametosauridae, Amphisbaenidae, Varanidae, and Anguidae. Commendable as his efforts were, they were hampered by the fragmentary and eroded nature of his material and by insufficient Recent comparative material. Consequently Estes (1964) revised the lizard genera recovered from the Lance Formation, Wyoming.

The lizard fauna of the Campanian, in comparison with the Maestrichtian, was quite poorly known until the current investigation, as no lizard genus had been reported from the Judith River Formation. Of the two genera described from the Oldman Formation of Alberta as lizards, *Palaeosaniwa canadensis* Gilmore (1928) and *Polyodontosaurus grandis* Gilmore (1932), only *P. canadensis* is actually a lizard. Sternberg (1951) and McDowell and Bogert (1954) showed that *P. grandis* was a dinosaur.

The lacertilian fauna was collected chiefly from Clayball Hill and Clambank Hollow, and is composed of six genera and six species previously known from the Lance Formation.

The presence of a new genus of lizard in the Judith River Formation is indicated by a number of varanoid-like vertebrae. These vertebrae cannot as yet be associated with any of the dentaries or maxillae in the collection. They are smaller and structurally dissimilar to the vertebrae of *Palaeosaniwa canadensis*, but resemble, in certain features, the ophidian, *Coniophis*. Other specimens are present in the Judith River Formation which are evidently different from those of the Lance Formation, but the material is too fragmentary and inadequate to make a meaningful comparison.

SUBORDER SCINCOMORPHA

FAMILY TEIIDAE

CHAMOPS MARSH, 1892a

Chamops segnis Marsh, 1892a

Figure 8A–D

A dentary, AMNH 8486 from Clayball Hill, is referred to *Chamops segnis* on the basis of its resemblance to the type dentary. The jaw is broken posteriorly and contains 13 worn and broken teeth (fig. 8A, B). The Meckelian fossa is open and extends anteriorly to the second most

anterior tooth. The roof of the Meckelian fossa consists of a thick border which considerably widens anteriorly in the form of a lingual expansion when seen in dorsal view. The lower border of the dentary is only slightly curved. The teeth are subpleurodont and tricuspid. The tricuspid nature of the teeth cannot be made out in AMNH 8486, because of excessive wear. A number of other dentary fragments, however, indicate that the teeth are similar to those referred to the genus by Estes (1964). The tooth row is heterodont; the anterior five or six teeth are anteroposteriorly compressed, whereas the posterior ones are less so and possess rounded tooth bases. The linguolabially compressed crowns have a prominent central cusp with smaller anterior and posterior accessory cusps delineated by short but distinct ridges. The anterior cusps are larger than the posterior cusps at the anterior end of the dentary; the anterior and posterior cusps are the same size toward the posterior end. Faint vertical striations are more prominent on the lingual than the labial side of the crowns. Labially the dentary is smooth except for the presence of prominent mental foramina. The foramina are situated closer to the dorsal edge of the dentary. The six foramina extend posteriorly to the ninth or tenth tooth from the front.

Chamops maxillae, which vary considerably in size, are present in the collection. AMNH 8487 from Clambank Hollow, is a partial tooth-bearing border of a maxilla. It corresponds closely to UCMP 46033, described in detail by Estes (1964, p. 106). AMNH 8488, also from Clambank Hollow, is considerably more robust than AMNH 8487 and probably corresponds to the more massive dentary just described (fig. 8C, D). The anterior part of the maxilla, bearing four teeth, is preserved. The teeth are quite large and show signs of wear. The anterior maxillary teeth are directed backward and are slightly recurved but are otherwise morphologically similar to corresponding teeth on the dentary.

LEPTOCHAMOPS ESTES, 1964

Leptochamops denticulatus (Gilmore, 1928)

Figure 8K

Chamops denticulatus GILMORE, 1928, p. 26.
Leptochamops denticulatus: ESTES, 1964, p. 110.

Estes (1964, p. 110) erected a new genus, *Leptochamops*, for *Chamops denticulatus* Gilmore

(1928) and distinguished the genus from the type of *Chamops*, *Chamops segnis* (Marsh, 1892b), on the following criteria: "greater number of teeth; higher crowned teeth; teeth with crests running up to the lateral cusps; lateral cusps closely pressed to the main cusp and lacking the well-defined tips present in *Chamops segnis*; the tooth bases generally not expanded, on the posterior teeth showing this condition weakly; the teeth more compressed and cylindric; the anterior teeth fully pleurodont; and the Meckelian fossa more restricted."

The Judith River material of *Leptochamops denticulatus* is identical to that from the Lance Formation. AMNH 8490, from Clambank Hollow, is a left dentary assigned to the species. It is more slender than that of *Chamops* even though the ventral border of the dentary is broken. The dorsal tooth-bearing border of the Meckelian fossa is relatively thinner and not anteriorly expanded as in *Chamops*. Thus, in occlusal view, the lingual outline of the dentary is straighter and not so concave as it is in *Chamops*. The mental foramina are small and not well developed.

The maxilla fragment, AMNH 8491, shows the extent of heterodonty (fig. 8K). The anterior four or five teeth are the smallest, which is a condition that prevails in the Recent genera *Crocodilurus* and *Tupinambis*. The maxillary teeth are similar to those on the dentary. They are long and slender, and have nonexpanded tooth bases. The anterior accessory cusp on the maxillary teeth is better developed than the posterior, and it is not so well separated from the central cusp as in *Chamops*.

Discussion: Two teiid genera are present in the Judith River Formation. *Chamops segnis* was first described by Marsh (1892b, p. 450) in a paper dealing with the reptiles of the "Laramie" Formation. Marsh (1892b) and Gilmore (1928) misidentified this type specimen as a maxilla, but it is actually a left dentary, as pointed out by Estes (1964, p. 106). The type specimen is peculiar in that it is one of the largest specimens of the genus. Other material referred to *Chamops* from the Lance and Judith River formations is morphologically similar but much smaller. *Chamops denticulatus* Gilmore (1928) was used by Estes (1964) for the type of a new genus, *Leptochamops*. In the Judith River Formation *L. denticulatus* is nearly as abundant as *Chamops* and is inseparable from the Maestrichtian form. The

two other teiid genera, *Meniscognathus* and *Haptosphenus*, described by Estes (1964) from the Lance Formation, have not been identified as yet from the Judith River Formation.

Marsh (1892b) did not assign a familial position to *Chamops*. Other early workers regarded it as possessing iguanid affinities (Camp, 1923; Gilmore, 1928). Reference of *Chamops* to the Teiidae was made initially by Boulenger and Nopsca, and has been conclusively demonstrated by Estes (1964, p. 105), who made a detailed comparison with the modern teiids *Crocodilurus* and *Tupinambis*. He pointed out that the teiids differ from the iguanids in having an open Meckelian fossa, less pleurodont teeth, straighter roof of the Meckelian fossa, and in the form of the tooth crown and base. The occurrence of *Chamops* and *Leptochamops* in the Campanian of North America is the oldest documented record of the Teiidae, and points to the antiquity of the family, which has undergone little change since the Cretaceous. A *Chamops*-like teiid may be present in the Albian Trinity Sandstone fauna of Texas (Estes, personal commun.) but this has yet to be studied in any detail.

Apart from its reported occurrences in the Lance Formation, Wyoming, and Hell Creek Formation, Montana, Sternberg (1951) reported *Chamops* from the Wapiti Formation of Alberta. Its presence there is significant in three respects: first, it is the northernmost occurrence of the genus; second, the horizon from which the specimen was obtained appears to be older than the Edmonton Formation with which Sternberg (1951) previously correlated it; third, the specimen is larger than average specimens referred to *Chamops*. The mandible, bearing a few teeth, was collected near Grand Prairie in northwestern Alberta in what Allan and Carr (1946) regard as Member B of the Wapiti Formation. According to Sternberg (1951), 2500 feet of the formation overlies Member B, placing it well down in the stratigraphic section. Recent studies by Williams and Burk (1964) indicated that the Wapiti Formation included not only sediments of the Maestrichtian but also some of the Campanian. They believe that Member A of the Wapiti Formation is equivalent to the Oldman Formation and that Members B, C, and D can in part be correlated with the Bearpaw Shale and the lower and middle members of the Edmonton Formation. Member E corresponds

to the Upper Edmonton of Allan and Sanderson (1945), which is generally reported as Lancian or Maestrichtian in age. The Wapiti *Chamops* consequently may well be in the Campanian and nearly contemporary with the fauna from the Judith River Formation.

SUBORDER ANGUIMORPHA

INFRAORDER DIPLOGLOSSA

FAMILY ANGUIDAE

SUBFAMILY GERRHONOTINAE

PELTOSAURUS COPE, 1873a

Peltosaurus piger Gilmore, 1928

Figure 8G, H

A right dentary, AMNH 8494 from Clambank Hollow, is not specifically distinguishable from that of *Peltosaurus piger* (fig. 8H).

Although its teeth are missing in the dentary, a number of other characteristics confirm the identification. Anteriorly the Meckelian fossa is ventral in position but posterior to the notch representing the internal mental foramina it becomes lingual. As in the Maestrichtian specimens of *P. piger* there are 10 or 11 teeth anterior to the notch. The intramandibular septum is broken posteriorly in the specimen but originates slightly anteroventral to the notch of the internal mental foramina. The distance from the foramina to the anterior of the dentary is 0.64 mm. in AMNH 8494, and is 0.9 mm. in UCMP 49772, from the Lance Formation. Externally the dentary is smooth and the mental foramina relatively large.

A maxilla fragment, AMNH 8495 from Clambank Hollow, can be referred to *Peltosaurus piger* (fig. 8G). The teeth are pleurodont, linguolabially expanded, and the transverse width is only slightly smaller than the height. The crown is expanded relative to the shaft and consists of a distinct anteroposteriorly directed crest rather than separate cuspules.

DISCUSSION: *Peltosaurus* is a common lizard in the faunas of the early Tertiary. Its range has now been extended down to the Campanian from the upper part of the White River Formation (late Oligocene). Geographically, it has been found in most of the Great Plains states and as far west as the late Eocene Sespe Formation, Ventura County, California (Brattstrom, 1955).

The presence of anguid lizards in the Campanian of North America is not surprising considering their presence in the Middle Cretaceous sediments of Mongolia. The Cretaceous *P. piger* has been differentiated from Tertiary species on the basis of "relatively shorter-crowned teeth, and shorter lower jaw" (Estes, 1964, p. 120). The Judith River material consists of three jaw fragments apparently similar in all respects to later Maestrichtian forms.

Peltosaurus piger was described originally from the Lance Formation by Gilmore (1928, p. 136) and placed in the Anguidae. McDowell and Bogert (1954, p. 116) were doubtful of such affinities and stated: "Gilmore (1928, p. 136) has assigned some jaw fragments from the Lance to *Peltosaurus* as *P. piger*. This material is probably not anguinid [anguid], and is too fragmentary to make certain the generic assignment." Recently Estes (1964, p. 121) has shown that *P. piger* should be placed in the Anguidae.

Gilmore (1943, p. 381) described the species *Isodontosaurus gracilis* from the Djadochta beds of Mongolia. This lizard, which is known by 18 well-preserved specimens, comes from the localities famous for their mammal skulls. *Isodontosaurus* was referred to the Anguidae on the basis of its resemblance to *Peltosaurus*. Gilmore (1943) and McDowell and Bogert (1954, p. 113) believed that a relationship to this family is unlikely and considered the genus to have scincinoid affinities. This is based on scincinoid-like morphology of the splenial, the internal mental foramina, and the anteriorly extended angular. Judged from Gilmore's (1943) illustrations, *Isodontosaurus* does not appear to have much in common with *Peltosaurus* and consequently the Campanian occurrence of the latter genus would seem to be the oldest record of the Anguidae.

FAMILY XENOSAURIDAE

EXOSTINUS COPE, 1873b

Exostinus lancensis Gilmore, 1928

Figure 8L

A right maxilla fragment, AMNH 8497, from Clambank Hollow, is referred to *Exostinus lancensis* (fig. 8L). As the specimen is broken, little can be said of the shape of the maxilla. The teeth are indistinguishable from those of *E. lancensis*, and are pleurodont with unexpanded bases and slightly recurved crowns. The crowns

consist of a principal central cusp with an anterior crest but no distinct anterior cusp. The posterior cusp is not developed. Faint vertical striations are present on the lingual side. The slender teeth project to one-third and one-half of their length above the jaw.

?XENOSAURIDAE

cf. *Exostinus* sp.

Figure 8E, F

Specimen AMNH 8498 has been referred tentatively to *Exostinus* (fig. 8E, F). It resembles the iguanid *Paraderma* in some features, particularly in the relatively fewer number of teeth, in the general shape of the maxilla, and in the sculpturing of the osteodermal scutes. Assignment to *Exostinus* is based primarily on the morphology of the tooth bases which are smooth and lack the prominent infolding present in parasaniwids.

Most of the maxilla, except for the dorsal edge and the posterior elongation, is present. Externally, the nasal process of the maxilla rises steeply and then gently slopes to the posterior. Ventral to the five superior alveolar foramina present, the external surface of the maxilla is smooth. Dorsal to the foramina, a few large osteodermal scutes are separated by unsculptured sinuous depressions. The osteoderms are polygonal in shape and extend anteriorly to the nasal process where they accentuate the steep rise of the process. The ornamentation of the scutes is fairly regular and different from that found in *E. lancensis* and *E. serratus*. It consists of anteroposteriorly elongate pits separated by irregular and "hummocky" ridges.

Internally, only the tooth bases of five teeth are present. The tooth bases are very unlike those of the Cretaceous iguanids *Parasaniwa* and *Paraderma* in that they are neither expanded nor externally folded into a number of ridges. Eight or nine teeth are estimated to have been originally present in the maxilla; this is far fewer than the number found in species of *Exostinus*, but is comparable with the number found in the maxilla of *Paraderma*.

DISCUSSION: The Judith River Formation material of *Exostinus* falls within the intraspecific range of variation of *E. lancensis* from the Maestrichtian. The species was originally described by Gilmore (1928, p. 23) and tentatively placed in the genus *Exostinus*. The genus was proposed by Cope (1873b) on the basis of a specimen consisting of a frontal, jugal, and dentary with teeth. The type was obtained from the Oligocene "Oreodon beds" of the White River Formation, Colorado. At that time Cope made no comments on the familial position of the genus. Later Cope (1900) compared it with *Xenosaurus grandis* and suggested that *Exostinus* should be placed in the Xenosauridae. Gilmore (1928), although realizing the evidence was inconclusive, placed the genus in the Iguanidae. McDowell and Bogert (1954, p. 32) clearly demonstrated the xenosaurid affinities of *Exostinus*, although they were skeptical as to the relationship of the Cretaceous species. Estes (1964) accepted their view regarding the placement of *Exostinus* in the Xenosauridae and established *E. lancensis* as a valid species. He also synonymized *Harpagosaurus parvus* (Gilmore, 1928, p. 156) and *Prionosaurus regularis* (Gilmore, 1928, p. 159) with *E. lancensis*.

The genus ranges in age from the Campanian through the Oligocene. *E. rugosus* was described from the Paleocene Polecat Bench Formation of Wyoming by Gilmore (1942), who was uncertain as to the generic identification. Estes (1965, p. 105) restudied the Princeton material and confirmed Gilmore's tentative assignment to the genus. The genotypic species from the Oligocene of Colorado, *E. serratus*, is found also in Wyoming and adjoining states and is similar in many respects to Recent *Xenosaurus*. The ancestry of *Xenosaurus* can be traced to the Cretaceous *E. lancensis*. The Paleocene *E. rugosus* is probably on an evolutionary side line as *E. serratus* appears to be closer to *E. lancensis* than to the Paleocene species.

INFRAORDER PLATYNOTA

SUPERFAMILY VARANOIDEA
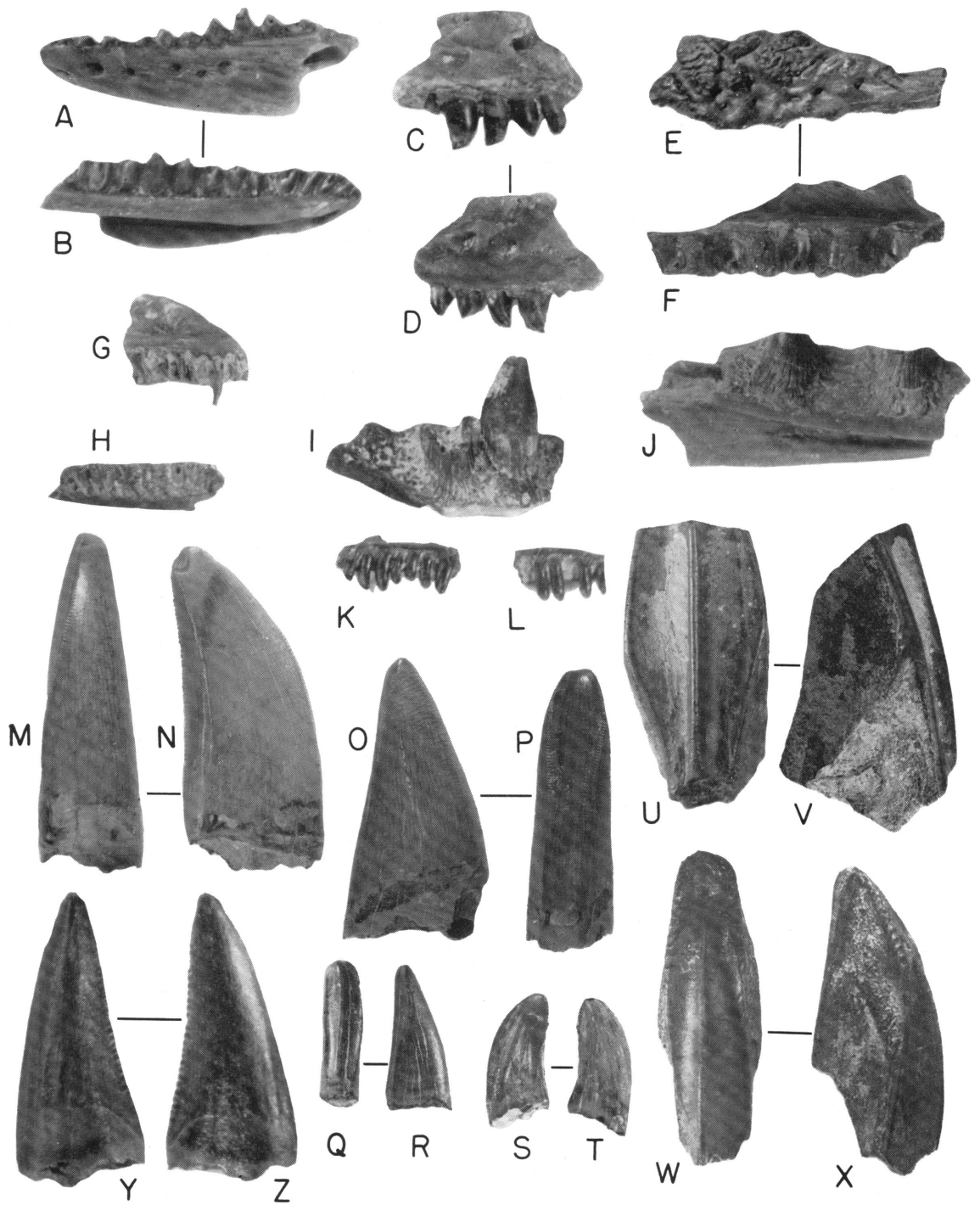
FAMILY PARASANIWIDAE

PARASANIWA GILMORE, 1928

Parasaniwa wyomingensis Gilmore, 1928

Figure 8J

A left dentary fragment of *Parasaniwa* containing three tooth bases, AMNH 8499 (fig. 8J), has been recovered from Clambank Hollow. The dentary consists of a large, ventrally convex

tooth-bearing border which descends anteriorly to the ventral edge of the lower jaw. The tooth bases are prominently folded externally as well as internally. The number of folds exceeds that found in *Paraderma* and may be as high as 10 on the lingual side. The tooth base is not expanded and usually a small foramen is present on its posterior side.

The anterior portion of a maxilla, AMNH 8503, has been recovered from Clambank Hollow. Its teeth are identical to those found on the dentary and the anterior two or three are much smaller than the posterior teeth. Externally, the maxilla is smooth and the sculpturing is not so marked as in *Exostinus* or *Paraderma*.

PARADERMA ESTES, 1964

Paraderma bogerti Estes, 1964

Figure 8I

Paraderma bogerti was originally described from the Lance Formation of Wyoming by Estes (1964). AMNH 8504, from Clambank Hollow, is the only fragment that can be referred to *Paraderma bogerti* from the Judith River Formation (fig. 8I). The teeth are pleurodont, and have transversely expanded and prominently infolded bases. AMNH 8504 is slightly smaller than UCMP 54261, a left maxilla described and figured by Estes (1964, p. 133).

DISCUSSION: The parasaniwids are represented by two genera, *Parasaniwa* and *Paraderma*, in the Judith River, Lance, and Hell Creek formations. These are quite distinct from contemporary lizards and are generically separable from each other by a number of characteristics discussed by Estes (1964). *Paraderma* differs from *Parasaniwa* in stoutness, in having fewer teeth, external maxillary sculpturing, and in the form of the maxilla.

The family Parasaniwidae was proposed by Estes (1964) for the reception of *Parasaniwa* and *Paraderma*. The relationship of this family to others is not clear as yet, although Estes believed the parasaniwids are primitive platynotans with some resemblances to the diploglossans. Estes (1964, p. 128) defined the family as follows: "teeth with simple basal fluting extending in to the medullary cavity; development of an intramandibular jaw hinge; unretracted nares; skull roof with well-defined scute areas; scutes tending towards multiplication." It is distinguished from the Varanidae by "the lack of complicated infolding of the tooth base into the medullary cavity and the lack of naris contraction."

A varanid, *Palaeosaniwa canadensis*, has been described from the Oldman Formation, Alberta, on the basis of a dorsal vertebra which closely resembles the living *Varanus* in structure. This species has not been found in the Judith River Formation and its absence is attributed to the rarity of the form and the fortunes of sampling. The type specimen, USNM 10864, was found near Steveville along the Red Deer River close to the localities from which Campanian marsupials have been recovered.

Telmasaurus grangeri, based on specimen AMNH 6645, was described by Gilmore (1943, p. 379) from the Djadochta Formation of Mongolia as a varanid related to *Saniwa*, *Palaeosaniwa*, and *Parasaniwa*. The general tooth form and size, judged from the illustrations by Gilmore (1943, p. 381), is similar to varanids rather than parasaniwids in that the teeth are sabreshaped and curved posteriorly.

FIG. 8. A. *Chamops segnis.* AMNH 8486, labial view of left dentary. B. Lingual view. Both × 5. C. AMNH 8488, lingual view of left maxilla. D. Labial view. Both × 5. E. cf. Xenosauridae, AMNH 8498, labial view of left maxilla. F. Lingual view. Both × 5. G. *Peltosaurus piger*, AMNH 8495, lingual view of left maxilla, × 5. H. AMNH 8494, lingual view of right dentary, × 5. I. *Paraderma bogerti*, AMNH 8504, lingual view of right maxilla. × 5. J. *Parasaniwa wyomingensis*, AMNH 8499, lingual view of left dentary, × 5. K. *Leptochamops denticulatus*, AMNH 8491, lingual view of right maxilla, × 5. L. *Exostinus lancensis*, AMNH 8497, lingual view of right maxilla, × 5. M. *Deinodon horridus*, AMNH 8513, posterior view of isolated tooth. N. Lateral view. Both × 1⅔. O. AMNH 8515, lateral view of anterior dentary tooth. P. Posterior view. Both × 1⅔. Q. AMNH 8514, posterior view of ?premaxillary tooth. R. Lateral view. Both × 1⅔. S. *Paronychodon lacustris*, AMNH 8522, lingual view of isolated tooth. T. Labial view. Both × 1⅔. U. *Kritosaurus* cf. *K. breviceps*, AMNH 8525, lateral view of isolated tooth. V. Posterior view. Both × 1⅔. W. *Procheneosaurus altidens*, AMNH 8527, labial view of isolated tooth. X. Anterior or posterior view. Both × 1⅔. Y, Z. ?Sebecosuchia, AMNH 8549, views of an solated tooth. Both × 10.

The varanids of the Campanian and Maestrichtian are large and comparable in size to some Recent forms. According to Estes (1964, p. 169), *Palaeosaniwa canadensis* was as large as the modern "komodo dragon," *Varanus komodensis*, and shared with it a number of common features. *Palaeosaniwa* was probably an active predator, and could have preyed on the smaller multituberculates and marsupials. *Paraderma* and *Parasaniwa* are similar in many respects to *Heloderma*, but little can be said about their ecologic characteristics until more information is forthcoming.

ORDER SAURISCHIA

SUBORDER THEROPODA

FAMILY DEINODONTIDAE[1]

DEINODON LEIDY, 1856

Deinodon LEIDY, 1856, p. 72.
Aublysodon LEIDY, 1868, p. 198.
Gorgosaurus LAMBE, 1914, p. 13.

Deinodon horridus Leidy, 1856

Figure 8M–R

Deinodon horridus LEIDY, 1856, p. 72.
Aublysodon mirandus LEIDY, 1868, p. 198.
Aublysodon lateralis COPE, 1876b, p. 248.
Laelaps incrassatus COPE, 1876a, p. 248; 1876b, p. 341.
Laelaps hazenianus COPE, 1876b, p. 343.
Ornithomimus grandis MARSH, 1890, p. 85.
Dryptosaurus kenabekides HAY, 1899, p. 348.
Gorgosaurus libratus LAMBE, 1914, p. 13.

