MULTIUBERCULATE MAMMALS FROM THE WAHWEAP (CAMPANIAN AQUILAN) AND KAIPAROWITS (CAMPANIAN, JUDITHIAN) FORMATLONS, WITHIN ANDENEAR GRAND StAIRCASE-ESCALANJE NATIONAL MONUMENT, SOUTHERN:UTAH


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# MULTITUBERCULATE MAMMALS FROM THE WAHWEAP (CAMPANIAN, AQUILAN) AND KAIPAROWITS (CAMPANIAN, JUDITHIAN) FORMATIONS, WITHIN AND NEAR GRAND STAIRCASE-ESCALANTE <br> NATIONAL MONUMENT, SOUTHERN UTAH 

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Cover photo by author:<br>Powell Point in "The Blues," the early Tertiary Claron Formation on the horizon and the Kaiparowits Formation in the foreground.

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# MULTITUBERCULATE MAMMALS FROM THE WAHWEAP (CAMPANIAN, AQUILAN) AND KAIPAROWITS (CAMPANIAN, JUDITHIAN) FORMATIONS, WITHIN AND NEAR GRAND STAIRCASE-ESCALANTE NATIONAL MONUMENT, SOUTHERN UTAH 

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#### Abstract

Multituberculate mammals from the Campanian Kaiparowits Formation of southern Utah include: two new species of Mesodma (M. archibaldi and M. minor) and a possible third new species (Mesodma sp. (large); three species of Cimolodon, including a new species (C.foxi); a new genus and species of a possible cimolodontid (Kaiparomys cifellii); a new species of Cedaromys (C. hutchisoni), a genus previously reported only from the mid-Cretaceous Cedar Mountain Formation; a taxon, Cimexomys magnus, is transferred to the genus Dakotamys (a genus previously reported only from the Cenomanian Dakota Formation); at least two species of Cimolomys close to C. trochuus and a new species questionably assigned to that genus (?C. butleria); two species of Meniscoessus (M. sp. cf. M. intermedius; M. sp. cf. M. major); and Cimexomys sp. cf. C. judithae. A possible relationship of Cimolomys to Cedaromys and Bryceomys is suggested. The fauna strongly supports an interpretation of a Judithian Land Mammal "Age" for the Kaiparowits Formation, however, the formation may be somewhat older than the type Judithian because of the close relationship of the fauna to the Aquilan fauna recovered from the underlying Wahweap Formation; however, this may be an artifact of both faunas being recovered from a continuous stratigraphic sequence.

Multituberculate mammals from the early Campanian Wahweap Formation include a species of Cedaromys (a genus also reported from the Kaiparowits Formation) and a species of Bryceomys (previously reported from the Turonian Smoky Hollow Member of the Straight Cliffs Formation and the older Cedar Mountain Formation). The fauna also contains the Aquilan species Cimolodon electus and C. similis. Several conferred species, including ones assigned to Cimex-


omys, Meniscoessus, Mesodma, Cimolodon, and Cimolomys, probably represent new species but are inadequately represented to diagnose new taxa. The fauna supports an Aquilan Land Mammal "Age" for the Wahweap Formation. The Wahweap fauna is enough different from that of the upper Milk River Formation (type Aquilan) to suggest either latitudinal controls or possibly a slightly older age for the Wahweap Formation. This age assessment is based on primitive characters found in the species of Mesodma and Cimolodon recovered from the Wahweap Formation.

## INTRODUCTION

Many of the specimens discussed here were originally described in an unpublished Ph.D. dissertation (Eaton, 1987), and subsequently the faunas were summarized by Eaton and Cifelli (1988) and Eaton and others (1999) (multituberculate faunal lists in both were based on Eaton, 1987). Since the time of original description, many specimens have been added to the sample as a result of continued collecting by Dr. Richard L. Cifelli (University of Oklahoma) and myself. Although the process of collecting new specimens continues, it was necessary to establish an arbitrary cut-off point and describe the material in hand. These specimens were recovered by screen-washing methods described in Cifelli and others (1996) from the Kaiparowits Plateau region within or near the Grand Staircase-Escalante National Monument (figure 1).

The present study was accomplished initially without reference to Eaton, 1987; after reevaluating the systematics, the results were then compared. The identifications made by Eaton (1987) are included in the list of referred specimens or underneath the species designation for cases in which the


Figure 1. Location map. Boundary of Grand Staircase-Escalante National Monument shown by the dark line. W - indicates areas of localities in the Wahweap Formation; K - indicates areas of localities in the Kaiparowits Formation.
identifications differ significantly from Eaton, 1987. Where instructive, these changes are discussed in the text. The higher-level systematics are based on Kielan-Jaworowska and Hurum (2001) with some modifications.

The purpose of this paper is the alpha-level systematic description of the multituberculate faunas recovered from the Wahweap and Kaiparowits Formations and assessment of their biostratigraphic correlations to North American Land Mammal "Ages."

## Stratigraphic Setting

The Wahweap Formation ranges in thickness from 360460 m and averages about 400 m (Eaton, 1991). Although the localities range stratigraphically from near the base of the formation (MNA localities 707-2, 707-6, 456-2) to the upper
member (below the capping sandstone member, see Eaton, 1991) of the formation (MNA localities 455-1, 455-2, and UMNH VP localities 77 and 130), there are no clear-cut vertical faunal changes (see Eaton and Cifelli, 1988). The formation is comprised of fluvial deposits consisting mostly of meandering river and floodplain facies (excluding the capping sandstone member from which no mammals have been recovered).

The Kaiparowits Formation is 855 m thick (Eaton, 1991) but there seems to be little faunal difference throughout the formation (see Eaton and Cifelli, 1988), suggesting rapid deposition. The stratigraphic positions of most of the localities from which multituberculates are described in this paper are shown in figures 15, 16, and 21 in Eaton (1991). Most of the localities occur in the lower $200-300 \mathrm{~m}$ of the formation (including localities discovered after 1991: UMNH localities $24,51,54,65$, and 108). Localities that occur higher in sec-
tion are TB2 (MNA 453-2; OMNH V14) at 370 m, JGE 8642 (OMNH V61) at 520 m , and TB8 (MNA 1004-1; OMNH V5) at 640 m .

The faunas are described in inverse formational order, because the number of specimens is much greater in the sample recovered from the Kaiparowits Formation than for the Wahweap Formation, providing a better basis on which to make diagnoses. Discussions of the fauna from the Wahweap Formation often refer back to discussions of taxa recovered from the Kaiparowits Formation.

## Photographic Figures

All specimens were photographed using a Nikon ${ }^{\circledR} 990$ digital camera mounted on a Meiji stereo zoom microscope. The photographs were modified in Adobe Photoshop ${ }^{\circledR}$ and arranged in Adobe Pagemaker ${ }^{\circledR}$. As there were no available guidelines for this kind of digital photomicrography, the photographic figures in the paper represent a first attempt. The usual problems of depth of field were encountered and it is strongly recommended that researchers utilize the stereo occlusal views when working from this paper. The sizes of the illustrations were determined by attempting to keep the scale as consistent as possible, while allowing for reasonable use of the printed page and permitting adequate space for stereo pairs. For this reason, there is sometimes more than one scale bar in a figure.

All specimens are oriented with their anterior margin facing the bottom of the page (except for the side view in figure 4 B , in which the anterior is oriented to the right).

## Measurements and Terminology

Specimens were measured using one ocular of a microscope mounted on a 2-axis micrometer measuring base with Mitutoyo 0.005 mm micrometers. Dimensions were measured as in Eaton (1995) except for additional measurements described below. All cusp formulae are given from the labial side of the tooth to the lingual. Several sets of ratios are provided to aid in comparisons of teeth. Crown height to anteroposterior dimension ratios ( $\mathrm{H}: \mathrm{AP}$ ) are provided to provide data for comparing crown heights relative to crown length for lower fourth premolars (figure 2). The climb ratio (CR) is a measure of how steeply the cusps of the medial row of upper fourth premolars increase in height from the front of the premolar to the tallest cusp of the premolar (figure 2). This measurement is too subtle to attempt from illustrated specimens and is only provided for specimens described here. The CR is determined by measuring the distance from the tip of the first cusp of the medial row to the deepest cusp of the row in one axis (CRH in figure 2) and the anteroposterior distance between these cusp apices on the other axis (CRL in figure 2). The CRL is divided by the CRH to get the climb ratio (CR). Length ratios of molars and premolars are provided to help compare dental proportions of taxa (M1:m1; M2:M1; P4:M1; m2:m1: p4:m1; P4:p4), which the author considers to be of considerable importance in multituberculate taxonomy. The term AL (anterior length) is used on p 4 s as a term somewhat comparable to the L1 of Novacek and Clemens (1977) and applied extensively by Archibald (1982). Novacek and Clemens (1977) established the antero-
posterior baseline on the labial side of the tooth, which I found difficult to apply on specimens other than those of Mesodma, such as Cimolodon. The baseline used here is on the lingual side of the tooth at the base of the enamel crown above the two roots (figure 2). Nevertheless, I found it difficult to consistently measure a maximum height as often there is apical crown wear and also in some of the specimens two of the serrations are essentially of the same height at the highest point of the crest. The PL (posterior length, figure 2) measurement taken on P 4 s is provided to help determine what proportion of the tooth's length is occupied by the posterior basin (PL:AP), which is highly variable among taxa.

Dental terminology follows that of Eaton (1995) except for additional terms discussed below. The term pyramidal is used to describe cusps with 4 distinct corners. Pyramidal cusps can be erect or lean anteriorly (M1, M2) or posteriorly ( $\mathrm{m} 1, \mathrm{~m} 2$ ). I consider the cusps to be subpyramidal if the posterior wall (in the case of upper molars) of the cusps is convex but maintains distinct posterior corners. A crescentic cusp (on upper molars) has lost the posterior corners (the anterior corners on lower molars) and has a convex posterior wall (anterior wall on lower molars) that meets the concave anterior face, forming only two strong edges of the cusp (unlike the 4 corners of pyramidal cusps).

## Abbreviations

UMNH - Utah Museum of Natural History, Salt Lake City
MNA - Museum of Northern Arizona, Flagstaff
MOR - Museum of the Rockies, Bozeman, Montana
OMNH - Oklahoma Museum of Natural History, Norman
AMNH - American Museum of Natural History, New York
UA - University of Alberta, Edmonton
UALP - University of Arizona Laboratory of Paleontology, Tucson
UCMP - University of California, Berkeley
UW - Collection of Fossil Vertebrates, Department of Geology and Geophysics, University of Wyoming, Laramie
$\mathbf{R}$ - right
L - left
M - upper molar
m - lower molar
$\mathbf{P}$ - upper premolar
p - lower premolar
$\mathbf{A P}$ - anteroposterior dimension
$\mathbf{L B}$ - lingual-buccal dimension
$\mathbf{H}$ - height of crown of fourth premolars (figure 2)
$\mathbf{C R}$ - measure of change in cusp depth over distance for cusps of medial row of P 4 (CRH:CRL in figure 2). CRL is measured along the AP axis from the tip of the first cusp of the medial row to the tip of the highest cusp (usually the last, but not always) and CRH is the change in height measured perpendicular to the AP axis (figure 2).
S:ER:IR - in tables including p4s: $\mathrm{S}=$ number of serrations, $E R=$ external ridges, $I R=$ internal ridges

*     - indicates some damage to specimen so that the measurement may not be accurate (in tables)
$\mathbf{e}$ - estimated values based on measuring figured specimens described in other papers (in tables)
? - denotes unavailable data such as ridge counts of p4s that are
not provided in some papers or uncertain values (in tables) !- unusual values that may suggest errors in assignment of specimens to a taxon (in tables)
$\mathbf{A L}$ - in p4s, the distance from the anterior of the tooth to the point of maximum height (figure 2)
$\mathbf{P L}$ - in P4s, distance from the last cusp of the medial row to the posterior of the tooth (figure 2)
$\mathbf{R i}$ - a non-cuspate anteroexternal ridge in the position of a third cusp row on some M2s


Figure 2. A, measurements taken on $\mathrm{p} 4 \mathrm{~s}(\mathrm{H}=$ height; $\mathrm{AL}=$ anterior length; $\mathrm{AP}=$ anteroposterior); B , measurements taken on $\mathrm{P} 4 \mathrm{~s}(\mathrm{H}=$ height; $\mathrm{AP}=$ anteroposterior; $\mathrm{AL}=$ anterior length; $\mathrm{PL}=$ posterior length; $\mathrm{CRH}=$ climb ratio height; $\mathrm{CRL}=$ climb ratio length .

# MULTITUBERCULATE FAUNA FROM THE KAIPAROWITS FORMATION 

Systematic Paleontology<br>Class MAMMALIA<br>Order MULTITUBERCULATA<br>Suborder CIMOLODONTA McKenna, 1975<br>Superfamily ?Ptilodontoidea Sloan and Van Valen, 1965<br>Family Neoplagiaulacidae Ameghino, 1890<br>Mesodma Jepsen, 1940<br>Mesodma archibaldi sp. nov.<br>tables 1-3; figures 3A-H, 4A-B

Holotype - OMNH 24039, RM1, Loc. V61.
Hypodigm - MNA V4502, Lm2, Loc. 453-2 (Paracimexomys n. sp. A in Eaton, 1987); MNA V5230, Lm2, Loc. 704-1 (Paracimexomys n. sp. A in Eaton, 1987); MNA V5303, Lm2, Loc. 704-1 (Paracimexomys n. sp. A in Eaton, 1987); MNA V5343, Rm1, Loc. 1004-1 (Mesodma sp. cf. M. hensleighi in Eaton, 1987); MNA V7524, LM1, Loc. 704-1; MNA V7531, Rp4-m2, Loc. 704-1; MNA V7533, Rp4, Loc. 704-1; MNA V7536, Rm1, Loc. 704-1; MNA V5284, RM1 (posterior part), Loc. 454-6 (Mesodma sp. cf. M. hensleighi in Eaton, 1987); OMNH 20511, LM1, Loc. V9; OMNH 20518, Lm2, Loc. V9; OMNH 20764, Lm1, Loc. V9; OMNH 22298, Rm1, Loc. V5; OMNH 22300, Rm1, Loc. V5; OMNH 22835, Lm1, Loc. V9; OMNH 22868, Rm2, Loc. V9; OMNH 24056, Lm1, Loc. V61; UMNH VP7643, Rm2, Loc. 51.

Distribution - Kaiparowits Formation of southern Utah and the Judith River Formation of Montana, Campanian.

Diagnosis - Small species of Mesodma in upper size range of $M$. hensleighi and smaller than M. formosa; p4 with fewer serrations and ridges than any species of Mesodma; M1 with fewer cusps (5:6:4) than any other species of Mesodma.

Etymology - named for J. David Archibald, who has greatly increased our knowledge of Mesozoic mammals and for his help with my fieldwork in southern Utah.

Description - p4. MNA V7533 (figures 3A-B) has 9 serrations, 7 external ridges and 6 internal ridges. The tooth is symmetrical, relatively low crowned (table 1), and reaches its apex at the third serration. The first two external ridges are short and ventrally directed. The third external ridge is oriented more anteriorly and intersects the second ridge. The posteromost three serrations are broadly separated, cusp-like, and oriented posteroventrally. The first internal ridge is short, the second and third almost meet and then diverge ventrally. The last three serrations have no internal ridges.
ml - OMNH 24056 (figure 3C) has a cusp formula of 6:4. The external cusp row is broader than the internal row. The first cusp of the external row is small, conical, and well separated from the second erect cusp. Cusps 3-6 are all crescentic, subequal in height, and lean strongly posteriorly. Cusps 5 and 6 are subequal in height, lean strongly posteriorly, and are only partially separated on the labial side of the tooth but are deeply separated adjacent to the central valley. The central valley is sinuous and unpitted. The first cusp of the internal row is small, low, erect and conical. It is connected to the second cusp at its base. The second, third and fourth cusps are subequal in height, well separated, and lean posteriorly. A low pit is present on the buccal wall of cusp 4. A few specimens have a small posteromost fifth cusp on the internal row (OMNH 22298, figure 3D).
m2 - MNA V5303 (figure 3E) has a cusp formula of 4:2. Cusps of the external row are spaced evenly along the row and are progressively more poorly separated posteriorly where they are separated mostly along the lingual wall. The central valley is complex because of crossing ridges, but it is not pitted. The cusps of the internal row are deeply divided and crescentic. MNA V5230 (figure 3F) is almost identical in size and is from the same locality (704-1) as MNA V5303, but the posterior two cusps of the external row are weakly separated. The central valley on this specimen bears some deep, round pits.

M1 - OMNH 24039 (the holotype, figure 3G) has a formula of 5:6:4, which is characteristic of all the M1s in this sample. The cusps of the external row narrow posteriorly. The first cusp of the row is low, connected to the anterior face of the tooth by a short ridge, and it has a distinct pocket on a shelf labial of the cusp. The remaining cusps are subequal in height and size and are well separated. The cusps are essentially pyramidal and erect. Cusps of the medial row are crescentic, recurved strongly anteriorly, and broaden posteriorly. Internal row cusps are conical, lingually-buccally compressed, and are lower than those of either the medial or external rows. The cusps are well separated and increase in size posteriorly and each is connected to the lingual side of the medial row by a small ridge. MNA V7524 (figure 3H) is quite similar to OMNH 24039, but the medial cusp row of MNA V7524 projects anteriorly, well beyond the external cusp row whereas on OMNH 24039 the cusp rows are of the same length, resulting in a squared front of the tooth.


Figure 3. Mesodma archibaldi, sp. nov.: A, (MNA V7533), Rp4, labial view; B, lingual view; C, (OMNH 24056), Lm1, stereo occlusal view; D, OMNH 22298), Rm1, stereo occlusal view; E, (MNA V5303), Lm2, stereo occlusal view; F, (MNA V5230), Lm2, stereo occlusal view; G, (OMNH 24039), holotype, RM1, stereo occlusal view; H, (MNA V7524), LM1, stereo occlusal view. Scale bar $=1 \mathrm{~mm}$.

Discussion - The single p4 assigned here is relatively low crested and symmetrical as is typical for Mesodma. In size, it is intermediate between specimens of M. hensleighi and M. formosa (table 1) and has fewer serrations and ridges than any other species of Mesodma. The ratio of its length (1.57) to the m 1 s of $M$. archibaldi is consistent with $\mathrm{p} 4: \mathrm{m} 1$ length ratios of other species of Mesodma (table 1). The m1s assigned here are in the size range of M. hensleighi (table 1) and could not be distinguished from that species without the associated M1s. The length ratio for M1:m1 (= 1.35) is typical for species of Mesodma (table 2). Perhaps most difficult is being certain that these molars represent Mesodma and not Cimexomys. It is characteristic for m 1 s of Mesodma to have a broad external row of strongly crescentic cusps and a narrower internal row (e.g., M. thompsoni, Lillegraven, 1969, figure 8-5b), whereas in Cimexomys the cusps of the external row are more erect, pyramidal, and not widely separated and the external cusp row is narrower than the internal cusp row (e.g., C. gratus, Archibald, 1982, figure 37d). This results in the anterior of m1s of Cimexomys being blunter than the tapering anterior of m 1 s of Mesodma (see discussion in Archibald, 1982, p. 50), with the exception of MOR 302 (Montellano and others, 2000), C. judithae. MNA V7531 (figures 4A-B) looks very similar to MOR 302 but is deeper jawed and has a distinct foramen on the labial side of the mandible just posterior of the lower incisor socket as in $M$. thompsoni and M. formosa but not MOR 302. For this reason, the jaw is considered to represent Mesodma; however, even in details, its morphology is strikingly similar to that of MOR 302.

The m 2 s assigned here are somewhat problematic because of difficulties in distinguishing m 2 s of Cimexomys and Mesodma. These are assigned here based on the occurrence of appropriately sized m1s of Mesodma in the sample and the absence of appropriately sized m1s of Cimexomys. Further difficulties in assignment arise because three of the specimens (MNA V4502, V5230, V5303) are about the same size and have similar LB:AP values (0.87-0.90) and three other specimens (MNA V7531, OMNH 20518, 22868) are larger, and have significantly lower LB:AP values (0.760.80 ). I was initially tempted to identify the later three specimens as Cimexomys because they do not taper posteriorly and posterior tapering of m 2 may be a characteristic of Mesodma (e.g., Mesodma sp., Clemens, 1964, figure 15a), whereas for the few illustrated M2s of Cimexomys, the tooth maintains its width or expands posteriorly (C. gratus, Archibald, 1982, figure 36b; but less so in figure 37e and on MOR 302, C. judithae, Montellano and others, 2000). However, MNA V7531 (figures 4A-B) has one of the larger m2s associated with an m 1 in a mandible considered to be $M$. archibaldi (see discussion above) and for that reason I have included these specimens within this species.

The M1s have fewer cusps than any described species of Mesodma and the specimens are in the upper size range of $M$. hensleighi and distinctly smaller than M. formosa (tables 13). These specimens fit within the range and cusp formula of specimens (UCMP 122182, 131486, 131493, 131494, 131996,131504 ) described by Montellano (1992) as Mesodma sp., and I consider those specimens from the Judith River Formation to belong to this species. Lillegraven and McKenna (1986) described a small species of Mesodma from the "Mesaverde" Formation of Wyoming that has similar
cusp formulae and lengths as the specimens described here, but seems to represent an unusual population of Mesodma in that the M1s are wider relative to length than other species of Mesodma (table 3) and one specimen has an internal cusp row as long as the tooth. It is uncertain if the "Mesaverde" sample represents the same species that is described here. Fox (1971) described a single M1 as ?Mesodma sp. that is somewhat more cuspate than the specimens described here (6:7:5 - the same formula as for M. primaeva) but is close to the size of M. archibaldi (table 3); however, the specimen has a very broad internal cusp row quite unlike these specimens.

## Mesodma sp. cf. M. archibaldi sp. nov. table 3; figure 4C

Referred Specimen - MNA V5291, LM1, Loc. 453-2 (Mesodma sp. cf. M. hensleighi in Eaton, 1987).

Description - M1. The external cusp row of MNA V5291 (figure 4C) has a small and lingually shifted first cusp that is connected to the larger second cusp by a high ridge. Cusps 2, 3, and 4 are well separated, subequal in height, and narrow slightly posteriorly due to the oblique angle of the central valley. The cusps are flattened lingually and bear deep grooves. Cusps of the medial row are strongly recurved anteriorly and become somewhat more erect, increase in height, and broaden posteriorly. A wall closes both valleys posteriorly. The internal row connects at about the midpoint of the third cusp of the medial row and extends more than $50 \%$ of the length of the tooth. The cusps are conical with the third cusp being the tallest of the row.

Discussion - This molar has a length most appropriate for M. hensleighi but has many fewer cusps than that species (table 3). The specimen is within the low end of the length range for M1s of M. archibaldi and its cusp formula (5:6:5) is appropriate for that species; however, the specimen is proportionally much broader $\mathrm{LB}: \mathrm{AP}=0.63$ ) than in that species ( $\overline{\mathrm{x}} \mathrm{LB}: \mathrm{AP}=0.51$ ). In this regard, the specimen is most similar to two M1s of Mesodma sp. described in Lillegraven and McKenna (1986) as they are proportionally broad relative to length (LB:AP values of 0.59 and 0.61 ). It is uncertain, due to the small sample size, if this specimen and those described by Lillegraven and McKenna (1986) should be included in M. archibaldi or another new species.

## Mesodma minor sp. nov. tables 2-3; figures 4D-G

Holotype - MNA V7525, RM1, Loc. 704-1.
Distribution - Kaiparowits Formation of southern Utah, Campanian.

Hypodigm - UMNH VP5606, Lm1, Loc. 51; UMNH VP7635, LM1, Loc. 108; MNA V4503, RM1, Loc. 453-2 (Cimexomys sp. cf. C. judithae in Eaton, 1987); MNA V5294, LM1 (posterior part), Loc. 453-2 (Cimexomys sp. cf. C. judithae in Eaton, 1987); MNA V7529, LM2, Loc. 704-1; MNA V7538, Rm1, Loc. 704-1; OMNH 20011, LM2, Loc. V5; OMNH 20364, RM2, Loc. V5; OMNH 20369, RM1, Loc. V5; OMNH 22296, RM2, Loc. V5; OMNH 22302, RM2, Loc. V5; OMNH 24045, LM1, Loc. V61.

Diagnosis - M1s $14 \%$ smaller than M. archibaldi with
cusp formula (4-6:6:4) lower than any other species of Mesodma except M. archibaldi, and mean lengths slightly less than M. hensleighi; m1s 16\% smaller than M. hensleighi or M. archibaldi.

Etymology - in reference to the small size of the taxon.
Description - m1. MNA V7538 (figure 4D) has a cusp formula of $6: 4$. The first cusp of the external row is tiny, low, and placed at the anteromost margin of the tooth. The second cusp is much larger. Cusp 3, the tallest of the row, and cusp 4 are weakly crescentic and are more deeply separated than the other cusps of the row. Cusps 5 and 6 are divided at their cusp apices labially but are much more deeply separated lingually. The cusps are distinctly broader than those of the internal row. The central valley is sinuous and a strong ridge connects cusp 3 of the internal row to cusp 4 of the external row. The first cusp of the internal row is very low, shifted labially, and does not lean posteriorly as do the other conical to subcrescentic cusps of the row.

M1 - MNA V7525 (holotype - figure 4E) has a cusp formula of $6: 6: 4$. The external row is formed of six conical cusps that become progressively smaller and lower anteriorly. The row narrows posteriorly. The first two cusps are not well separated and are connected by a ridge. The third and fourth cusps are well separated with cusp 4 being the tallest of the row. Cusps 5 and 6 are connected and smaller than cusp 4 . The sixth cusp is shifted slightly lingual of the straight row formed by cusps 1-5. The central valley is somewhat oblique to the anteroposterior axis of the molar. The cusps of the medial row are strongly crescentic and increase slightly in height posteriorly. The first two cusps of the internal row are small and conical with the first cusps being taller than the second. Cusp 3 is the tallest cusp of the row and, with the small weakly separated fourth cusp, forms a continuous posterolingual wall that connects to the last cusp of the medial row. There is a slight swelling anterior of the internal cusp row lingual of cusps 2 and 3 . The internal row connects to the main body of the tooth at the back of the second cusp of the medial row. OMNH 20369 (figure 4F) is similar to MNA V7525, but it has one less cusp in the external row (although a tiny cuspule is present in that position) and the internal row connects to the main body of the tooth at the third cusp of the medial row.

M2 - OMNH 22296 (figure 4G) has a cusp formula of Ri:3:3. The anteroexternal platform is narrow. The anterolabial ridge forming the margin of the platform has 3 distinct cuspules produced by the continuous ridge and are not counted as cusps. There is a well-developed recess for M1 at the front of the external cusp row. The swelling of the anterior ridge is counted as a cusp of the internal cusp row but would have functioned as a cusp only after considerable wear. The second cusp is crescentic and strongly recurved anteriorly. The last cusp is also crescentic. Cusps of the internal row are distinct but closely appressed and not deeply divided.

Discussion - The M1s clearly belong to Mesodma as the internal cusp row distinctly exceeds $50 \%$ of the length of the molar (but see discussion below in the section on the fauna from Wahweap Formation, Cimexomys sp. cf. C. antiquus) and the cusps of the medial row are strongly crescentic. The M1s have a cusp formula close to that of M. archibaldi and lower than other species of Mesodma. If the M1s were included in M. archibaldi the standard deviation of the sample rises to 0.29 . However, if these were considered as sep-
arate samples the standard deviation of M. archibaldi becomes 0.16 and for $M$. minor, 0.08 . The size of the m 1 s and M1s plot distinctly on graphs (respectively, figures 5 and 6). The upper molars of M. minor are $18 \%$ shorter and the m 1 s are $16 \%$ shorter than those of $M$. archibaldi. In terms of size, they fit within or are slightly below the known length range of $M$. hensleighi but are proportionally broader and have fewer cusps. The lower first molars are also somewhat broader relative to length than those of either M. hensleighi or $M$. archibaldi and are $16 \%$ shorter than m 1 s of $M$. hensleighi (based on mean values for M. hensleighi in Lillegraven, 1969; Archibald, 1982).

The anterior faces of the M2s fit well with the posterior ends of the M1s assigned to M. minor. The length ratio of M2:M1 is similar to that seen in M. thompsoni and M. garfieldensis but larger than that of $M$. hensleighi and $M$.formosa (table 3). This is consistent with the mean M2 LB:AP ratio for M. minor which is comparable to those of M. thompsoni and M. garfieldensis and lower than the values for $M$. hensleighi and M. formosa (table 3); however, in size, these specimens are closest to samples of $M$. hensleighi (table 3).

## Mesodma sp. (large)

tables 1-3; figures 7A-H, 8 A-D
Referred Specimens - MNA V4584, L?p4, Loc. 704-1; MNA V5267, Rm2, Loc. 454-6; MNA V5275, Lp4, Loc. 454-6; MNA V5315, LP4; Loc. 704-1; MNA V5338, Rm1, Loc. 1004-1; OMNH 20351, LP4, Loc. V5; OMNH 20356, Lm1, Loc. V5;OMNH 20366, LP4, Loc. V5; OMNH 20506, RP4 (anterior part), Loc. V9; OMNH 24041, LM2, Loc. V61; UMNH VP7633, Lp4, Loc. 108; UMNH VP7642, Rp4, Loc. 24.

Description - p4. UMNH VP7642 (figures 7A-B) has 10 serrations and 7 external and internal ridges. The specimen is high crowned (table 1) but gently arched and reaches its apex at the fourth serration at slightly more than half the length of the tooth. The posterior serrations form bulbous cusp-like projections. The posteroexternal platform is well worn.
m1 - MNA V5338 (figure 7C) has a cusp formula of 6:4 and the molar tapers anteriorly. The external cusp row is slightly broader than the internal row and the cusps are crescentic and oriented strongly posteriorly. The central valley is aligned with the anteroposterior axis of the tooth. The first cusp of the internal row is tall and well separated from the second cusp, the second and third cusps are crescentic and essentially erect, and the last cusp of the row is blade-like. OMNH 20356 (figure 7D) is similar to MNA V5338 but is more rectangular in shape and cusps $2-5$ of the external row are connected to a cusp of the internal row by well-developed ridges crossing the central valley.
m2 - MNA V5267 (figure 7E) has a cusp formula of 4:2. The cusps of the external row are progressively closer together posteriorly. The first two cusps are well separated apically, and cusps 3 and 4 are only separated lingually. The cusp row broadens slightly at the valley between cusps 2-3. Grooves that lingually separate the cusps are arch-shaped and convex anteriorly. Ridges cross the central valley and a few deep pits are present. The cusps of the internal row bear lingual wear. The first cusp and the larger second cusp have deep grooves on their labial sides.



Figure 5. Graph comparing ml AP and LB dimensions of Mesodma archibaldi sp. nov., M. minor sp. nov., Mesodma sp. (large), and Cimexomys or Mesodma indeterminate.


Figure 6. Graph comparing M1 AP and LB dimensions of Mesodma archibaldi sp . nov., M. minor sp. nov., and M. sp. cf. M. archibaldi.


Figure 7. Mesodma sp. (large): A, (UMNH VP7642), Rp4, labial view; B, lingual view; C, (MNA V5338), Rm1, stereo occlusal view; D, (OMNH 20356), Lm1, stereo occlusal view; E, (MNA V5267), Rm2, stereo occlusal view; F, (MNA V5315), LP4, stereo occlusal view; G, labial view; H, lingual view. Scale bar $=1 \mathrm{~mm}$.

P4 - MNA V5315 (figures 7F-H) has a cusp formula of 2:6 and is a broad, robustly crowned tooth that bears striations. A small anteriorly positioned cusp is present on the moderately expanded anteroexternal platform and a second larger cusp is positioned much more posteriorly on the platform. The cusps of the medial row climb steeply, making the tooth deep-crowned relative to its length. The posterior basin is a deep pit bounded on the labial side by a well-developed and bulbous cusp and on the lingual size by a lower and smaller cusp. OMNH 20351 (figures 8A-C) has a cusp formula of 1:6 and is more strongly arched (in occlusal view) and more gracile in form than MNA V5315. The posterior basin is complex with an additional cusp present on the posterolabial wall above the basin.

M2 - OMNH 24041 (figure 8D) has a cusp formula of $2: 3: 4$. The anteroexternal platform is very small and is not expanded labially. Two cusps are present on the anteroexternal corner of the tooth and three deep pits are present on the platform basin. The first cusp of the medial row is narrow and low. The second cusp is bulbous, weakly crescentic in form, and it is separated from the first cusp by deep pits. A deep valley separates the second and third cusps. The central valley is deeply pitted. The cusps of the lingual row are weakly separated lingually and are divided by deep grooves buccally. The first two cusps are closely appressed, and the third and fourth are more widely spaced.

Discussion - The p4s are deep crowned and gently arched as is characteristic for p 4 s of Mesodma. The size range of the p 4 s (table 1) is within that of M. garfieldensis, but these p 4 s have fewer serrations and ridges than those of that taxon. The size range is also similar to the p 4 s of M. primaeva described both by Lillegraven and McKenna (1986) and Montellano (1992); however, those p4s are much smaller than those described as M. primaeva in Sahni (1972) and Novacek and Clemens (1977) (table 1) and probably do not belong to that species. The upper and lower fourth premolars Lillegraven and McKenna (1986) and Montellano (1992) assigned to M. primaeva probably do not belong together in the same species because their $\mathrm{P} 4: \mathrm{p} 4$ length ratios indicate that the P 4 s are the same size or longer than the p 4 s (table 1), a condition not seen in any other species of Mesodma (length range of $\mathrm{P} 4: \mathrm{p} 4=0.64-0.74$ ).

The two m1s overlap in size with the m1s assigned to Cimexomys or Mesodma sp. later in this paper (figures 7CD). I consider them to represent Mesodma because of the alignment of the central valley with the anteroposterior axis of the tooth, the narrowness of the internal cusp row relative to the external, the strongly crescentic nature of the external row cusps, and the tendency of the molars to narrow anteriorly. In length, these molars would fit in the upper range of m 1 s of $M$. formosa and close to the mean length of m1s of $M$. garfieldensis, although these molars have a higher LB:AP ratio than those of M. garfieldensis (table 2). In the diagnosis of M. garfieldensis (Archibald, 1982, p. 47), it is stated that the M1 and m1 cusp formula averages are higher than in other species of Mesodma. However, the stated cusp formula for m1s of M. garfieldensis is 6-7:4-5 (Archibald, 1982), which is identical to the formula of M. formosa provided by Lillegraven (1969, p. 21). As such, there is no basis on which to identify these lower molars to species.

The m 2 assigned here (MNA V5267) is similar to those identified as Cimexomys judithae in various collections (e.g.,

AMNH 77105) except this tooth is proportionally broader. The tooth is considered to represent Mesodma because the cusps of the external row become more closely positioned posteriorly, unlike the condition in m 2 s of $C$. gratus (Archibald, 1982, figure 37c). In the specimens illustrated in Montellano and others (2000) as Cimexomys (C. judithae, MOR 302 , figure 2), the cusps of the external row do decrease in size posteriorly but the last cusp is shifted slightly lingually. The second internal cusp is elongated on some specimens of Mesodma (e.g., M. formosa, Lillegraven, 1969, figure 7-4a) but not all (e.g., M. primaeva on which the first cusp is longer than the second; Sahni, 1972, figure 10G). The internal cusp row is worn prior to the external row in Mesodma, unlike the condition in m 2 s of Cimexomys (Archibald, 1982, figure 37e; Lofgren, 1995, figure 21). However, the m2 of MOR 302 (Montellano and others, 2000, figure 2), C. judithae, is unlike most specimens assigned to Cimexomys in being relatively squared posteriorly. Also, the second cusp of the internal row is elongated. This makes identification of the molar described here difficult. Also, the pitting present in the central row appears to be more a characteristic of Cimexomys than Mesodma. This characteristic is also strongly developed in molars of Cimolomys, but this specimen does not appear to represent that genus. The m 2 is appropriate in size and morphology to complement the M2 (OMNH 24041) assigned here, and I am at least certain that these two molars belong to the same species, but the assignment to Mesodma must be considered tentative.

A single P 4 is robust in form (MNA V5315) compared to the other more gracile P 4 s assigned here. It is not certain if these two forms represent the same taxon; however, they are close in length and the appropriate size for the p 4 s assigned here ( $\mathrm{P} 4: \mathrm{p} 4=0.70$; table 1 ), and they appear to be too large for the p 4 s assigned to $M$. archibaldi $(\mathrm{P} 4: \mathrm{p} 4=0.90)$. In size and cusp formula, these P 4 s are closest to those of M. senec$t a$, Fox, 1971, and very similar to Mesodma sp. of Montellano (1992) (table 1). The p4s assigned here are smaller and have fewer serrations and ridges than do those of M. senecta (table 1). However, it is possible that the upper and lower fourth premolars are incorrectly associated here and there are specimens in the sample close to M. senecta (particularly MNA V5315). Unfortunately, only fourth premolars are described for M. senecta and it is not possible to compare the rest of the dentition.