Deinodon horridus was proposed by Leidy (1856) for about a dozen teeth collected by Hayden from the Judith River Formation. This species was the first of the carnivorous dinosaurs to be recovered from the Upper Cretaceous sediments of the American continent. The collection of teeth on which the genus was based consists of two distinct morphological types, although Leidy (1856, p. 73; 1860, p. 144) considered them as belonging to a single species. Leidy (1860, p. 145) correctly guessed that the differences involved in the two groups of teeth

[1] [Russell (1970) revised the taxonomy of Upper Cretaceous carnosaurs and argued that *Deinodon horridus* is a *nomen dubium* and that individual teeth are not generically determinable (*Ibid*, p. 3). According to the classification presented by Russell (1970) and Colbert and Russell (1969) large carnivorous dinosaur teeth could be assigned most appropriately to the family Tyrannosauridae.] M. C. McKenna.

were positional in nature and suggested that the teeth with U-shaped cross sections were incisors. Later, Leidy (1868, p. 198) erected a separate genus, *Aublysodon*, for the inclusion of those teeth he had earlier regarded as incisors. These teeth have serrated crests on the posterior side. Cope (1876a, 1876b) described a number of species from the Judith River Formation under the genus *Laelaps*, the type of which is *L. aquilunguis*, obtained from New Jersey. The genus *Aublysodon* was placed in synonymy with *Deinodon* by Matthew and Brown (1922). Of the three species of *Laelaps* collected from the Judith River Formation, two, *L. explanatus* and *L. falculus*, were referred to *Dromaeosaurus* and the other, *L. incrassatus*, was transferred to *Deinodon* by Matthew and Brown (1922).

On the basis of the dentition it is not possible to separate the closely related genera *Gorgosaurus* and *Deinodon*. As suggested by a number of authors including Matthew and Brown (1922, p. 383), and Russell (1964, p. 13), the genus *Gorgosaurus* is probably synonymous with the Judith River Formation *Deinodon*. Lambe (1914) described *G. libratus* from the Oldman Formation and then restudied it in greater detail (Lambe, 1917) on the basis of more complete material than that known for *Deinodon*. The name *Deinodon*, however, has priority and no differences can be shown to exist between the type specimen of *Deinodon* and material of *Gorgosaurus*. The name *Deinodon* should be retained for the large carnivorous dinosaur found in the Judith River and Oldman formations.

The present collection consists of a number of teeth similar to those described by Leidy (1856) and later figured by him (Leidy, 1860, pl. 9, figs. 21–48). AMNH 8513 is a large saber-shaped linguolabially compressed tooth. Both its anterior and posterior edges are serrated. It is either a maxilla or dentary tooth (fig. 8M, N). The premaxillary teeth are small with a U-shaped cross section. Morphologically similar, but larger, teeth come from the anterior part of the dentary. The premaxillary teeth (AMNH 8514, fig. 8Q, R) are usually smaller than the anterior dentary teeth (AMNH 8515, fig. 8O, P) and have serrated crests lateral to the apex of the tooth that become more posterior toward the base of the tooth. A strong median keel is present that is not found in the larger dentary teeth.

The type specimen of *Ornithomimus grandis*

Marsh (1890) was supposedly recovered from the Eagle Sandstone, but probably came from the Judith River Formation, and was referred by Gilmore (1920) to *Deinodon*.

DROMAEOSAURUS[1] MATTHEW AND BROWN, 1922

Dromaeosaurus albertensis Matthew and Brown, 1922

Figure 9I

Dromaeosaurus albertensis MATTHEW AND BROWN, 1922, p. 383.
Laelaps explanatus COPE, 1876a, p. 249.
Laelaps falculus Cope, 1876a, p. 249.
Laelaps laevifrons COPE, 1876b, p. 344.

Dromaeosaurus albertensis is a small carnivorous dinosaur described from the "Belly River Formation" of Alberta by Matthew and Brown (1922, p. 383). These authors stated that the length of the skull is one-third to one-fourth the linear size of that of *Deinodon*, and differs from it by "reduced number of teeth, the large pre-maxillary teeth and the unsymmetric form of the maxillary teeth as well as the light skull construction, large fenestrae and numerous details that might be largely associated with its small size."

Teeth similar to those of *Dromaeosaurus* have been reported and figured (Russell, 1935, fig. 9) from the Milk River Formation of Alberta. They have also been reported from the Judith River Formation (Matthew and Brown, 1922, p. 378). AMNH 8516 is referable to the genus (fig. 9I). The teeth are usually smaller versions of those of *Deinodon*, with relatively strongly convex anterior borders. Serrations on the posterior edge of most teeth are coarser than those on the anterior, and in some specimens the anterior crest may be completely unserrated.

TROODON LEIDY, 1856

Troodon formosus Leidy, 1856

Figure 9L, M

Troodon formosus LEIDY, 1856, p. 72.

[1] [Colbert and Russell (1969) presented a study of *Dromaeosaurus* in which they placed this form in the family Dromaeosauridae, infraorder Deinonychosauria, along with the genera *Deinonychus* and *Velociraptor*.] M. C. McKenna.

Troodon formosus: LAMBE, 1902, p. 47.
Polyodontosaurus grandis GILMORE, 1932, p. 117.
Troodon formosus: RUSSELL, 1948, p. 629.

Troodon was originally described by Leidy (1856) on the basis of a single unworn tooth recovered by Hayden from the Judith River Formation. Leidy (1856, p. 72; 1860, pp. 147–148) suggested that *Troodon* had lacertilian affinities. The genus was also considered to have lacertilian affinities by Lambe (1902, p. 47), who described a few teeth from the "Belly River Series" of Alberta. Stanton and Hatcher (1905) were the first to tentatively regard *Troodon* as a dinosaur. Russell (1948) showed that *Troodon* was a theropod and quite distinct from *Stegoceras*. Consequently, the synonymy of *Stegoceras* with *Troodon*, as proposed by Gilmore (1924) and supported by Brown and Schlaikjer (1943), is incorrect. *Polyodontosaurus grandis* Gilmore (1932) has been shown by Sternberg (1951) and McDowell and Bogert (1954) to be synonymous with *Troodon formosus*.

There are a number of teeth recently collected from the Judith River Formation that closely resemble the type specimen of *Troodon formosus*. AMNH 8518, from Clambank Hollow, is a small laterally compressed tooth in which the coarser serrations are found on the posterior, and the finer ones, on the anterior crest (fig. 9L, M). The serrations are much better developed than in teeth of *Deinodon* or *Dromaeosaurus*, and usually consist of small, well-separated conules. A wear facet is present on the internal side of the crown apex.

A tooth considered to belong to *Troodon formosus*, AMNH 8519, from Clambank Hollow, differs from AMNH 8518 in a number of minor features. The base of the tooth is not laterally compressed but is oval in cross section, and coarse denticles are present on both anterior and posterior sides of the relatively straighter crown. The tooth resembles GSC 8841 in these features (Sternberg, 1945, pl. 70, figs. 2, 3). AMNH 8520 is probably from the posterior end of the dentary. Its crown height is about 3.4 mm., and the crown is linguolabially compressed with a slight constriction at its anterior junction with the crown. The anterior crest is distinct but not serrated, and the posterior crest has about 11 well-separated denticles. The tooth resembles ROM 1445 (Russell, 1948, p. 628, fig. 10) although the latter is slightly larger.

PARONYCHODON COPE, 1876a

Paronychodon lacustris Cope, 1876a

Figures 8S, T; 9J, K

Paronychodon lacustris COPE, 1876a, p. 256.
Zapsalis abradens COPE, 1876b, p. 345.
Tripriodon caperatus MARSH, 1889b, pl. 3, figs.18–22.

The genus was originally described by Cope (1876a, p. 256) from detached teeth obtained from the Judith River Formation. *Zapsalis abradens* was also described by Cope (1876b, p. 345) from the same area and is a larger, worn tooth of *Paronychodon*. Teeth referable to *Paronychodon lacustris* were named *Tripriodon caperatus* (Marsh, 1889b, pl. 3, figs. 18–22) because of a supposed identity as the incisors of the multituberculate *Meniscoessus* Cope (=*Dipriodon* Marsh). Clemens (1963b, pp. 85–86) showed that *Meniscoessus* incisors were significantly different from *Paronychodon* and Estes (1964) has demonstrated that *P. lacustris* is a carnivorous dinosaur.

The rare genus *Paronychodon* is represented in the collection by about six teeth of various sizes. The largest (AMNH 8522, fig. 8S, T) has a length of 13 mm. and a basal width of about one-third the length, and the smallest (AMNH 8523, fig. 9J, K) has a height of 4.8 mm. and a basal width of about 2.8 mm. Other differences in morphology also exist. AMNH 8522, from Clambank Hollow, is relatively less curved than teeth of *Deinodon*. At least four ridges were present on the internal side of the crown but these have been worn down. The smaller teeth are more curved and are not denticulated on the posterior or anterior side, although sharp ridges are present.

ORDER ORNITHISCHIA

SUBORDER ORNITHOPODA

FAMILY HADROSAURIDAE

SUBFAMILY HADROSAURINAE

KRITOSAURUS BROWN, 1910

Kritosaurus cf. *Kritosaurus breviceps* (Marsh, 1889a)

Figure 8U, V

Hadrosaurus breviceps MARSH, 1889a, p. 335.
Trachodon breviceps: MARSH, 1896a, p. 224.
?*Kritosaurus breviceps*: LULL AND WRIGHT, 1942, p. 170.

About a dozen teeth of a large flat-headed (hadrosaurine) ornithopod are present in the collections. AMNH 8525 consists of a crown (30 mm. long) making an obtuse angle of about 120 degrees with the fang (fig. 8U, V). The teeth are similar in size and morphology to each other and appear to belong to a single species. The crown is diamond-shaped with a bluntly rounded apex. A distinct medial keel is present above the slightly concave lateral edges. No ornamentation is found on the sides or keel. These teeth are probably referable to *Kritosaurus*, the only flat-headed ornithopod to be reported from the Judith River Formation (Lull and Wright, 1942, p. 171). The species was originally described by Marsh (1889a, p. 335) as *Hadrosaurus breviceps*, and later (Marsh, 1896a, p. 224) as *Trachodon breviceps*. The systematic position of *Hadrosaurus* and *Trachodon* has been discussed at length by Sternberg (1936). *Trachodon mirabilis* seems to be more closely related to the crested lambeosaurines rather than to the flat-headed hadrosaurines. Sternberg (1936) has suggested that use of *Trachodon mirabilis* be abandoned.

Lull and Wright (1942, p. 171) described and figured the dental battery of *K. breviceps* obtained from the Judith River Formation. The teeth recently collected probably belong to the same species. Comparison of *K. breviceps* with other species of *Kritosaurus* from the Oldman Formation is of little use as the Judith River material is still not sufficiently well known.

SUBFAMILY LAMBEOSAURINAE

PROCHENEOSAURUS MATTHEW, 1920

Procheneosaurus altidens (Lambe, 1902)

Figure 8W, X

Trachodon (Pteropelyx) altidens LAMBE, 1902, p. 76.
Procheneosaurus? altidens: LULL AND WRIGHT, 1942, p. 222.

A crested ornithopod is indicated by a small group of teeth, AMNH 8527 from Clambank Hollow, which are markedly different from those of *Kritosaurus* (fig. 8W, X). The teeth are large, with a long, narrow and elongated enamel face having a prominently raised medial keel. Sides of the enamel face are ornamented toward the apex of the crown with small papillae. Unlike teeth of *Kritosaurus*, the crown is not diamond-shaped but is rectangular in lateral view.

The teeth, which vary greatly in size, closely resemble teeth of *Trachodon* (*Pteropelyx*) *altidens* Lambe (1902, pl. 4, fig. 4). The species was later tentatively transferred to the genus *Procheneosaurus* by Lull and Wright (1942, pp. 222–223).

FAMILY PACHYCEPHALOSAURIDAE BROWN AND SCHLAIKJER, 1943

?*Stegoceras validus* Lambe, 1902

Figure 9N, O

A number of teeth recovered from the Judith River Formation closely resemble those of *Stegoceras validus*, an ornithopod not previously reported from the Judith River Formation, but quite frequent in the Oldman Formation of Alberta.

Specimen AMNH 8530, from Clambank Hollow, is representative of the group. The tooth is small with a crown height of 5.2 mm., a length of 4.8 mm., and a transverse width 3.6 mm. (fig. 9N, O). The crown is conical with a pointed apex showing a horizontal wear surface. Denticles are large compressed cones, better separated on the labial than on the lingual side. Valleys between the denticles extend as flutings to the base of the crown. The base is swollen on the internal face, thereby considerably increasing the basal width of the crown. The crown is markedly constricted at its junction with the cylindrical root.

These teeth are distinctly different from those of *Troodon*. Gilmore (1924) put the genus *Stegoceras* in synonymy with *Troodon* and this was followed by Brown and Schlaikjer (1943). Sternberg (1945), on the basis of his comparative study of the teeth of *T. formosus* and *Stegoceras*, maintained that the genera were distinct. Later, Russell (1948), in his description of the dentary of *Troodon*, also supported the separation of the ornithopod *Stegoceras* from the theropod *Troodon*.

FAMILY HYPSILOPHODONTIDAE

THESCELOSAURUS GILMORE, 1913

Thescelosaurus cf. *T. neglectus* Gilmore, 1913

Figure 9E, F

The material, consisting of about 12 teeth from the Judith River Formation, is the first record of the genus from the Campanian of the North American continent. Gilmore (1913, 1915), described *T. neglectus* from the Lance Formation of Wyoming. Later Parks (1926) described in detail the skeleton of *T. warreni* from the Edmonton Formation of Alberta. Sternberg (1937) erected a new genus, *Parkosaurus*, for the reception of this species. Sternberg (1940b) described yet another species, *T. edmontonensis*, from the Edmonton Formation of Alberta, and reviewed the classification of the Hypsilophodontidae.

Based on criteria listed by Sternberg (1940b, p. 483), premaxillary, maxillary, and dentary teeth appear to be present in the Judith River Formation. They are all approximately of the same size with one notable exception, AMNH 8538 from Clambank Hollow, which may not be a hypsilophodont. The other teeth are consistently smaller than those figured by Sternberg (1940b, p. 484, figs. 2–8). AMNH 8536 is triangular in shape with a sharply pointed apex (fig. 9E, F). The anterior and posterior ridges may be straight or slightly concave, and the presence and development of denticles is variable. Denticles may be well developed on the anterior and posterior crests, or may be restricted only to the posterior crest. The anterior edge is usually straight as a result of development of a principal wear facet on the internal side.

Judging from the figures of Sternberg (1940b, p. 484, figs. 2, 3), AMNH 8539 from Clambank Hollow is probably a premaxillary tooth of *Thescelosaurus*. The denticles are faint but appear to be developed on both the anterior and the posterior edges. A wear facet is present on the anterior half of the crown, on the internal face. The crown is higher than long and constricted at the base. No cingulum is present. The root is subcylindrical in cross section and hollow. Despite the small size and early stratigraphic occurrence of these specimens it does not seem advisable to name a new species based on them.

SUBORDER CERATOPSIA

FAMILY CERATOPSIDAE

Figure 9G, H

Although worn ceratopsian teeth form a sizable portion of the ornithischian remains, they cannot be differentiated at the generic level. Unworn teeth indicate that at least two genera
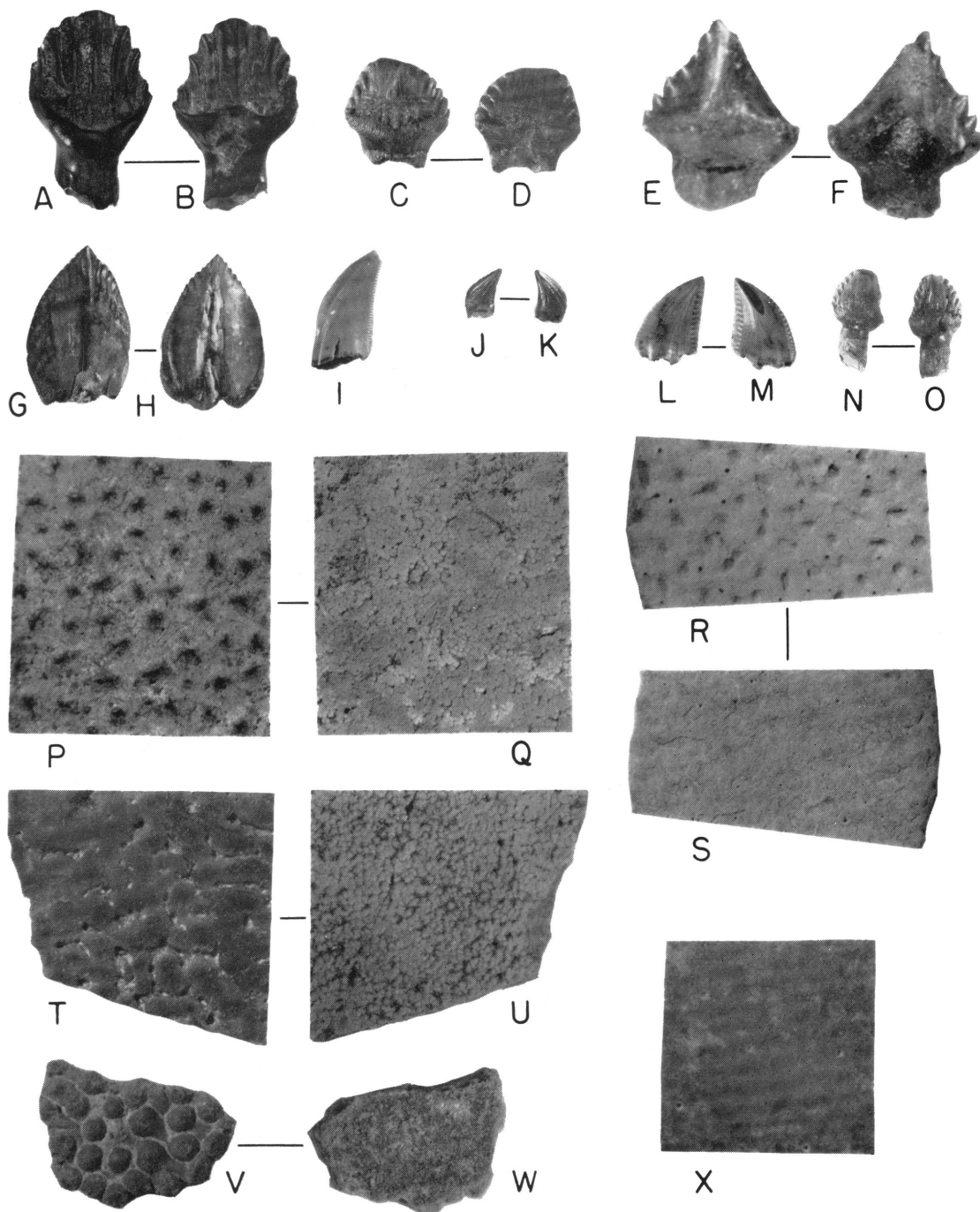
FIG. 9. A, B. *Edmontonia longiceps*, AMNH 8543, lateral views of an isolated tooth, ×1⅔. C, D. *Palaeoscincus costatus*, AMNH 8542, lateral views of an isolated tooth, ×1⅔. E, F. *Thescelosaurus* cf. *T. neglectus*, AMNH 8536, lateral views of an isolated tooth, ×10. G, H. Ceratopsidae, AMNH 8540, lateral views of an unworn tooth, ×1⅔. I. *Dromaeosaurus albertensis*, AMNH 8516, lateral view of an isolated tooth, ×1⅔. J, K. *Paronychodon lacustris*, AMNH 8523, lateral views of an isolated tooth, ×1⅔. L, M. *Troodon formosus*, AMNH 8518, lateral views of an isolated tooth, ×1⅔. N. O, ?*Stegoceras validus*, AMNH 8530, lateral views of an isolated tooth, ×1⅔. Dinosaur egg shell fragments. P. AMNH 8545, external view of shell (Class B). Q. Internal view. Both ×10. R. AMNH 8546, external view of shell (Class B). S. Internal view. Both ×10. T. AMNH 8548, external view of shell (Class C). U. Internal view. Both ×10. V. AMNH 8547, external view of shell (Class B). W. Internal view. Both ×10. X. AMNH 8544, external view of shell (Class A), ×10.

of ceratopsians may have been present. The ceratopsians of the Judith River Formation have been discussed by, among others, Lull and Hatcher (1907) and Lull (1933). Based mostly on fragmentary material, a number of species of *Monoclonius* and *Ceratops*, the only two genera known from the formation, have been described. *Brachyceratops montanensis* was described by Gilmore (1917) from the Two Medicine Formation of Montana. The Oldman Formation of Alberta has produced better known forms such as *Eoceratops*, *Brachyceratops*, *Monoclonius*, *Centrosaurus*, *Styracosaurus*, *Chasmosaurus*, and *Anchiceratops* (Sternberg, 1940a; Langston, 1965, p. 4).

An unworn tooth, AMNH 8540, from Clambank Hollow, has a sharply pointed apex (fig. 9G, H). The sides of the crown are serrated toward the apex, and a strong median keel must have been present but it is broken away in the specimen.

A much larger tooth, AMNH 8541, also from Clambank Hollow, with rougher ornamentation, probably belongs to a distinct genus.

SUBORDER ANKYLOSAURIA

FAMILY NODOSAURIDAE

PALAEOSCINCUS[1] LEIDY, 1856

Palaeoscincus costatus Leidy, 1856

Figure 9C, D

Palaeoscincus costatus Leidy is based on a single tooth and is the only ankylosaur species to have been reported from the Judith River Formation until the present study. The tooth was figured by Leidy (1860, pl. 9, figs. 49–52). AMNH 8542 from the present collection is similar to Leidy's specimen. AMNH 8542 has large and sometimes distinct denticles with well-separated cones (fig. 9C, D).

The flutings, however, do not extend to the base of the crown. A basal cingulum is present on the lingual side.

EDMONTONIA STERNBERG, 1928

Edmontonia longiceps Sternberg, 1928

[1] [*Palaeoscincus* is regarded as a *nomen dubium* by Walter P. Coombs in his review of the nodosaurs, which is now in an advanced stage of preparation. The specimens referred to *Palaeoscincus costatus* and to *Edmontonia longiceps* may all belong to *Panoplosaurus* Lambe, 1919, *fide* Coombs (personal commun.).] M. C. McKenna.

Figure 9A, B

The presence of *Edmontonia* is indicated by AMNH 8543, from Clambank Hollow (fig. 9A, B). Sternberg (1928) distinguished the teeth from those of *Palaeoscincus costatus* by the fact that they are "considerably higher in the crown, thicker transversely and the cingulum is more strongly developed . . . the transverse diameter of the tooth through the cingulum is three-fifths the height of the crown above the cingulum, while in *P. costatus* the transverse diameter is about one-half the height."

DINOSAUR EGG SHELL FRAGMENTS

Figure 9P–X

The discovery of dinosaur egg shell fragments from Clambank Hollow in the Judith River Formation unfortunately was made after most of the material had been etched in 10 per cent formic acid. Surprisingly, the external and internal sculpture pattern is well preserved in the etched as well as in the nonetched material. The internal stratification of mineral and organic layers, however, is less clear in radial sections of the acid-treated material, indicating that these substances have been leached out.

At least five separate external sculptured patterns can be seen, including all three of the categories devised by Jensen (1966) for distinguishing fossil egg fragments from the North Horn Formation of Utah. According to Jensen's (1966) criteria, the egg shells probably belong to those of dinosaurs, although Jensen's Class A eggs bear certain resemblances to bird eggs. The egg shells described here are all believed to be dinosaurian.

The most common egg shell fragments from the Judith River Formation are those that belong to Jensen's Class B. Fragments from Jensen's Class A and Class C are rare in the Judith River Formation.

CLASS A: Shells in this class are characterized by a smooth external surface with little or no sculpturing. No color mosaic can be noticed. Pores are distinct and well spaced and their density in AMNH 8544 is about 10/sq. cm. (fig. 9X). The pore openings are either subcircular or pentagonal with straight sides, and do not appear to be elongated parallel to the length of the shell as mentioned by Jensen (1966, p. 61). The internal surface consists of mammillae which reach a maximum diameter of

0.1 mm. The thickness of the shell is 1.0 mm. Stratification, in radial section, is indistinct or, at places, absent.

CLASS B: These shells are ornamented with nodose or linear ridges raised above the general surface of the shell. This, by far, is the most common class in the Judith River Formation. AMNH 8545 is a fairly large fragment (1.5 × 2.0 cm.) with external sculpturing of small, well-spaced nodes (fig. 9P, Q). Pores occur in the valleys between the nodes, are indistinct and few in number. The thickness of the shell is 1.0 mm.

The nodes in specimen AMNH 8546 coalesce to form meandering ridges (fig. 9R, S). There is a possibility that this type is identical to the one described above and that the differences are positional in nature. The thickness of the shell is 1.2 mm.

Different from the other nodular types is AMNH 8547 (fig. 9V, W). The nodes are not circular in outline but have squared off bases and are relatively more closely spaced. Pores do not occur between the nodes but are deep gutter-like depressions that incompletely encircle the nodes. The thickness of the shell is 1.0 mm. As in some North Horn Formation forms, the internal surface consists of small mammillae with an average diameter of about 0.01 mm.

CLASS C: Specimen AMNH 8548 probably belongs to the Class C category of Jensen (1966). The sculpture pattern is impressed into the external layer of the shell and consists of deeply incised grooves and irregular pits (fig. 9T, U). Two distinct shell layers are visible in side view, as well as in radial section. The upper layer is 0.7 mm. thick and appears to be porous and spongy; the lower layer is 1.2 mm. thick, quite dense and extremely hard. No distinct pores are present, and their function must have been carried out by the irregular grooves and pits. On the internal surface, the mammillae are small and relatively well separated.

The presence of fragile dinosaur egg shell pieces in the Clambank Hollow Quarry certainly indicates that the eggs were laid quite close to the site of deposition. The variety of the shells also indicates that their discovery at the locality is not a chance occurrence, but that the stream bank was a suitable laying area for a number of different dinosaurs. No generic names have been assigned to the egg shell fragments and as yet

little can be said even about the familial affinities of the eggs. The presence of grossly similar types in the Campanian and in the Maestrichtian suggests that similar reptiles existed during the two epochs. Although members of the major groups of dinosaurs were more diverse during the Campanian, all the families persisted into the Maestrichtian.

The material from Campanian Clambank Hollow adds yet another locality where eggs of dinosaurs have been found. Eggs and egg shell fragments have been reported from Mongolia (Van Straelen, 1928), Southern China (Young, 1965), India (Sahni, 1957), France and Brazil (Thaler, 1965), and North America (Jepsen, 1931; Jensen, 1966).

CLASS MAMMALIA

SUBCLASS ALLOTHERIA

ORDER MULTITUBERCULATA

The Campanian multituberculates from the Judith River Formation afford clear evidence for ancestry of later Maestrichtian forms. Evidently well advanced from the plagiaulacids reported from the Trinity Sandstone (Albian) of Texas, they are much closer to the multituberculates of the Lance Formation. Most of the genera recognized by Clemens (1936b) in the Lance Formation of Wyoming are present in the Judith River Formation. Additional genera have been described by Sloan and Van Valen (1965) from a series of Upper Cretaceous localities in eastern Montana; of these, only *Cimexomys* has so far been identified in the present collection.

Allotherian teeth greatly outnumber those of the Metatheria and Eutheria. The occurrence of isolated teeth makes generic and specific identification in some instances quite tentative. Most assignments are based on the criteria used by Clemens (1963b) in associating various multituberculate dentitions, and consist of comparative morphology, frequency of occurrence, and size. Unfortunately, size is not so useful a criterion in the Judith River multituberculates as it is in those from the Lance Formation. *Cimexomys judithae*, the smallest multituberculate, is the easiest to differentiate. Except for the largest species, *Meniscoessus major*, the others tend to

approach each other in size. The Campanian *Mesodma primaevus* is significantly larger than *M. formosa* and *M. thompsoni*, but *Cimolomys clarki* and *Meniscoessus major* are smaller than their later descendants, *Cimolomys gracilis* and *Meniscoessus robustus*, and much closer to each other in size. The only specimen that can be referred to *Cimolodon* is a single left P_4 fragment.

As is usually the case with isolated multituberculate teeth, the fourth lower premolar is most useful for generic and specific identification. Sloan (personal commun.) has pointed out the merits of using the labial rather than the lingual side of the lower blade as suggested by Jepsen (1940) for diagnostic purposes. In addition to the relative height of the anterior serration above the top of the depression for P_3, and the number and pattern of the ridges discernible on either side of the blade, the labial side shows more sculpture, particularly on the posterolabial corner of the crown. The shape and wear pattern of the posterolabial cuspule and the fine surface sculpture dorsal to that cuspule in this region are of diagnostic value. The shape of the labial enamel on the anterior root is also taxonomically useful.

P^4s have not been used as much for taxonomic differentiation. Complete P^4s are more common than P_4s in the collection and present morphological details that can be used for generic and specific identification. The following features are useful for diagnostic purposes: the number and shape of the cusps on the medial row; the number of cusps on the labial row; the height to length ratio (height taken as the vertical distance to enamel base from the penultimate cusp of the medial row); the inclination of the ridge connecting the posterior basal cusp with the penultimate cusp of the medial row; and the wear pattern and the number of cusps in the triangular area on the posterior medial slope of the crown.

SUBORDER PTILODONTOIDEA SIMPSON, 1927

FAMILY ECTYPODONTIDAE
SLOAN AND VAN VALEN, 1965

CIMEXOMYS SLOAN AND VAN VALEN, 1965

Cimexomys judithae, new species
Figure 10L–R

ETYMOLOGY: Named for Julia "Judith" Hancock Clark, for whom the Judith River was named by Lewis and Clark.

HOLOTYPE: AMNH 77100, a right P_4.

TYPE LOCALITY: Clambank Hollow, Chouteau County, Montana.

KNOWN DISTRIBUTION: Judith River Formation.

DIAGNOSIS: Teeth smaller than those of *Cimexomys priscus* and larger than those of *Cimexomys minor*. The lower molars are small, average length of M_1 is 1.8 mm.

DESCRIPTION: P_4; there is only one complete P_4, the holotype (AMNH 77100), that can be referred to the genus *Cimexomys* (fig. 10L, M). It has nine serrations and a length of 3.0 mm. The first external ridge is weakly developed and converges on the second external ridge at an acute angle; the other ridges are wide-spaced and curve anteroventrally except at the posterior two serrations where they are feebly developed. The apogee of the lateral profile is at the third or fourth serration, dorsal to the ventrolabial expansion of the enamel on the anterior root. The anterobasal cavity for P_3 is covered with enamel except for the posterior wall. The posterolabial cusp is represented in *Cimexomys* by a faint ledge. The anterior root is much larger than the posterior and an interradicular crest is present. Wear appears to be the greatest on the posterolabial side of the premolar.

M_1; M_1s have been referred to *Cimexomys judithae* on the basis of size rather than on any noticeable morphological difference from other M_1s in the collection. Cusp formula of AMNH 77103 is 6/4 (fig. 10N). The conical first external cusp is linked to the first internal cusp by a low ridge, notched by the median valley. External cusps are smaller and more crescentic than the lingual ones. Roots have transversely rectangular cross sections with a feebly developed interradicular crest. Length of the crown is 1.8 mm.

M_2; cusp formula of AMNH 77105 is 4/2 (fig. 10O). This small tooth (length 1.4 mm.) has four external cusps of which the most posterior may be considered divided, as the valley separating the last and next to last cusp is very narrow and shallow. External cusps are approximately equal in height to the two larger internal cusps. All the cusps are crescentic with their apexes deflected posteriorly. The cross section of the anterior root is transversely rectangular, whereas that of the posterior is triangular; no interradicular crest is present.

P^4; there are two P^4s in the collection that are quite small in comparison to the others, and are

referred to *Cimexomys judithae*. One of these is thoroughly worn, but the other, AMNH 77109, is complete and is illustrated in figure 10P, Q. Although the uncertainty of referring this tooth to the present species is even more apparent because of the slightly larger than expected length of the tooth (2.4 mm.), its distinct morphology separates it from the premolars of *Mesodma* with which it can be most easily confused. Sloan and Van Valen (1965), in their description of *Cimexomys minor* from the Hell Creek Formation of Montana, did not distinguish P4. The cusp formula of AMNH 77109 is 3/5/2. The external row consists of three well-separated cusps that are parallel or converge only slightly with the medial row. Cusps are as well spaced on the external row as they are on the medial row; on the latter, they are nearly equal in size but the posterior cusps tend to be higher because the height of the crown increases posteriorly. The crown in the case of *Cimexomys*, however, is much lower than in *Mesodma* species, not only of the Campanian, but also of the Maestrichtian. Height to length ratio for P4 of *Cimexomys judithae* is 0.4, whereas that for *Mesodma formosa* is 0.6. Its roots are rectangular in cross section and a prominent interradicular crest is present.

M1; there are two *Cimexomys* upper first molars that are morphologically similar but differ from each other in size. Both have the identical cusp formula of 5/5/1. The distinctive feature of these molars is that the internal row is extremely short and in all cases is less than one-half length of the molar. *Cimexomys* has the shortest internal row of all multituberculates except the M1s of the plagiaulacids, which have only two rows. Of the two molars, the smaller (AMNH 77110) is of the size expected for *C. judithae*. The larger M1 is discussed later.

Specimen AMNH 77110 is a worn tooth with five conical external cusps (fig. 10R). The anteroexternal cusp is connected to the anterior cusp of the medial row by a short, low ridge. Conical to pyramidal medial row cusps are parallel to the cusps of the external row except for the posteromedial cusp, which is more labial in position. The tendency for the posterolabial cusp to be situated more labially is seen also in the illustration of M1 by Clemens (1963b, p. 46) of ?*Mesodma* sp., later referred by Sloan and Van Valen (1965) to *C. minor*. The internal row is more like an elevated ridge than a separate cusp

and its anterior termination is usually at the next to last cusp on the medial row. The length of AMNH 77110 is 2.4 mm.

M2; an M2, AMNH 77111, resembles M2 of *C. minor* and is of a size that one would expect for *C. judithae*. Its cusp formula is 1/3/3. The most anterior cusp of the internal row is conical in shape and it is preceded by two cusps, the apexes of which are deflected anteriorly. The anterior cusp of the medial row is more a part of the anterior ridge than a separate cusp. A worn external ridge bearing a cuspule joins the posteromedial cusp. Its length is 1.5 mm. The cross section of the anterior root is transversely rectangular, whereas that of the posterior is rounded; no interradicular crest is present.

Cimexomys magnus, new species

Figures 10S–U; 11L

ETYMOLOGY: Latin *magnus*, large.

HOLOTYPE: AMNH 77120, a right M1.

TYPE LOCALITY: Clambank Hollow, Chouteau County, Montana.

KNOWN DISTRIBUTION: Judith River Formation.

DIAGNOSIS: Teeth larger than *Cimexomys minor* or *C. priscus*.

DESCRIPTION: P4; two large P4s in the collection are tentatively referred to *Cimexomys magnus*. AMNH 77112 is illustrated in figure 11L. A study of the posterior part of the P4s reveals that the ridges arising from the posterior serrations are bifurcate, a feature also characteristic of ?*Mesodma* sp. Clemens (1963b, p. 43) referred by Sloan (McKenna, Clemens, and Sloan, MS.) to *Kimbetohia campi* Simpson (1936). The two branches of the ridges are not equal in length. On the middle serrations the anteroventral branch is much longer than the posteroventral, whereas on the anterior serrations the anteroventral branch is much shorter. The present species could be ancestral to *Kimbetohia campi* from the Lancian and Puercan, and, through *Kimbetohia*, to the various species of *Ptilodus*.

P4; the upper blade (AMNH 77114, fig. 10S, T) is morphologically similar to, but larger than, P4 of *Cimexomys judithae*. The premolar appears to be a relatively primitive tooth, similar to P4s of mid-Cretaceous Djadochta multituberculates except in the possession of a few more cusps (personal commun. to Sloan from

Kielan-Jaworowska) and, in structure, intermediate between them and the Maestrichtian upper blades of *Cimolodon*, *Cimolomys*, and *Mesodma*. Its cusp formula is 3 or 4/6 or 7/1 and its length is 3.2 mm.

M^1; cusp formula of AMNH 77120 (fig. 10U) is 5/5/1. It is more than one-third longer than M^1 of *Cimexomys judithae*, and it is also larger than *Cimexomys priscus* Lillegraven (1969) and an undescribed species of *Cimexomys* from the Puercan of Montana (Sloan and Van Valen, 1965). The average length of the Puercan species is 3.2 mm. in comparison to 3.91 of AMNH 77120.

DISCUSSION: Prior to the current study, two species of *Cimexomys* had been described. One, *C. minor*, ranged in age from the Maestrichtian to the Puercan, and the other, *C. priscus*, restricted to the Maestrichtian of Alberta. An unnamed, larger species also occurred in the Puercan (Sloan and Van Valen, 1965). The discovery of two more species from the Judith River Formation in Montana has extended the range of the genus down to the Campanian.

The lower dentition has been reconstructed with greater certainty by reference to the type of *C. minor* (SPSM 62. 2115, a left mandible with P$_3$ and P$_4$ and alveoli for the lower incisor, M$_1$ and M$_2$), and other comparative material from the Bug Creek Anthills Quarry (Maestrichtian) of eastern Montana. The upper dentition, however, is more difficult to restore as no upper and lower jaws have been found in association. Since *Cimexomys judithae* is the smallest multituberculate in the collection, size has been used as a main criterion for identification. Size is important from another aspect; it is a probable cause for the under-representation of the species in the collection, as small teeth are suspected of being selectively eliminated in the screening process.

The similarity of M^1 of *Cimexomys* to that of the plagiaulacids has been discussed by Clemens (1963b, p. 48), who has pointed out that "the small size of the internal row of these molars (M^1,s) could be interpreted as a primitive character indicating little modification from the double-rowed M^1's of the plagiaulacids."

MESODMA JEPSEN, 1940

Mesodma JEPSEN, 1940, p. 267.
Mesodma: CLEMENS, 1963b, p. 30.

Mesodma primaevus (Lambe, 1902)

Figures 10A–J; 11K

Ptilodus primaevus LAMBE, 1902, p. 79.
Cimolomys primaevus: SIMPSON, 1929, p. 114.
Mesodma primaevus: CLEMENS, 1963b, p. 53.

HOLOTYPE: NMC 1890, left mandible with P$_4$ and M$_1$.

TYPE LOCALITY: Near Steveville, Red Deer River Valley, Alberta.

KNOWN DISTRIBUTION: Oldman Formation, Alberta, and Judith River Formation, Montana.

REVISED DIAGNOSIS: *Mesodma primaevus* is larger than *M. formosa* but smaller than *M. ambigua*; it is about the size of *M. thompsoni*. P$_4$s have 11 serrations and an average length of 3.0 mm., and closely resemble the type specimen, NMC 1890, from the Oldman Formation of Alberta. The profile of the serrate crest is generally higher than in *M. thompsoni* and *M. ambigua*; it is more like that of *M. formosa*.

DESCRIPTION: Lower incisor; AMNH 77273 and similar teeth are tentatively assigned to *Mesodma primaevus* on the basis of size and morphological similarity to lower incisors figured and described by Clemens (1963b, p. 33).

P$_4$; similar to the type specimen of *Mesodma primaevus*, a P$_4$, in size, morphology, and in having 11 serrations, are specimens AMNH 77121, 77122, and 77123. First and second external ridges of the P$_4$ of *M. primaevus* are short and run ventrally at an acute angle to the ridges of the posterior serrations. The profile of the serrate crest of both P$_4$s, AMNH 77121 and 77122, is a high, near symmetrical arc with its apogee at the fourth or fifth serration. The posterolabial side of the tooth is worn, but external ridges from the posterior three serrations in AMNH 77121 (fig. 10H, I) indicate that the ridges are not directed anteriorly. Ventral to the posterior two serrations a short, worn ledge represents what, in the primitive condition, was a row of cusps.

Height of the slightly convex anterior edge of the crown, measured from the top of the anterobasal cavity to the first serration, is approximately one-third the length of the crown. The anterobasal cavity is covered on all except the posterior side by bulging enamel; at the dorsal roof of the concavity the enamel may be cleft.

The first internal ridge on P$_4$ is usually longer than, or equal to, the second internal ridge. The longest ridge seems to originate from the fifth serration, or from the serrations immediately adjacent to it. The anterior root is larger than
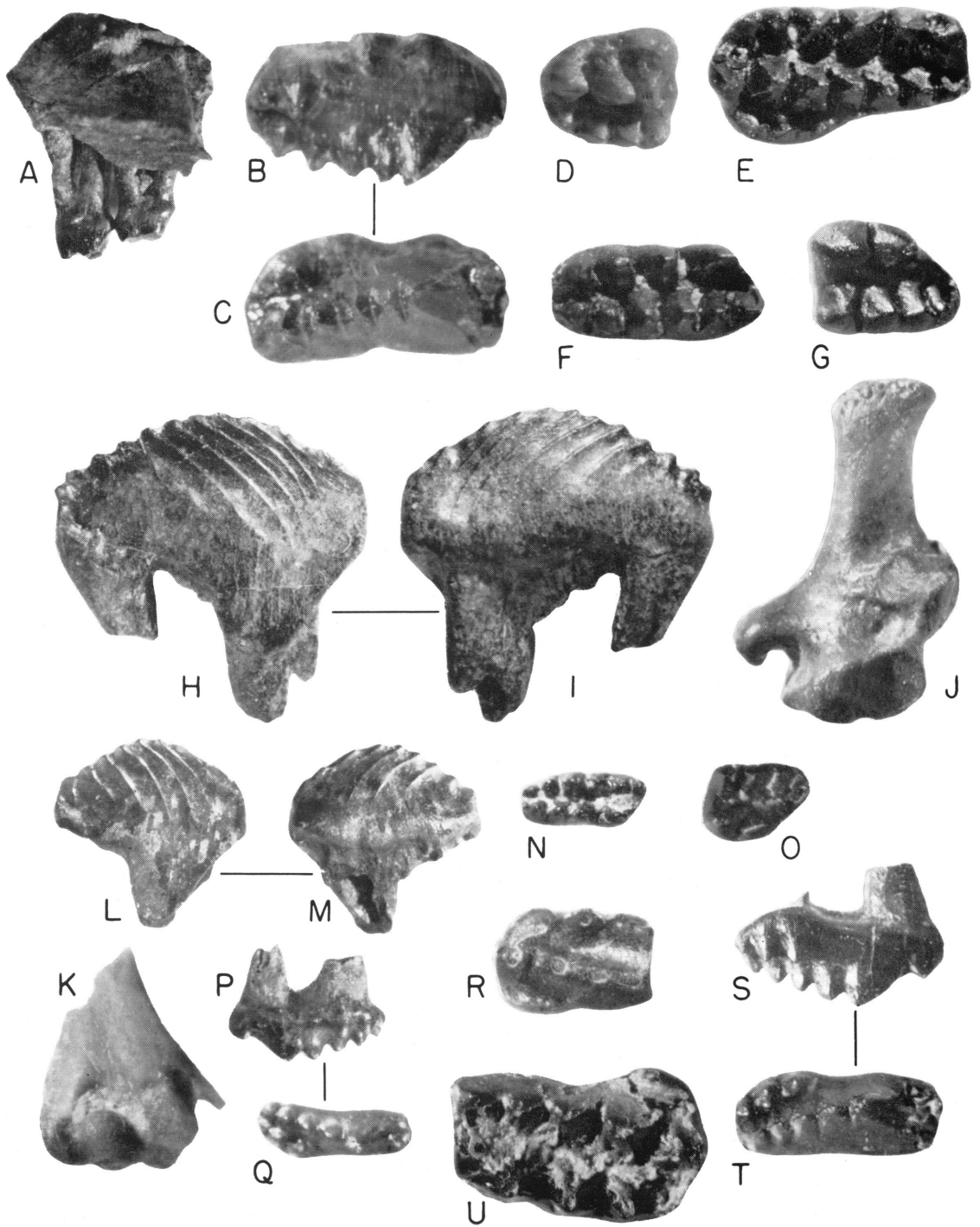
the posterior, and a prominent interradicular crest is present.

M_1; discrimination of isolated M_1s of *Mesodma primaevus* and *Cimolomys clarki* is not possible as their size and cusp formulae are either identical, or overlap. These M_1s have an average length of 3.4 mm., and an observed range of 3.15 mm. to 3.6 mm., and a cusp formula of 5 or 6/4.

Molars referred to *Mesodma* in this work are tentatively identified on cusp formulas and similarity to the M_1 figured by Lambe (1902). Cusp formula of AMNH 77125 is 6/4 (fig. 10F). The first external cusp is the smallest and is succeeded by cusps that are crescentic with their apexes deflected posteriorly. Internal cusps are higher than external cusps and stand more upright; the posterointernal cusp is the largest. The teeth are rectangular in outline in occlusal view. Roots of the M_1s are transversely rectangular in cross section and a prominent interradicular crest is present. There are no accessory roots.

M_2; allocation of M_2 to this species is also doubtful. Cusp formula of AMNH 77126 (fig. 10G) is 4/2, as compared with 3/2 of the later species of *Mesodma*. The anteroexternal cusp of M_2 is conical, the other external cusps are crescentic with posteriorly directed apexes. The two internal cusps are much larger than the external ones. The anterointernal cusp is linked to the second external cusp by a ridge cutting off the median valley. This feature seems to be fairly consistent in similar M_2s in the collection. The average length of M_2 is 2.4 mm.

The anterior root has a transversely rectangular cross section, and an interradicular crest is absent.

Maxilla containing P^2 and P^3; a fragmentary maxilla (AMNH 77149) was obtained from the productive clam/bone bed about 40 feet east of Clambank Hollow Quarry and on the opposite side of the gully. The maxilla (fig. 10A) is the only multituberculate jaw fragment found

during the three years of collecting. Anterior premolars bear close resemblance to the maxillary fragment, UCMP 46600, from the Lance Formation (Clemens, 1963b). Clemens tentatively identified the premolars as belonging to *Mesodma* "on the basis of the small size of the upper premolars and the circumstantial evidence of the joint occurrence" (of a broken P_4 of *M. thompsoni*). AMNH 77149, from the Campanian, probably represents *Mesodma*, although the possibility of its belonging to *Cimexomys judithae* cannot be ruled out.

P^2; the tooth is three cusped, and it is more elevated than the adjoining P^3. Two of the three conical cusps are more lingual in position than the third, and the anterior of these is higher and more slender. The posterolabial cusp is larger than the other two, and the area posterior to it is expanded and slopes gently. P^2 is two rooted, with a length of 1.0 mm. and a width of 0.7 mm.

P^3; the crown of P^3 has four cusps and the anterior edge of the tooth appears to be displaced lingually relative to P^2. Although P^3 is worn, it is possible to tell that the posterior pair of cusps is larger and better separated from each other than the anterior pair. The crown is 1.0 mm. long and 0.65 mm. wide. P^3 has two roots.

P^4; the upper blade, AMNH 77150, is tentatively assigned to *Mesodma primaevus* (fig. 10B, C). It has a cusp formula of 2/6/2. The posteroexternal cusp is much larger than the anterior, and the medial row consists of six, well-separated conical cusps. The penultimate cusp is the highest, and the included angle between the anterior and the posterior slopes of the shearing face is around 120 to 125 degrees. The same angle in the Maestrichtian species *M. formosa* and *M. thompsoni* is less, and varies between 115 and 120 degrees. The crown of AMNH 77150 is unworn and the two to three basal cusps are distinct. The length of the tooth is 4.0 mm.

FIG. 10. *Mesodma primaevus* (Lambe). A. AMNH 77149, lingual view of right maxilla with P^2 and P^3. B. AMNH 77150, labial view of left P^4. C. Occlusal view. D. AMNH 77159, occlusal view of right M^2. E. AMNH 77154, occlusal view of right M^1. F. AMNH 77125, occlusal view of left M_1. G. AMNH 77126, occlusal view of left M_2. H. AMNH 77121, labial view of right P_4. I. Lingual view. J. AMNH 77176, medial view of left calcaneum. K. AMNH 77175, distal end of right humerus. *Cimexomys judithae*, new species. L. AMNH 77100, labial view of right P_4. M. Lingual view. N. AMNH 77103, occlusal view of right M_1. O. AMNH 77105, occlusal view of right M_2. P. AMNH 77109, labial view of right P^4. Q. Occlusal view. R. AMNH 77110, occlusal view of right M^1. *Cimexomys magnus*, new species. S. AMNH 77114, labial view of left P^4. T. Occlusal view. U. AMNH 77120, occlusal view of right M^1, holotype. All × 10.

M^1; cusp formula of AMNH 77154 is 6/7/5 or 6 (fig. 10E). Of the external cusps, the anterior tend to be conical and the posterior subpyramidal, rather than crescentic, and their apexes are only slightly deflected anteriorly. The anterior cusp of the medial row is separated from the anterior cusp of the external row by a valley. The lingual side of the external row cusps is grooved. The internal row extends slightly more than one-half the length of the crown, although these five to six cusps on the internal row are not well separated from each other and are more like cuspules. M^1s of *Mesodma primaevus* are distinct from those of other species from the Judith River Formation in size, cusp formula, and the ratio of length of the internal row to crown length. They can be distinguished from M^1s of later Maestrichtian species of *Mesodma* by two, apparently primitive, features. The first is the tendency to have fewer cusps in the external and medial rows than in later species, and the second is the presence of five to six very small cuspules in the internal row in comparison to five to six distinct and well-separated cusps in the Maestrichtian species of *Mesodma*. The cross section of the anterior root is elongated, whereas that of the posterior is transversely lengthened, and an interradicular crest is present. The average length of M^1 is 4.0 mm.; the width is 2.0 mm.

M^2; cusp formula of AMNH 77159 is 1/3/4 (fig. 10D). The internal row consists of four well-separated cusps, with the anterointernal cusp linked to the anteromedial cusp by a short ridge. Three medial cusps are large and crescentic. On the anteroexternal side of the crown, the single external cusp, or cuspule, is situated on a ridge. The tooth is 2.1 mm. long and 1.6 mm. wide.

DISCUSSION: *Mesodma primaevus* (Lambe, 1902) was one of the earliest Campanian mammals to be described from the "Belly River Series" (Oldman Formation) of Alberta. Simpson (1929), in his review of the Mesozoic Mammalia, included Lambe's holotype in *Cimolomys* (*sensu lato*) as had been suggested previously by Matthew (1916). Both of these authors, and later Russell (1952) noted the similarity of the type specimen, NMC 1890, to some of the later Lance allotherians; a situation resulting partly, but not entirely, from the initial inclusion of most Lance multituberculates in the genus *Cimolomys* used in a "wastebasket sense." Additional evidence from the Judith River Forma-

tion tends to confirm the tentative assignment by Clemens (1963b) of Lambe's type to *Mesodma*. There is a close resemblance between the Judith River specimens and the type specimen of *Mesodma primaevus*, NMC 1890, which is a broken right mandible containing P_4 and M_1 (not from the left side as suggested by Russell, 1952).

Stanton and Hatcher (1905) reported a specimen of this species from the Judith River Formation. The new material greatly adds to our knowledge of this species. *Mesodma primaevus* is a satisfactory ancestor for *Mesodma formosa* and *Mesodma thompsoni* of the Maestrichtian Lance and Hell Creek formations, and through them to the later ectypodontids.