The M2 is similar to specimens assigned to both Cimexomys and Mesodma. Mesodma tends to have a very straight central valley (M. formosa, Lillegraven, 1969, figure 7-5b; M. garfieldensis, Archibald, 1982, figure 12d) whereas it is somewhat oblique to the central axis in at least some species of Cimexomys (C. gratus, Archibald, 1982, figure 38e; but not in MOR 322, C. judithae, Montellano, 1992, figure 6; or MOR 302, Montellano and others, 2000, figure 1). As a result of the orientation of the central valley, the internal cusp row of M2s of Mesodma will tend to narrow (or in some case maintain) its width posteriorly whereas in Cimexomys (at least C. gratus) the cusp row broadens posteriorly. Also, on the M2s of Cimexomys represented by MOR 322 (Montellano, 1992, figure 6) and MOR 302 (Montellano and others, 2000, figure 1) the last cusp of the internal row is distinctly separated (labially and lingually) from the penultimate cusp. It is also evident that on MOR 322 the first and second cusps are well separated. On specimens of Mesodma, the cusps of
the internal row form a ridge and the cusps are only slightly separated at their apices and divided labially by vertical grooves. On these tentative grounds, OMNH 24041 is assigned to Mesodma rather than the less-well preserved M2s assigned later in this paper to Cimexomys or Mesodma sp. A difficulty (also noted for the m 2 ) in placing this M2 in Mesodma is the presence of distinct pits present in the central valley that I have not observed in other specimens assigned to Mesodma.

The molars are all in the uppermost size range or exceed that of M. formosa and are distinctly smaller than molars of M. thompsoni or M. garfieldensis (tables 2, 3). Within this sample there probably exists a new species of Mesodma. However, uncertainties about whether all the specimens assigned here really belong to a single species and the lack of knowledge of molars of the potentially most similar taxon, M. senecta, indicates that a formal taxon should not be proposed at this time. A better sample of this large taxon of Mesodma, as well as improved sampling M. senecta from the type area, would help in resolving whether another species of Mesodma is present.

## Comments on Relationships of Species of Mesodma

The species of Mesodma described here retain the most primitive characters of any described species. M. primaeva was considered the most primitive taxon by Novacek and Clemens (1977); but all of the taxa described here have fewer cusps on molars and lower numbers of serrations and ridges on p4s. Oddly, the P4 of M. senecta would be considered primitive whereas the p 4 , with 15 serrations, would represent the most derived condition for p4. Novacek and Clemens (1977, figure 12) considered M. hensleighi to be nearly as primitive as $M$. primaeva. I agree that the p 4 s of $M$. hensleighi retain a low serration and ridge count; however, the elongation of the m 1 relative to its width (at least in Lillegraven's 1969 sample - Archibald's 1982 sample is proportionally broader) is a derived character as is the low $\mathrm{m} 2: \mathrm{m} 1$ length ratio (table 2). In regards to $\mathrm{m} 2: \mathrm{m} 1$ length ratios, $M$. thompsoni and M. primaeva are the most primitive, M. formosa and M. archibaldi intermediate, and M. hensleighi and M. garfieldensis the most derived. In terms of P 4 s, M. primaeva, M. senecta and the species of Mesodma described here all have distinct posterior basins considered here to be a primitive characteristic. M. formosa is somewhat variable in that regard and M. thompsoni, M. garfieldensis, and M. hensleighi lack a distinct posterior basin. In terms of M1s, the taxa described here have the lowest cusp formula, and the number of cusps increase in the following order: M. primaeva, M. hensleighi, M. thompsoni, M. formosa, and M. garfieldensis.

From analysis of these characters it appears that the taxa described here, along with M. primaeva, represent the most primitive known taxa of Mesodma. Mesodma formosa and M. thompsoni are more derived, and M. garfieldensis and M. hensleighi are the most derived. The position of M. senecta is unclear due to lack of knowledge of more than the fourth premolars. Attempts to generate meaningful cladograms were fruitless as each dental position yielded significantly different results.

Family Cimolodontidae<br>Cimolodon Marsh, 1889<br>Cimolodon foxi sp. nov. tables 4-5; figures 8F-J, 9A-I, 10A-B

Holotype - OMNH 24038, RM1, Loc. V61.
Hypodigm - MNA V4635, LM2, Loc. 454-6 (Cimolomys sp. B in Eaton, 1987); MNA V4638, LM1, Loc. 454-6 (Mesodma sp. cf. M. thompsoni in Eaton, 1987); MNA 4508, LP4 (anterior part), Loc. 453-2; MNA V5270, LP4, Loc. 454-6; MNA V5302, RP4, Loc. 1004-1; MNA V5339, RP4, Loc. 1004-1 (Cimolodon sp. B in Eaton, 1987); MNA V7540, Rm2, Loc. 704-1; OMNH 20005, Lm2, Loc. V5 (?Cimolomyid, gen. \& sp. indet., in Eaton, 1987); OMNH 20483, Rp4, Loc. V9; OMNH 20491, Lm2, Loc. V9; OMNH 20492, Rm2, Loc. V9; OMNH 22316, LM2, Loc. V5; OMNH 24040, RM1, Loc. V61; OMNH 24043, RM2, Loc. V61; OMNH 24044, RM2, Loc. V61;OMNH 24326, RM1, Loc. V61; OMNH 24329, LP4 (anterior part), Loc. V61; UMNH VP7630, LP4, Loc. 108.

Distribution - Kaiparowits Formation of southern Utah, Campanian.

Diagnosis - Smallest species of Cimolodon, molars more than $15-20 \%$ smaller than C. similis; P 4 with formula of 4:5-6, with medial row cusps only somewhat taller than external row cusps; cusp formula M1 5-6:7:4-6 similar to $C$. similis but internal row longer relative to molar length than in C. similis.

Etymology - For Dr. Richard Fox's contributions to our knowledge of Cretaceous mammals, and the similarity of this taxon to that named by Dr. Fox, Cimolodon similis.

Description - p4. OMNH 20483 (figures 8E-F) is a small, high-crowned $(\mathrm{H}: \mathrm{AP}=0.61)$, flat-crested blade with 12 serrations, 10 external ridges, and 9 internal ridges. The valley separating the two posteromost serrations is oriented posteroventrally and extends to the top of the posteroexternal cusp.
m2 - OMNH 20005 (figure 8G) is a worn specimen with a formula of $4: 2$. The molar broadens posteriorly. Narrow notches divide the cusps of the external row and the cusps are not divided labially. Internal cusps are also not well divided lingually.

P4 - These P4s have a formula of 4:5-6, the teeth are low crested, and are arched in occlusal view. The posterior basin is small (PL:AL $=0.34-0.35$ on relatively unworn specimens) and the climb ratio for the cusps of the medial row is low ( $\mathrm{CR}=0.27$ ). UMNH VP7630 (figures $8 \mathrm{H}-\mathrm{J}$ ) has four distinct cusps on the external row. The first is the smallest and lowest, the second and third are larger than the cusps of the medial row, with the third cusp being the tallest. The fourth cusp is about the same size as the second. Five cusps are counted on the medial row although there is a tiny anterior cuspule not included in the formula. The cusps are progressively broader and more widely separated posteriorly with the last cusp being the tallest. The cusps have crenulated enamel and the premolar is low crowned $(\mathrm{H}: \mathrm{AP}=0.36$; CR not measurable). MNA V5270 (figures 9A-C) has conical cusps on the anteroexternal platform and the third cusp is the largest and tallest of the tooth, although the medial cusp row is well worn on this specimen. The cusps of the medial row are well separated and striated. MNA V5302 (figures 9D-F) is similar to the other P4s but is less worn, the medial


Figure 8. Mesodma sp. (large): A, (OMNH 20351), LP4, stereo occlusal view; B, labial view; C, lingual view; D (OMNH 24041), LM2, stereo occlusal view. Cimolodon foxi: E, (OMNH 20483), Rp4, labial view; F, lingual view; G, (OMNH 20005), Lm2 in mandibular fragment, stereo occlusal view; H, (UMNH VP7630), LP4, stereo occlusal view; I, labial view; J, lingual view. Scale bar $=1 \mathrm{~mm}$.


Figure 9. Cimolodon foxi sp. nov.: A, (MNA V5270), LP4, stereo occlusal view; B, labial view; C, lingual view; D, (MNA V5302), RP4, stereo occlusal view; E, labial view; F, lingual view; G, (MNA V5339), RP4, stereo occlusal view; H, labial view; G, lingual view. Scale bar = 1 mm.
cusp row is taller than the cusps of the external row, and there is an additional cusp in the medial row. MNA V5339 (figures 9G-I) is tentatively included here. It is strongly arched in occlusal view and is larger than the other specimens included here (table 4), but its cusp morphology is almost identical to the other specimens.

M1 - OMNH 24038 (holotype, figure 10A) has a formula of $5: 7: 4$. All of the cusps of the external row are separated labially and attached lingually by a low, sharp crest that parallels the central valley. Each cusp of the row becomes taller, narrower, and more deeply separated posteriorly. Cusps are erect and conical. The central valley is oblique to anteroposterior axis of the molar. The cusps of the medial row are crescentic to subcrescentic (posteriorly) and are more deeply divided and taller than the cusps of the external row. Cusps of the medial row broaden posteriorly. The central valley is lower than the valley separating the medial and internal cusp rows. Cusps of the internal row are essentially conical. The first three cusps of the row are well separated and the two posteromost cusps are connected. The internal row is broad and terminates just posterior of the first cusp of the medial row.

M2 - OMNH 22316 (figure 10B) has a cusp formula of $\mathrm{Ri}: 2: 5$. The medial cusp row has a strong anterior ridge that is unworn, uncusp-like, and is too low to function as a cusp and as such is not counted as one here (although it might well be counted as a cusp by other workers). The external ridge is comprised of lingual-buccally compressed cuspules, but none is distinct enough to be counted as an individual cusp. The first cusp (not counting the anterior ridge) of the medial row is large, oriented strongly anteriorly, and is deeply ribbed on its sides and pitted at its base. The central valley is complex with ribs and pits in this narrow valley. Cusps of the internal row are only divided at their apices. The labial wall of this row is deeply ribbed and complex. The first two cusps are large and the posterior three cusps are subequal in height and smaller.

Discussion - The p4 is high crowned as are the p4s of other species of Cimolodon. The p4 is smaller than those of C. similis (table 5) but not as small relatively as are the molars of C. foxi. It may be that the $\mathrm{p} 4: \mathrm{ml}$ ratio for this taxon is higher than that of $C$. similis (1.4) and closer to that of C. electus (1.8). The P4s have the typical arch-shaped low crown and short posterior basin (primitively at least) of Cimolodon and are markedly smaller ( $27 \%$ ) than those of $C$. similis (table 4).

The second lower molars of Cimolodon are distinguished from those of Cimolomys in that those of Cimolodon have the cusps of the external cusp row divided lingually, but not labially, such that the external row forms a high continuous ridge. The cusps of the external row of Cimolomys are well separated lingually and labially (C. clarki, Sahni, 1972, figure 11E; Lillegraven and McKenna, 1986, figure 7B; C. gracilis, Clemens, 1964, figure 35). In Cimolodon, there is also a tendency for the last cusp of the external row to shift somewhat lingually relative to the other cusps of the row, whereas in Cimolomys the cusps are in a straight row. OMNH 20005 is damaged at its posterolabial corner so this character cannot be assessed. One specimen tentatively included here, MNA V7540, is also damaged, making assessment of the presence and position of the last cusp of the external row impossible. MNA 7540 may also have a cusp
formula too low for Cimolodon, ?3:2, and its rounded cusps are not very similar to those of OMNH 20005; however, the cusps of the external row are poorly divided as in Cimolodon. The tooth might be considered to represent Mesodma, but this specimen clearly broadens posteriorly, unlike illustrated specimens of Mesodma (Mesodma sp., Clemens, 1964, figure 16b; M. formosa, Lillegraven, 1969, fig, 7a; M. garfieldensis, Archibald, 1982, figure 12C). This specimen has a LB:AP ratio identical to that of OMNH 20005 (table 4).

The P4s are considered to represent Cimolodon because of the well-developed external cusp row on a broadly expanded anteroexternal platform, the strong arch of the premolar in occlusal view, the low-crowned nature of the tooth, and the low climb ratio of the cusps of the medial row (e.g., C. nitidus, Clemens, 1964, figure 30b). The P4s are smaller than any previously described for Cimolodon (table 4) except for UALP 15629 described by Flynn (1986) as Cimolodon n. sp. which is very close in size $(\mathrm{AP}=3.07 ; \mathrm{LB}=181)$ to these specimens and may represent the C. foxi.

The M1s of C. foxi are similar to those of Cimolodon similis in cusp formula and proportions; however, the length and width of the molars (table 4) are at least $20 \%$ smaller than those of C. similis. Fox (1971) separated C. similis and C. electus solely on the basis of size, a difference of $12-15 \%$ depending on the dimension measured. If that difference is adequate to distinguish two species, then most certainly $C$. foxi can be separated from C. similis on the basis of size as well as the elongation of the internal cusp row.

The M2s are thought to represent Cimolodon and not Cimolomys because: 1) the cusps of the internal row are poorly separated in Cimolodon (C. nitidus, Clemens, 1964, figure 31b) and better separated in Cimolomys (C. gracilis, Archibald, 1982, figure 23d); 2) the cuspules along the external platform form a sharp ridge in Cimolodon (C. electus, Fox, 1971, figure 5a; C. nitidus, Lillegraven, 1969, figure 11) and are more cusp-like in Cimolomys; and 3) the medial and internal cusp rows of Cimolodon are parallel to each other and oriented at an angle to the anteroposterior axis of the molar (as do the rows and valleys of the M1) whereas in Cimolomys the rows are aligned essentially anteroposteriorly (C. clarki, Sahni, 1972, figure 11F; Lillegraven and McKenna, 1986, figure 7D; C. gracilis, Clemens, 1964, figure 38b). These M2s are smaller than those described for any other species of Cimolodon (table 4). The primitive condition of the M2 length being close to that of the M1 is seen in C. similis and C. electus, but this species has M2:M1 length ratios within the range of the more derived taxon C. nitidus (table 4).

## Cimolodon sp. cf. C. nitidus Clemens, 1964 table 4; figures 10C-F

Referred Specimens - MNA V5285, anterior part RP4, Loc. 453-2; MNA V5337, RP4, Loc. 1004-1; OMNH 24035, RP4 (posterior part), Loc. V61; OMNH 20477, LM1-2, Loc. V9.

Description - P4. MNA V5337 (figures 10C-E) has a cusp formula of $3: 7$. The tooth has the arched shape in occlusal view and low crest $(\mathrm{H}: \mathrm{AP}=0.44)$ typical of P 4 s of Cimolodon. The three cusps of the external row arise from a broadly expanded anteroexternal platform and are broader based than the cusps of the medial row. There is a small cuspule at the anterior margin of the tooth between the two cusp


Figure 10. Cimolodon foxi sp. nov.: A, (OMNH 24038), holotype, RM1, stereo occlusal view; B, (OMNH 22316), LM2, stereo occlusal view. Cimolodon sp. cf. C. nitidus: C, (MNA V5337), RP4, stereo occlusal view; D, labial view; E, lingual view; F, (OMNH 20477), LM1-2, stereo occlusal view; Cimolodon sp. cf. C. similis; G, (OMNH 20484), Rp4, labial view; H, lingual view. Scale bars $=1 \mathrm{~mm}$.
rows. The cusps of the medial row are only divided apically, and the row reaches its apex at the sixth cusp. The posterior heel is short ( $\mathrm{PL}: \mathrm{AL}=0.31$ ) and positioned just below the last cusp of the medial row. The cusps are strongly striated.

M1 - OMNH 20477 (figure 10F) has a cusp formula of 6:7:5. The central valley is oriented somewhat transversely to the anteroposterior axis of the tooth such that the cusps of the labial row narrow posteriorly while the cusps of the medial row broaden. The medial valley is higher than that separating the medial and internal cusp rows. The cusps of the medial row increase in height posteriorly. The internal cusp row is about two-thirds the length of the tooth.

M2 - OMNH 20477 (figure 10F) has a cusp formula of 3:3:2. There are two distinct cusps on the anteroexternal corner of the platform and a series of small cuspules that descend posteriorly. The first two cusps of the medial cusp row are closely positioned with the third cusp more broadly separated. The central valley has deep pits. The first two cusps of the internal row are not deeply divided, and there is a much deeper separation between cusps 2 and 3 .

Discussion - The P4 is similar in length to C. similis but is broader and more cuspate than the P 4 s of that taxon (table 4). The tooth is also broader relative to length than either $C$. similis or C. electus and is very close to the value recorded by Lillegraven (1969) for C. nitidus (table 4). The P4s are in the lower size range for those of $C$. nitidus in the Lance Creek sample (Clemens, 1964) but are below the range of values provided for the Scollard sample by Lillegraven (1969, table 2) (table 4). The cusp formula is in the range of C. nitidus (table 4). The presence of striations, as in C. similis and C. electus, suggests a form of Cimolodon close to $C$. nitidus in size but retaining many primitive features. Also primitive is the high climb ratio of the cusps of the medial row ( $\mathrm{CR}=0.49$ ) which is more like the condition seen in P 4 s of C. electus (Fox, 1971, figure 5a-b) than in P4s of $C$. nitidus (Clemens, 1964, figure 30b). The retention of some primitive characteristics and the small size of the sample only permit conferring this species to C. nitidus. It is difficult to evaluate the proportion of the posterior basin to the total length of the tooth (PL:AP) as this appears to be highly variable in C. nitidus, based on calculations made from illustrated specimens (table 4).

The slight narrowing of the external cusp row of the M1 (OMNH 20477; figure 10F) is similar to that of the specimen figured by Lillegraven (1969, figure 12-3) as C. nitidus. The cusp formula and size of the M1 (OMNH 20477) are within the range for C. nitidus (in Lillegraven, 1969, but are larger than the samples described by Clemens, 1964 and Archibald, 1982) (table 4). Making certain species assignment of the M1 is complicated by the P4:M1 ratio based on the P4 (MNA V5337) described above. The resultant ratio (0.76) is well below recorded values for Cimolodon nitidus (see table 4). This raises a question of whether the P 4 represents the same species as the M1. It could be that two species similar to $C$. nitidus are present, or a new species is present with dental proportions different than $C$. nitidus. A larger sample is required to resolve this issue. It should also be noted that the M2 (OMNH 20477; figure 10F) has one less cusp in the internal row than recorded previously for Cimolodon nitidus (table 4). The M2:M1 length ratio is close to the value of the sample of Cimolodon nitidus provided by Archibald (1982).

Cimolodon sp. cf. C. similis Fox, 1971 table 5; figures $10 \mathrm{G}-\mathrm{H}$

Referred Specimens - MNA 7532, Rp4, Loc. 704-1; OMNH 20347; Rp4; Loc. V5; OMNH 20484, Rp4, Loc. V9; OMNH 22313, Lp4, V5.

Description and Discussion - p4. These are high-arched, symmetrical p4s typical of Cimolodon. OMNH 20484 (figures $10 \mathrm{G}-\mathrm{H}$ ) has 12 serrations with 7 external and 12 internal ridges. This specimen is more highly arched and has more serrations than the other specimens conferred here to C. similis. The other specimens are less high crowned and there is considerable variation in the number of internal and external ridges (table 5). As such, these p4s may represent more than one taxon. The size of these specimens and their serration count place them closer to $C$. similis than to any other species of Cimolodon (table 5).

## Family ?Cimolodontidae Marsh, 1889 <br> Kaiparomys gen. nov.

Type and only species - Kaiparomys cifellii.
Distribution - Kaiparowits Formation of southern Utah, Campanian.

Diagnosis - m1 with formula (7:4), cusps more broadly separated than in Mesodma or Cimolodon, molars elongate and taper strongly anteriorly, cusps erect pyramidal on external row, crescentic on internal row, unlike Cimolodon. Molars complexly pitted unlike Mesodma.

Etymology - Named after the Kaiparowits Formation and mys, the Latin for mouse.

> Kaiparomys cifellii sp. nov.
> table 6; figures 11A-D
> ?Cimolodon sp. Eaton, 1987

Holotype - UCM 50420, Lm1-2, Loc. 83240.
Hypodigm - UCM 50384, Rm2, Loc. 83258; MNA V5264, Rm2, Loc. 454-6, MNA V5286, LM2 (part), Loc. 697-2; MNA V7530, RM2, Loc. 704-1; OMNH 20362, RM2, Loc. V5; OMNH 22325, RM2, Loc. V5; OMNH 22325, RM2, Loc. V5; OMNH 22842, Rm2, Loc. V9.

Distribution - As for genus.
Diagnosis - As for genus.
Etymology - For Dr. Richard L. Cifelli's remarkable contributions to our knowledge of Cretaceous mammals and his labors collecting many of the specimens described in this paper.

Description - m1. UCM 50420 (figure 11A) is a ramus with $\mathrm{m} 1-2$. The m 1 has a cusp formula of $7: 4$. The molar is anteroposteriorly elongate relative to its width and narrows markedly anteriorly. The first two cusps of the external row are low and close together. The third cusp is well separated from and taller than the first two cusps. Cusp 4 is small, low, and labially placed. The fifth cusp is erect and in the form of an anteroposteriorly compressed pyramid. The fifth and sixth cusps are well separated lingually but, unlike the more anterior cusps, there is a low wall connecting the cusps labially closing off the valley between the cusps. This wall is tallest between the sixth and seventh cusp of the external row. These two cusps are positioned posterior to the last two


Figure 11. Kaiparomys cifelli gen. \& sp. nov.: A, (UCM 50420), holotype, Lm1-2, stereo occlusal view; B, (UCM 50384), Rm2, stereo occlusal view; C, (MNA V7530), RM2, stereo occlusal view; D, (OMNH 22325), RM2, stereo occlusal view. Meniscoessus sp. cf. M. intermedius: E, (OMNH 20507), Lm1, stereo occlusal view; F, (OMNH 20481), LM1, partial, stereo occlusal view. Scale bars $=1 \mathrm{~mm}$.
cusps of the internal row, forming a sharp inflection on the posterior wall of the molar.

The central valley is open posteriorly, probably as a result of wear. The valley is sinuous, resulting in part from the strong corners of the pyramidal cusps of the external row that cross the central valley.

Cusps of the internal row are taller than those of the external row. The first two cusps are closely appressed. The third cusp is distinctly crescentic with a rounded anterior face and a concave posterior wall bounded by strong ridge-like corners on both sides. There is a broad, deep valley between cusps 3 and 4. The fourth cusp is elongate and ribbed on its labial wall and is concave on its anterior face.
m2 - UCM 50420 (figure 11A) has cusp formula of 4:2. The valleys separating the cusps of the external row are closed buccally. The cusps of the external row lengthen posteriorly. The first cusp of the internal row has a deep pit on its labial wall. The valley separating the first and second cusps is broad and very similar to the valley separating the third and fourth cusp of the internal row of the ml . The second molar is significantly broader than the m 1 (table 6 ).

UCM 50384 is an unworn m 2 (figure 11B) with a cusp formula of 5:2. The external cusp row forms a tall wall with cusps decreasing slightly in size and height posteriorly. The cusps are separated only at their apices with deep valleys plunging into the central valley. The central valley is crossed by ribs generated from interior walls of the cusps of both rows. Deep pits are present along the valley. The first cusp of the internal row is large with a concave posterior face. The second cusp is much narrower. There is a small cuspule at the posterior margin of the second cusp.

M2 - MNA V7530 (figure 11C) has a cusp formula of $\mathrm{Ri}: 3: 4$. The first cusp of the external row is ribbed and surrounded at its base by pits. The second cusp is about the same height and size. A distinct wall surrounds the anterior and labial margin of the tooth. The central valley is very complex as it is crossed by ribs and deeply pitted. The first three cusps of the internal row are close together and only slightly separated at their apices. The fourth cusp is more widely and deeply separated than the first three cusps. The tooth is slightly constricted in occlusal view due to slight indentations behind the third cusp of the internal row and between the two cusps of the external row. OMNH 22325 (figure 11D) has a cuspate wall with four distinct cusps along the anterolabial corner of the tooth. The first cusp of the medial row is ridge-like, whereas the second and third cusps are larger and have their apices oriented anteriorly. There is some ribbing on the posterior wall of cusp 2. The central valley has deep pits with ridges crossing it, connecting the cusps of the medial and internal rows. The cusps of the internal row are deeply separated on the labial wall and moderately well separated lingually. A deep pit is present posterior to cusp 3 at the terminus of the central valley.

Discussion - This taxon superficially resembles Mesod$m a$ in the elongation and the sinuous central valley of the m 1 , but Mesodma has more consistently crescentic cusps in both cusp rows of the ml and the cusps are not as broadly separated as in Kaiparomys. The m 1 is like that of Cimolodon in having the cusps of the external row pyramidal and a pitted central valley (but also see Mesodma, Archibald, 1982, figure 12a). But Kaiparomys lacks the well-developed and complex ribbing seen in the molars of $C$. similis and C. elec-
tus. The ratio of $\mathrm{m} 2: \mathrm{m} 1(0.65)$ is similar to that of $C$. nitidus, Archibald, 1982 (table 8; $\mathrm{m} 2: \mathrm{ml}=0.63$ ) but is dissimilar to the value calculated for C. nitidus, Lillegraven, 1969 ( $\mathrm{m} 2: \mathrm{m} 1=0.71$ ). It is interesting to note that the size range for m 1 s of $C$. nitidus in Archibald (1982) does not overlap with those reported by Lillegraven (1969), suggesting that there may be more than one species present in their two samples. The $\mathrm{m} 2: \mathrm{m} 1$ length ratio is also similar to that of Mesodma thompsoni, Lillegraven, 1969 ( $\mathrm{m} 2: \mathrm{m} 1=0.68$ ) but not close to the value for M. thompsoni presented in Archibald (1982; $\mathrm{m} 2: \mathrm{m} 1=0.75$ ). It may be that m 2 s are often incorrectly assigned or that the lengths of m 2 s may be highly variable. The somewhat low, paired, and slightly offset anterior cusps of both cusp rows on ml are more like the condition seen in m 2 s of C. electus (see Fox, 1971, figure 4) than in those of Mesodma (except for a somewhat odd tooth described as $M$. formosa by Lillegraven, 1969, figure 7 and some of the specimens of Mesodma described herein).

The m2 resembles that of Cimolodon electus (see Fox, 1971, figure 5), in that the cusps of the external row are not well separated labially, but the external cusp row of C. electus becomes taller and broadens posteriorly unlike the external cusp row of this taxon. The elongation of the second cusp of the internal row is more like the m 2 s of Cimolomys (see Archibald, 1982, figure 23e), but the cusps of the external row of the m 2 s of Cimolomys are deeply divided (see $C$. clarki, Sahni, 1972, figure 11E; Lillegraven and McKenna, 1986, figure 7B). The m 2 is not similar to any figured specimens of Mesodma, although the length to width ratio is similar (table 6). The length-to-width ratio is intermediate between that of the m 2 s of Cimolodon similis and C. nitidus (table 6). The M2s appear to be more squared (mean LB:AP=0.96) than the M2s of either Mesodma or Cimolodon (table 6).

The M2 is also unlike described specimens of Mesodma in having strong ribs and deep pits. The ribbing and pitting are most similar to the condition seen in M2s of Cimolomys (C. gracilis, Archibald, 1982, figure 23), but the close position of the anterior two cusps of the internal cusp row is similar to the condition seen in Cimolodon (C. nitidus, Lillegraven, 1969, figure 11-5b). Cimolodon electus has a similar internal cusp row but has a broadly expanded anterolabial platform unlike Kaiparomys. The well-divided internal cusp row is more similar to M2s of Cimolomys than Cimolodon.

In overall form of the cusps, the presence of some ribs and pits, and the way in which cusps of the molars are separated, this taxon more closely resembles Cimolodon than any other described taxon. The resemblance however, may just be the retention of primitive characters as the strong anterior tapering of the ml may suggest closer affinities with Mesod$m a$. In many other regards the teeth, particularly the second molars, are distinctly unlike any described for Mesodma.

Superfamily unknown<br>Family Cimolomyidae Marsh, 1889<br>Meniscoessus Cope, 1882<br>Meniscoessus sp. cf. M. intermedius Fox, 1976<br>table 7; figures $11 \mathrm{E}-\mathrm{F}$

Referred Specimens - OMNH 20481, LM1 (posterior part), Loc. V9; OMNH 20507, Lm1, Loc. V9; OMNH

24057, Lm1 (anterior part), Loc. V61; UMNH VP7636, RM1 (fragment), Loc. 108.

Description - m1. OMNH 20507 (figure 11E) has a cusp formula of $6: 4$. The first cusp of the external row is low, cusps 2-4 are pyramidal in form and well separated, and cusps 5 and 6 are not separated labially but are separated lingually by a vertical groove. The central valley is sinuous with pitting in the posterior half of the valley. The first cusp of the internal row is small and conical with a wear facet facing the central valley. Cusps 2, 3, and 4 are pyramidal and well separated but not as deeply divided as the cusps of the external row.

M1 - OMNH 20481 (figure 11F) is the posterior part of an M1. The cusp formula is uncertain, but there are at least six cusps in the internal row. Cusps of the external and medial rows are about the same height, but those of the medial row are broader. The largest cusps of the internal row are about the same size as those of the medial row but are lower. Cusps of the external row are conical but flattened on the lingual side and are connected medially by small anteroposter-ior-oriented ridges. The cusps of the medial row are subpyramidal with a flattened anterior face and with cusp apices oriented slightly anteriorly. The internal cusps are basically conical and separated from the medial row by a valley that is deeper than that which separates the medial and external rows. Cusps of the medial and external rows are ribbed on the sides facing valleys.

Discussion - The m1 is smaller and less cuspate than those of M. major and smaller, with much less crescentic cusps than m1s of M. robustus (table 9). Although the specimen is also smaller than M. intermedius, it is just below the known range of that taxon both in terms of size and number of cusps (table 9). Older, presumably more primitive forms of Meniscoessus (M. major, Sahni, 1972, figure 12E; M. intermedius, Fox, 1976) have more erect and less crescentic cusps than Lancian forms (e.g., M. robustus, Clemens, 1964, figs. 43, 44). The taxon described here has erect subpyramidal cusps, placing it among the more primitive forms of Meniscoessus. The internal cusp row is not as expanded as that of the incompletely prepared M1 of $M$. intermedius (illustrated by Fox, 1976, figure 3) but otherwise appears to be very similar. Both the molars are somewhat smaller than known specimens of $M$. intermedius, and part of the lack of certainty about assignment of these specimens occurs because Fox (1971) described a smaller species, M. ferox. Meniscoessus ferox is based on a P4 (Fox, 1971). An M2 was subsequently identified (Fox, 1976), but there are no description or measurements available for that specimen. As there is a smaller species named, and the only complete measurable molar here is $12 \%$ smaller than $M$. intermedius, I confer the taxon to the better-known species recognizing that with more complete knowledge of M. ferox, these specimens might be more appropriately placed within that species.

## Meniscoessus sp. cf. M. major Sahni, 1972

Referred Specimen - MNA V4587, LM1 (anterior part), Loc. 704-3.

Description and Discussion - A single partial M1 is significantly larger than the specimens described above, but there are no complete dimensions available to measure. The fragmentary specimen compares closely to M1s from the

Judith River Formation (UCMP collections) in size, number of cusps, and deep grooves present at the base of the cusps, but the internal cusp row is longer, relative to the total molar length, in the Judith River specimens. However, the internal row is very similar to those described from Fox's (1980) sample of M. major in that the anteromost cusp of the internal row is opposite the fourth cusp of the medial row, which has a low ridge continuing to the anterior margin of the tooth. Because of the tooth size and morphology, this partial molar is tentatively conferred to M. major.

> Cimolomys Marsh, 1889
> Cimolomys sp. A cf. C. clarki Sahni, 1972 table 8 , figures $12 \mathrm{~A}-\mathrm{B}$

Referred Specimens - OMNH 24037, RM1, Loc. V61; OMNH 24324, LM2, Loc. V61; OMNH 24325, LM1 (posterior part), Loc. V61.

Description - M1. The cusp formula of OMNH 24037 (figure 12 A ) probably is $5: 6: 7$, although the anteromost part of the tooth is missing and there is the slight possibility of an additional external or medial cusp. The first three cusps of the external row are conical but have flat wear facets on their lingual sides. A large, deep, broad valley separates cusps 2 and 3. The fourth cusp is conical but anteroposteriorly compressed. The fifth cusp is small, low, and connected to the posteromost cusp of the medial row by a ridge that closes off the central valley posteriorly. Although the cusps of the external row get smaller posteriorly, the width of the row does not narrow posteriorly.

The central valley is slightly sinuous and crossed by ribs at the position of the valley separating cusps 2 and 3 of the external row and also near the posterior end of the central valley. The central valley has a slight arch to it in occlusal view but is essentially oriented with the anteroposterior axis of the tooth, and it does not cross the tooth diagonally. The cusps of the medial row are subpyramidal with the four posterior cusps having apices oriented slightly anteriorly. The cusps increase in size and height posteriorly.

The internal cusp row reaches or closely approaches the anterior margin of the tooth (estimated due to the small amount of breakage anterior of the external and medial cusp rows). At the anterior of the internal cusp row are three low, connected cuspules, of which only the third is counted as a cusp in the formula. Cusps 2, 3, and 4 are distinct, conical, and well separated. Cusps 5, 6, and 7 are connected and form a high ridge. The cusps increase in height to the sixth cusp, but the seventh cusp is distinctly lower. In occlusal view the row is arched, reaching its maximum lingual breadth at the position of the fourth cusp.

M2 - OMNH 24324 (figure 12B) has a cusp formula of 3:3:4. There are three distinct cusps present anteriorly on the anteroexternal platform that grade posteriorly into a cuspate ridge. The first cusp of the medial row is low and narrow. The second cusp is strongly ribbed all the way around, and the third is well-ribbed on its posterolabial side and subequal in size to the second cusp. The central valley is finely pitted and open posteriorly. Cusps of the internal row are progressively better separated posteriorly. A tiny cuspule is present posterolabially of the fourth cusp.

Discussion - The M1 is thought to represent Cimolomys because of the well-developed internal cusp row, the conical
cusps on the outside rows of the tooth, the anterior-leaning subpyramidal cusps of the medial row, and because the external and medial cusp rows maintain their width such that the central valley of the molar is aligned approximately with the anteroposterior axis of the tooth. The specimen is too small to represent C. trochuus or C. gracilis. It is close to the estimated size of the specimen described by Sahni (1972) as $C$. clarki (Sahni provided no dimensions but stated m1s of $C$. clarki were the same size as those of Mesodma primaeva) and is very similar to that specimen in overall form and cusp formula; however, the specimen appears to be significantly smaller than the sample of C. clarki described by Lillegraven and McKenna (1986) (see table 8). The first cusp of the external row of this specimen is subequal to the second, whereas in the specimen of C. clarki figured by Sahni (1972, AMNH 77219, figure 11-G) the first cusp is small and positioned lingually of the other cusps.

The M2 is considered to represent Cimolomys because the relatively well-separated cusps of the internal row, unlike the ridge-like cusp row of Cimolodon (see discussion above under Cimolodon foxi). It fits well against the posterior margin of OMNH 24037 (an M1), and has LB:AP and M2:M1 length ratios identical to described specimens of Cimolomys (table 8). The specimen is distinctly smaller than any other described M2s of Cimolomys and possibly, along with the M1, indicates the presence of a smaller population of C. clar$k i$ than previously sampled, or a new smaller species. A larger sample would be required to determine this with certainty.

Cimolomys sp. B cf. C. clarki Sahni, 1972
table 8; figures 12C-F
Referred Specimens - MNA V4586, RP4, Loc. 704-1; MNA V7526, RP4, Loc. 704-1; OMNH 24327, RM1 (posterior part), Loc. V61.

Description - P4. MNA V7526 (figures 12C-E) has a cusp formula of $1: 5$. The tooth is broad with rounded margins (in occlusal view) with a moderate crown height. The cusp apices are striated. There is a single anteroexternal cusp on the anteroexternal platform that is not broadly expanded relative to the width of the tooth. Cusp apices of the medial cusp row are well separated with the apogee reached at the fifth cusp. A complexly enameled and flattened surface descends from the apex of cusp 5 to a large posterior cusp. A small basin is formed lingual to the cusp and another smaller cusp terminates the basin internally. MNA V4586, another RP4, has a cusp formula of 1:5 and is slightly larger and more robust than MNA V7526 (table 8).

M1 - OMNH 24327 is the posterior half of a RM1 (figure 12 F ). The posterior four cusps of the external and medial rows are much like those of OMNH 24037, referred above to Cimolomys sp. A cf. C. clarki, but all of the cusps are more elongated anteroposteriorly. The width of the molar is less than that of OMNH 24037 (table 8). The internal row is unusual in having at least seven distinct, equal-sized, closely appressed cusps.