SUBORDER TAENIOLABIDOIDEA
SLOAN AND VAN VALEN, 1965

FAMILY CIMOLOMYIDAE (MARSH, 1889c)

The family was proposed by Marsh (1889c) but never defined. Clemens (1963b) preferred to place the genus in the Ptilodontidae, *incertae sedis*. Material from the Judith River Formation, however, indicates that the genera *Cimolomys* and *Meniscoessus* are closely related and should be included in the family *Cimolomyidae*. The affinity of the two genera as cimolomyids had already been anticipated by Sloan and Van Valen (1965) in their discussion of the Hell Creek multituberculates. The family as here defined contains two genera, *Cimolomys* and *Meniscoessus*, and the following six species:

Cimolomys clarki, new species
C. gracilis Marsh, 1889b
Meniscoessus major (Russell, 1937)
M. robustus (Marsh, 1889b)
M. conquistus Cope, 1882
M. borealis Simpson, 1927a

The Cimolomyidae comprise medium- to large-sized multituberculates, with a tendency to increase in size in later forms. P_4 is a high, arcuate tooth, with fewer serrations than in most contemporary allotherians. The posterior two or three serrations of P_4s in both genera are more distinct than the other serrations and may be deflected posteriorly; on the labial sides, grooves are present on or between these serrations and lead ventrally to a prominent posterolabial ledge containing one to three cuspules. P^4 differs in the two genera. It is long and low in *Cimolomys*, but

in *Meniscoessus* it is short and high. The internal row of M^1 is well developed, terminating at or near the second cusp from the anterior end of the medial row. The species of these genera from the Judith River Formation are more similar to each other than they are to later species.

CIMOLOMYS MARSH, 1889b

Cimolomys MARSH, 1889b, p. 84.
Cimolomys: CLEMENS, 1963b, p. 75.
TYPE-SPECIES: *Cimolomys gracilis* Marsh, 1889b.

Cimolomys clarki, new species

Figure 11A–J

ETYMOLOGY: For Captain William Clark, pioneer explorer of the Missouri River.

HOLOTYPE: AMNH 77179, right P_4.

TYPE LOCALITY: Clayball Hill, Judith River Formation, Montana.

KNOWN DISTRIBUTION: Chouteau County, Montana.

DIAGNOSIS: *Cimolomys clarki* is smaller than, but similar to, its Maestrichtian descendant, *C. gracilis*.

DESCRIPTION: P_4; no complete P_4 of *C. clarki* has yet been found. A reconstruction of the premolar was made from AMNH 77179 and 77180 (fig. 11A–D). P_4 probably had eight or nine serrations arranged in a nearly symmetric arc. Ridges arising from the anterior two or three serrations are extremely short; those from the middle are well developed and extend antero-ventrally to the level of the posterolabial ledge. The posterior two or three serrations are distinct, and are grooved labially. The posterolabial ledge is well developed and indicates the presence of three worn cuspules.

The anterolabial lobe of the crown at the anterior root is poorly formed, as in *C. gracilis*; the anterobasal cavity is small and enamel covered except for the posterior wall. The anterior root is much larger than the posterior, and a low interradicular crest is present.

M_1; this tooth is apparently identical in size and cusp formula with that of *Mesodma primaevus*, suggesting a P_4/M_1 length ratio of about 1.0 ± 0.1, which is similar to that in the other species of this family (Clemens, 1963b, p. 80).

M_2; morphologically, these teeth bear close resemblance to M_2s of *C. gracilis* except that they are slightly smaller. Cusp formula of AMNH 77212 is 4/2 (fig. 11E). External cusps are four in number, subcrescentic with deep intervening

valleys. The posteroexternal cusp occupies the posterolabial portion of the crown and is linked to the internal row by a low ridge, in some instances bearing small cuspules. The internal row consists of two large cusps which are much higher than the external ones and separated from them by broad valleys. An anterior ridge usually joins the anterior cusps of the external and internal rows.

Upper incisor; a right upper incisor, AMNH 77266, is referred to *Cimolomys clarki* on the basis of size and the presence of two distinct cusps (fig. 11J).

P^4; two specimens of P^4, AMNH 77217 and 77218, both from Clambank Hollow, are referred to *C. clarki*. Cusp formula of AMNH 77217 is 2/5 or 6/2 (fig. 11H, I). Medial cusps gradually increase in height posteriorly and have prominent vertical striations on both their lingual and labial sides. The crown is low, and at its base enamel thickens and bulges on both external and internal sides. As is the case with *C. gracilis*, to which the teeth are similar, a distinct ridge connects the highest medial cusp to the basal cusps situated on the posterolabial corner of the crown. Lingual to the basal cusp, there is a depressed triangular area with two to three deep pits and grooves. Two external cusps in AMNH 77217 are situated on the anterolabial expansion of the crown; the posterior cusp is usually much larger than the anterior.

The coronal shape of P^4 in occlusal view is roughly rectangular, with a constriction on both the lingual and the labial sides of the crown. Roots of AMNH 77217 are broken but their sockets indicate a subrounded cross section, and a small interradicular crest is present.

M^1; there are at least a dozen M^1s in the collection from Clambank Hollow. They are similar to M^1s of *C. gracilis* except that their dimensions are much smaller and they possess fewer medial cusps. Cusp formula of AMNH 77219 is 5/6/6 (fig. 11G). External cusps are conical or pyramidal in shape. The anterior cusps are joined by a ridge to the anteromedial cusp. Other external cusps are well separated from each other by distinct valleys, especially the posterolabial cusp, in which the valley is wide and projects labially. Cusps of the medial row are crescentic with their apexes directed forward. Those on the internal row diminish in size anteriorly and are six in number. Anterolingual cusps are conical in shape, with circular bases, and extend to the secondmost anterior cusp of the medial row.
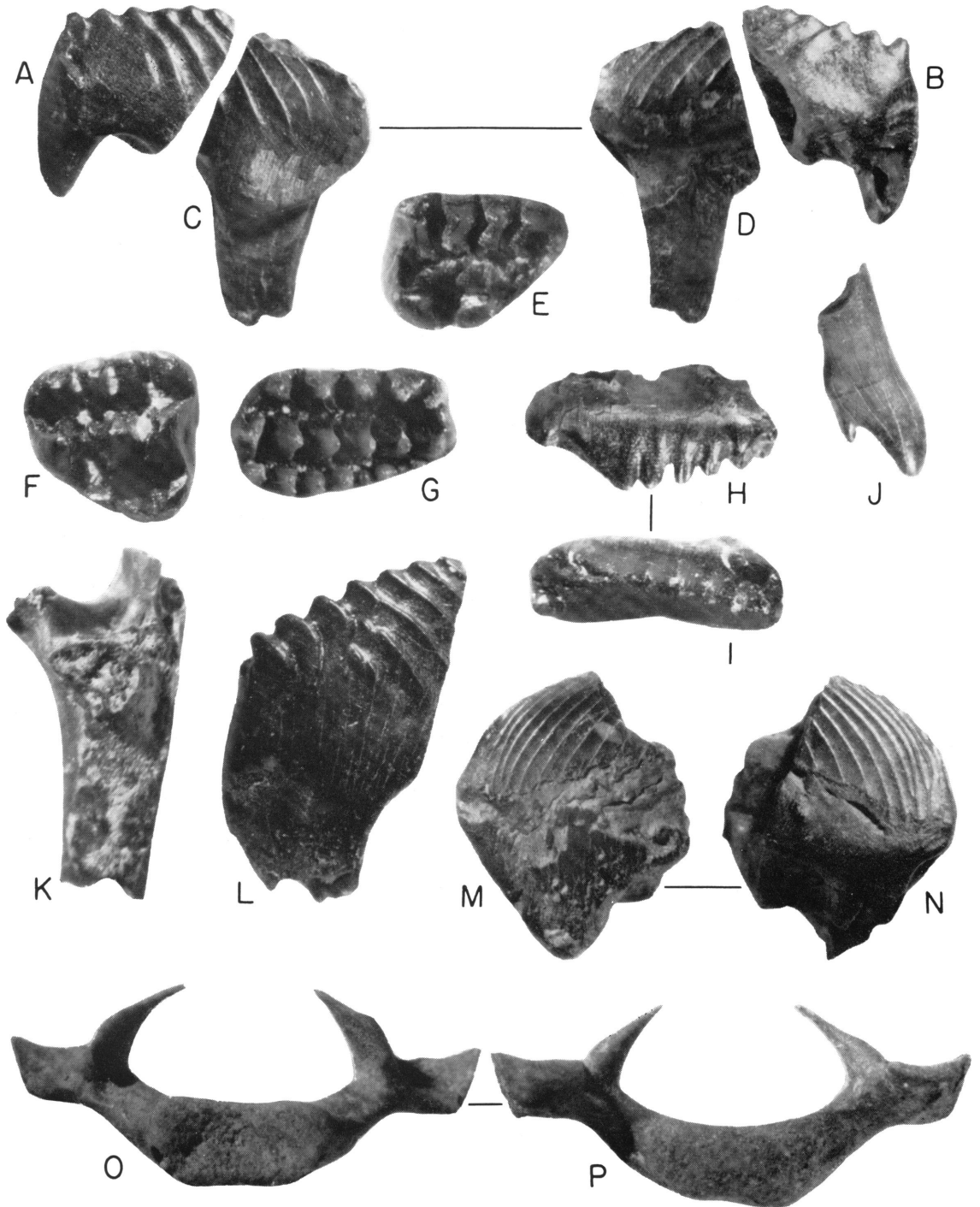
FIG. 11. *Cimolomys clarki*, new species. A. AMNH 77179, labial view of right P_4. B. Lingual view. C. AMNH 77180, labial view of right P_4. D. Lingual view. E. AMNH 77212, occlusal view of right M_2. F. AMNH 77241, occlusal view of left M^2. G. AMNH 77219, occlusal view of right M^1. H. AMNH 77217, labial view of right P^4. I. Lingual view. J. AMNH 77266, labial view of right upper incisor. K. ?*Mesodma primaevus* (Lambe), AMNH 77178, proximal portion of right femur. L. *Cimexomys magnus*, new species, AMNH 77112, lingual view of posterior fragment of left P_4. M. *Cimolodon* sp., AMNH 77267, labial view of anterior fragment of left P_4. N. Lingual view. O. Anuran, AMNH 8424, anterior view of vertebra. P. Posterior view. All × 10.

The cross section of the anterior root is elongated, whereas that of the posterior is transversely rectangular. Two small accessory roots are present near the posterior root and on either side of the interradicular crest.

M^2; cusp formula of AMNH 77241 is 2/3/4 (fig. 11F). The internal row consists of four pyramidal cusps, which are well separated from each other by deep valleys. The anterointernal cusp is linked by a low ridge to the anteromedial cusp and also to the anteroexternal cusp, forming the anterior ridge which closely fits against the posterior side of M^1. Medial cusps are well separated, and the most posterior one is crescentic and joined to the external cusps by a cuspidate ridge. Roots are equal in size, and an interradicular crest is feebly developed.

DISCUSSION: Although five species have been assigned to the genus *Cimolomys*, only three, *C. clarki*, from the Campanian and *C. gracilis* and *C. trochuus*, from the Maestrichtian, are validly included. *Ptilodus primaevus* Lambe (1902) from the Oldman Formation was referred to *Cimolomys* by Simpson (1929), and then later transferred to *Mesodma* by Clemens (1963b). *Cimolomys major* Russell (1937) is herein transferred to *Meniscoessus*. All teeth of *Cimolomys clarki*, except P^4, are approximately 70 per cent of the size of their counterparts in *C. gracilis*. P^4, on the other hand, is larger; the average length of the two specimens of *C. clarki* is 4.0 mm. in comparison with the average length of the specimens of *C. gracilis* (Clemens, 1963b, p. 81) of 3.0 mm. This observation can be explained as the result of the progressive tendency toward reduction of size of the shearing premolars relative to the other teeth in species of the family. Morphologically, however, the teeth in the two species are similar and it seems reasonable to derive *Cimolomys gracilis* from *C. clarki*.

Absence of associated teeth in mandibles and maxillae from the Lance or Judith River formations has resulted in casual reference of teeth to specific taxa. All jaws previously described as belonging to *Cimolomys* have been removed from the genus; thus, in the Judith River and Oldman formations, mandibles referred to *Cimolomys primaevus* (Lambe, 1902) and *Cimolomys major* Russell (1937) are placed in different genera. Also, with the removal of *Mesodma* and *Cimolodon* by Clemens (1963b) from the group of multituberculates that had been included by Simpson (1929) in *Cimolomys, sensu lato*, there are

now no jaws that can be referred to *Cimolomys, sensu stricto*. The method used by Clemens (1963b, p. 80) for distinguishing *Cimolomys, sensu stricto* was to eliminate teeth referable to *Mesodma, Cimolodon*, and *Meniscoessus* and to assign the few remaining teeth to *Cimolomys*. He corroborated his findings by computing ratios for various upper and lower teeth. Material from the Judith River Formation tends to confirm Clemens's identification.

Cimolomys major Russell (1937, 1952) from the Oldman Formation is in reality closer to *Meniscoessus* than to *Cimolomys* and is discussed later. Only the reasons for excluding it from *Cimolomys* will be mentioned here. The type specimen is NMC 8743, a broken mandible with M_1–M_2, and the root of the incisor. Later a P_4 was obtained at another locality. The root of this P_4 is the same size as that expected for the alveolus of the type specimen. The teeth are large and the combined length of P_4–M_2 is 17.2 mm., nearly twice that of *C. clarki*. They are almost identical in size and morphology to teeth of the smallest species of *Meniscoessus*, found in the Judith River Formation. All species of *Meniscoessus* have characteristic grooves on the cusps, especially on the molars. In some cases similar grooves are present on the incisor and P^4. Such grooves are present on M_1 and M_2 of Russell's type specimen NMC 8743. The structure of P_4 of *Cimolomys* and *Meniscoessus* is also different; in the Campanian *Meniscoessus* and NMC 8820 (P_4 referred by Russell, 1952), 11 serrations are present instead of the usual eight or nine found in P_4 of *Cimilomys clarki* and *C. gracilis*.

MENISCOESSUS COPE, 1882

[*non*] *Paronychodon* COPE, 1876a, p. 256.
Meniscoessus COPE, 1882, p. 830.
Dipriodon MARSH, 1889b, p. 85.
Tripriodon MARSH, 1889b, p. 86.
Selenacodon MARSH, 1889b, p. 86.
Halodon MARSH, 1889b, p. 87.
Oracodon MARSH, 1889c, p. 178.

Meniscoessus major (Russell, 1937), new combination

Figure 12

Cimolomys major RUSSELL, 1937, p. 75.
Cimolomys major: RUSSELL, 1952, p. 111.

HOLOTYPE: NMC 8743, a lower jaw with an M_1 and M_2, and incisor root, from the Oldman Formation of Alberta.

TYPE LOCALITY: Legal subdivision 10, sect. 29, T. 21, R. 12, W. 4th meridian; Red Deer Valley, near Steveville, Alberta.

KNOWN DISTRIBUTION: Judith River Formation, Montana, and Oldman Formation, Alberta.

REVISED DIAGNOSIS: *Meniscoessus major* is the smallest species of *Meniscoessus* yet described. P_4 with 11 serrations, lateral profile of the blade is a symmetrical arc, anterobasal cavity enamel covered except for a part of the posterior wall, posterior two serrations with prominent grooves leading into a well-developed posterolabial ledge. M_1 cusp formula is 8/6 with more cusps than in any contemporary allotherian. M^1 with a high width/length ratio, M^2 with an accessory root near the posterior root.

DESCRIPTION: Incisor; one partial incisor, AMNH 77254 (fig. 12F), can tentatively be referred to *Meniscoessus* on the basis of its large dimensions and the presence of deep longitudinal labial grooves that appear to be characteristic of the genus. The cross section at the junction of enamel and the root is ovoid.

P_4; no complete P_4s have been recovered from the Judith River Formation. Fragments of the lower premolar present in the collection include the anterior half of the tooth, AMNH 77247 (fig. 12A, B). A similar number of serrations are present on P_4, NMC 8820, referred to *Cimolomys major* by Russell (1952) from the Oldman Formation. P_4 is from the left side, as stated by Russell (1937), and not from the right side as stated by Russell (1952). The lateral profile of the serrate crest is a high symmetrical arc, with its apogee at the fourth or fifth serration. The anterobasal cavity is enamel covered except for the ventral portion of the posterior wall. The last two or three serrations are characteristic and resemble the condition in *Cimolomys* to a certain degree. These posterior serrations are well separated from those anterior and their apexes may be deflected posteriorly. Grooves are present on the serrations which terminate ventrally at the prominent posterolabial ledge.

The roots of all three specimens from the Judith River Formation referred to *Meniscoessus* have been broken, although a striated interradicular crest is present in most cases.

M_1; the only M_1 that can be assigned confidently to the genus is AMNH 77253 (fig. 12D, E). It is very similar to specimen NMC 8743 in most respects. Cusp formula in both the holotype and referred specimens is 8/6, and is thus much higher than that of *M. robustus*. This formula is within the range of variation of *C. gracilis* Clemens (1963b), but *M. major* differs from this species in other features.

The conical anteroexternal cusp is the smallest cusp on M_1 and is succeeded by seven other cusps that are pyramidal in shape and ornamented by grooves on both the labial and lingual side. The posteroexternal cusp is not fully separated from the adjoining cusp. There are six conical internal cusps that are much taller than the external cusps and are grooved only on the labial side. The anterior root is only slightly larger than the posterior, and an interradicular crest links them together. A subsidiary root is present labial to the crest.

M_2; not present in the collection.

Upper incisor; AMNH 77265 is a left incisor (fig. 12M). The upper incisors of cimolomyids are typically bifid in contrast to ectypodontid incisors.

P^4; there are two P^4s that can confidently be assigned to the genus. AMNH 77257 (fig. 12I, J) is complete, except for breakage at the anterolabial border and the absence of roots. Its cusp formula is 2/4, 5/2, or 3. The posterior cusp is the larger of the two external cusps. External cusps are closely appressed to those of the medial row, and a deep valley separates the two rows. The anterolabial side of the crown is damaged but was probably expanded. There are four or five cusps on the medial row, and they only slightly increase in height posteriorly. Vertical striations are present on the cusps of the two rows. The posterior slope of the posteromedial cusp is quite steep and terminates ventrally in a basal cusp. Two other cusps are situated in this region lingual to the basal cusp. A ridge connects the anterior of these lingual cusps to the base of the posterolabial cusp.

Shape of P^4, in occlusal view, is characteristically constricted in the middle. Although the roots are missing in both P^4s, their cross sections, which are subrounded, indicate that the two roots were equal in size. P^4 differs from P^4 of *Meniscoessus borealis* in having one additional cusp in the medial row.

A deciduous upper posterior premolar, AMNH 77255 (fig. 12K), is tentatively referred to *Meniscoessus*. Its cusp formula is 2/4, and its length is 2.5 mm. The two external cusps are equally large, well separated, and closely appressed to the medial row. The medial row consists of four small cusps ornamented with
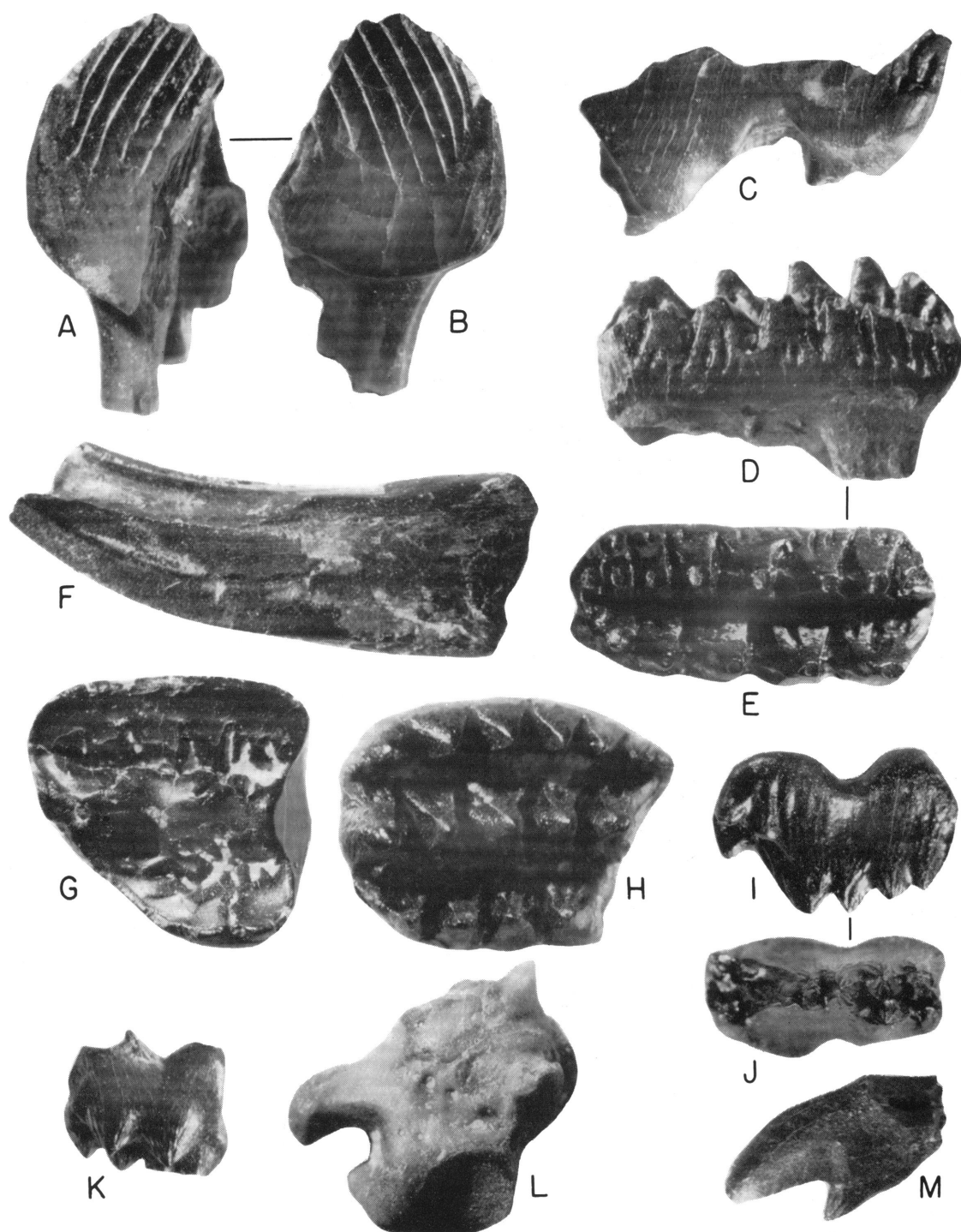
Fig. 12. *Meniscoessus major* (Russell), new combination. A. AMNH 77247, labial view of anterior fragment of left P_4. B. Lingual view. C. AMNH 77248, labial view of ventral fragment of left P_4. D. AMNH 77253, labial view of right M_1. E. Occlusal view. F. AMNH 77254, lingual view of right lower incisor. G. AMNH 77261, occlusal view of left M^2. H. AMNH 77259, occlusal view of right M^1. I. AMNH 77257, lingual view of left P^4. J. Occlusal view. K. AMNH 77255, labial view of left upper posterior premolar. L. AMNH 77264, medial view of left calcaneum. M. AMNH 77265, labial view of left upper incisor. All $\times 10$.

vertical striations. There is a distinct constriction in the middle of the tooth, in occlusal view, as in P^4.

M^1; although the anterior portion of AMNH 77259 is broken, it confidently can be referred to *Meniscoessus*. Cusp formula, however, cannot be determined because of the fragmentary nature of the tooth (fig. 12H). Its cusps are conical, and those of the medial row are deflected strongly anteriorly. External cusps are more conical and less deflected anteriorly than those of the medial row. Vertical grooves and striations are present, not only on the labial and lingual side of the crown but also on the sides of the valleys separating the two rows.

The crown of AMNH 77259 is relatively unworn; thus the apexes of the cusps are sharp and pointed. Roots are absent in the specimen.

M^2; although worn, M^2s can be assigned to *Meniscoessus* on the basis of size and morphological similarity to M^2s of the Maestrichtian species of the genus. The cusp formula of AMNH 77261 is difficult to decipher because of the worn and eroded nature of the tooth, but the external row appears to have two or three cusps (fig. 12G). There are four medial cusps, with some vertical striations still present on their lingual and labial sides. The internal row is so worn that the number of cusps cannot be discerned. The anterior root is slightly larger than the posterior one, and both have rectangular cross sections; as in *Meniscoessus robustus*, an interradicular crest is absent.

DISCUSSION: *Meniscoessus major*, the largest multituberculate from the Judith River Formation, is nevertheless the smallest species of that genus. The reconstructed dentition is fairly complete except for anterior premolars. M_2 has not been found in the present collection but this tooth is present in association with M_1 in the type mandible (NMC 8743) from the Oldman Formation (Russell, 1952). Several characteristics, including large size, enlarged molars, and vertical grooves and striations on the face of the cusps, make the genus easily distinguishable from all other contemporary allotherians.

Russell's type specimen had originally been referred to *Cimolomys*, *sensu* Clemens (1963b). Although the obvious similarity between the two genera cannot be denied, it is unlikely that NMC 8743, the holotype of *Meniscoessus major*, is a large species of *Cimolomys*. The presence of a small *Meniscoessus* in the Judith River Formation, with teeth comparable in size to the teeth de-

scribed by Russell (1937, 1952), is indicated by the distinctive P^4, M^1, and M^2, which are about 70 per cent of the size of comparable teeth of *M. robustus*. M^2 of *M. major* is smaller by about 30 per cent than M^2 of *M. conquistus*, the type species (AMNH 3011) and the smallest and perhaps the earliest of the Maestrichtian species. Coincidentally, as in *Cimolomys clarki*, P^4 of *M. major* is the same size as the average size of 34 P^4s of *M. robustus* measured by Clemens (1963b, p. 93). This is another indication that the shearing premolars of this family, especially P^4s, were undergoing reduction relative to the molars during the Maestrichtian.