Discussion - The differentiation of P4s of Cimolodon and Cimolomys is not easy. Although most of the described P4s of Cimolodon have several cusps in the external row they may have as few as one (e.g., C. electus). P4s of Cimolodon usually have more cusps in the medial cusp row than in P4s of Cimolomys, but they may overlap in number (e.g., 6 cusps
in some specimens of Cimolodon nitidus and in Cimolomys clarki). In general, the P 4 s of Cimolodon have an arched shape in occlusal view such that they are concave lingually and convex labially. This appears to reflect a change in direction of the cusps to correspond to curvature of the maxillary (Clemens, 1964, figure 29C). In Cimolomys, the medial cusp row tends to be essentially straight (Clemens, 1964, figure 36b; Sahni, 1972, figure $11-\mathrm{H}$; Lillegraven and McKenna, 1986, figure 7F); however, there is a slight curvature to the specimen of C. gracilis shown in Archibald (1982, figure 23 C ) and in the specimens assigned here to Cimolomys.

The height of the crown relative to the tooth length also shows certain trends. The H:AP is generally relatively low for Cimolodon as estimated from figures ( 0.33 for C. electus, Fox, 1971, figure 5b; 0.36 for C. nitidus, Clemens, 1973, figure 30c) but is estimated to be as high as 0.48 (C. nitidus, Archibald, 1982, figure 20b). The crown tends to be higher in Cimolomys, but the values overlap with those of Cimolodon ( 0.42 for C. clarki Sahni, 1972, figure 11-H; 0.45 for C. gracilis in Archibald, 1982, figure 23b; and 0.50 for ?Cimolomys sp. A in Fox, 1971, figure 6c). The specimens here have a H :AP range of $0.50-0.54$, exceeding the known range for Cimolodon. This suggests affinities of these specimens to Cimolomys.

An attempt was made to distinguish P4s of Cimolodon and Cimolomys on the basis of the proportion of the posterior basin to the anterior part of the tooth (PL:AL). However, C. electus and some illustrated specimens of Cimolomys have a short posterior basin (range of PL:AL $=0.38-0.47$ ). But many illustrated specimens of Cimolodon nitidus have relatively long posterior basins ( $\mathrm{PL}: \mathrm{AL}=0.7$ ), as does the P 4 of Cimolomys gracilis (PL:AL $=0.67$ ) figured by Clemens (1964, figure 36) and the P4 of Cimolomys clarki depicted by Sahni (1972, figure 11-H). So this aspect of tooth proportion may be highly variable, or apical wear has strongly altered the apparent proportions. It is also possible that the attempt to determine these proportions from illustrations yielded inaccurate data.

In overall tooth appearance, high crest, and low cusp count these specimens most closely resemble Cimolomys. The teeth are too large to be those of C. gracilis and exceed the range of described specimens of C. clarki. P 4 s assigned to C. clarki by both Sahni (1972) and Lillegraven and McKenna (1986) were unusually large as the teeth of C. clar$k i$ are usually $30 \%$ smaller than those of $C$. gracilis. The P4s they assigned to $C$. clarki are actually larger than those of $C$. gracilis. An alternate hypothesis is that the P 4 assigned by Sahni (1972) to $C$. clarki may be from a species closer to $C$. trochuus, an observation consistent with Archibald's (1982, p. 122) comment that the similar-sized ?Cimolomys sp. A of Fox (1971) may possibly represent C. trochuus. MNA V7526 is close to the size of the specimen described by Fox (1971) as ?Cimolomys sp. A (table 8) and MNA V4586 is more robust than Fox's specimen. Fox's (1971) specimen is close to those described by Sahni (1972) as C. clarki, but all of Sahni's specimens may actually represent C. trochuus. If Fox's specimen represents $C$. trochuus, then the specimens described here should also be referred to that species. Comparison of the M1 (OMNH 24037, figure 12F) referred to here as Cimolomys sp. A cf. C. clarki with these two P4s indicates that the P 4 s are too large to appropriately fit the M1.


Figure 12. Cimolomys sp. A cf. C. clarki: A, (OMNH 24037), incomplete RM1, stereo occlusal view; B, (OMNH 24324), LM2, stereo occlusal view. Cimolomys sp. B cf. C. clarki: C, (MNA V7526), RP4, stereo occlusal view; D, labial view; E, lingual view; F, (OMNH 24327), partial RM1, stereo occlusal view. Scale bar $=1 \mathrm{~mm}$.

Either the size range of C. clarki is greater than previously known or there is a species of Cimolomys larger than C. clarki such as C. trochuus in this sample. As such, it is possible that there are two species of Cimolomys present in the sample recovered from the Kaiparowits Formation.

The partial M1 included here (OMNH 24327) may be significantly longer and have an internal row that differs from that of the M1 referred above to Cimolomys sp. A cf. C. clarki. The specimen is inadequate to assign this M1 with certainly to C. clarki.

Family ?Cimolomyidae Marsh, 1889<br>?Cimolomys butleria sp. nov. table 8; figures 13A-G

Holotype - MNA V5226, LM1, Loc. 704-1 (?Cimolomyid, gen. \& sp. indet. in Eaton, 1987).

Hypodigm - MNA V5341, RP4, Loc. 1004-1 (Paracimexomys n. sp. C in Eaton, 1987); OMNH 20010, RP4, Loc. V5 (Cimexomys sp. in Eaton, 1987); OMHH 22306, LP4, Loc. V5; OMNH 22837, Lm1, Loc. V9.

Distribution - Kaiparowits Formation of southern Utah, Campanian.

Diagnosis - Smaller than any other species of Cimolomys; first lower molar formula 6:4, cusps pyramidal unlike those of other species Cimolomys; P4 formula 1:5, low crested and straight as in other species of Cimolomys; M1 squared with internal row as long as molar, cusp formula 4:6:5, external row cusps pyramidal, medial row cusps pyramidal and leaning anteriorly, medial valley crosses tooth diagonally. Molars are smaller and less cuspate than described species of Cimolomys or Cimolodon.

Etymology - for my wife, Linda Butler (her maiden name) Eaton, in recognition of her never-ending support and help with my field work, her acceptance of the never-ending parade of students and colleagues at our summer home, and her patience with my many long absences, both in the field and while writing manuscripts.

Description - m1. OMNH 22837 (figure 13A) has a cusp formula of $6: 4$ and the tooth narrows medially in occlusal view. The external cusp row is much longer than the internal row. The first cusp of the external row is small and low. The second cusp is the tallest of the row, and the remaining cusps are subequal in height, widely and deeply separated, and pyramidal in form. The last three cusps lean posteriorly. The central valley is deeply pitted and crossed by well-developed ridges connecting the cusps of both rows. The first cusp of the internal row is tiny and shifted medially. The second cusp is larger and leans posteriorly. The third cusp is larger still and is pyramidal in form. The fourth cusp is the broadest and tallest of the tooth. The internal cusp row is slightly higher than the external row. Cusps of the internal row are widely separated.

P4 - OMNH 22306 (figures 13B-D) has a cusp formula of $1: 5$. The tooth is straight and very low crowned. The anteroexternal platform has little swelling and the single cusp is placed anteriorly. The cusps of the medial row are broadly separated and the climb ratio is low $(C R=0.32)$, and the row reaches maximum depth at cusp 4. Cusps 3 and 5 are only slightly lower. The posterior basin is deep and is bounded on both sides by two cusps. On the labial side the posteromost cusp is small and the more anterior cusp is much
larger. On the lingual side of the basin the posterior cusp is well developed and there is a hint of a small, more anteriorly placed cuspule. OMNH 20010 (figures 13E-G) is tentatively placed here due to being significantly narrower than the other P 4 s (table 8). The specimen is similar in cusp formula (1:5) to the other specimens but is straight and narrow and the climb ratio for the cusps of the medial row is intermediate in value $(\mathrm{CR}=0.36)$; however, the last cusp of the medial row is the tallest, unlike in the other two specimens on which the fourth cusp was the tallest.

M1 - MNA V5226 (holotype, figure 13H ) has a cusp formula of 4:6:5 and is a squared molar with all cusp rows reaching the front of the tooth. There are four distinct cusps in the external row. The middle two cusps are erect and pyramidal. There is a small cuspule positioned anterolabially that is not counted in the cusp formula. This cusp row markedly narrows posteriorly. The central valley runs diagonally across the tooth. It is pitted and crossed by complex ribbing. The cusps of the medial row are essentially pyramidal but lean anteriorly, unlike the cusps of the external row. The cusps increase in size to the fourth cusp. Cusps 4, 5 , and 6 are subequal in size.

The internal cusp row is positioned low on the tooth. The cusps of this row are widely separated and the anteromost cusps are linguobuccally compressed (however the first cusp of the row is missing). There is a small cuspule positioned posterolingual to the third cusp. The anterior of the tooth has a broad facet for the P4.

Discussion - Of illustrated specimens, the m 1 is closest to ?Cimolomys sp. A of Fox (1971, figure 6d) and C. clarki of Lillegraven and McKenna (1986, figure 7A) in terms of cusp formula and shape. The cusps in all of these specimens are to a high degree pyramidal, rather unlike the revised diagnosis of the genus by Clemens (1964, p. 76) which states "Molar cusps, particularly those of lower molars, are strongly crescentic." The cusp formula of these specimens is also lower than defined for the genus by Clemens, 1964 (7-8:5-7). As such, it is questionable if these teeth actually represent Cimolomys. The m1 occludes perfectly with the M1 and certainly belongs to the same species. I originally thought that the ml assigned to $C$. clarki by Lillegraven and McKenna (1986) was incorrectly assigned due to its lack of crescentic cusps; however, there are significant similarities between that tooth, and the ml described here as ?Cimolomys butleria, and Bryceomys in terms of the broad, open valleys between lower molar cusps. It may be that a taxon similar to Bryceomys gave rise to Cimolomys such that the earliest forms of Cimolomys had not yet developed fully crescentic cusps (see discussion below). It may be appropriate to erect a new genus for these Cimolomys-like taxa that lack crescentic cusps. This new genus could include the Wahweap taxon ?Cimolomys sp. described later in this paper, ?Cimolomys butleria, ?Cimolomys sp. A of Fox (1971), and possibly C. trochuus of Lillegraven (1969).

The P4s are not strongly arched in occlusal view (or are essentially straight in the case of OMNH 20010), the cusp of the anteroexternal platform is very anteriorly placed, the crown is shallow, the medial cusp row reaches its greatest depth before the last cusp (except on OMNH 20010 in which the last cusp is the deepest), and the posterior basin is complex. These are all characters seen in specimens of Cimolomys (see Archibald, 1982, figure 23C, and Clemens, 1964,


Figure 13. ?Cimolomys butleria sp. nov.: A, (OMNH 22837), Rm1, stereo occlusal view; B, (OMNH 22306), LP4, stereo occlusal view; C, labial view; D, lingual view; E, (OMNH 20010), RP4, stereo occlusal view; F, labial view; G, lingual view; H, (MNA V5226), holotype, LM1, stereo occlusal view. Scale bar $=1 \mathrm{~mm}$.
figure 36b). If these P 4 s are correctly associated with the other teeth assigned here to ?C. butleria, then this species probably could be referred to Cimolomys without question. The cusps of the posterior basin of P4 are the same width as the anteromost two cusps of the M1, and the ratio of the lengths of P4s to the M1s ( $\mathrm{P} 4: \mathrm{M} 1=0.86$ ) is close to that observed for C. clarki by Lillegraven and McKenna (1986) but quite different from the value for C. gracilis provided by Clemens (1964) (table 8). This may in part relate to the rather large size of P4s assigned to C. clarki by Sahni (1972)
and Lillegraven and McKenna (1986) (see discussion above). The P4s included here are in the lower range of the anteroposterior dimensions of C. gracilis (see Archibald, 1982) but are distinctly narrower than in that species (table 8). OMNH 20010 was originally assigned to Cimexomys sp. by Eaton (1987), but the low cusp formula suggests that the specimen was incorrectly assigned. The identification of the specimen here is also tentative.

The squared shape of the M1 and the internal cusp row extending the entire length of the molar strongly suggests
affinities with Cimolomys. However, the diagonal nature of the central valley with the cusp of the external row narrowing posteriorly is unlike most illustrated specimens of Cimolomys (C. gracilis, Clemens, 1964, figure 37b; C. clarki, Sahni, 1972, figure 11G; C. trochuus, Lillegraven, 1969, figure 13-4b). However, the specimen of Cimolomys clarki (AMNH 88485) shown in Lillegraven and McKenna (1986, figure 7C) has a diagonal central valley. Also, the cusps of the medial row of this specimen are less crescentic than those usually assigned to Cimolomys, a condition acknowledged by Lillegraven and McKenna (1986, p. 22). It is possible that this specimen would be more properly assigned to Cimolodon, because upper molars of Cimolodon have anteriorly directed pyramidal cusps in the medial row and a diagonal central valley (e.g., C. electus, Fox, 1971, figure 4d). The diagonal central valley is also present in Mesodma primaeva, Paracimexomys, Cimolodon, and in bolodontoids (e.g., Bolodon, Kielan-Jaworowska and Ensom, 1992, textfigure 6A). Djadochtatherioids (e.g., Buginbaatar, KielanJaworowska and Sochava, 1969, pl. 1), however, show no tendency for a transverse central valley on M1.

The length of the internal row on M1 being as long as the tooth is found in some specimens of Cimolomys (C. clarki, Sahni, 1972, figure 11G; C. trochuus, Lillegraven, 1969, figure 13-4b) but not in others (C. gracilis, Clemens, 1964, figure 37b; C. clarki, Lillegraven and McKenna, 1986, figure 7c). This condition has not been described for M1s of Cimolodon. MNA V5226 is smaller ( $\mathrm{AP}=3.07$; $\mathrm{LB}=1.85$ ) and bears fewer cusps than the M1s of all other taxa of Cimolomys and Cimolodon.

If the M1 identified as Cimolomys by Lillegraven and McKenna (1986; AMNH 88485) is correctly assigned, there would be little question of the close affinity of ?Cimolomys butleria to Cimolomys. However, it is hard to accept that a major functional feature such as the orientation of the central valley and the external and medial cusp rows would be variable within a genus. For this reason the taxon is questionably assigned to the genus Cimolomys while recognizing a possible closer link to cimolodontids.

Both the molars bear some similarity to the much older taxon Bryceomys Eaton, 1995. The broad separation of the molar cusps and tooth shape are shared by Bryceomys, ?Cimolomys butleria, and to a lesser extent by certain cimolomyids. It may be possible that Bryceomys represents the primitive state from which later cimolomyids were derived (see discussion in Eaton and Cifelli, 2001). Based on the sample described by Eaton (1995), it is unlikely that Bryceomys has a lower incisor completely covered in enamel, a condition required in the revised diagnosis of the Cimolomyidae by Archibald (1982, p. 72); however, the condition of the lower incisor of Cimolomys is unknown. Archibald (1982) also stated in the revised diagnosis of Cimolomyidae that M2s are long relative to M1s. However, a long M2 relative to M 1 is a primitive condition that is better developed in taxa like Paracimexomys ( $P$. priscus, Archibald, 1982, table 17, M2:M1 $=0.9$ ), primitive cimolodontids (C. electus, C. similis; Fox, 1971, table 2, M2:M1 $=0.8$ ), and Bryceomys (see Eaton, 1995, M2:M1 $=0.8$ ) than it is in Cimolomys (C. gracilis, Clemens, 1964, table 9, $\mathrm{M} 2: \mathrm{M} 1=0.7$ ). As such, the phylogenetic position of Cimolomys is uncertain as is the position of the cimolomyidlike taxa described here.

Family unknown
Cimexomys Sloan and Van Valen, 1965
Cimexomys sp. cf. C. judithae Sahni, 1972
table 9; figures 14A-J
Referred Specimens - MNA V4639, LP4, Loc. 454-6; MNA V5312, Rp4, Loc. 704-1; OMNH 20190, LP4, Loc. V14; OMNH 22315, Rp4, Loc. V5.

Description - p4. OMNH 22315 (figures 14A-B) has 10 serrations and 6 external and 7 internal ridges. The highest part of the crest is reached at the fourth serration. MNA V5312 (figures 14C-D) has 9 serrations, 8 external and 7 internal ridges. The tooth is low crested and the ridges are widely spaced.

P4 - MNA V4639 (figures 14E-G) has a formula of 2:5. The anteroexternal platform is broadly expanded such that the anterior of the tooth is much broader than the posterior. The platform bears two cusps and there is a small cuspule positioned at the anterior margin of the tooth, which is not counted in the formula. The medial cusp row is low and worn. The crest posterior of the last cusp of the row is convex posterodorsally. The posterior basin bears one welldeveloped cusp labially, but the entire basin lingual to this cusp has been removed by wear. OMNH 20190 (figures $14 \mathrm{H}-\mathrm{J}$ ) has a higher cusp formula (4:6) than MNA V4639. The anteroexternal platform is only slightly broadened. The first cusp of the platform is tiny and each successive cusp is larger. The last cusp is coarsely ribbed lingually. The cusps of this row are only slightly lower than those of the medial row. The first cusp of the medial row is tiny and the remainder become progressively larger posteriorly. The climb ratio is low ( $\mathrm{CR}=0.33$ ). The posterior basin has one large cusp bordering it labially and a small cusp lingually. Cusps are separated by a deep pit that is open posteriorly.

Discussion - The p4s are included here largely because they are low crested and have few serrations and ridges. They are very similar to the p4s of Mesodma. Montellano (1992) rediagnosed Cimexomys as having fewer serrations (8-10) than comparably sized species of Mesodma, but M. archibaldi is very similar in terms of serrations and ridges to specimens described here. Montellano (1992) also maintained that the last 2-3 serrations form distinct cusps and lack internal or external ridges in Cimexomys. This can also be the case in Mesodma (see Clemens, 1964, figure 10a-b). In the specimen figured as C. gratus by Archibald (1982, figure 37) only the last cusp lacks a ridge. Lower fourth premolars of Cimexomys were distinguished here from those of Mesodma based on the broad spacing of the serrations in Cimexomys, the tendency for the first two anteroexternal ridges to converge with the third ridge in Cimexomys (see Montellano, 1992, figure 8a), and the high point of the crest being reached at the fourth serration in Cimexomys and more posteriorly in Mesodma. This last character does not result in a dramatic difference in AL:AP between this small sample and other species of Cimexomys (table 9) or species of Mesodma (table 1), possibly a result of the difficulty in determining the AL dimension (see discussion above, under "Measurements and Terminology"). The p4s are in the size range of $C$. judithae (and potentially $C$. antiquus, for which p 4 s are unknown) (table 9) but have more internal ridges than described for that species. Otherwise, they are very close to those of C. judithae.

The P4s are included with Cimexomys rather than Mes-


Figure 14. Cimexomys sp. cf. C. judithae: A, (OMNH 22315), Rp4, labial view; B, lingual view; C, (MNA V5312), Rp4, labial view; D, lingual view; E, (MNA V4639), LP4, stereo occlusal view; F, labial view; G, lingual view; H, (OMNH 20190), LP4, stereo occlusal view; I, labial view; J, lingual view. Scale bar $=1 \mathrm{~mm}$.
odma because they are lower crowned (H:AP) and have a lower climb ratio for the cusps of the medial row than in P 4 s of Mesodma (compare tables 1 and 9). More distinctive is the convex posterodorsal ridge posterior of the last cusp of the medial row that gives the cusp the impression of being anteriorly directed (C. judithae, Montellano, 1992, figure 7; C. minor, Archibald, 1982, figure 35a) rather than upright as in Mesodma. These P4s are in the size range of C. judithae but are also within the range of $C$. minor; however, the P 4 s of this taxon have a much different width-to-length ratios than do those of C. minor, which are almost identical to the values for $C$. judithae (table 9). The reported range of cusp formulae for P 4 s of $C$. judithae is 2-3:5 (Sahni, 1972; Montellano, 1992), and one of these P 4 s falls within that range, the other is more cuspate (4:6). Specimens in the UCMP collections identified as $C$. judithae from locality UCMP Locality V77083 (uncatalogued at the time I examined them), however, had cusp formulae of 3:6.

Although the species of Cimexomys described here is very close to $C$. judithae, it is not certain if that species is represented. Until a larger sample is available, this species is conferred to C. judithae.

> Cimexomys or Mesodma sp. table 10; figures $15 \mathrm{~A}-\mathrm{D}$

Referred Specimens -MNA V5269, Lm1, Loc. 454-6 (?Mesodma sp. cf. M. formosa in Eaton, 1987); OMNH 20006, Rm1, Loc. V5; OMNH 20343, LM2, Loc. V5; OMNH 20344, RM2, Loc. V5; OMNH 20359, Lm1, Loc. V5; OMNH 20494, Lm1, Loc. V9; OMNH 22314, Rm1, Loc. V5; OMNH 22847, Rm1, Loc. V9; OMNH 24053, Lm1, Loc. V61; OMNH 24055, Lm1, Loc. V61; UMNH VP5604, Lm1, Loc. 51; UMNH V5611, Lm1, Loc. 54; UMNH VP7640, Rm1, Loc. 56.

Description - m1. OMNH 22314 (figure 15A) has a cusp formula of $6: 4$. The tooth is slightly $(0.01 \mathrm{~mm})$ broader posteriorly than anteriorly. The cusps of the internal row are broad relative to those of the external row and there is a broad facet for p 4 at the anterior end of the tooth. The first two cusps of the external row are low, erect, and conical. The third and fourth cusps are about the same size and height, are well separated, and subpyramidal. Cusps 4, 5, and 6 are more deeply separated lingually than labially and lean slightly posteriorly. The central valley is slightly oblique to the anteroposterior axis of the tooth and is crossed by ribs and is deeply pitted. The first cusp of the internal row is low and occurs on the anterior edge of the second cusp. Cusps 2, 3, and 4 are of about the same height. The third cusp is the most separate and distinct. MNA V5269 (figure 15B) is broader anteriorly than posteriorly and is strongly waisted in occlusal view. OMNH 20494 (figure 15C) also is broader anteriorly than posteriorly, has a strong anterior notch for p4 visible in occlusal view, and has the cusps of the external cusp row more crescentic than in other specimens in the sample. The longest two specimens in the sample (OMNH 24053, figure 15D; UMNH VP5611) have an additional cusp in the external row. OMNH 24053 (figure 15D) is slightly broader anteriorly than posteriorly and is strongly waisted in occlusal view. The first three cusps of the external row are closely appressed, the fourth and fifth cusps are much larger and distinct, and are pyramidal in form. The sixth and seventh cusps
are formed from the lingual subdivision of the posteroexternal ridge. The last four cusps lean posteriorly. The central valley is sinuous and lined with deep pits. The internal cusp row is broader anteriorly than posteriorly. The first cusp is closely appressed to the second and both are essentially conical with the labial sides of the cusp worn flat along the central valley. Cusps 2 and 3 are widely separated by a deep valley bearing two distinct pits. The valley separating cusps 3 and 4 is narrower than that separating cusps 2 and 3 .

M2 - Two worn M2s assigned here have a narrow ridge that is not expanded labially and a probable cusp formula of Ri:2?:4.

Discussion - The distinction between isolated lower first molars of Cimexomys and Mesodma is difficult if not impossible to ascertain. It is likely that both molars assigned by Sahni (1972) to C. judithae are not Cimexomys at all (Archibald, 1982, p. 112). Archibald (1982), Montellano (1992), and Lofgren (1995) did not separate m1s of Cimexomys from Mesodma as both were present with overlapping size ranges. Possible methods for separating m 1 s , based on previously figured specimens, are as follows: 1) the internal cusp row of Mesodma (M. thompsoni, Lillegraven, 1969, figure $8-5 \mathrm{~b}$ ) tends to be narrow and blade-like relative to the broader external cusp row, whereas in Cimexomys (C. gratus, Archibald, 1982, figure 37d) the rows tend to be of equal width or the internal cusp row may even be broader than the external; 2) the m1s of Mesodma taper anteriorly, whereas those of Cimexomys tend to be blocky (see discussion in Archibald, 1982, p. 50); 3) the cusps of the external row of Mesodma tend to be strongly crescentic whereas they are more pyramidal and narrowly divided in Cimexomys (C. gratus, Archibald, 1982, figure 37d); and 4) the central valley is aligned with the anteroposterior axis in Mesodma (M. garfieldensis, Archibald, 1982, figure 12a, 12b; M. hensleighi, Lillegraven, 1969, figure 6-3c), and is somewhat oblique in C. gratus (see Archibald, 1982, figure 37d) and possibly in C. antiquus (see Fox, 1971, figure 3C). The only illustrated specimen of Mesodma in which the central valley is oblique to the anteroposterior axis is that of M. primaeva (see Sahni, 1972, figure 10F), which may indicate that early forms of Mesodma and Cimexomys share the primitive state.

The m1s here are thought most likely to represent Cimexomys because they have relatively broad internal cusp rows, the anterior of the teeth are broad, blunt, and have a notch for p 4 evident in occlusal view, the central valley is somewhat oblique to the anteroposterior axis, and the cusps of the external cusp row tend not to be strongly crescentic (although there is variation in this character as shown by OMNH 20494, figure 15C). However, direct comparison of MNA V5269 (figure 15B) to UA 5396, C. antiquus, also revealed distinct differences in that the UA specimen is not waisted in occlusal view and its anterior cusps are much more closely positioned such that they appear to be fused. In size, these m 1 s should approach the lower end of the size range of m 1 s of $C$. minor based on comparison of M1:m1 length ratios for Cimexomys (close to $1: 1$ ) and measurements provided for M1s of C. minor by Lofgren, 1995. Comparison of the lengths of the p4s described above as Cimexomys sp . cf. $C$. judithae to these m 1 s yields a $\mathrm{p} 4: \mathrm{m} 1$ value of 1.32 . The range of $\mathrm{p} 4: \mathrm{ml}$ for known species of Cimexomys is 1.061.24 (table 9), which suggests that the P 4 s of Cimexomys sp . cf. C. judithae are probably too large for the sample of mls


Figure 15. Cimexomys or Mesodma sp.: A, (OMNH 22314), Rm1, stereo occlusal view; B, (MNA V5269), Lm1, stereo occlusal view; C, (OMNH 20494), Lm1, stereo occlusal view; D, (OMNH 24053), Lm1, stereo occlusal view. Scale bar = 1 mm .
included here. That might suggest that these m1s would most closely approach the size of m 1 s of $C$. minor, but neither Archibald (1982) nor Lofgren (1995) attempted to separate m 1 s of Cimexomys from those of similar-sized species of Mesodma.

The M2s assigned here are almost identical in size to OMNH 24041, tentatively assigned to Mesodma sp. (large) (see discussion above); however, the differences between Cimexomys and Mesodma M2s are likely to be subtle, and certain morphologic criteria on which to base a distinction are lacking.

## Cedaromys Eaton \& Cifelli, 2001

 Cedaromys hutchisoni sp. nov. tables 11, 12; figures 16A-H Paracimexomys n. sp. A (in part), Eaton, 1987Paracimexomys n. sp. B (in part), Eaton, 1987
Paracimexomys n. sp. C (in part), Eaton, 1987
Holotype - OMNH 22861, LM1, Loc. V9.
Hypodigm - MNA V4583, LM1, Loc. 704-1; MNA V4657, Rm1, Loc. 453-2; MNA V5260, Lm1, Loc. 453-2; MNA V5266, Rm1, Loc. 454-6; MNA V5274, LM1, Loc. 704-1; MNA V5288, LM1, Loc. 704-1; MNA V5306, Rm1, Loc. 704-1; MNA V5316, LM1, Loc. 704-1; MNA V5340, LM1, Loc. 1004-1; MNA V5342, RM1, Loc. 1004-1; MNA V7535, Rm1, Loc. 704-1; MNA V7537, Lm1, Loc. 704-1; OMNH 20008, Rm1, Loc. V5; OMNH 20009, LM1, Loc. V5; OMNH 20340, RM1, Loc. V5; OMNH 20350, Lm1,

Loc. V5; OMNH 22295, RM1, Loc. V5; OMNH 22318, Rm1, Loc. V5; OMNH 22323, Rm1 (part), Loc. V5; OMNH 22834, LM1, Loc. V9; OMNH 24054, RM1, Loc. V61; UMNH VP5608, Lm1, Loc. 51; UMNH VP7631, Lm1, Loc. 108.

Distribution - Kaiparowits Formation of southern Utah, Campanian.

Diagnosis - Smallest species of Cedaromys; m1s (4-5:3) proportionally broader than species of Paracimexomys, Bryceomys, and Dakotamys; M1s (3-4:4:0-1) lacking an internal row or having a small, posteriorly placed, internal cusp.

Etymology - Named after Dr. J. Howard Hutchison, who has contributed enormously to our knowledge of Mesozoic and Tertiary vertebrates, has led me to many excellent microvertebrate localities on the Kaiparowits Plateau, and taught me the virtues of quarrying.

Description - m1. OMNH 20350 (figure 16A) has a formula of $4: 3$. The tooth broadens anteriorly; however, the cusp rows converge slightly anteriorly. There is an indentation on the labial wall of the tooth but none on the lingual side, so there is no "waist" in occlusal view. Cusps of the external row are well separated. The first two cusps of the internal row are joined together and only divided apically, and the second and third cusps are well separated. OMNH 20008 (figure 16B) has a formula of 5:3. The first cusp of the external row is erect and conical. The second cusp is larger than the other cusps, subcrescentic to conical in form, and the third cusp is linguobuccally compressed. The fourth and fifth cusps of the row are formed by a slight division of


Figure 16. Cedaromys hutchisoni sp. nov.: A, (OMNH 20350), Lm1, stereo occlusal view; B, (OMNH 20008), Rm1, stereo occlusal view; C, (MNA V7537), Lm1, stereo occlusal view; D, (OMNH 22861), holotype, LM1, stereo occlusal view; E, (OMNH 20009), RM1, stereo occlusal view; F, (OMNH 20340), RM1, stereo occlusal view; G, (MNA V5340), LM1, stereo occlusal view; H, (OMNH 22295), RM1, stereo occlusal view. Scale bar $=1 \mathrm{~mm}$.
a ridge that extends well posterior of the internal row. The first two cusps of the internal row are weakly separated, and the second and third are well separated. Cusps of both rows become lower anteriorly. MNA V7537 (figure 16C) also has a cusp formula of $5: 3$ and the central valley is sinuous. The first cusp of the external row is low, the second and third are equal sized and well separated, and the fourth and fifth cusps form a subdivided posterolabial ridge. The fifth cusp is the tallest cusp of the tooth. The labial cusp row is relatively high prior to wear compared to the lingual cusp row. Both

MNA V7537 and OMNH 20008 have strong indentations on the labial wall of the tooth but lack an indentation on the lingual wall.

M1 - OMNH 22861 (holotype, figure 16D) has a formula of 3:4:1, which is the most common formula in this sample of M1s. The external row has three conical cusps that are completely separated from each other. There is a tiny cuspule at the anterior margin of the row that is not included in the cusp formula. The second cusp bears well-developed striae. The last cusp is connected to the last cusp of the medi-
al row by a high wall that closes off the central valley. The central valley terminates posteriorly and appears to branch lingually between the third and fourth cusps of the medial row and continue to the single internal cusp. The medial row has four cusps that increase in width and height posteriorly. The cusps of the medial row are basically conical, well separated, and their apices lean anteriorly. The external and medial cusp rows appear to diverge slightly on this specimen, although on most of the M1s in this sample they do not. There is a single posteriorly placed cusp low on the lingual wall of the tooth. OMNH 20009 (figure 16E) shows the well-developed striae on cusps of the external row. OMNH 20340 (figure 16F) shows the strong convex labial side of the tooth (in occlusal view) that emphasizes the lack of a "waist" (opposite indentations on both sides of the tooth in occlusal view). On MNA V5340 (figure 16G) the cusp rows clearly do not diverge anteriorly, and this specimen differs from the other M1s in having a countable fourth cusp in the external row. OMNH 22295 (figure 16H) is the smallest tooth in the sample and is an example of an M1 that lacks an internal cusp. The external cusps are conical, coarsely striated, and well separated. The third cusp is lower and smaller than the first two cusps. The medial valley is oblique to the anteroposterior axis of the tooth. The cusps of the medial row are conical and broaden posteriorly. There is only a slight swelling in the position of the internal cusp.

Discussion - Many of the teeth here were assigned to Paracimexomys by Eaton (1987). This was prior to recognizing that retained primitive characters like small size and few cusps would doom about 50 million years of similar multituberculates to be lumped into a single genus, Paracimexomys. Since that time I have undertaken study of middle Cretaceous multituberculates (Eaton, 1995; Eaton and Cifelli, 2001) and I now believe that considerable generic diversity is present among small multituberculates with low cusp formulae (including Dakotamys, Bryceomys, Cedaromys, and Janumys).

The first lower molars of Cedaromys hutchisoni lack a waist in occlusal view, although some specimens have an indentation on the labial wall. A diagnostic character of Paracimexomys is the present of a waist on first molars (Archibald, 1982). The first molars assigned here to Cedaromys are broad relative to width (table 11), a character shared by other species of Cedaromys. These teeth are in many regards similar to those of Eobaatar magnus, KielanJaworowska and others (1987), in having a convex lingual tooth wall (in occlusal view). The cusp formula for E. magnus was described as $4: 2$ by Kielan-Jaworowska and others (1987). Based on their plate 2, figure 2B, however, I interpret it as $4: 3$ with the first two cusps of the internal row being closely approximated as in this species of Cedaromys. Also note that the $\mathrm{p} 4: \mathrm{m} 1$ length ratio for $E$. magnus is very high (1.94), which is the condition found in species of Cedaromys and Bryceomys; it is significantly lower for Paracimexomys and Dakotamys (table 11).

The M1s are morphologically close to those of Cedaromys from the Cedar Mountain Formation, near the AlbianCenomanian stage boundary, of central Utah described by Eaton and Cifelli (2001). The characteristic central valley that is lingually directed between cusps 3-4 of the medial row and the striae on the cusps of the external row are like the condition present in previously described species of

Cedaromys. The cusps of the external row are better separated and less ridge-like than in previously described species of Cedaromys. The teeth are not similar to those of Paracimexomys as their cusp formulae differ, the internal and external rows of Cedaromys either diverge weakly or not at all anteriorly, and there is no waisting (indentation in occlusal view) of the molars. The M1s are quite distinct from those of Dakotamys in having greater width relative to length, conical cusps, and no reduction in height of external cusp row. The teeth are also similar to those of Bryceomys, a taxon possibly derived from Cedaromys (see Eaton and Cifelli, 2001). Bryceomys differs from Cedaromys principally in having a broad cuspate internal cusp row on M1. The similarity of M1s of Cedaromys hutchisoni and Eobataar is intriguing as they are similar in form, cusp formulae (3:4:1), and in having cusps, most markedly those of the external row, that bear striae. Cusps of the medial row of Eobaatar magnus, however, are pyramidal and deeply, but narrowly, separated unlike the anterior leaning conical cusps of the species described here.

## cf. Cedaromys sp.

figures 17A-F
Referred Specimens - OMNH 20007, RP4, Loc. V5 (Paracimexomys n. sp. B in Eaton, 1987); OMNH 20479, RP4, Loc. V9.

Description - OMNH 20007 (figures 17A-C) is a relatively small P4 ( $\mathrm{AP}=2.38$; $\mathrm{LB}=1.13$ ) with a cusp formula of 1:5. The tooth is low crested ( $C R=0.36$ ), low crowned ( $\mathrm{H}: \mathrm{AP}=0.46$ ), broad relative to length (LB:AP=0.48), and strongly waisted in occlusal view. There is a single small cusp anteriorly placed on the anteroexternal platform. The cusps of the medial cusp row are not well separated, which may reflect wear. The posterior basin is worn flat but appears to have lacked a deep pit at the posterior base of the tooth. OMNH 20479 (figures 17D-F) is significantly larger ( $\mathrm{AP}=2.59 ; \mathrm{LB}=1.40$ ) than OMNH 20007, heavily worn, and appears to have a cusp formula of $1: 4$. The tooth is waisted in occlusal view with a broadly expanded anteroexternal platform (LB:AP=0.54) bearing one small, anteriorly placed cusp. The medial cusp row is well worn, and it is possible that a fifth cusp may have been completely removed by wear.

Discussion - These P4s may represent Cedaromys because of the low cusp formula (Cedar Mountain specimens have a formula of $4: 2$, Eaton and Cifelli, 2001) and low climb ratio of the medial cusp row. Cedar Mountain species of Cedaromys are weakly waisted and lack the broadly expanded anteroexternal platform of OMNH 20479. No P4s of Paracimexomys have been illustrated except for specimens questionably assigned to Paracimexomys (see Eaton and Cifelli, 2001) by Eaton and Nelson (1991) and Eaton (1995) that consistently have a cusp formula of 5:1. The P4 of cf. P. robisoni (see Eaton and Nelson, 1991: figure 2D-E; table 2) has strongly striated cusps, is not waisted in occlusal view, and has a larger less anteriorly placed cusp on the anteroexternal platform than on these specimens.