Cimolomys and *Meniscoessus* are similar in gross morphology. The lateral profile of the serrate crest of P_4 in both is a high symmetrical arc with relatively few serrations (eight to 11). Posterior serrations, usually two to three in number, are demarcated with well-defined ridges leading into a prominent posterolabial ledge that may bear up to three cuspules. Similarity of the two M_1s has already been discussed. P^4, on the other hand, is apparently dissimilar. P^4 in *Cimolomys* is lower and longer relative to the molars than in *Meniscoessus*. M^1s have similar internal row/length and width/length ratios.

Four species of *Meniscoessus* have been proposed, *M. major* in the Campanian, and *M. conquistus* Cope (1882), *M. robustus* (Marsh, 1889b), and *M. borealis* Simpson (1927a) confined to the Maestrichtian. Clemens (1963b), in his discussion of Lance mammals, described only *M. robustus* in detail; he confined *M. conquistus* to the type specimen, and regarded *M. borealis* as a species of "questionable validity" within the range of variation of *M. robustus*. Additional work by Sloan (personal commun.) in Montana, however, and Wilson (personal commun. to Sloan) in South Dakota indicates that the three Maestrichtian species are distinct.

SUBORDER PTILODONTOIDEA
SLOAN AND VAN VALEN, 1965

FAMILY CIMOLODONTIDAE MARSH, 1889b

CIMOLODON MARSH, 1889b

Cimolodon MARSH, 1889b, p. 84.
Cimolodon: CLEMENS, 1963b, p. 56.

Cimolodon sp.

Figure 11M, N

There is only one tooth, a fragment of P_4, that can be referred with confidence to *Cimolodon*.

P₄; the anterior half of a P₄ from Clambank Hollow, AMNH 77267 (fig. 11M, N), has been referred to *Cimolodon*. It is morphologically similar to P₄ of *C. nitidus* Marsh (1889b), but slightly smaller. The tooth, in labial view, shows a high arched profile of the serrate crest. The first external ridge is very short and meets the longer second external ridge at an acute angle. Twelve anteroventrally curving ridges are visible on P₄, but evidently more than 12 serrations were present. The anterobasal cavity is deep and covered by enamel on all sides except the posterior wall.

MULTITUBERCULATE POSTCRANIAL ELEMENTS

Recovery of limb and girdle elements associated with dentitions of small Cretaceous mammals is impossible by screening techniques. It is therefore practically impossible to make any generic identification of isolated postcranial material. Gidley (1909), Broom (1914), Simpson (1928), Simpson and Elftman (1928), Granger and Simpson (1929), McKenna (1961), Clemens (1963b), and Deischl (MS) have been the principal contributors to our knowledge of the postcranial osteology of allotherians.

Deischl (MS) tried to differentiate various postcranial elements present in the large Hell Creek collections from the Bug Creek Anthills locality, McCone County, Montana, on the basis of size, frequency of occurrence, and morphological differences. Although the three criteria listed above are not conclusive in themselves, they are the principal means of identifying and associating allotherian teeth, limb, and girdle elements.

A few multituberculate limb bone elements have been found in the Judith River Formation. These include the distal portion of a humerus, three calcanea, and three fragmentary shafts of femora. These limb elements, in general, bear close resemblance to the specimens described by Deischl.

HUMERUS

The distal portion of a humerus, AMNH 77175, is referable to *Mesodma* (fig. 10K). Although much smaller than a fragmentary humerus of *M. thompsoni*, UMVP 1406, described by Deischl (MS, fig. 9), AMNH 77175 is morphologically similar to it in the shape of the ulnar condyle and the position of the ulnar pit. These two characteristics were used by Deischl in the differentiation of the humeri of *Cimexomys*

minor, *Mesodma formosa*, *M. thompsoni*, and *Stygimys kuszmauli*.

Width or length of AMNH 77175 cannot be estimated as the extremities are broken, but measurements taken from the entepicondylar foramen to the ectepicondyle indicate that the limb bone may belong to a juvenile of *Mesodma primaevus*, or, less likely, to an adult of *Cimexomys judithae*. Measurements of AMNH 77175 are nearly identical with those of the distal fragment of a *Cimexomys minor* humerus, UMVP 1404 (Deischl, MS, fig. 7), and would tend to support the less likely alternative, that it belongs to an adult of *C. judithae*, but a number of morphological differences exist. The ulnar pit in AMNH 77175, and in UMVP 1406 (*Mesodma thompsoni*), is situated at the proximal termination of the ulnar condyle, whereas in specimen UMVP 1404, of *Cimexomys minor*, it is situated on the anterolateral surface of the ulnar condyle. Also, in UMVP 1404, the entepicondylar foramen is situated more proximal to the ulnar condyle and not lateral to it as in AMNH 77175 and UMVP 1406. The shape of the ulnar condyle is also different in the two genera.

AMNH 77175 is incomplete; the entepicondylar region and most of the hollow shaft is missing. The shape of the ulnar condyle in this specimen is similar to that in specimen UMVP 1406, of *Mesodma thompsoni*, and the proximal termination of the condyle does not taper as in *M. formosa*.

ALLOTHERIAN FEMORA

Proximal portions of three eroded and damaged allotherian femora have been found. A right multituberculate femur (AMNH 77178) recovered by surface picking at the Ankylosaur Point locality (fig. 11K) has a relatively long and narrow neck, but lacks its head. The proximal digital fossa is deep. Most of the greater trochanter is not preserved and distally the femur is broken and the gluteal crest is weak. The lesser trochanter is relatively large. Width of the femur shaft taken below the lesser trochanter is 1.76 mm., which indicates that the femur is smaller than the multituberculate femora described by Deischl (MS, figs. 26–28).

The femur AMNH 77178, however, reveals some morphological differences from UMVP 1421, a left femur fragment of *Cimexomys minor*. Its neck is relatively longer, and the distal digital fossa is less well developed. Some resemblances to

Mesodma femora are apparent, especially in the shape and development of the lesser trochanter. Perhaps AMNH 77178 is the femur of a young individual of *Mesodma primaevus*.

CALCANEA

Only a few papers have been published discussing calcanea of Cretaceous and early Tertiary allotherians, notably those by Marsh (1889b), and Granger and Simpson (1929). The work of Deischl (MS) also needs mention. The distinctive morphology of multituberculate calcanea makes them easy to distinguish from calcanea of therians. Proximally, the groove for the tendon of Achilles is feebly developed or absent from the calcanea. The posterior astragalar facet is large and highly convex; a deep groove separates it from the sustentaculum which is situated farther distally and medially. The trochlear process also is characteristically hook-shaped and situated medioventrally. The cuboid facet is usually oval to subrounded but invariably slightly concave and distomedially positioned.

?*Mesodma primaevus* CALCANEUM

One calcaneum from the Judith River Formation, AMNH 77176, is similar to UMVP 1432, a right calcaneum of *M. thompsoni*, described by Deischl (MS, pl. 9, fig. 36). The shaft of AMNH 77176 is almost one-half the length of the calcaneum and is expanded at its proximal terminus (fig. 10J). The posterior astragalar facet is a large, knoblike, and highly convex articulating surface. It is separated from the smaller, oval sustentaculum by a deep groove, the interosseous fossa. The sustentaculum is narrowly bridged to the distomedial slightly concave cuboid facet, ventral to which is the prominent hook-shaped trochlear process. Length of the calcaneum is 4.9 mm.

Meniscoessus major CALCANEUM

A large calcaneum, AMNH 77264, is referable to *Meniscoessus* (fig. 12L). The specimen is incomplete, because it lacks most of the shaft. The calcaneum is robust, and the convex posterior articular facet is large. The sustentaculum is subrounded with a flat articulating surface, and is connected to the concave, rounded depression of the cuboid facet by a broad bridge. The foramen nutriens is present on both calcanea recovered from the Judith River Formation,

proximal to the cuboid facet, ventral to the sustentaculum, and lateral to the bridge connecting these facets.

INFRACLASS METATHERIA

SUPERORDER MARSUPIALIA

ORDER MARSUPICARNIVORA RIDE, 1964

SUPERFAMILY DIDELPHOIDEA OSBORN, 1910

FAMILY DIDELPHIDAE GRAY, 1821

SUBFAMILY DIDELPHINAE SIMPSON, 1927a

ALPHADON SIMPSON, 1927b

Alphadon SIMPSON, 1927b, p. 125.
Alphadon: CLEMENS, 1966, p. 5.

Alphadon praesagus (Russell, 1952),
new combination

Figure 13A–N

Delphodon? praesagus RUSSELL, 1952, p. 113.
Delphodon? praesagus: CLEMENS, 1966, p. 109.

HOLOTYPE: NMC 114, a right mandible with M$_3$ and roots of M$_4$.

TYPE LOCALITY: Four miles below the mouth of Berry Creek, southeast of Steveville, Alberta.

KNOWN DISTRIBUTION: Oldman Formation, Alberta; Judith River Formation, Montana.

REVISED DIAGNOSIS: A common Campanian didelphid with close similarities to the slightly smaller *A. marshi*. The type specimen, NMC 114, from the Oldman Formation, is a partial right lower mandible with M$_3$, roots of M$_4$, and an alveolus for the posterior root of M$_2$. The stylar shelf of M^3 is broad, and the stylar cusp is better developed than in most contemporary marsupials. It is separated from stylar cusp B by a short valley. Stylar cusp B is the largest stylar cusp, with a low ridge joining the only slightly higher paracone, another ridge extends to stylar cusp C. This latter elongate cusp is variously oriented, it may be inclined to the anteroposterior direction (M^1) or less inclined (M^2) or situated on the labial margin (M^3 and M^4). Cusp C is smaller than stylar cusp B but larger than stylar cusp D. A high ridge links the metastyle to the metacone. The metacone is as tall or slightly taller than the paracone. The protocone is a low cusp. The lower teeth have a crista obliqua that intersects the protoconid-metaconid wall just ventral

to the notch separating the posterior trigonid cusps.

DESCRIPTION: M¹; specimen AMNH 77344, an M¹, is assigned to *Alphadon praesagus* (fig. 13C). It is less transverse than the other upper molars. The tooth is only slightly wider than it is long and the stylar shelf is wide. Stylar cusp A is well developed but smaller than the other stylar cusps. A narrow, short valley separates it from stylar cusp B, and it is connected to the paraconule by a crest. Stylar cusp B is a large cusp with at least three distinct ridges leading from its apex. One ridge extends anteriorly, another low ridge joins the paracone, and a third trends posteriorly toward stylar cusp C. Stylar cusp C is situated centrally on the incipiently bilobate stylar shelf. Its elongate orientation is not anteroposterior, but at an angle to this direction, leaving a small, flat shelf between itself and stylar cusp B. Stylar cusp D is smaller than stylar cusp C.

The paracone and metacone are well separated by a broad valley, as in *A. marshi*, and the metacone is noticeably taller than the paracone. No anterolingual cingulum is present. Both conules are well developed. Although the roots are broken, it is possible to make out an interradicular crest that joins the lingual side of the labial roots together.

M²; an M², AMNH 77343 (fig. 13B), is relatively more transverse than M¹ but is relatively less transverse than M³. The stylar shelf of M² is asymmetrically bilobate. Stylar cusp A is situated at the anterolabial corner of the crown on an expanded shelf area, and is separated from stylar cusp B by a valley similar to that found in M¹. Stylar cusp B is well developed, and joined by a ridge to the paracone, and the cusp is farther separated from the paracone than the corresponding cusp in M¹. An indistinct ridge arises from the apex of stylar cusp B and joins the smaller stylar cusp C, situated at the stylar cleft. Stylar cusp D, although slightly worn, still appears to have been smaller than stylar cusp C. The paracone and metacone are separated by a broad valley and there does not seem to be much difference in the relative heights of these cusps. The protocone is a low cusp. The lingual portion of the crown is broken, but there appears to be a small anterolingual cingulum. An interradicular crest is present as in M¹.

M³ and M⁴; a maxilla fragment containing M³ and M⁴, AMNH 77342 (fig. 13A), has been recovered. The stylar shelf on its M³ is worn, but stylar cusp B seems to have been well developed as indicated by the labial expansion of the stylar shelf in that area. Stylar cusp A is much smaller than cusp B and is separated from it by a short valley. Stylar cusp C is smaller than cusp B, and is situated on the labial margin of the stylar shelf at the stylar cleft. Stylar cusp D is present and is smaller than cusp C. A high, worn ridge links the metastyle to the metacone, and the paracone is broken and missing. Both conules are present, and the premetaconular wing terminates at the rounded anterolingual side of the metacone. The protocone is relatively low. A short but distinct anterior cingulum is present, and extends from about the base of the paraconule to the anteroventral side of the protocone.

M⁴; few M⁴s have been found in association with other teeth of *Alphadon* and consequently their assignment to the genus is tentative. Two M⁴s of *A. rhaister* were described by Clemens (1966), and a complete maxilla with M¹–M⁴ of *A. marshi* from the upper Edmonton Formation of Alberta was described by Lillegraven.

M⁴ is smaller than M³ and is characterized by an anterolabial expansion of its stylar shelf. Stylar cusp A is present and a well-developed cingulum connects this cusp to the paraconule. Stylar cusp B is the best-developed stylar cusp. It is connected by a high ridge to the conical paracone, which is much larger and taller than the metacone. Stylar cusp C is present on the labial side of the crown and is smaller than cusp B. Posterior to cusp C, the stylar shelf rapidly narrows and forms the posterolabial part of the metacone. Both the paraconule and the metaconule are present, and the protocone is a low cusp. An anterior cingulum, similar to that found on M³, occurs on M⁴.

Russell (1952) described an incomplete lower jaw with M₃ collected below the mouth of Berry Creek, southeast of Steveville, in the Oldman Formation, as *Delphodon? praesagus*. Clemens (1966, p. 109) suggested that this molar pertained to the genus *Alphadon* but, in the absence of upper molars, the assignment could not be certain. A large number of isolated teeth and two jaw fragments with teeth, from Clambank Hollow, confirm Clemens's suggestion. This is the most common marsupial from the Judith River Formation. Dimensions of the complete lower molars are given in table 1. Fragmentary molars are useful only in establishing the relative

frequency of occurrence of *Alphadon praesagus*. Comparisons of lengths of the upper and lower molars of *A. praesagus* agree with the general principle proposed by Clemens (1966, p. 83) that in didelphoid marsupials the lengths of the "lower molars tend to be equal to or greater than the lengths of their upper counterparts."

P_3; some premolars have been found that most likely belong to *A. praesagus*. It is not possible to clearly distinguish between isolated P_2 and P_3 because they are morphologically and dimensionally very similar. Only a few differences can be made out, principally in the degree and development of the lingual and labial cingula adjacent to the posterior accessory cusp.

Specimen AMNH 77355 (fig. 13D, E) is tentatively identified as P_3 on the basis of a large anterior "spirelike" cusp (protoconid), the development of cingula that are lingual and labial to the posterior accessory cusp, and on the basis of size. The mean length of P_3 in *Alphadon marshi* is 1.75 mm. (Clemens, 1966), whereas the length of AMNH 77355 is much greater (2.4 mm.). This difference is in keeping with size of molars of *A. praesagus*, which are larger than those of *A. marshi*.

The primary cusp on P_3 is a large, transversely compressed cusp with steep anterior and more gentle posterior margins. A short anterolingual cingulum is present at the base of the cusp. The posterior accessory cusp is much smaller but well separated from the larger anterior cusp by the presence of a short valley. Two ridges, one originating from the apex of the large primary cusp, and the other from the apex of the posterior accessory cusp, terminate in this valley. Two other ridges arising from the poste-

rior accessory cusp extend lingually and labially. The lingual ridge is higher and longer than the labial one. A basal cingulum is present on the posterolabial corner of the crown. The tooth is two rooted.

DP_3; a left DP_3, AMNH 77398. is similar to the deciduous premolar figured by Clemens (1966, p. 108). This tooth is tentatively assigned to *Alphadon praesagus* on the basis of size (length 2.5 mm.). Its trigonid is anteroposteriorly elongated, and the protoconid is situated anterior to the metaconid. The talonid cusps are distinct and well separated (fig. 13K, L).

M_1; two teeth have been tentatively identified as M_1s. They are smaller but otherwise similar to M_2s.

M_2; there are at least four isolated lower molars similar in size and morphology to M_2 in the mandible of *Alphadon praesagus* (AMNH 77358, illustrated in fig. 13M, N). A comparison with UCMP 50299 and 50300, a right and left mandible, respectively, of *A. marshi* (Clemens, 1966, p. 89) reveals that they are significantly smaller but otherwise morphologically very similar to the Campanian mandible, AMNH 77358. The posterior extension of the symphysis in both Lance species, *Alphadon lulli* and *A. marshi*, is below P_2, and a similar condition is present in the Campanian mandible. A prominent mental foramen occurs ventral to M_1 in the Lance mandibles, and also in the Campanian specimen. These features confirm identification of the preserved teeth as P_3 and M_2.

The molar has a well-developed, anteriorly projecting paraconid. The paraconid is the smallest cusp of the trigonid and is well separated from the metaconid. All trigonid cusps are conical with broad bases. An anterobasal cingulum extends ventrolabially from the paraconid. The talonid is slightly wider than the trigonid, and the crista obliqua connects the prominent hypoconid to the posterior wall of the trigonid, ventral to the notch separating the protoconid from the metaconid. The hypoconulid and the entoconid are twinned, and the hypoconulid is posterior to the lingually situated entoconid. A broad cingulum extends posterolabially to the hypoconid.

M_3; an isolated M_3, AMNH 77356, is assigned to *Alphadon praesagus* (fig. 13H–J). Its trigonid is anteroposteriorly compressed, and the protoconid is the tallest cusp and is situated

TABLE 1

DIMENSIONS (IN MILLIMETERS) OF LOWER MOLARS
OF *Alphadon praesagus*

Tooth	Catalogue Number	Length	Trigonid Width	Talonid Width
M_1	AMNH 77359	2.5	broken	1.8
M_1	AMNH 77365	2.6	1.6	1.5
M_2	AMNH 77358	2.8	1.6	1.7
M_2	AMNH 77357	2.8	1.8	1.6
M_2	AMNH 77363	2.8	1.6	1.6
M_2	AMNH 77364	2.8	2.0	1.8
M_3	AMNH 77356	3.2	2.0	1.8
M_3	AMNH 77366	3.3	1.8	1.6

slightly anterior to the metaconid. The metaconid is only slightly higher than the paraconid. An anterior cingulum is feebly developed. The width of the trigonid (2.0 mm.) of AMNH 77356 is greater than that of the talonid (1.8 mm.). The hypoconid is well developed and separated from the other two talonid cusps. A prominent posterolabial cingulum is present at its base. Entoconid and the hypoconulid are elevated in position and situated close to each other. The entoconid is completely lingual in position.

Specimen AMNH 77356 and an additional M_3, AMNH 77366, resemble the type specimen of *Alphadon praesagus*. Length and width of AMNH 77356 is 3.2 mm. and 2.0 mm., respectively, whereas in the type specimen, NMC 114, the corresponding dimensions are 3.3 mm. and 2.2 mm., respectively.

M_4; an isolated molar, AMNH 77361, is probably an M_4, as based on its trigonid/talonid width ratio and on its large anteroposteriorly elongated posterior root (fig. 13F, G). The protoconid is the highest trigonid cusp, and the metaconid is equal to, or slightly taller than, the paraconid. An anterobasal cingulum is present. The hypoconid is a prominent cusp with a posterolabial cingulum, and the hypoconulid is twinned with the lingual entoconid. The crista obliqua intersects the protoconid-metaconid ridge at a point posterior to the metaconid.

Alphadon halleyi, new species

Figure 13U–W

ETYMOLOGY: Named in honor of the Warren Halley family on whose ranch most of our prospecting was done.

HOLOTYPE: AMNH 77367, a lower molar.

TYPE LOCALITY: Clambank Hollow, Chouteau County, Montana.

KNOWN DISTRIBUTION: Judith River Formation, Montana.

DIAGNOSIS: Smaller than *Alphadon praesagus* but larger than *A. lulli* from the Lance Formation. Upper molars with stylar cusp D well developed and larger than stylar cusp C; metaconule and protoconule distinct, protocone low.

DESCRIPTION: Several lower molars from Clambank Hollow show morphological differences from teeth that can be assigned to *A. praesagus*. AMNH 77367 is significantly smaller (length 2.1 mm., fig. 13U, V) than lower molars of *A. praesagus*. Its paraconid is a conical cusp

and it is slightly medial to the metaconid. The metaconid is anteroposteriorly elongated, particularly at its base, and tapers toward the apex. The protoconid is taller than the metaconid and situated anterior to it. The talonid is deep and basined and the crista obliqua is oriented in the manner characteristic of *Alphadon*. The hypoconid is a well-developed cusp, and the hypoconulid is directed posteriorly and more separated from the entoconid than in most contemporary marsupials. The width of the talonid (1.2 mm.) is equal to that of the trigonid.

A partial upper molar, AMNH 77370, is small enough to be included within *A. halleyi* (fig. 13W). The width of the crown is 1.7 mm. and it is approximately equal to the estimated length. The stylar shelf anterior to stylar cusp C is broken. Stylar cusp D is well developed and larger than stylar cusp C. The metacone is as high as the paracone and separated from it by a narrow valley. Both conules are present, and the protocone is a low cusp. *Alphadon halleyi* is a possible ancestor to the Maestrichtian *A. lulli*.

Alphadon cf. *A. rhaister* Clemens, 1966

Figure 14L–P

Alphadon cf. *A. rhaister* CLEMENS, 1966, p. 34.

The presence of a large didelphid, only slightly smaller than *Boreodon matutinus*, is suggested by two teeth in the collection. AMNH 77372 is an upper molar which resembles the teeth described by Clemens (1966, p. 15) as *Alphadon* cf. *A. rhaister* obtained from the Lance Formation of Wyoming. Another tooth, AMNH 77371, is also a large lower molar morphologically similar to teeth of *Alphadon* cf. *A. rhaister*. These two teeth are provisionally included within *Alphadon* cf. *A. rhaister*. Both teeth are morphologically different from corresponding teeth of *Boreodon matutinus*.

The status of *Alphadon* cf. *A. rhaister* is subject to question. It is unlikely that the two specimens figured by Clemens (1966, fig. 12) are in fact an "extreme in intraspecific variation" of *A. rhaister*. More probably they represent a new metatherian genus. Additional material from Clambank Hollow indicates that two taxa are present. All stylar cusps are present in AMNH 77372. Stylar cusps B, C, D are well developed, and A and E are distinct (fig. 14O–P). Stylar cusp A is small and conical, and has a cingulum leading from it to the paraconule. Stylar cusp B
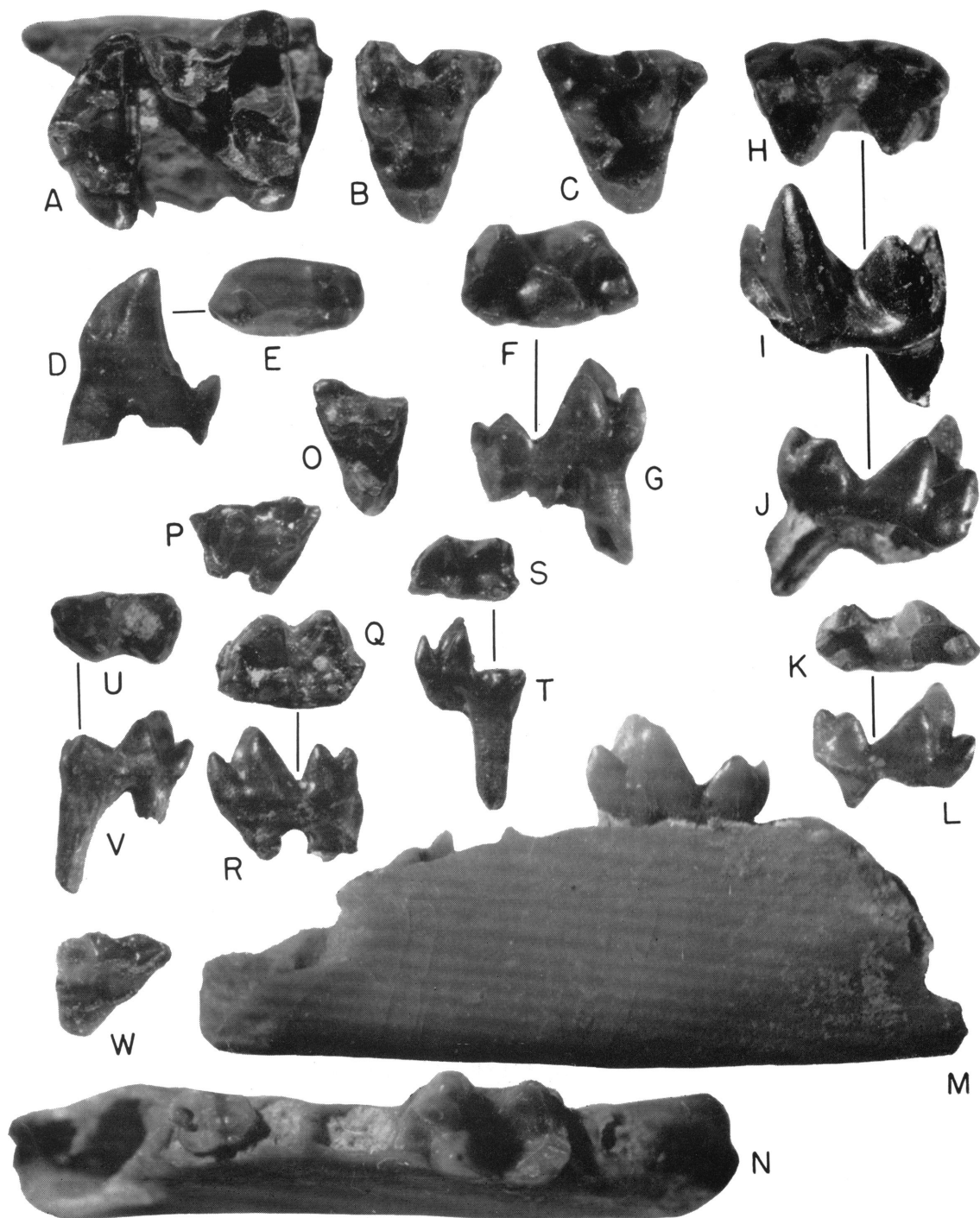
is a large anteroposteriorly elongated cusp, only slightly smaller than the paracone, and connected to the paracone by a high ridge which intersects cusp B anterolingually. Cusp C is smaller than cusp B and is situated slightly lingual to it. Stylar cusp D is larger than cusp C. A ridge extends from the posterior metastyle to the metacone. The stylar shelf is broad and the labial margin relatively straight. The paracone and metacone are separated by a broad valley, and the metacone is the larger of the two cusps. The disposition of the crests arising from the paracone is characteristic. The anterior crest, originating from the metacone, is anterolabially directed toward stylar cusp C and meets the posterior crest originating from the paracone at a high angle. This condition is uncommon in species of *Alphadon* and *Boreodon*. Both paraconule and the metaconule are present. The protocone is a low cusp with relatively short ridges leading to the conules. Although its size and greater length/width ratios would indicate that it is a DP^3 of *Boreodon*, this is unlikely. The tooth, AMNH 77372, is highly molariform, its stylar shelf is straight and very different from the condition seen for *Boreodon* upper molars. Its cusps are well developed and anteroposteriorly elongate, its metacone is higher than the paracone, and both conules are present. Also, the tooth bears little resemblance to AMNH 77386, considered here to be a DP^3 of *Boreodon*, and also to DP^3 of *Didelphodon vorax* (Clemens, 1966, p. 70).