These specimens are similar in most regards to P4s of Cedaromys described by Eaton and Cifelli (2001) but are different from each other and cannot be confidently placed in Cedaromys. Also, comparison of the P4:M1 length ratio of these specimens with $C$. hutchisoni provides a value of 1.30 ,
whereas previously described species of Cedaromys (see Eaton and Cifelli, 2001) have P4:M1 values between 1.031.13 , indicating the P 4 is only slightly larger than M1. If these P4s represent Cedaromys, it is unlikely that they belong to $C$. hutchisoni.

Dakotamys Eaton, 1995<br>Dakotamys magnus new combination (Sahni, 1972)<br>table 12, figures 17G-H

Cimexomys magnus Sahni, 1972
Paracimexomys magnus (Archibald, 1982)
Holotype - AMNH 77120, RM1.
Type Locality - Clambank Hollow Locality, Chouteau County, Montana.

Distribution - Judith River Formation of Montana, Kaiparowits Formation of southern Utah, Campanian.

Revised Diagnosis - Larger than any species of Paracimexomys and Dakotamys. M1 cusp formula of 5:5:12, greater than Paracimexomys and Dakotamys malcolmi. Internal cusp row short and cusps alternate position unlike Cimexomys; asymmetrical waist present in occlusal view.

Referred Specimens - MNA V5301, RM1, Loc. 1004-1; OMNH 20354, LM1, Loc. V5.

Description - M1. MNA V5301 (figure 17G) has a cusp formula of $5: 5: 2$ or 3 and is large ( $\mathrm{AP}=4.03 ; \mathrm{LB}=2.62$; $\mathrm{LB}: \mathrm{AP}=0.65$ ). The tooth has an asymmetric waist in occlusal view due to the lingual indentation present between cusps 3-4 and a more anterior indentation, between cusps 23 , on the labial wall. The internal cusp row has two (or possibly three) small cusps that are well separated from the main body of the tooth. The medial row broadens posteriorly. The first three cusps are closely joined with only apices separated prior to wear. The fourth cusp is well separated and bears striae. The fifth cusp is the widest, and tallest cusp is the last of the row. The central valley is slightly oblique to the anteroposterior axis of the molar. The cusps of the external row are conical in form, deeply striated, and narrow posteriorly. The first cusp is low and small. The second cusp is the largest of the row and forms a bulge on the labial wall of the tooth. The cusps become smaller and less separated posteriorly. OMNH 20354 (figure 17H) clearly has a formula of 5:5:2 and is also large ( $\left.\mathrm{AP}=4.02^{*} ; \mathrm{LB}=2.59 ; \mathrm{LB}: \mathrm{AP}=0.64^{*}\right)$. This specimen clearly shows the pit present labial to cusps 1 and 2 of the external cusp row (also present on MNA V5301). The internal cusp row has two distinct cusps separated by a deep valley from the lingual wall of the medial cusp row.

Discussion - Sahni (1972) named a new species of Cimexomys, C. magnus. The molars described here are almost identical in size, morphology, and cusp formula to the type of C. magnus (AMNH 77120, AP=3.91; formula $=$ 5:5:1). Archibald (1982, p. 111) recognized that the taxon did not fit in Cimexomys and tentatively transferred it to Paracimexomys. This species is not considered here to represent Paracimexomys because the medial and external cusp rows do not diverge anteriorly and the cusps are deeply ribbed. The species is included in Dakotamys as that genus was erected to include M1s with low cusp formulae, narrow internal cusp rows, parallel medial and external cusp rows, well-ribbed cusps, and an external row in which the cusps
become smaller and more poorly defined posteriorly (Eaton, 1995; see revised diagnosis of Dakotamys in Eaton and Cifelli, 2001). Also, comparison of these specimens to M1s of Dakotamys malcolmi shows that they share the presence of a deep labial pit between the first two cusps of the external row, and the second cusp of that row is the largest and is deeply striated. The enlarged second cusp is reflected in the swelling on the labial side of the tooth; on D. malcolmi this results in a waist that is close to transverse to the anteroposterior axis. The elongation and addition of cusps in D. magnus results in the indentations being offset such that the resultant waist is oblique to the anteroposterior axis.

## Relationships of Taxa from the Kaiparowits Formation

Most of the teeth described here are isolated and most of the attempts at taxonomy were directed toward separating what appear to be relatively closely related taxa. For this reason, the characters used to identify these taxa are virtually absent in multituberculate cladograms (e.g., Simmons, 1993; Rougier and others, 1996) and so this study provides little data for directly arguing or comparing larger-scale relationships. It would be desirable to collect more complete specimens so that dental associations can be made with more certainty and it would be ideal to be able to include cranial characteristics. Lacking these kinds of data, I hesitate to generate cladograms based on isolated teeth and find it frustrating that such attempts by me have yielded different results depending on the tooth position selected for analysis. This appears to lend some support for hypothesizing a mosaicstyle evolution, at least in some multituberculate dental characteristics.

One potential relationship that may be emerging is that among Cedaromys, Bryceomys, and Cimolomys. This relationship is based on the similarity of lower first molars of these taxa, which have broad open valleys separating the pyramidal cusps of both rows. That is particularly the case if the m1 (UW 15535) Lillegraven and McKenna (1986) identified as Cimolomys clarki does belong to that genus. This suggests a transition from the erect pyramidal cusps seen in Bryceomys to the strongly crescentic cusps of Lancian species of Cimolomys. The lower incisor is not known in Cimolomys, which raises fundamental questions about the systematic relationships of that taxon. The lower incisor is also unknown with certainty for Cedaromys and Bryceomys.

## MULTITUBERCULATE FAUNA FROM THE WAHWEAP FORMATION

Systematic Paleontology Class MAMMALIA Order MULTITUBERCULATA Suborder CIMOLODONTA McKenna, 1975 Superfamily ?Ptilodontoidea Sloan and Van Valen, 1965 Family Neoplagiaulacidae Ameghino, 1890<br>Mesodma Jepsen, 1940<br>Mesodma sp. cf. M. formosa (Marsh, 1889) Clemens, 1964<br>table 13, figures 18A-G

Referred Specimens - MNA V4571, Rm2, Loc. 456-2; MNA V5241, Lm2, Loc. 456-2; MNA V5244, RM2, Loc. 456-2; MNA 5250, LM2, Loc. 456-2 (all of these second


Figure 17. cf. Cedaromys sp.: A, (OMNH 20007), RP4, stereo occlusal view; B, labial view; C, lingual view; D, (OMNH 20479), RP4, stereo occlusal view; E, labial view; F, lingual view. Dakotamys magnus: G, (MNA V5301), RM1, stereo occlusal view; H, (OMNH 20354), LM1, stereo occlusal view. Scale bars $=1 \mathrm{~mm}$.
molars were all assigned to Cimexomys or Mesodma sp. by Eaton, 1987); MNA V5254, RP4, 456-1;OMNH 20782, LM2, Loc. V11; OMNH 23340, Lm2, Loc. 707-2; UMNH VP7984, LM1 (part), Loc. 130; UMNH VP7989, Rm1, Loc. 130.

Description - m1. UMNH VP7989 (figure 18A) has a cusp formula of $6: 5$. The first cusp of the external row is small, three-sided, and leans anteriorly. The second cusp is
pyramidal in form and leans slightly anteriorly. The third cusp is the largest of the tooth and is upright and pyramidal. The fourth and fifth cusps are equal in size and subcrescentic with their apices oriented posteriorly. The sixth cusp is a small erect cone with a concave lingual side. Cusps 1-5 have deep grooves at their lingual and labial bases. These grooves cross the pitted central valley that is closed posteriorly.

The first cusp of the internal row is small but distinct and
is directly opposite the first cusp of the external row. The second cusp is taller than the first and essentially conical and erect. The third and fourth cusps are equal in size and taller than the second cusp. They are crescentic in form and lean posteriorly. Cusps 1-4 are well separated but to a depth higher than the central valley. The fourth and fifth cusps are more deeply divided by a valley that reaches the level of the central valley. The fifth cusp is elongate with a concave labial face. On this unworn specimen the cusps of both rows increase in height posteriorly.
m2 - MNA V5241 (figure 18B) has a cusp formula of $4: 2$. The apices of the cusps of the external row are separated labially. The cusps are separated lingually by deep grooves. The cusps decrease in length and increase in height posteriorly. The last cusp has a deep vertical groove on its lingual side. The central valley is sinuous with deep pits. The cusps of the internal row are about equal in size, although the second cusp is slightly longer than the first. The two cusps are well separated and no wear is apparent on either cusp.

MNA V4571 (figure 18C) also has a cusp formula of 4:2. The cusps of the external row broaden posteriorly and are about equal in height, rather than increasing in height posteriorly, probably reflecting wear. The apices of this worn cusp row are only separated at the apices labially and by deep grooves lingually. The anteromost groove crosses the pitted central valley. The first cusp of the internal row is much taller than the first cusp of the external row. It is worn apically and there is a deep groove on the wall of the cusp that faces the central valley. The second cusp is lower, unworn and not as long as the first cusp. There is a strong notch posterior of the second cusp.

P4 - MNA V5254 (figures 18D-F) has a cusp formula of 2:5. The anteroexternal platform is broad and the anterior width exceeds the posterior width of the tooth. The platform bears two cusps that are much lower than those of the central cusp row. The cusps are well striated. The cusps of the central row are deeply striated and have a moderate climb ratio such that the row reaches its apex at the subequal fourth and fifth cusps (although without wear it is likely that the fifth cusp would have been taller than the fourth). The posterior basin is poorly developed with a small, shallow basin.

M1 - UMNH VP7984 is the anterior part of an M1 with an estimated formula of 5:6:?. There are three well-striated conical cusps on the external row. The cusps of the medial row are crescentic and broaden posteriorly. The internal row is missing, but it attaches to the medial row below the third cusp, indicating the internal row exceeded half of the molar length.

M2 - OMNH 20782 (figure 18G) is a M2 with a formula of Ri:3:4. The external platform is moderately expanded and there is no evidence of cusps on the margin (ridge) of the platform. The first cusp of the medial row is weakly pyramidal and the same height as the second cusp. The second cusp has its apex oriented strongly anteriorly. The last cusp is small and well separated from the second cusp. The central valley is slightly sinuous and pitted. The first two cusps of the row are equal sized and closely positioned. The third cusp is slightly lower, has a deeper apical separation, with a deeper labial groove than between the first two cusps. The fourth cusp is the lowest of the row and is separated from the third cusp by a deep labial groove.

Discussion - The m 1 is larger than the m 1 s of $M$. hensleighi and too small for those of M. thompsoni and M. primaeva. It is within the length range of Lillegraven's (1969) sample of M. formosa (table 13) but the width exceeds that of the specimens in Lillegraven's sample. The molar is at the lowest AP value for Archibald's (1982) sample of $M$. garfieldensis, and the width slightly exceeds that of Archibald's sample (table 13). No m1s are known for $M$. senecta (see Fox, 1971), but the size of the p 4 s indicates that taxon is close in size to M. thompsoni.

The basis for assigning these m 2 s to Mesodma is provided above under Mesodma sp. (large) described from the Kaiparowits Formation. The well-developed posterolingual notch is not found on figured specimens of Cimexomys, but the feature is absent on depicted specimens of Mesodma, except for M. primaeva (see Sahni, 1972, figure 10G). The pitting on these may also seem atypical for m 2 s of Mesodma, but the m 1 included here is also pitted. These m 2 s (relative to the m 1 , UMNH VP7989) have an $\mathrm{m} 2: \mathrm{ml}$ length ratio appropriate for Mesodma (table 13). Clemens (1964; p. 31) provided a cusp formula for $M$. formosa of 3:2, but Lillegraven (1969, figure 7-4a) illustrated a specimen of M. formosa with a formula of $4: 3$ which is characteristic of all of the m 2 s included here. The specimens are well within the size range of M. formosa and are in the lower part of the range of M. garfieldensis (table 13).

The P4 is very similar to that illustrated by Lillegraven (1969, figure8-1) as Mesodma formosa in the climb ratio of the medial cusp row, cusp formula, and the weakly developed posterior basin. The MNA specimen has a more broadly expanded anteroexternal platform. The specimen is below the size range of M. garfieldensis and is within the size range of M. formosa (table 13). The M1 is similar to M1s of Mesodma in terms of the length of the internal row exceeding half the molar length, the crescentic medial row cusps, and in that the cusps of the external and medial row are offset anteriorly but aligned transversely farther back on the tooth.

The M2s are similar to those from the Kaiparowits Formation assigned above to Mesodma minor, but they are larger and in the size range of M. formosa and M. garfieldensis (table 13).

It is difficult to distinguish this sample from among either of the similar-sized species $M$. formosa and $M$. garfieldensis. The P 4 has fewer cusps and is smaller than those of M. garfieldensis (table 13). The molars are close to being within the range of both species. Archibald (1982, p. 47) distinguished M. garfieldensis from other species of Mesodma in that "M1 and m1 longer relative to M2 and m2, respectively, than in any Cretaceous species of Mesodma ... " The $\mathrm{m} 2: \mathrm{m} 1$ length ratio for M. garfieldensis is 0.56 , whereas various samples of $M$. formosa range in value from 0.58-0.61 (table 13). The mean of the ratios of the m 2 s to the single m 1 in this sample is 0.59 and is therefore slightly closer to the ratios of M. formosa than those of M. garfieldensis. This, coupled with the size and cusp formula of the single P4, suggests that this species is closer to $M$. formosa than to $M$. garfieldensis. However, the pits present in the molar valleys may indicate the presence of a species morphologically distinct from and more primitive than either M. formosa or M. garfieldensis.


Figure 18. Mesodma sp. cf. M. formosa: A, (UMNH VP7989), Rm1, stereo occlusal view; B, (MNA V5241), Lm2, stereo occlusal view; C, (MNA V4571), Rm2, stereo occlusal view; D, (MNA V5254), RP4, stereo occlusal view; E, labial view; F, lingual view; G, (OMNH 20782), LM2, stereo occlusal view. Scale bar $=1 \mathrm{~mm}$.

Family Cimolodontidae Marsh, 1889
Cimolodon Marsh, 1889
Cimolodon electus Fox, 1971
table 14, figures 19A-G
Referred Specimens - MNA V4613, Lm1, Loc. 455-1; MNA V5200, Rm2, Loc. 456-2 (Cimolomys n. sp. in Eaton, 1987); MNA V5234, RM1, Loc. 456-2 (Cimolodon sp. in Eaton, 1987); MNA V5273, Lm2, Loc. 455-1 (Cimolomys n. sp. in Eaton, 1987); MNA V5277, Lm1 (partial), Loc. 456-2; MNA V5280, RP4 (partial), Loc. 456-2; MNA V5282, LM1 (partial), Loc. 456-2; UMNH VP7562, Rm1, Loc. 82.

Description - m1. UMNH VP7562 (figure 19A) is from the base of the Wahweap Formation and has a cusp formula of $6: 4$. The first cusp of the external row is low and conical. The second cusp is taller and sub-pyramidal. Cusps 3 and 4 are well separated, pyramidal, and lean slightly posteriorly.

Cusps 5 and 6 are small and conical, developed on the posteroexternal ridge. The central valley is slightly sinuous. The four cusps of the internal row are taller and larger than those of the external row. The first two cusps of the internal row are closely positioned. Deep valleys separate cusps 2-4. There is some weak grooving of the lingual and labial sides of cusps and a hint of a posteroexternal shelf. MNA V4613 (figure 14B) was recovered approximately 200 m higher in the section and, compared to UMNH VP7562, is more striated on the lingual and labial cusp walls, has an additional external cusp, and a better-developed posteroexternal shelf below cusps 6-7 of the external row.
m2 - MNA V5200 (figure 19C) has a cusp formula of $5: 2$. The external row is higher and broader and the cusps become more closely compressed posteriorly. The cusps of the row are narrowly separated. The first and second cusp appear to have been deeply divided prior to wear, but the val-
leys separating cusps 2-4 are progressively less deeply divided posteriorly and are mostly divided on the lingual wall of the cusp row. The central valley is deep and pitted and the cusp row walls are deeply grooved at their bases on both sides of the valley. The two cusps of the internal row are narrowly but deeply divided. There is a well-developed notch posterior of the second cusp.

P4 - MNA V5280 (figures 19D-F) is incomplete but clearly is part of a very high-crowned P4. The walls of the premolar are deeply striated. The posterior basin comprises a small part of the tooth. The basin is bounded by two cusps, the lingual being much lower than the labial.

M1 - MNA V5234 (figure 19G) has a cusp formula of $6: 7: 5$. The first three cusps of the external row are striated and conical and are not deeply divided. The fourth cusp is slightly smaller than the third but is better separated, both anteriorly and posteriorly. Cusps 5 and 6 form a posterolabial ridge. The cusps of the row narrow slightly posteriorly due to the somewhat oblique nature of the central valley. The cusps of the medial row are strongly striated and crescentic, well worn on their labial side, and become better separated posteriorly. The valley between the internal and medial cusp rows is deeper than that of the central valley. The internal row is broad, and the cusps become larger and taller posteriorly.

Discussion - The m1s clearly belong to Cimolodon because of the isolated robust pyramidal cusps, the striated cusp walls, the largest of the internal row cusps occurring posteriorly, and the largest of the external row cusps occurring medially. They can be referred to C. electus because of their size (table 14), cusp formulae, pyramidal nature of the cusps, and the presence of a posterolabial cingulum. UMNH VP7562 (figure 19A), from near the base of the formation, may express primitive characters for this species in being weakly striated, having a low cusp formula, and in the weak development of the posterolabial cingulum. The partial P4 is remarkably similar to UA 5323, C. electus (see Fox, 1971, figure $4 \mathrm{a}-\mathrm{b}$ ). The M1 (MNA V5234, figure 19G) shown is similar to UA 5326 (Fox, 1971, figure 4d), C. electus, except for having one or two fewer cusps in each row (table 14) and a longer internal cusp row relative to the total length of the molar. The m 2 s are most similar to those of Cimolodon in that the cusps of the external row are not divided labially; however, other characters are less consistent. The broadening of the external cusp row posteriorly and the presence of a strong posterior notch are seen on m 2 s of Cimolodon electus (see Fox, 1971, figure 5b) but not on C. nitidus (see Clemens, 1964, figure 26-b; Lillegraven, 1969, figure 11$5 \mathrm{~b})$. The external cusp row broadens posteriorly also on m 2 s of Cimolomys (see Archibald, 1982, figure 23e; Lillegraven and McKenna, 1986, figure 7B), and the posterior notch is present on the m 2 of $C$. clarki illustrated by Lillegraven and McKenna (1986) but not on the m 2 of C. gracilis shown in Archibald (1982). A direct comparison of MNA V5200 (figure 19C) with UA 5336, Cimolodon electus (depicted by Fox, 1971, figure 5b), indicates that the specimens are almost identical except the two cusps of the internal row are less widely separated on the MNA 5200 than on the UA specimen. In this regard, MNA V5200 appears to be more similar to Cimolomys clarki (see Lillegraven and McKenna, 1986, figure 7B).