The following features set this group of teeth apart: large size, straight stylar shelf, prominent development of all stylar cusps, particularly cusps B and D, the presence of a ridge linking cusp B with the paracone, a metacone slightly higher than the paracone, a stylar shelf narrower than in *Boreodon*, metacone and paracone ridges directed posteriorly, W-shaped, bulbous teeth

usually less transverse than in other marsupials, and finally the presence of a low protocone.

Specimen AMNH 77371 from Ankylosaur Point is probably an M_4 of this species (fig. 14L–N). Its trigonid is anteroposteriorly compressed, the paraconid is as high as the metaconid, and the protoconid is broken. A short anterobasal cingulum is present. The talonid consists of a prominent hypoconid and a closely twinned, posterolingually placed, hypoconulid and entoconid. The orientation of the crista obliqua is more lingual than in molars of contemporary marsupials, and connects the hypoconid with the posterior margin of the metaconid. This results in narrowing of the talonid (talonid width 1.9 mm., trigonid width 2.4 mm.). The valley separating the protoconid and hypoconid is wide and shallow. A posterolabial cingulum encircles the hypoconid. The posterior root is larger than the anterior.

Characteristics of AMNH 77371, a presumed M_4, and *Boreodon* molars are compared in table 2.

M_4, AMNH 77371, is the expected size for M_4 of *Eodelphis browni* Matthew (1916), the type and only species of the genus. *Eodelphis browni* is based on a single jaw, and resembles *Alphadon* as much as it does *Boreodon* or *Didelphodon*, genera to which it is usually assigned.

DISCUSSION: Cretaceous marsupials are differentiated primarily on the degree and development of the stylar cusps of the upper molars, and on the orientation of the crista obliqua on the lower molars. Other features used are the relative heights of the paracone and metacone, the width of the stylar shelf, and the relative development of the conules. The stylar shelf in *Alphadon* consists of five cusps of which cusp B is the best developed. Cusp B is separated from the parastyle (cusp A) by a valley. It is also connected to the slightly higher paracone by a high ridge. Cusp C is larger than cusp D. Specific

FIG. 13. *Alphadon praesagus* (Russell), new combination. A. AMNH 77342, occlusal view of right maxilla with M^3, M^4. B. AMNH 77343, occlusal view of right M^2. C. AMNH 77344, occlusal view of right M^1. D. AMNH 77355, lingual view of right P_3. E. Occlusal view. F. AMNH 77361, occlusal view of left M_4. G. Lingual view. H. AMNH 77356, occlusal view of left mandible with M_3. I. Labial view. J. Lingual view. K. ?*Alphadon praesagus* (Russell), new combination, AMNH 77398, occlusal view of DP_3. L. Lingual view. M. *Alphadon praesagus* (Russell), new combination, AMNH 77358, lingual view of right mandible with M_2 and P_3 talonid. N. Occlusal view. O. ?Pediomyidae, AMNH 77375, occlusal view of right upper molar. *Pediomys clemensi*, new species. P. AMNH 77373, occlusal view of left upper molar. Q. AMNH 77376, occlusal view of right lower molar. R. Lingual view. S. AMNH 77377, occlusal view of right lower molar. T. Lingual view. *Alphadon halleyi*, new species. U. AMNH 77367, occlusal view of left lower molar. V. Lingual view. W. AMNH 77370, occlusal view of left upper molar. All × 10.

TABLE 2

Comparison of Morphological Features of AMNH 77371(?M_4) with Corresponding Features of *Boreodon* Molars

AMNH 77371	Boreodon
1. Paraconid crescentic, anteroposteriorly compressed	1. Cylindrical
2. Anterior cingulum short	2. Better developed, continuous on labial side, marked by rugosities
3. Hypoconulid and entoconid close together	3. Farther apart
4. Crista obliqua intersects protoconid-metaconid wall posterior to metaconid, and lingual to the valley separating the metaconid and protoconid	4. Crista obliqua intersects posterior to protoconid, labial to the valley separating the metaconid and protoconid
5. Talonid very narrow and basined (talonid width 1.9 mm., trigonid width 2.4 mm.)	5. Talonid broad

differences between the Lance species of *Alphadon* were made chiefly on the basis of size (Clemens, 1966). The orientation of the crista obliqua of the lower molars has been used for generic differentiation (Clemens, 1966).

The three Campanian species of *Alphadon*, *A. praesagus*, *A. halleyi*, and *Alphadon* cf. *A. rhaister*, are ancestral to later Maestrichtian forms. *A. halleyi* is poorly known and similar in size to *A. lulli*. *Alphadon* cf. *A. rhaister* may be synonymous with *Eodelphis browni* but this cannot be shown conclusively as yet. Among the commonest marsupials in the two faunas are *A. praesagus* in the Campanian and *A. marshi* in the Maestrichtian. Apart from a size difference between the two forms, other morphological dissimilarities seem to be present, but these are at a specific, rather than at a higher level. The most obvious of these differences are in the structure of the lower premolars, structure of the upper molar stylar shelf, and the morphology of M^4. Clemens's (1966) and Lillegraven's (1969) detailed discussions of the ancestors and descendants of *Alphadon* greatly increase knowledge about marsupial origins, and also about their Tertiary history.

At the time Clemens published on the Lance marsupials little was known about the earlier Campanian fauna. Clemens rightly pointed out that *Boreodon*, although primitive in certain respects, is more advanced than *Alphadon*. *Boreodon*, however, shares with *Alphadon* common features, such as the great width of the stylar shelf, and the prominence of stylar cusp B and prominence of the ridge connecting this cusp to the paracone.

Holoclemensia texana (Slaughter, 1968b, 1968c) from the Albian Trinity Formation of Texas seems appropriate as an ancestor for all the Campanian marsupials.

PEDIOMYIDAE SIMPSON, 1927a

The term Pediomyinae was used first in the discussion of the Hell Creek fauna by Simpson (1927a). Clemens (1966) raised the subfamily to familial status by proposing the name Pediomyidae, but restricted it to include only a single genus, *Pediomys*.

PEDIOMYS MARSH, 1889b

Pediomys Marsh, 1889b, p. 89.
Synconodon Osborn, 1898, p. 171.
Protolambda Osborn, 1898, p. 172.
Pediomys: Clemens, 1966, p. 34.

Pediomys clemensi, new species

Figure 13P–T

ETYMOLOGY: For W. A. Clemens, University of California, Berkeley.

HOLOTYPE: AMNH 77373, an upper molar (M^2 or M^3).

TYPE LOCALITY: Clambank Hollow, Chouteau County, Montana.

DISTRIBUTION: Judith River Formation, Montana.

DIAGNOSIS: A small Campanian pediomyid most closely similar to *P. elegans* from the Maestrichtian. Stylar cusp A (parastyle) and D are well developed. Cusp B is feebly formed and is situated posterolabial to the paracone, close to the equally small stylar cusp C.

DESCRIPTION: Two labial fragments of upper molars, AMNH 77373 and 77374, are similar to each other. Specimen AMNH 77373, however, has conules (fig. 13P), whereas the other, AMNH 77374, lacks conules and is slightly larger. The stylar shelf in the specimens is not

bilobate and the stylar shelf is weakly developed. Cusp A is better developed than in the other contemporary metatherian genera, and a crest connects it to the paraconule. Cusp B is small and posterolabial to the paracone. The stylar shelf narrows labial to the paracone, and the external rim of the paracone extends to the shelf. Cusp C is posterior to cusp B and slightly larger. The stylar shelf widens posteriorly just lingual to the prominent stylar cusp D, which is the largest stylar cusp. The metastyle is weakly developed and linked to the metacone by a high ridge. The paracone is situated more labial to the metacone and is about the same height.

There are five lower molars that can be referred to *Pediomys* by use of the criterion developed by Clemens (1966), which is the position of the crista obliqua on the posterior wall of the trigonid. The crista obliqua in pediomyid molars intersects the trigonid wall at the protoconid, a position labial to the usual position in other Cretaceous marsupials. These pediomyid lower molars are small, ranging in length from 1.8 to 2.6 mm. The paraconid is a slender, conical, anteriorly directed cusp in AMNH 77377 (fig. 13S, T). It is only slightly smaller than the metaconid and well separated from it. The protoconid is anterior and taller than the metaconid, and has a small anterobasal cingulum. The talonid is wide, and the hypoconid is a large, high cusp, which is well separated from the twinned hypoconulid and the broken entoconid. The hypoconulid is a small pointed cusp, directed posteriorly and linked to the entoconid by a short ridge. A broad cingulum is present on the posterolabial side of the crown. AMNH 77376 (fig. 13Q, R) is a larger lower molar than AMNH 77377.

?PEDIOMYID

Figure 13O

The pediomyid affinities of the right upper molar, AMNH 77375, from Clambank Hollow, are indicated by the prominence of stylar cusp D, the narrowing of the stylar shelf labial to the paracone, and the presence of an anterolingual cingulum which often occurs as a variation in later Maestrichtian species, particularly in *P. elegans*. AMNH 77375 (fig. 13O) is small and as transverse as M³ of *P. elegans* Clemens (1966, p. 37). A ridge connects the apex of the paracone to the parastyle.

It is likely that AMNH 77375 belongs with the other small lower and upper molars assigned to *Pediomys clemensi* but such an association cannot be demonstrated.

DISCUSSION: *Pediomys clemensi* is a relatively rare member of the fauna from the Judith River Formation, and is closest morphologically to *P. elegans* from the Lance Formation of Wyoming. *Pediomys elegans* is the Maestrichtian species that Clemens (1966, p. 34) regarded as most primitive of those then known. Only one species of *Pediomys* appears to be present as ascertained from the upper molars. Unfortunately, there is not a single complete upper molar of *Pediomys*; thus there is no way of determining whether the three upper molar fragments belong to the same species. The pediomyid stylar shelf is radically different from that of other marsupials not only in the nonuniform width of the stylar shelf but also in the relative development of the stylar cusps. Buccal to the paracone, the stylar shelf narrows considerably and is little more than a narrow cingulum. The shelf in some later Maestrichtian species may even be absent and discontinuous in this area. Posteriorly, the shelf widens buccal to the metacone. Stylar cusp B is feebly formed and situated closer to cusp C than to cusp A. Cusp D is the largest stylar cusp. The paracone is more labial than the metacone.

STAGODONTIDAE MARSH, 1889c

The family Stagodontidae was proposed by Marsh (1889c, p. 178) for the inclusion of *Stagodon nitor*, the genotypic species, and *S. tumidus*. The type specimen of *S. nitor*, a worn premolar, however, was later shown by Clemens (1966, p. 55) to belong to *Didelphodon* Marsh (1889b). In accordance with the rules established by the International Code of Zoological Nomenclature [Art. 23(d) and 40], Clemens (1966) retained the family Stagodontidae in preference to the other family group names, Thlaeodontinae Cope (1892), Didelphodontinae Simpson (1927b), and Thlaeodontinae Hay (1930).

The family Stagodontidae as redefined by Clemens (1966, p. 55) consists of "Large, late Cretaceous, North American marsupials in which the trigonids are anteroposteriorly shortened and paraconid and protoconid are of subequal height, and higher than the metaconid. Epitympanic sinus is large and of complex
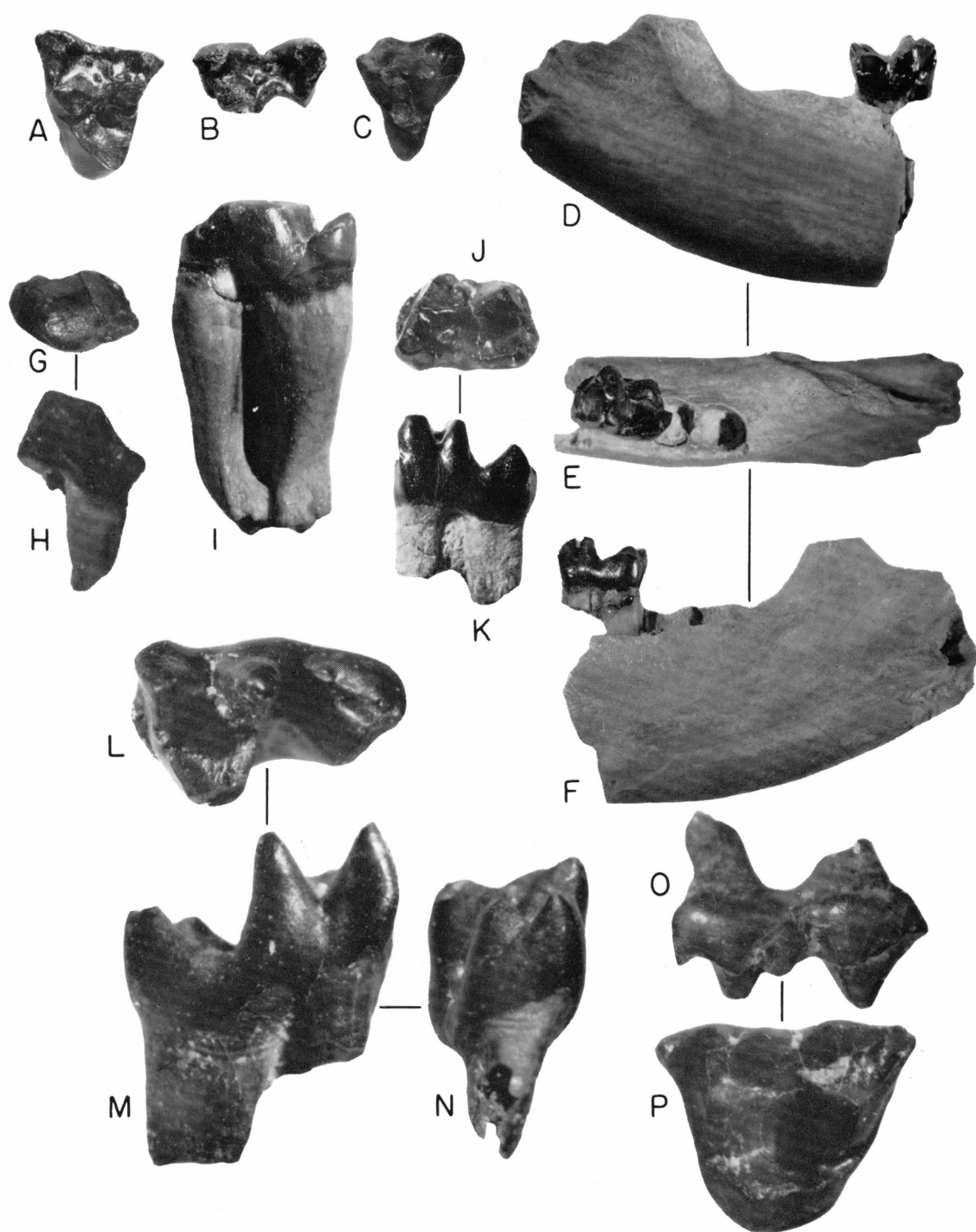
structure. Alisphenoid lacks an entoglenoid process. Bullae are well developed, apparently formed of both alisphenoid and petrosal elements." *Boreodon* and *Didelphodon* are included in the family Stagodontidae in the present paper, but *Eodelphis* is excluded.

<div align="center">

BOREODON LAMBE, 1902

Boreodon matutinus Lambe, 1902

Figure 14A–K

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Boreodon matutinus LAMBE, 1902, p. 79.
Boreodon matutinus: STANTON AND HATCHER, 1905, p. 128.
Cimolestes cutleri WOODWARD, 1916a (May), p. 30; 1916b (Sept.), pp. 525–528.
Eodelphis cutleri: SIMPSON, 1928, p. 148; 1929, pp. 128, 129; 1930, pp. 29–32.

TYPE LOCALITY: Near Steveville, Red Deer River Valley, Alberta.

DISTRIBUTION: Judith River Formation, Montana; Oldman Formation, Alberta.

REVISED DIAGNOSIS: A large didelphoid with robust upper teeth which have wide, thick, prominent stylar shelves, becoming progressively more asymmetrically bilobate from M¹ to M³, and stylar cusp B D A=C E.

DESCRIPTION: although many isolated lower teeth and mandibles of *Boreodon* have been recovered in the Oldman Formation (Russell, 1952), the upper dentition has yet to be described. At least four upper teeth are here assigned to the genus on the basis of size, morphology, and a similarity to those of *Didelphodon*. The only complete upper tooth is an M¹ and possibly a DP³. Other teeth referable are the labial and lingual halves of either M² or M³. DP³, AMNH 77386, is a large, worn, but almost complete DP³ of *Boreodon* (fig. 14C). The width of the crown is 3.6 mm. and this is approximately equal to the estimated length of the tooth. The stylar shelf is broken posteriorly and the most prominent cusp is stylar cusp B. The parastylar area is expanded. The paracone is

higher than the closely situated metacone and is linked to stylar cusp B by a ridge. Both conules are present. The protocone is anteroposteriorly compressed.

M¹; a worn, but complete M¹, AMNH 77385 (fig. 14A), has been recovered. Its stylar shelf is incipiently bilobate with a long posterior wing. Stylar cusp A is small and connected by a ridge to cusp B, which is the largest stylar cusp. Two ridges originate from the apex of cusp B, one connecting it to the paracone and the other to cusp C. Cusp C is situated at the stylar cleft or slightly anterior to it. Three small cuspules lie on the wide stylar shelf labial to the paracone and metacone and between stylar cusps C and D. Cusp D is elongated anteroposteriorly, and a small cuspule is present slightly anterior to it. The shelf is not expanded labial to cusp D as it is in the posterior molars. Cusp E (metastyle) is connected to the metacone. The conules are well developed, the paracone is distinctly larger and is connected to stylar cusp A by a cingulum. The protocone is a low cusp. Although roots are not present it is possible to make out an interradicular crest linking the lingual sides of the two labial roots.

M² or M³; a tooth fragment, AMNH 79383, is probably the labial part of an M², but it could be part of an M³ (fig. 14B). Its stylar shelf is asymmetrically bilobate, and stylar cusp A is small and well separated from cusp B. Stylar cusp B is not connected to the paracone by a ridge and is situated farther from that cusp than in M¹. Stylar cusp C is situated slightly anterior to the stylar cleft, and it is smaller than stylar cusp D. As in M¹, three cuspules are present on the broad stylar shelf lingual to cusps C and D. Stylar cusp D is relatively well developed and the shelf area labial to it is expanded. A similar condition is found on molars of *Didelphodon*.

Another tooth fragment, AMNH 77381, is the lingual portion of either an M² or an M³. Both its conules are present, but the paraconule is the better developed. Pre-paraconular and post-

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FIG. 14. *Boreodon matutinus* Lambe. A. AMNH 77385, occlusal view of right M¹, × 5. B. AMNH 77383, occlusal view of left upper molar, × 5. C. AMNH 77386, occlusal view of right DP³, × 5. D. AMNH 77394, labial view of mandible with M₃ and alveoli for M₄. E. Occlusal view. F. Lingual view. All × 2½. G. AMNH 77387, occlusal view of right P₂. H. Lingual view. Both × 5. I. AMNH 77388, lingual view of right P₃, × 5. J. AMNH 77393, occlusal view of right lower molar. K. Lingual view. Both × 5. *Alphadon* cf. *A. rhaister* Clemens. L. AMNH 77371, occlusal view of left lower molar (probably M₄). M. Lingual view. N. Posterior view. All × 10. O. AMNH 77372, labial view of left upper molar (probably M¹). P. Occlusal view. Both × 10.

paraconular wings diverge at a greater angle than the pre-metaconular and post-metaconular wings. The protocone is a low cusp.

P_2; the partial tooth, AMNH 77387, is probably a P_2 (fig. 14G, H). It is large, robust, and double rooted (length 4.0 mm., width 2.4 mm.) with two cusps. The anterior cusp is massive and its apex is worn. The posterior accessory cusp is not so sharply differentiated from the anterior cusp as in P_3 but is connected to it by a ridge. I consider the type specimen of *Boreodon matutinus* Lambe (1902) to be P_2 of the species generally known as *Eodelphis cutleri* Simpson (1928) and not a P_3 as was suggested by Russell (1952).

P_3; this premolar is larger than P_2 and M_1. The anterior cusp of AMNH 77388 is so worn that it is not possible to make out many details (fig. 14I). The large cusp is narrow transversely with a worn ridge leading from its apex to its valley separating the posterior accessory cusp. The latter is a small, pointed cusp with two ridges arising from its apex, one extending toward the anterior cusp, the other extending labially. P_3 is two rooted, and the posterior root is larger than the anterior.

M_2; although AMNH 77393 (length 4.4 mm., fig. 14J, K) is nearly the same length as M_2 in the mandible, BM M11532, described by Woodward (1916) as the type specimen of *Cimolestes cutleri*, the tooth is narrower (2.8 mm.). Width of M_2, BM M11532, is 3.5 mm. The trigonid is anteroposteriorly compressed, the paraconid is a large, lingual cusp. The metaconid is slenderer and smaller than the paraconid in AMNH 77393. The protoconid, although worn, is the largest cusp of the trigonid and is situated slightly anterior to the metaconid. The rugose anterobasal cingulum is well developed but does not extend to the labial side of the protoconid. Width of the trigonid is equal to that of the talonid.

The hypoconid is the largest cusp in the talonid and well separated from the hypoconulid and entoconid. The hypoconulid is broken, but a cingulum encircles its labial side. The crista obliqua intersects the posterior wall of the trigonid slightly labial to its center. The posterior root is larger than the anterior.

M_3; a mandible, AMNH 77394, found during the first year of prospecting (1964) fortunately has an unquestionable contact with an M_3 found from the same locality. This specimen, AMNH 77394, from the Judith River Formation, consists of the posterior part of the ramus with the associated M_3 and the alveolus for M_4. M_3 (fig. 14D–F) is larger (length 5.5 mm.) than AMNH 77393, which is discussed above. But the trigonid is similarly anteroposteriorly compressed, and the paraconid is slightly taller than the slender metaconid. The talonid cusps are similar in the two teeth, except that the hypoconulid is directed posteriorly. The anterobasal cingulum extends to the labial side and is not so restricted as in AMNH 77393. All articular surfaces are broken away from the mandible (fig. 14D–F). The masseteric fossa is deep and well defined. The greatest transverse width of the dentary is at M_4, 6.8 mm., but in BM M11532 it is 8.0 mm.

DISCUSSION: *Boreodon matutinus* was a species proposed by Lambe (1902) on the basis of a large lower premolar (NMC 1887) from the Oldman Formation, near Steveville, where most of the Campanian mammals from Alberta were collected (Russell, 1952). Although Lambe (1902) placed the specimen in the Multituberculata, Matthew (1916) pointed out its therian affinities. Simpson (1929) was the first to comment on its didelphid relationships. Its didelphid relationships were supported by Russell (1952), who suggested that the holotypic premolar of *Boreodon matutinus* was probably a P_3 of "*Eodelphis*" *cutleri*. Clemens (1966) in his study of the Lance marsupials also considered this likely. No author, however, formally put *Eodelphis* in synonymy with *Boreodon*. The chief reasons for not synonymizing the two was because the isolated premolar, NMC 1887, which is the holotype of *Boreodon matutinus*, was worn and fragmentary, and also because there was lack of information on the kind and size of other marsupials that may have been present in the Judith River and Oldman formations. Also, little notice was taken of an edentulous jaw referred to *B. matutinus* by Stanton and Hatcher (1905). This lower jaw is similar to the many mandibles assigned to "*Eodelphis*" *cutleri* (Russell, 1952).

The holotype of *Boreodon matutinus*, NMC 1887, is a P_2 not a P_3 as was suggested by Russell (1952) and accepted by Clemens (1966). The reasons for considering NMC 1887 as P_2 rather than P_3 are the following. Dimensionally, the tooth is nearly identical with P_2 (AMNH 77387, with a length of 4.4 mm.) rather than P_3 (AMNH 77388, with a length of 5.6 mm.).

Morphologically, the posterior median ridge on NMC 1887 arises from the apex of the anterior cusp and extends to the small posterior accessory cusp as in P_2 (AMNH 77387).

The anterior cusp is sharply separated from the distinct posterior accessory cusp in AMNH 77383, and the posterior median ridge descends only to the deep valley separating the two cusps. Differences that exist between specimens NMC 1887 and AMNH 77387 are mainly produced by wear.

The question of synonymy of *Cimolestes cutleri* Woodward (1916), based on a right mandible with P_3, M_2, and M_3, BM M11532, and *Eodelphis browni* Matthew (1916) based on a left mandibular ramus with a complete but worn dental series, AMNH 14169, has been repeatedly discussed in the literature (Simpson, 1928, 1929, 1930; Russell, 1952; and Clemens, 1966). The specimens on which these genera are based were collected close to each other, and from the same stratigraphic horizon, near Little Sandhill Creek, near Steveville, Alberta. The description of *Cimolestes cutleri* Woodward (1916) was published on May 30 of that year, whereas that of *Eodelphis browni* Matthew (1916) was published on July 24. Woodward's (1916) reference of specimen M11532 to *Cimolestes* was based on its resemblance to *C. curtus*. Later the specimen was used by Simpson (1927b) as the holotype of *Diaphoradon*, and still later it was put in synonymy with *Didelphodon vorax* by Clemens (1966). Simpson (1928, 1929) in his review of the Mesozoic mammals, commented on the similarity of the two forms and finally (Simpson, 1929) put *E. browni* Matthew (1916) in synonymy with *Cimolestes cutleri* Woodward. Russell (1952) agreed with Simpson's point of view on the basis of the many mandibles at his disposal. More recently, however, Clemens (1966, p. 59) has shown that *Eodelphis browni* Matthew (1916) and *Cimolestes cutleri* Woodward (1916) are not conspecific, as there are differences in incisors and premolars. The present material from the Judith River Formation includes an upper molar of *Alphadon* cf. *A. rhaister*, AMNH 77372, and a lower molar, AMNH 77371, comprising a large species consistent in morphology with the holotype of *Eodelphis*. There is no really satisfactory reason for *Eodelphis browni* and "*Cimolestes*" *cutleri* being considered to be congeneric except for their similar size. This implies that "*Cimolestes*" *cutleri* does not belong to any described

genus except for the long abandoned *Boreodon* Lambe (1902), with which Simpson (1929), Russell (1952), and Clemens (1966) have suggested a close relationship. None of these authors, however, put the material referred to "*Eodelphis*" *cutleri* in synonymy with *Boreodon matutinus* because of the eroded and worn nature of the type specimen of *B. matutinus*, now established as P_2. Evidence provided by the premolars (AMNH 77387 and 77388) from the Judith River Formation indicate that *Boreodon matutinus* Lambe (1902) is conspecific with "*Eodelphis*" *cutleri* (Woodward, 1916). Consequently, material previously referred to *Eodelphis cutleri* is put in synonymy with *Boreodon matutinus* Lambe (1902). Alternatives to this solution would be referral of "*Cimolestes*" *cutleri* to *Didelphodon*, or the erection of a new generic name to substitute for *Boreodon*. Neither of these alternatives seems useful.

A few upper teeth have been discovered that may belong to *Boreodon*. Description of a DP^3 and of upper molars is the first attempt to establish the morphology of the upper teeth of this genus. Upper teeth have not been found in association with lowers, and the referral of the teeth is based on their large size and similarity to those of *Didelphodon vorax*. *Boreodon matutinus* of the Campanian apparently occupies the same ecolological niche that *D. vorax* does in the Maestrichtian. Both are large omnivorous marsupials with carnivorous tendencies.

Clemens (1966) has discussed the possible ancestry of the stagodonts *Boreodon* and *Didelphodon*. He rightly pointed out that the wide stylar shelf with many cusps, especially the prominent stylar cusp B, are primitive features and indicative of a lineage that must have originated sometime before the Campanian and after the advent of the Forestburg therians. The pediomyids differ from the stagodontids in the same way as they differ from the various species of *Alphadon*, namely in the narrowing of the stylar shelf labial to the paracone, the absence of the feeble development of cusp B, and of the ridge linking that cusp with the paracone. The lower molars of *Didelphodon* and *Boreodon*, however, differ from those of the other Cretaceous marsupials by a more prominent anterobasal cingulum, and by more anteroposterior compressed trigonids, on which the metaconid was the shortest and most slender cusp. The paraconid and protoconid are of the same height and

form an effective shearing blade. The talonid is relatively wider than in *Alphadon* and the orientation of the crista obliqua is more labial.

SUBCLASS THERIA

INFRACLASS EUTHERIA

ORDER INSECTIVORA

SUBORDER PROTEUTHERIA ROMER, 1966

FAMILY LEPTICTIDAE GILL, 1872

SUBFAMILY GYPSONICTOPSINAE VAN VALEN, 1967

GYPSONICTOPS SIMPSON, 1927a

Gypsonictops SIMPSON, 1927a, p. 6.

TYPE SPECIES: *Gypsonictops hypoconus* Simpson, 1927a.

KNOWN DISTRIBUTION: Campanian, Judith River Formation, Montana; Maestrichtian, Lance Formation, Wyoming; Hell Creek Formation, Montana; Upper Edmonton Formation, Alberta.

REVISED DIAGNOSIS: These insectivores are medium-sized relative to contemporary mammals, and have submolariform posterior premolars. P^3 of *Gypsonictops lewisi* has a separate metacone. Both precingulum and postcingulum are present in the more molariform specimens. P^4 is quite molariform, with separated paracone and metacone. Upper molars have narrow stylar shelves, buccally placed paracone and metacone, a stronger postcingulum than precingulum, and a well-developed parastylar area. M^2 is more transverse with better developed lingual cingula than M^1. P_3 has a basined talonid bearing two to three cusps, and a strong posterolingual ridge arising from the protoconid and representing the metaconid. P_4 has a separate protoconid and metaconid and a basined talonid composed of three cusps, with a very poorly developed paraconid. Lower molars are of the standard primitive eutherian pattern, and have elevated trigonids.

Gypsonictops lewisi, new species

Figure 15

ETYMOLOGY: For Captain Meriweather Lewis, pioneer explorer of the Missouri River.

HOLOTYPE: AMNH 77429, a right P_4.

TYPE LOCALITY: Clambank Hollow, Chouteau County, Montana.

KNOWN DISTRIBUTION: Campanian, Judith River Formation.

DIAGNOSIS: Similar in most respects to *Gypsonictops hypoconus* and *G. illuminatus*, but with less molariform P^3 and P_2, and a more molariform P_3.

DESCRIPTION: Lower dentition: P_2; two teeth are probably P_2s referable to *G. lewisi*. Their size and morphology sets them apart from the posterior premolars of a reconstructed dental series. Their resemblance to those of placental mammals is indicated by presence of a small metaconid that is not fully separated from the long and slender protoconid, and a shallow talonid bearing two cusps. Anterior lower premolars of Cretaceous metatherians have a protoconid that is linked to a posterior accessory cusp by a median ridge, and cingula that may be developed on either side of this ridge.

A double rooted tooth, AMNH 77426 (fig. 15A–C), is smaller than P_3. The specimen lacks its anterolabial part and the anterior root. The protoconid is a large cusp with a steep anterior margin. A small metaconid arises from the lingual cingulum and is not well separated from the protoconid. Buccal to the protoconid there is a well-developed labial cingulum that terminates at the labial accessory cusp of the talonid. This latter cusp is also linked to the apex of the protoconid by a shear ridge. There is at least one other cusp lingual to, and higher than, the labial accessory cusp. The talonid basin is shallow.

The identification of the tooth as a P_2 is based primarily on occlusal relationships and comparison with P_3. Although present, the talonid is too shallow to be functional and probably occluded with a P^2 which had a small protocone without root support. Unfortunately, P^2 of *Gypsonictops lewisi* has not been found. P_2 of *G. lewisi* is smaller than P^3, and it lacks the lingual ridge arising from the posterior side of the protoconid apex.

P_3; reference to specimen AMNH 77428 as P_3 is based in part on the occlusal relationship of the tooth and in part on the development and degree of separation of the major cusps. This submolariform tooth has an anterior cingulum extending from the anterolingual side of the protoconid ventrally to the anterolabial side (fig. 15D–F). A small cuspule, more a basal

swelling than a distinct cusp, is present at the paraconid position, and probably represents that cusp. The most prominent cusp is the protoconid, which is high and conical with convex anterior slopes. Two ridges arise from the posterior border of the protoconid; one extends from its lingual slope to the heel of the tooth, and the other extends more medially and joins the two major cusps of the talonid. A groove is present on the posterior wall of the protoconid between the two ridges. The metaconid is not clearly visible, represented only by a swelling on the lingual ridge at a point one-half the height of the protoconid.

The talonid is basined and deeper than that of the supposed P_2. Two cusps are situated close together and probably correspond to the hypoconid-hypoconulid. A ridge bearing a small cuspule arises from the more lingual of these cusps and probably represents the entoconid. A shallow cingulum marks the posteroventral border of the tooth on the labial side.

P_3 of *Gypsonictops lewisi* is distinct from P_3 of *G. petersoni*, *G. illuminatus*, and *G. hypoconus*. The Campanian specimen has a better developed and more basined talonid which bears two cusps. Simpson (1951, pp. 10, 17) commented on the P_3 "being simple and abruptly different from the molariform P_4."

P_4; three teeth can be considered P_4s on the basis of their similarity to similarly placed teeth in jaws of *Gypsonictops hypoconus* from the Lance and Hell Creek formations, CM 11657, and UMVP 2316, 2317, and 2311. A distinct paraconid is present on the anterobasal cingulum in front of the groove separating the metaconid from the protoconid in AMNH 77429 (fig. 15G–I). Metaconid is not fully separated from the protoconid and in all three specimens at hand, it is a slender, conical cusp that is much smaller than the protoconid. A high ridge links the posterior wall of the protoconid to the hypoconid. An anterior ridge arises from the protoconid apex, and joins the paraconid ventrally in AMNH 77429. This is similar to the condition seen in the P_4, UMVP 2311.

The talonid of P_4 is basined and well developed, and all three cusps are represented. The hypoconulid is separated from the hypoconid, and it is only slightly smaller than the hypoconid. The entoconid is a feebly developed cusp situated on the lingual ridge of the talonid anterior to the other cusps. Labial to the crista

obliqua, the crown extends ventrally, and a distinct cingulum is present on the posteroventral border.

P_4 of *G. lewisi* is distinguishable from that of other species because it has a stouter, broader-based protoconid, it has less separation of the metaconid from the protoconid, and it has a less-developed talonid.

M_1 and M_2; there are five lower molars that are either M_1 or M_2. The criterion used here to distinguish between molars is the tendency for the talonid to get progressively narrower (transversely) toward M_3. On this basis, two teeth are probably M_1s and the remainder M_2s. One tooth, AMNH 77432 (fig. 16J–L), is tentatively identified as M_1, and follows the basic therian pattern. Its trigonid is anteroposteriorly compressed, and its smallest cusp is the anteriorly projecting paraconid, the worn apex of which is only slightly labial to the apex of the metaconid. Its paraconid is connected to the protoconid by a ridge. A short anterobasal cingulum is present labial to the paraconid. The metaconid is a well-developed cusp and slightly smaller than the protoconid. The talonid of AMNH 77432 is basined and wide, and the hypoconid is large with a short cingulum extending down its posterior wall. The hypoconulid is well separated from the adjacent talonid cusp and is medial in position. The entoconid appears to be the highest talonid cusp. Of the two roots, at the enamel base, the anterior one is more anteroposteriorly compressed.

M_2; specimen AMNH 77434 (fig. 15M–O) is probably an M_2. It differs from M_1 by having a shorter, more anteroposteriorly compressed, and narrower talonid.

M_3; a possible M_3 is specimen AMNH 77438 (fig. 15P–R) because its talonid is elongated anteroposteriorly and is much narrower in comparison to the trigonid width of either M_1 or M_2. The anterobasal cingulum flattens to form a small shelf. The trigonid is similar to those of the other molars but the talonid is very different. It narrows considerably at the point where the crista obliqua intersects the protolophid (metaconid-protoconid ridge). The three cusps of the elongate talonid are well developed, the hypoconulid and the entoconid are situated closer to each other.

UPPER DENTITION: A reconstruction of the upper dentition of *Gypsonictops* was made by Simpson (1951) and had been accepted until
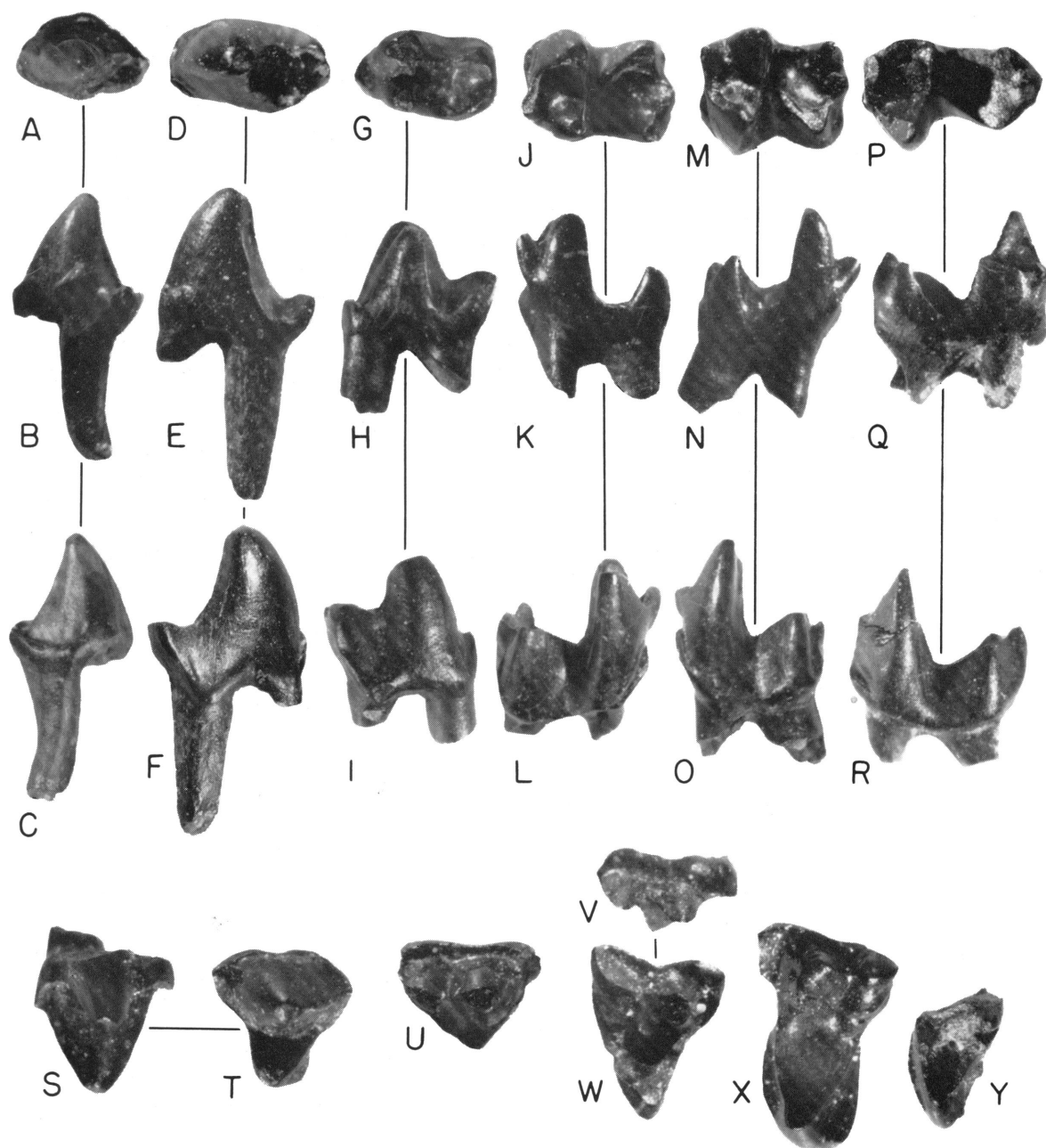
FIG. 15. *Gypsonictops lewisi*, new species. A. AMNH 77426, occlusal view of right P_2. B. Lingual view. C. Labial view. D. AMNH 77428, occlusal view of right P_3. E. Lingual view. F. Labial view. G. AMNH 77429, occlusal view of right P_4. H. Lingual view. I. Labial view. J. AMNH 77432, occlusal view of right M_1. K. Lingual view. L. Labial view. M. AMNH 77434, occlusal view of left M_2. N. Lingual view. O. Labial view. P. AMNH 77438, occlusal view of left M_3. Q. Lingual view. R. Labial view. S. AMNH 77442, lingual view of left P^3. T. Occlusal view. U. AMNH 77451, occlusal view of right P^4. V. AMNH 77452, labial view of broken right M^1. W. Occlusal view. X. AMNH 77456, occlusal view of left M^2. Y. AMNH 77457, occlusal view of left M^3. All $\times 10$.

recently when doubts about the identity of P^4 were expressed by McKenna (1960) and Slaughter (1968a). According to these authors, P^4 figured by Simpson (1951) is most probably P^3. P^4, then, is probably an even more molariform tooth. McKenna based his conclusions on a fragmentary maxilla with P^2, P^3, and roots of P^4, UCMP 51386. This specimen is currently under study by W. A. Clemens in his survey of the eutherians of the Lance Formation. The holotype maxilla of *Gypsonictops illuminatus* Lillegraven (1969), UAPC 2447, with P^3 to M^3, from the upper part of the Edmonton Formation, conclusively demonstrates that McKenna (1960) and Slaughter (1968a) are correct in their interpretation. *Gypsonictops* material from the Judith River Formation, although clearly ancestral to the Maestrichtian species, differs from them in structure of its premolars. Premolars of *G. lewisi* are less molariform than those of later species.

P^3; there are seven teeth in the collection that I consider to be P^3 rather than P^2 because of the occlusal relationship with the submolariform lower anterior premolars, particularly P_2, and because it is unlike P^2 in the *Gypsonictops* maxilla, UCMP 51386.

Specimen AMNH 77442 (fig. 15S, T) is subtriangular in shape. Its most prominent cusp is the large, conical, broad-based paracone. Labial slopes of the paracone descend into a well-developed ectocingulum particularly in the parastylar and metastylar regions. The stylar shelf narrows at the ectoflexus where the paracone forms the buccal edge of the crown. A sharp crest, the metacrista, extends posteriorly from the apex of the paracone to the metastyle. Just anterior to the metastyle a slight swelling is present on the stylar shelf. The protocone is much smaller than the paracone with steeper lingual slopes. A definite postcingulum is present in three of the seven complete teeth and in two of these three teeth a smaller anterior cingulum is also present. Two ridges link the protocone to the paracone, but conules are absent. These three teeth have roots with rounded cross sections, and the most lingual root is placed beneath the protocone.

P^3 is submolariform because the paracone is undivided and has a sharp metacrista, and because the protocone has root support and lingual cingula. P^3s of the later species of *Gypso-*

nictops are more molariform, chiefly because the metacone is more separated from the paracone. Separation of the metaconid on the lingual side of the paraconid is seen in a specimen of *Gypsonictops*, UMVP 2316, from the Hell Creek beds. P_3 of *G. lewisi* is approximately at the same stage of molarization as P^3.

P^4; there is only one tooth, AMNH 77451 (fig. 15U), that is considered P^4. The reasons for this are not its similarity to P^4 of *G. hypoconus*, as identified by Simpson (1951) (now considered to be P^3), but because of its degree of molarization relative to P^3 and M^1, and because of its occlusal relationship to P_4. This specimen, AMNH 77451, lacks the area lingual to the paracone and metacone. A trace of a paraconule was present but during preparation this region broke away and thus the protoconule is not visible in the illustration. The tooth is more molariform than P^3, as indicated by the greater separation of the paracone from the metacone. These cusps, however, are undivided at the base and only a narrow valley separates their apexes. Absence of a prominent ectoflexus and less transverseness also imply that it is less molariform than the upper molars. A small protocone with root support, a paraconule, and both precingulum and postcingulum must have been originally present. P^4 of *G. lewisi* closely resembles P^3 of *G. hypoconus*. The parastylar area is more prominent than the metastylar area and no ectoflexus is present. The apex of the metacone is separated from the larger paracone by a short centrocrista and is connected to the metastyle by a metacrista.

M^1; three teeth have been identified as M^1s. They are more molariform than the supposed P^4, less transverse, with less prominent lingual cingula than M^2. The stylar shelf extends above the entire labial margin of the crown in AMNH 77452 (fig. 15V, W), and the parastylar area is well developed with a prominent parastyle connected to the paracone by a short, low ridge. The metastyle is joined to the metacone by a metacrista. The paracone is taller than the metacone and separated from it by a deep valley. Conules are present, the preparaconular wing of the paraconule is bounded anteriorly by a ridge extending anterobuccally, and a prominent premetaconular wing is also present. The protocone is a narrow, thin cusp with nearly vertical lingual slopes. The preprotocrista and the postprotocrista join the paraconule and the

metaconule, respectively. The postcingulum is larger than the precingulum and bears a worn area representing the hypocone.

M^1 of *G. lewisi* is similar to the upper molar, USNM 5044, figured by Simpson (1951, fig. 2b).

M^2; there is only one worn but complete M^2 (AMNH 77456, fig. 15X). It is distinguished from M^1 by having a narrower stylar shelf with a more anterobucally expanded parastylar region, by being shorter and more transverse, and by fuller development of the precingulum and the postcingulum.

The paracone and metacone are set buccally, and the precingulum is better developed than on M^1 and extends from a point just ventral to the paraconule, to the anterolingual side of the protocone. The postcingulum, bearing a hypocone, is even larger than the precingulum, extending from a point ventral to the base of the metacone, and terminating on the posterolingual side of the protocone. The tooth is three rooted, and its lingual root is very compressed anteroposteriorly. Its labial roots are small in comparison and have rounded cross sections.

M^3; the third upper molar is known by a lingual fragment, AMNH 77457 (fig. 15Y). Its paracone is missing, but the metacone is a small, conical cusp. The paraconule is better developed than the metaconule, and the postcingulum is broken in the specimen.

DISCUSSION: Patterson's (1956) description of mammals at the eutherian-metatherian grade has greatly increased our knowledge about placental origins. Mammal remains recovered from the Trinity Sandstone of Texas, of Albian age (Lower Cretaceous), indicate that they had already differentiated into placental and marsupial types, as based on presence or absence of submolariform premolars. Submolariform premolars indicate a specialization unknown in marsupials (Slaughter, 1968a, 1968b, 1968c). The next record of eutherians in North America is during the Campanian, and the new material from the Judith River Formation is the principal source of this information. During the Maestrichtian, placentals increased in diversity in various western states of North America, and at the close of the Cretaceous represent the orders: Insectivora, Deltatheriidia (*sensu* Van Valen, 1966), Condylarthra, and Primates (Sloan and Van Valen, 1965; Van Valen and Sloan, 1965).

Gypsonictops was first described by Simpson (1927a) on the basis of isolated upper teeth from the Lance Formation. These teeth had originally been assigned by Marsh (1892c) to *Batodon* and *Telacodon*. Simpson (1951) brought together previous information on this Cretaceous insectivore and made a hypothetical reconstruction of its dentition. This reconstruction was based partly on upper teeth assigned to *Gypsonictops* and partly on lower teeth assigned to *Euangelistes*. Later, it was found that probably two different species were involved, because the dimensions of the lower teeth were considerably larger than those of the upper teeth. Two species were thus retained, *G. hypoconus*, based on the smaller upper molars, and *G. petersoni*, based on the larger lower molars.

Although the hazards of such a hypothetical reconstruction were obvious to Simpson (1951), subsequent finds have shown that, at least in the association of upper and lower dentitions, he was correct, but owing to misidentification of P^3 as P^4 and of P^4 as an upper molar Simpson was led to believe that *Gypsonictops* possessed simple, not incipiently molariform, P^1–P^3.

The placental mammal, *G. lewisi*, from the Judith River Formation, is represented by about 45 teeth, comprising slightly over 5 per cent of the total mammal teeth recovered, and a calcaneum quite similar to that of *Prodiacodon* (Szalay, 1966). It probably belongs to *Gypsonictops* and is currently under study by W. Nelson. The majority of the isolated teeth are broken or worn. None of the edentulous jaws can be referred with any certainty to the species. Still, by comparison with other eutherian material in the Maestrichtian of Alberta and Montana, it has been possible to identify the series of teeth, P_2 to M_3, and P^3 to M^3. Teeth anterior to P_2 and P^3 may be present in the collection, but are as yet unidentified. If the reconstruction of the dentition of *G. lewisi* proves to be correct, then the Campanian species differs from those of the Maestrichtian, at least at the species level.

Absence of *Cimolestes* and other members of the Palaeoryctidae from the Judith River Formation lends some credence to the viewpoint that deltatheridians were an immigrant group that invaded the coastal plains east of the rising Rocky Mountains sometime during the Maestrichtian. *Gypsonictops* is considered here to be a primitive placental and, by virtue of its presence in pre-Maestrichtian sediments, is a likely ancestor for some later North American eutherians.

ENVIRONMENT OF THE FAUNA

GEOGRAPHIC AND TECTONIC SETTING

AT THE CLOSE of the Cretaceous the geologic history of the western interior of the United States is a record of the intermittent pulsations of Laramide Orogeny, and of the accompanying deposition of sediments eastward toward the Pierre Sea. During the late Cretaceous, two transgressive and three regressive phases of the sea, approximately cyclical in nature, can be traced (Weimer, 1960). The Milk River Formation of Alberta, and the Judith River and Hell Creek formations of Montana, and their regional equivalents are continental coastal plain deposits which contain terrestrial vertebrate faunas. These coastal plain regressive sediments are separated by marine transgressive shales which, in north-central Montana, in ascending order, are the Marias River, Claggett and Bearpaw shales. Strandline deposits such as the Fox Hills Sandstone mark the transition from marine to nonmarine sedimentation, and are particularly prominent at the base of the continental wedges during the regressions. The sequence of fluctuations of late Cretaceous seas has been traced by Reeside (1957), Weimer (1960), and Williams and Burk (1964).

During the 15 million years of the Campanian, the sea retreated three times and transgressed twice. During the late Santonian, the Colorado Sea probably extended to the Arctic as a broad epeiric seaway. The first impulse of the Laramide Orogeny occurred in the early Campanian, with the resulting seaward movement of the shoreline. Strandline and freshwater deposits consisting of fluviatile sands and silts with occasional coals and lignites were laid down in southern Alberta and comprise the Milk River Formation. Farther south, in Montana, shallow-water marine sediments of the Eagle Sandstone were being deposited contemporaneous to the Milk River Formation. Westward, near the disturbed belt of Alberta and Montana, continuous continental deposition prevailed from the time of the final withdrawal of the Colorado Sea to the time of the transgression of the Bearpaw Sea.

Another transgression of the sea took place in the early Campanian, resulting in the deposi-tion of marine shales known as the Claggett Shale on the United States side, and the Pakowki Shale on the Canadian side of the international boundary. The transgression, however, was minor relative to the one before it and the one that was to come after. Pakowki Shale, when traced westward to the foothills of southern Alberta, thins to a few feet (Lerbekmo, 1961). The next major upheaval of the Cordilleras, in the middle Campanian, resulted in deposition of about equivalent clastics, but because of differences in geographic locations these are called the Belly River Formation, the Foremost and Oldman formations of southeastern Alberta, and the Judith River Formation in Wyoming. The Two Medicine and Belly River formations are closer to the source area of the clastics than are the others and for this reason their sediments are coarser, thicker, and of continental origin. Farther east, the sediments become progressively brackish and less freshwater in nature until they interfinger with the marine shales of the Pierre Sea (Tourtelot, 1962). The last major transgression of the sea took place in the late Campanian, and blanketed vast areas of the Great Plains region with deposits that are known in Alberta and Montana as the Bearpaw Shale. The western limit of this sea is demarcated by Weimer (1960, p. 17) and Williams and Burk (1964, p. 187).

By the very nature of the deposits laid down during the slow regressive phases of the sea, the contacts with overlying nonmarine sediments are time-transgressing and, accordingly, the boundaries between such formations become progressively younger in the direction of the regression. An example is cited by Lerbekmo (1963) in which coal seams are found at the base of the Belly River Formation of the Alberta foothills along the Bow River. Farther south the seams are found progressively higher in the stratigraphic section so that near the Drywood River some 150 miles away, they occur at the top of the formation. Transgressive cycles such as that of the Bearpaw Shale appear to have occurred more rapidly than the regressive cycles and consequently the contacts between the nonmarine and overlying marine beds are more likely to be synchronous.

With reference to the fossil localities in the Judith River Formation at the mouth of the Judith River, it can be said that they represent the deposits of a fairly large stream or river, flowing eastward or southeastward on a coastal plain toward a sea not more than 100 miles distant (Weimer, 1960). The detritus was obtained primarily from the emerging highlands some 400 or 500 miles away. Few studies have been made in Montana which trace the source of the sediments of the Judith River Formation. Petersen (1961) inferred on the basis of a heavy mineral study made in central Montana that the source area lay to the west, that its climate was semiarid, and that it had moderate relief. McMannis (1965) and Viele and Harris (1965) described thick sequences of volcanic sediments in western and southwestern Montana that are roughly contemporaneous with those of the Judith River Formation. That area was probably the source of at least part of the volcanic ash beds (bentonites) that occur extensively throughout the Campanian sequence. The Boulder Batholith also may have been introduced during this time (Knopf, 1964).

A number of petrographic studies have been carried out recently in Alberta on fine and coarse clastic sediments of the Belly River Formation in an attempt to determine their source, environment of deposition, and stratigraphic relationships (Lerbekmo, 1961, 1963). Lerbekmo (1963, p. 79) stated that the major terrains of the source area of the Belly River Formation consisted of shelf sediments, or metamorphic and volcanic rocks. Based on the settling velocity of large crystals in a bentonite occurring along the Drywood River, Lerbekmo estimated that the contributing volcanoes must have been as close as 100 miles.

CRETACEOUS CLIMATE AND PALEOTEMPERATURE

Measurement of paleotemperatures from the isotopic composition of oxygen in calcite of marine invertebrates was initiated by Urey et al. (1951) and Epstein et al. (1951). Since that time a number of studies have dealt with the reconstruction of late Mesozoic climates (Lowenstam and Epstein, 1954; Bowen, 1961a, 1961b, 1961c, and 1963). Results of the last author seem to indicate that there were two temperature maxima, one during the Albian and the other during the Coniacian-Santonian. The climate

started cooling in mid-Campanian time with a steady trend of decreasing temperatures toward the close of the Maestrichtian. Studies in Germany and Poland (Bowen, 1961a), in Australia (Bowen, 1961b), and in Europe and India (Bowen, 1961c) indicate synchronous worldwide temperature fluctuations during the same times. Samples from Japan, however, apparently do not conform to the general pattern.

Unfortunately no such studies have been undertaken with Pierre Shale belemnites and pelecypods, and the climate during the late Cretaceous in the Great Plains region is best inferred by the ecologic consideration of the contemporary floras.

FLORA

The macroflora of the Judith River Formation was originally studied by Knowlton (1900, 1905, 1915, and 1919). The flora of the Oldman Formation was studied by Dawson (1886). As the formations are essentially equivalent, and the plants were collected in a relatively restricted area, the floras are pooled (table 3).

Pollen from the Judith River Formation is currently under study by Robert Shoemaker. Although the study is incomplete, samples taken from the upper part of the Claggett Shale, the Judith River Formation, and the Bearpaw Shale indicate a greater diversity of plant types than those found in the Lance and Hell Creek formations of Wyoming and Montana. The material consists of 211 distinct pollen types, 135 of which have been assigned to previously described species and 76 of which are believed to be new. Based on ecological considerations, Shoemaker (personal commun.) traced the floral changes that occurred during the deposition of the Judith River Formation. He found that coastal species predominate at the base and top of the formation, whereas continental types occur in the middle. *Fide* Shoemaker (personal commun.) the climate was somewhat similar to that of the cool and wet rain forest of eastern Costa Rica today.

Hall and Norton (1967) have traced climatic changes across the Cretaceous-Tertiary boundary in eastern Montana, based on a study by Fischer (1960) on the relation of biotic diversity to latitude and temperature. These authors believed that the decrease in floral diversity in similar lithologic units and under similar conditions of preservation is indicative of relatively

TABLE 3

COMPOSITE LIST OF PLANT TAXA KNOWN FROM THE JUDITH RIVER AND OLDMAN FORMATIONS

Flora	Judith River Formation	Oldman Formation
Lemna	—	X
Nelumbium	—	X
Nelumbo	—	X
Nymphaea	X	—
Pistia	X	X
Trapa	X	X
Cyperacites	X	—
Araucarites	X	—
Berchemia	X	—
Betula	X	X
Betulites	X	—
Carpites (?)	X	—
Cercidiphyllum	X	—
Cunninghamites	X	—
Damara	X	—
Diospyros	X	—
Dryopteris	X	—
Osmunda	X	—
Phyllites	X	—
Platanus	X	X
Populites	X	—
Populus	X	X
Quercus	X	—
Sapindus	X	—
Sequoia	X	X
Taxodium	X	—
Thuja	X	X
Viburnum	X	X
Acer	—	X
Carva	—	X
Ginkgo	—	X
Pityoxylon	—	X
Podocarpites	—	X
Taxites	—	X
Ulmus (?)	—	X

TABLE 4

NUMBER OF POLLEN TYPES PRESENT IN VARIOUS PALEOCENE AND CRETACEOUS FORMATIONS

Formation		Number of Pollen Types
Paleocene	Lebo	41
	Tullock	56
Cretaceous	Hell Creek	100
	Fox Hills (marine)	36
	Bearpaw (marine)	33
	Judith River	211

Formation were first described in a comprehensive manner by Meek (1876). Later, Stanton (1905) reviewed the gastropods and pelecypods from the Judith River Formation. Recently, Russell (1964, pp. 8–9) has compiled a faunal list of the nonmarine molluscs of the Cretaceous formations of northwestern North America. His list is presented in part below.

Judith River Formation

  Pelecypoda

    Anodonta propatoris White

    Plesiellptio subspatulatus (Meek and Hayden)

    P. abbreviatus (Stanton)

    Rhabdotophorus senectus (White)

    Fusconaia? danae (Meek and Hayden)

    Quadrula? primaevus (White)

    Q.? superawensis (Stanton)

    Sphaerium planum Meek and Hayden

    S. recticardinale Meek and Hayden

  Gastropoda

    Valvata montanensis Meek

    Viviparus conradi (Meek and Hayden)

    Lioplacodes vetula (Meek and Hayden)

    L. judithensis (Stanton)

    Hydrobia subconica Meek

    Goniobasis sublaevus (Meek and Hayden)

    G. invensta (Meek and Hayden)

    G. gracilenta Meek

    G.? omitta (Meek and Hayden)

    G.? subtortuosa (Meek and Hayden)

    Menetus amplexus (Meek and Hayden)

    Physa copei White

    Aplexa subelongata (Meek and Hayden)

    A. atava (White)

    Vitrina obliqua Meek and Hayden

cooler climates. They have documented such a decrease in the number of pollen types in the Maestrichtian and Paleocene sediments of eastern Montana. Shoemaker's study furnishes additional data on floral diversity in the Campanian and older sediments. The data from Hall and Norton (1967) and Shoemaker (personal commun.) were obtained from samples that are comparable and were processed in the same laboratory. These data are given in table 4.

FRESHWATER MOLLUSCS

The freshwater molluscs of the Judith River

During this investigation, lenses of sediment containing freshwater molluscs were found to be common in the upper part of the Judith River Formation. The shells are usually crushed and fragmentary and occur as molds or steinkerns. All the forms listed below were obtained from the principal mammal locality at Clambank

Hollow. The species identified are the following:

Pelecypoda
  Unio sp.
  Sphaerium planum (Meek and Hayden)
Gastropoda
  Goniobasis sp.
  G.? subtortuosa (Meek and Hayden)
  Lioplacodes judithensis (Stanton)
  Viviparus sp.
  ?Valvata montanensis Meek

COMMUNITY STRUCTURE

Reconstruction of paleocommunities is an attempt to reestablish the interrelationship of past animals and plants to their environment and to assign the animal components to their interpreted ecological niches and feeding habits. Although such a reconstruction is an approximation of reality, it nevertheless serves as a useful unit with which to work, as it results from the synthesis of diverse geological and biological fields. Analysis of community structure not only involves compiling a complete faunal and floral list with the relative abundance of taxa, but also involves a knowledge of physical conditions, such as climate, paleogeography, and environment of sediment deposition. The community can be visualized as a living, dynamic system, deriving its energy from complex food-chain patterns and its longevity from the stability of interacting forces. Study of paleocommunities through time and space provides an insight into the mechanics of change in animal populations.

Paleocommunities differ from living communities in several respects. They represent accumulation of diverse elements over a span of time extending in some cases to many years, in contrast to neoecological studies where observations apply to shorter periods of time. Community structure of past animals and plants is analyzed on the basis of several elements from one or many localities. Because quarries of late Cretaceous age in Montana and Wyoming are mainly in stream deposits, the fossils are a mixture of contemporary but different communities in a combined death assemblage. Some of these contemporary communities are close to the basin of deposition, whereas others are more distant. The criteria for distinguishing proximal and distal communities have been discussed by Shotwell (1955, 1958) and are based primarily on frequency of individuals, representation of the various elements, and the fragility of the bones. Under-representation and over-repre-

sentation of genera is dependent on size sorting, differential preservation, and proximity to the basin of deposition. Throughout the late Cretaceous, the percentage of members of the stream and streambank community is remarkably constant from locality to locality (Estes, 1964) although significant changes take place in the megaterrestrial and arboreal communities.

Estes (1964) followed in part the procedures adopted by Shotwell (1955, 1958), and reconstructed the Lance Formation community of lower vertebrates based on the minimum number of individuals. Other late Cretaceous and early Tertiary communities have been described in a similar manner (Sloan, 1964; Sloan and Van Valen, 1965; and Van Valen and Sloan, 1966). Relative frequency of abundance of various taxa, in the present study, as indicated by the minimum number of individuals, is based on data from Clambank Hollow and Clayball Hill (table 5).

Three contemporary vertebrate communities are recognized in the Judith River Formation. These have been designated as the stream and streambank community, the megaterrestrial community and the arboreal community (fig. 16). These are differentiated on the basis of the ecological niches of community members. The stream and streambank community is a proximal aquatic community and the best represented. The other two terrestrial communities inhabit a multistory rain forest whose presence is indicated by macrofloral and pollen samples from the sediments of the Judith River Formation in the area. The megaterrestrial community comprises the larger herbivorous and carnivorous dinosaurs occupying the understory and forest floor, whereas the arboreal community consists of mammals and lizards occupying the canopy. The components of each community are listed and their relative abundances indicated by rectangular areas in the community structure diagram. The chart is so organized that energy flow is essentially upward, i.e., toward the larger carnivores. Some energy flow does occur between the two terrestrial communities, but in general terms, the three communities are broadly independent in subsequent history.

The stream and streambank community comprises more than 50 per cent of the minimum number of individuals represented. Dominants in the sense of Estes (1964, p. 164) are *Kindleia*, the discoglossids, *Lisserpeton*, *Scapherpeton* and

TABLE 5
RELATIVE FREQUENCY OF INDIVIDUALS, OR PARTS
THEREOF, FROM THE JUDITH RIVER FORMATION

Faunal list	No. of Counted Elements	Min. No. of Individuals
Myledephas bipartitus	35	1
Kindleia fragosa	44	25
Belonostomus longirostris	6	2
Lepisosteus occidentalis	3	3
?Paralbula sp.	44	1
Teleost indet.	21	1
Discoglossid A	8	8
Discoglossid B	4	4
Discoglossid C	4	4
Pelobatid	1	1
Lisserpeton bairdi	10	10
Scapherpeton tectum	15	15
Habrosaurus dilatus	8	8
Prodesmodon copei	4	4
Opisthotriton kayi	12	12
Basilemys sp.	17	1
Trionyx sp.	23	1
?Baenid	8	2
Champsosaurus sp.	4	4
Leidyosuchus canadensis	157	3
Brachychampsa montana	31	1
?Sebecosuchian	12	1
Chamops segnis	87	14
Leptochamops denticulatus	31	17
Exostinus lancensis	1	1
cf. Xenosauridae	1	1
Peltosaurus piger	5	3
Parasaniwa wyomingensis	6	6
Paraderma bogerti	1	1
Deinodon horridus	56	2
Dromaeosaurus albertensis	164	3
Paronychodon lacustris	10	1
Troodon formosus	33	1
Kritosaurus sp.	700	5
Procheneosaurus altidens	14	1
?Stegoceras validus	63	2
Thescelosaurus cf. *T. neglectus*	13	1
Ceratopsidae gen. et sp. indet.	33	3
Palaeoscincus costatus	6	2
Edmontonia sp.	8	1
Cimexomys judithae	14	2
Cimexomys magnus	3	2
Mesodma primaevus	56	3
Cimolomys clarki	62	11
Meniscoessus major	19	4
Cimolodon sp.	1	1
Alphadon praesagus	34	3
A. halleyi	3	1
A. cf. *A. rhaister*	2	1
Pediomys clemensi	6	1
Boreodon matutinus	23	2
Gypsonictops lewisi	45	6

Opisthotriton. Kindleia is the single best represented genus in the Judith River Formation and its frequency of occurrence is comparable to that in the Lance Formation. Cranial elements assigned to this genus indicate the presence of immature as well as mature individuals. Frequency of the carnivorous *Lepisosteus*, however, is low. Of fish that are not primarily freshwater, *?Paralbula* sp. and *Myledephas* have a common but lower frequency of occurrence than *Belonostomus*. This probably is the result of collecting bias, as the estimate on *Belonostomus* is based on jaws and not on isolated teeth. Teleost vertebrae of various sizes are abundant but they are probably under-represented because of their fragility. *Lonchidion* and *Ischyriza*, which are common in the Oldman, Mesaverde, Lance, and Hell Creek formations, have not been found in any of the Judith River Formation quarries. Conspicuously rare in the fauna is *Acipenser*, a form that had originally been described from the Judith River Formation (Stanton and Hatcher, 1905; and Estes, 1964, p. 12). Sturgeons are quite common in the majority of late Cretaceous stream communities.

Dominance of anurans which comprise approximately 14 per cent of the streambank community is another contrast between the Judith River and Lance formations. The frogs appear to be generically distinct from those of the Maestrichtian Lance fauna and closer to those described from the Morrison Formation of Wyoming (Hecht and Estes, 1960). The scapherpetonids, *Lisserpeton* and *Scapherpeton*, are well represented only because of the durability of their atlas vertebrae. Estimates on the minimum number of individuals based on other elements produce drastically reduced figures. *Opisthotriton* is more common than *Habrosaurus*. The remainder of the fluvial community is composed of active, piscivorous, semiaquatic reptiles and turtles. Turtles appear to be under-represented mainly as a result of the fragmentary nature of the carapace and plastron bones, making positive generic identification impossible. Structure of the stream and streambank community has remained remarkably stable throughout the fluvial deposits of the late Cretaceous and early Paleocene in central and eastern Montana (Van Valen and Sloan, 1965) and in Wyoming (Estes, 1964).

Members of the megaterrestrial community comprise only 13 per cent of the total number of

Fig. 16. The vertebrate communities of the Judith River Formation.

individuals represented. This is to be expected from a distal community composed primarily of large saurischian and ornithischian dinosaurs living in forested interfluve areas. The presence of worn, shed teeth, and delicate egg shell fragments, however, indicate that dinosaurs must have spent a considerable part of their time close to the river. Hadrosaurs, now regarded as active terrestrial herbivores rather than semi-aquatic forms (Ostrom, 1964), form the bulk of the Judith River Formation ornithischians, but they certainly could have swum or waded across small rivers. The Ceratopsidae are only half as common as ornithischians and the Nodosauridae are even less so. The theropods are well represented by four genera. The most common of these is the small active carnivore, *Dromaeosaurus*. The megaterrestrial community shows a progressive decline in the numbers and variety of dinosaurs from the Campanian to the Maestrichtian. The hypsilophodont *Thescelosaurus* is found in the Judith River Formation as well as in the Lance Formation. It appears, however, to be much more common in the Campanian. It has been generally regarded as an arboreal form. An analysis of the skeleton of *Hypsilophodon* by Peter Galton (personal commun.) indicates that this cannot be the case.

The estimation of the minimum number of individuals for the various dinosaur groups poses a problem. First, as dinosaurs form part of the distal community, they will in general be underrepresented relative to other communities. Second, worn teeth of the ornithischians are less diagnostic than those of saurischians and usually only a subfamilial assignment can be made. Last, in any estimation of the minimum number of individuals the absolute number of teeth in the jaw is not so important as the number of teeth shed during the time it took for the accumulation of the bone concentration. Tentative figures compiled on the basis of number of lateral and vertical tooth rows show that ornithischians are much more common than saurischians, which agrees with the census of the skeletons of the Oldman Formation dinosaurs made by Dale Russell (1967).

The microterrestrial and arboreal community is composed mainly of mammals and lizards. Birds and insects were undoubtedly part of this system. Allotherians comprise 58.8 per cent of the total number of mammals present. Cimolomyids are more common than ectypodontids, a situation that contrasts sharply with that found in later mammal communities, where the reverse is true. Incidentally, both *Cimolomys* and *Meniscoessus* are smaller than their Maestrichtian descendants of the Lance and Hell Creek formations of Wyoming and Montana. *Cimolodon* is extremely rare and may have belonged to a more distal community. Only specific differences exist between the Campanian and the Maestrichtian multituberculates, and the Judith River Formation forms undoubtedly occupied niches similar to those of the Lance. As pointed out by Van Valen and Sloan (1966, p. 269) ecological niches were relatively broad in the late Cretaceous and were probably occupied by multituberculates in a manner similar to some present-day rodents. The multituberculates must have lived closer to the site of deposition as is attested by numerous but fragile post-cranial elements. Marsupials are less diversified than those in the Lance Formation. The metatherians of the Judith River Formation are clearly ancestral to later Maestrichtian forms. *Alphadon* is the most common and the least specialized; *Pediomys* is rare and represented by a single species, whereas *Boreodon* is a large omnivorous, or possibly carnivorous marsupial, close to the Maestrichtian *Didelphodon*. Eutherians are represented by a single species of the insectivore *Gypsonictops*, *G. lewisi*, in contrast to the greater placental diversity in the Maestrichtian. No deltatheridians (*sensu* Van Valen, 1966) have been recovered from the Judith River Formation and their absence may be a result of an inadequate sample, or the fact that deltatheridians had not as yet immigrated to the area. Current work in the Oldman and Upper Edmonton formations of Alberta will increase knowledge about the history of the group.

Study of Campanian vertebrate communities of Montana reveals a number of features. The stream and streambank communities underwent little change from the Campanian to the end of the Paleocene in Montana and adjacent states despite the major changes in temperature and flora. The megaterrestrial, microterrestrial, and/or arboreal communities, however, were progressively modified from the Campanian to the end of the Maestrichtian. There was greater floral diversity and a greater variety of dinosaurs in the Campanian than later. Beginning with the cooling trend that started in the late Campanian, there was a decline in the number of

species of plants, and this was associated with rapid reduction in variety of dinosaurs within a 2 million year interval. Mammals, however, were stable throughout this time interval until the close of the Cretaceous when three new orders of mammals were added, presumably by immigration. The added forms were condylarths (Sloan and Van Valen, 1965), primates (Van Valen and Sloan, 1965) and deltatheridians (*sensu* Van Valen, 1966).

CONCLUSIONS

1. THE JUDITH RIVER FORMATION of Montana and its regional equivalents in Alberta and Wyoming were deposited as a result of a late regressive phase of the Pierre Sea during the middle Campanian.

2. The Judith River Formation is roughly equivalent to the Foremost and Oldman formations of the southern plains of Alberta. The formations thicken westward.

3. Geochronologic methods used in dating the regression of the Bearpaw Sea indicate that the regression started between 72 and 74 million years ago. The age of mammal localities in the Judith River Formation, at the mouth of the Judith River, is considered to be 75 ± 2 million years.

4. Prior to the present study, the vertebrate fauna of the Judith River Formation was poorly known with the exception of fish, turtles, and dinosaurs. Screening and acid-etching methods has resulted in the recovery of a large and varied microvertebrate fauna consisting of mammals, lizards, salamanders, and frogs.

5. *?Paralbula* sp. is the only occurrence of a new genus of fish to be reported from the Judith River Formation and it is similar to material recently collected from the Oldman Formation of Alberta.

6. Anurans comprise 14 per cent of the stream and streambank community. They appear to be at least generically distinct from Maestrichtian forms and closer to types of the Jurassic Morrison Formation.

7. Salamanders are as diversified as in the later Lance and Hell Creek Formations of Wyoming and Montana, and are specifically indistinguishable.

8. Lizards were well represented, although the Lance genera, *Meniscognathus*, *Haptosphenus* cf. *Gerrhonotus*, *Colpodontosaurus*, *Palaeosaniwa* (originally reported from the Oldman Formation), *Litakis*, and *Cuttysarkus* have not been identified in the present collection.

9. *Hadrosaurs* are better represented than ceratopsians.

10. *Thescelosaurus* cf. *T. neglectus* is reported for the first time in the Judith River Formation.

11. Theropods are represented by *Deinodon horridus* and the smaller *Dromaeosaurus albertensis*;

coelurids by *Troodon formosus* and *Paronychodon lacustris*.

12. Dinosaur egg shell fragments show three major patterns of external sculpturing with minor variations. The shell structure closely resembles that of shell fragments from the North Horn Formation (Maestrichtian) of Utah.

13. There are some significant size changes between the Judith River Formation allotherians and their Lance Formation descendants. *Cimexomys judithae* and *Mesodma primaevus* are slightly larger than their descendants, *Cimexomys minor*, *Mesodma formosa*, and *M. thompsoni* from the Lance and Hell Creek formations of Wyoming and Montana. *Cimolomys clarki* and *Meniscoessus major*, however, are smaller than *Cimolomys gracilis*, *Meniscoessus conquistus*, *M. robustus*, and *M. borealis*.

14. Cimolomyids are relatively more abundant than ectypodontids in the Judith River Formation in contrast to the situation in the Lance and Hell Creek formations.

15. *Alphadon praesagus* is probably ancestral to *A. marshi*, and *A. halleyi* to *A. lulli*. *Alphadon* cf. *A. rhaister* is a large form comparable in size to *Boreodon matutinus* and similar to some specimens recovered from the Lance Formation of Wyoming. It may prove to be conspecific with *Eodelphis browni*.

16. *Pediomys clemensi* is known from six fragmentary teeth and is close to *P. elegans* from the Maestrichtian.

17. *Boreodon matutinus* is not considered congeneric with *Eodelphis browni*. The name *Boreodon matutinus* is retained for all teeth previously referred to *Cimolestes cutleri*.

18. *Gypsonictops lewisi* is the only eutherian species in the Judith River Formation and differs specifically from the Maestrichtian species of *Gypsonictops* in the less molariform nature of the premolars.

19. Three communities are distinguished in the Judith River Formation: the stream and streambank, the megaterrestrial, and the microterrestrial, and/or arboreal communities. The stream and streambank community is stable in comparison to the megaterrestrial community, which consists of carnivorous and herbivorous dinosaurs occupying the understory and forest

floor. The microterrestrial and/or arboreal community comprises the mammals and lizards.

20. The megaterrestrial community under-goes great modification in the decrease of the number and variety of its dinosaur taxa from the Campanian to the close of the Cretaceous.

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