This sample appears to represent a slightly less cuspate
population of C. electus than that described by Fox (1971), but in size, construction of the teeth, and details of morphology these teeth are almost identical to the Milk River sample. This broadens the definition of the species only by increasing the lower range of the cusp formulae.

Cimolodon similis Fox, 1971
table 14; figures 20A-H, 21A-F
Referred Specimens - MNA V4595, LP4, Loc. 455-1; MNA V5214, LP4 (part), Loc. 1015-1; MNA V5217, LP4, Loc. 1015-1; MNA V5221, RP4, Loc. 455-1; MNA V5245, Rm1, Loc. 456-2; UMNH VP7592, Rp4, Loc. 77; UMNH VP7980, Lm1, Loc. 130; UMNH VP7987, Rm1, Loc. 130; UMNH VP7989, Lm1 (part), Loc. 130; UMNH VP7990, Rm2, Loc. 130.

Description - p4. UMNH VP7592 (figures 20A-B) is a high crowned, symmetrically arched p4 with 11 serrations, 8 external, and 10 internal ridges. The anteroexternal lobe is deep and broad. External ridges descend from all but the most posterior serration and become more widely separated ventrally. The crest of the blade is reached at the fifth serration. Internal ridges 2-4 intersect anteriorly with the steeper ridge descending from the first serration. There is no internal ridge developed from the posteromost serration. The interior ridges maintain approximately the same separation ventrally, unlike the external ridges.
ml - MNA V5245 (figure 20C) has a cusp formula of 6:4 and is waisted in occlusal view. The first three cusps of the external row are closely appressed and have little separation between the cusps. Cusps 3 and 4 are well separated, but the more posterior cusps of the row are less well separated. The central valley is lined with deep pits. The first two cusps of the internal row are closely positioned. The valley separating cusps 2-3 and cusps 3-4 are progressively more deeply divided compared to the valley separating the first two cusps. Cusps 2-3 are more pyramidal in form than the other cusps of the row as a result, in part, of their distinct separation.

UMNH VP7987 (figure 20D) is smaller than MNA V5245 (figure 20C) and has only a rudimentary cuspule in the position of the first cusp on the internal row, resulting in a cusp formula of $6: 3$. The first cusp of the external row is low and round. The second cusp is larger, taller, and weakly pyramidal in form. The third and fourth cusps are large, pyramidal in form, and well separated. The fifth and sixth cusps form a subdivided elongate ridge. The central valley is complexly pitted as a result of the presence of ribbing at the base of the cusps of both rows. On the internal row, there is a rudimentary anterior cuspule not counted in the cusp formula. The first cusp is tall, rounded anteriorly, flattened labially, and has a concave posterior face. The second cusp is similar but larger. The third cusp is squared anteriorly and rounded posterolingually.
m2 - UMNH VP7990 (figure 20E) has a cusp formula of 4:2. The external row is tall relative to the central valley of the tooth and rises higher posteriorly. The cusps are only separated at their apices and are divided lingually by narrow grooves. The central valley has a few pits. The cusps of the internal row are well worn apically. There is a basal vertical groove labially on the face of the first cusp. The first and second cusps are separated labially by a narrow groove. There is a well-developed notch posterior to the second cusp.


Figure 19. Cimolodon electus: A, (UMNH VP7562), Rm1, stereo occlusal view; B, (MNA V4613), Lm1, stereo occlusal view; C, (MNA V5200), Rm2, stereo occlusal view; D, (MNA V5280), partial RP4, stereo occlusal view; E, labial view; F, lingual view; G, (MNA V5234), RM1, stereo occlusal view. Scale bar $=1 \mathrm{~mm}$.


Figure 20. Cimolodon similis: A, (UMNH VP7592), Rp4, labial view; B, lingual view; C, (MNA V5245), Rm1, stereo occlusal view; D, (UMNH VP7987), Rm1, stereo occlusal view; E, (UMNH VP7990), Rm2, stereo occlusal view; F, (UMNH VP4595), LP4, stereo occlusal view; G, labial view; $H$, lingual view. Scale bar $=1 \mathrm{~mm}$.

P4 - UMNH VP4595 (figure 20F-I) has a cusp formula of $1: 8$. It has a broadly expanded anteroexternal platform bearing one large cusp and a tiny, more anteriorly placed cuspule (not included in cusp formula). The medial row appears to have a low climb ratio, although this is not directly measurable due to wear on the last two cusps of the row. The posterior basin comprises a small part of the total length of the
tooth ( $\mathrm{PL}: \mathrm{AP}=0.28$ ). The tooth is strongly striated on both sides. This specimen is almost identical in size, form, and cusp formula to those assigned by Fox (1971) to C. similis (table 14). MNA V5217 (figures 21A-C) has one more cusp on the anteroexternal platform, one less cusp in the medial row, and is smaller than MNA V4595 but in other regards similar. MNA V5221 (figures 21D-F) is similar in size to

MNA 5217 (table 14), but the last cusp in the medial row is subdivided, resulting in a cusp formula of 2:7. The anteroexternal platform is broadly expanded and bears one small and one large cusp. The cusps of the medial row have a low climb ratio $(C R=0.32)$, the sixth cusp is higher than the seventh, and the cusps are only separated at their apices. The wall posterior to the last cusp of the medial row is rugose. The posterior basin is short and has deep pits.

Discussion - The deep, wide anteroexternal lobe and high, symmetrical arch are characters of Cimolodon p4s (e.g. C. nitidus, Archibald, 1982, figure 18a). This specimen is about $11 \%$ smaller than that described by Fox (1971) as $C$. similis (table 14), a size difference also present in some of the P 4 s included here. The specimen is also similar in size to the p4s of Cimolodon foxi sp. nov. from the Kaiparowits Formation described earlier in this paper, but the p4 from the Wahweap Formation is less serrate than the p4s of $C$. foxi.

The ml is considered to be Cimolodon because the cusps of both rows are pyramidal, the cusps of the external row are largest in the middle of the row, and the tooth is as broad anteriorly as posteriorly. The specimen compares almost identically with UA 5372 included by Fox (1971) in the hypodigm of $C$. similis and is within the size range of that species (table 14); however, one of the m1s (UMNH VP7987, figure 20D) is smaller than the range given by Fox (1971) for the species and is perhaps more primitive in having a lower cusp formula of $4: 3$. Another specimen from the same locality (UMNH VP7980, Loc. 130) is also smaller than the Milk River sample of $C$. similis but does have a bet-ter-developed first cusp such that its cusp formula is $6: 4$ as in C. similis. As such, although slightly smaller specimens having perhaps more primitive characters are present, designation of a new species is not warranted.

The P4s in this sample broaden both the size range and cusp formulae attributable to $C$. similis. The cusp formula in the diagnosis of the species (Fox, 1971) is 1:8-9. If the specimens described here are properly identified, the range of the cusp formula would be broadened to 1-2:6-9 and the anteroposterior range expanded to 3.6-4.1. MNA V4595 is certainly $C$. similis, and the other P 4 s included here are very similar to that specimen but are outside the range of size and cusp formula provided by Fox (1971). Fox's sample is small and the sample from the Wahweap Formation occurs considerably south of where Fox recovered his sample in Alberta, Canada. As such, it is not surprising that the sample described here is somewhat different. Alternatively, this sample could include two species, one in the size range of $C$. similis and a second smaller species. A much larger sample would be required to justify two species.

Cimolodon sp. cf. C. nitidus Marsh, 1889 table 14 ; figures $21 \mathrm{G}-\mathrm{I}$

Referred Specimens - UMNH VP7978, Lp3-4 (in partial mandible), Loc. 130; UMNH VP7988, Lp4 (in partial mandible), Loc. 130; UMNH VP7981, LM1, Loc. 130.

Description - p4. UMNH VP7978 (figures 21G-H) has 11 serrations with 9 external and 10 internal ridges. The arcuate crest reaches its apex at the fourth serration. On the labial wall of the blade the first ridge is nearly vertical, the second ridge is oriented posterodorsally-anteroventrally and the remaining ridges parallel the second. The posterior wall
of the blade is well worn and an additional ridge may be obliterated. The orientation of the ridges on the lingual face of the tooth is very similar to the buccal side. A small single cusped p 3 is positioned directly below the anterior face of the p4. Another p4 (UMNH VP7988) from the same locality as UMNH VP 7978 is almost identical.

M1 - UMNH VP7981 (figure 21I) was an extraordinarily well-preserved M1 but virtually exploded when touched by a tool during preparation (the specimens from this locality are extremely brittle). This description is limited by the extent to which the molar could be reconstructed. The cusp formula of the specimen is estimated to be $6 ?: 7: 5$ or 6 . The first cusp of the external row is small, low, and shifted slightly lingually. The second cusp is only slightly larger and about the same height as the first cusp (at least after wear). The third cusp is small, weakly pyramidal, and leans anteriorly. The fourth cusp is similar to the third in form but is much taller and longer. The fifth cusp is three-sided and slightly smaller than the fourth cusp. The part of the tooth possibly bearing the sixth cusp is missing. The central valley is complex and pitted due to the ribs formed at the bases of the cusps of the external and medial rows. The ribs cross the valley and connect to the cusps of the other row. Cusps of the medial row become larger and broader posteriorly. The first four cusps of the row are weakly pyramidal and cusps 2-4 lean anteriorly. The fifth and sixth cusps are pyramidal and the posteromost cusp is missing due to breakage. There are 5 distinct cusps in the internal row and a series of small swellings along the row. The valley between the medial and internal row is ribbed posteriorly. The internal row connects anteriorly just behind the second cusp of the medial row.

Discussion - The H:AP of these two p4s (0.60-0.61) is appropriate for p 4 s of Cimolodon (table 5) and generally greater than for p 4 s of Mesodma (table 1). The specimen is larger than those assigned to C. similis and smaller than those assigned to C. electus by Fox, 1971 (table 14). The specimens have fewer serrations (11) than does C. electus (15). The size of the specimens (table 14) is within the lower range of p4s assigned to C. nitidus by Archibald (1982) and Clemens (1964) but is below the size range of the sample described by Lillegraven (1969). The specimens have one fewer serration (11) than described for p 4 s of $C$. nitidus. The M1 is estimated to be larger than those of C. electus and within the lower range of length and upper range of width for the samples of $C$. nitidus described by Archibald (1982) and Clemens (1964). It is slightly shorter and narrower than the sample described by Lillegraven (1969).

It is likely that these specimens represent a new species of Cimolodon in which the molars are broader relative to width than those of $C$. nitidus. The proportions of these molars and premolars are different than in other species of Cimolodon, and there are fewer serrations on p4 (11) than on C. nitidus, C. electus, or C. similis. Had the M1 not shattered during preparation, it likely would have provided sufficient characters on which to base a new species. Lacking adequate data to establish a new species, the specimens are conferred to the closest of described species of Cimolodon, C. nitidus. All of the specimens were recovered from UMNH Locality 130 and nothing like them has been recovered from other Wahweap localities. This suggests that there can be very localized controls on the distributions of mammalian taxa.


Figure 21. Cimolodon similis: A, (MNA V5217), LP4, stereo occlusal view; B, labial view; C, lingual view; D, (MNA V5221), partial RP4, stereo occlusal view; E, labial view; F, lingual view. Cimolodon sp. cf. C. nitidus: G, (UMNH VP7978), Lp3-4, labial view; H, lingual view; I, (UMNH VP7981), LM1, stereo occlusal view. Scale bars $=1 \mathrm{~mm}$.

## Cimolodon sp. (small)

table 14; figures 22A-C
Referred Specimens - MNA V4525, Rp4, Loc. 455-1 (Cimexomys sp. cf. C. antiquus in Eaton, 1987); MNA V4537, Lm2, Loc. 456-2 (?Cimolodon sp. in Eaton, 1987).

Description - p4. MNA V4525 (figures 22A-B; note that the bottom of the anteroexternal lobe is not shown as it is obscured by glue on the specimen) has 10 serrations and six internal and external ridges. The tooth forms a nearly symmetrical arch. The second serration is spaced far posterior to the first serration, and the remaining serrations are approximately equally spaced. The crest of the blade reaches its apex at the fourth serration slightly anterior to the midpoint of the blade. The posteroexternal pocket is low on the labial wall of the tooth and slopes anteroventrally. There are six closely spaced serrations on both sides of the blade and no serrations associated with the posteromost two cusps.
m2 - MNA V4537 (figure 22C) has a cusp formula of $4: 2$. The first cusp of the external row is anteroposteriorly narrow and broadly separated from the larger second cusp. Cusps 2 and 3 are separated slightly apically and by a deep groove lingually. There is little separation of cusps 3 and 4. The central valley is complexly pitted. The first cusp of the internal row is well separated from the smaller second cusp. There is a distinct notch posterior of the second cusp.

Discussion - This p4 was assigned to Cimexomys sp. cf. C. antiquus in Eaton, 1987. This choice reflects the small size of the tooth (very close to that of C. judithae, see table 9 ), the low number of serrations and ridges, and that the posteromost serrations were cusp-like and lacked ridges (as in $C$. judithae, Montellano, 1992, p. 32). However, the blade is high crowned and has a high H:AP ratio (0.65), much higher than that of any known species of Cimexomys (table 9). Also, the large gap between the first two serrations is not seen on either Cimexomys or Mesodma but is consistently present on p4s of Cimolodon (e.g., C. similis, Fox, 1971, figure 5; C. nitidus, Archibald, 1982, figure 18). However, it is somewhat difficult to access the relative position of the first two serrations on the figure of p4 of C. gratus (see Archibald, 1982, figure 37), as the anterior portion of the blade appears to be worn. Of species of Cimexomys, C. gratus has the most serrations (up to 10 ) and the highest H :AP ratio ( 0.52 ), but $C$. gratus is much larger than the MNA specimen and still has a significantly lower H:AP ratio (table 9). MNA V4525 is shorter and appears to be higher crowned than the partial p4 assigned above to Cimolodon foxi sp. nov. from the Kaiparowits Formation. The specimen is also similar to, but smaller than, a p4 (MNA V5870, figure 5C-D) described by Eaton (1995) as an indeterminate cimolodontid from the Dakota Formation. The blade is considered to represent Cimolodon because of its high H:AP ratio and the broad separation of the anteromost two serrations.

The cusps of the internal row of the m 2 are not as narrowly divided and the external cusp row is less divided than in most illustrated m2s of Cimolomys (Sahni, 1972, figure 11 E ; Clemens, 1964, figure 35b; but less so than on the m2 illustrated in Archibald, 1982, figure 23e). Pitting and grooves are evident in specimens of both taxa. The specimen is smaller than described m2s of Cimolodon (or Cimolomys) and compares closest to the m 2 s of Cimolodon foxi sp. nov. from the Kaiparowits Formation described earlier in this
paper. Taken together, these two specimens suggest the presence of a species of Cimolodon in the Wahweap Formation similar to $C$. foxi from the Kaiparowits Formation.

Superfamily unknown<br>Family Cimolomyidae Marsh, 1889<br>Meniscoessus Cope, 1882<br>Meniscoessus sp. cf. M. intermedius Fox, 1976<br>table 15; figures 22D-G

Referred Specimens - MNA V5281, LM1 (posterior part), Loc. 456-1; MNA V5287, RP4, Loc. 455-1.

Description - P4. MNA V5287 (figures 22D-F) has five cusps in the medial row. The first four cusps have a high climb ratio, and there is less difference between the height of the fourth and fifth cusps. The posterior face of the tooth is complexly crenulated with two cusps on the lingual side and one cusp on the labial side.

M1 - MNA V5281 (figure 22G) is the posterior portion of a large M1. The cusps of all three rows are pyramidal and the cusps of each row are deeply separated, almost to the depth of the anteroposterior valleys. The valleys that separate each cusp in the external and medial rows are aligned transversely. The cusps of the medial row broaden slightly posteriorly. The internal row has five cusps and joins the main body of the tooth just about at the position of the fifth from the last cusp.

Discussion - The P4 is unlike the P4 illustrated by Fox (1971, figure 8a, b) as Meniscoessus ferox. In overall form, the P 4 looks more like that of the much larger M. robustus (e.g., Archibald, 1982, figure 29a, b). The P4 of M. intermedius is unknown. The number of cusps on the internal row of the M1 and the position the row meets the main body of the tooth are the same as in the M1 of M. intermedius (table 15), from the Oldman Formation (Judithian) of Canada (Fox, 1976). As there is only one M1 described for M. intermedius, it is not known if the specimen described here is within the size range for that taxon, or represents a smaller taxon. Of described species of Meniscoessus, M. intermedius is the closest in size and morphology to MNA V5218.

## Genus Cimolomys Marsh, 1889

Cimolomys sp. cf. C. trochuus Lillegraven, 1969
table 16; figures 23A-C
Referred Specimens - MNA V4524, LP4 (part), Loc. 455-1 (Cimolodon sp. near C. clarki in Eaton, 1987; MNA V5326, LP4, Loc. 707-6 (Cimolodon sp. near C. clarki in Eaton, 1987); OMNH 23350, RP4, Loc. 702-2.

Description and Discussion - P4. MNA V5326 (figures $23 \mathrm{~A}-\mathrm{C}$ ) has a cusp formula of $1: 5$ and has only a slight arch in occlusal view. The anteroexternal platform is moderately expanded and bears one large, ribbed cusp. The cusps of the medial row have a high climb ratio $(\mathrm{CR}=0.58)$, are well separated, ribbed, and become larger posteriorly. The posterior wall that descends into the posterior basin from the last cusp of the medial cusp row is convex rather than flat. Two small cusps border the small posterior basin ( $\mathrm{PL}: \mathrm{AP}=0.34$ ).

These P4s are considered to represent Cimolomys because they have relatively few cusps, the cusps are large and distinct, and the cusps are ribbed. They are all near or with-


Figure 22. Cimolodon sp. (small): A, (MNA V4525), Rp4, labial view; B, lingual view; C, (MNA V4537), Lm2, stereo occlusal view. Meniscoessus sp. cf. M. intermedius: D, (MNA V5287), RP4, stereo occlusal view; E, labial view; F, lingual view; G, (MNA V5281), partial LM1, stereo occlusal view. Scale bar $=1 \mathrm{~mm}$.
in the size range of P 4 s attributed to $C$. clarki by Sahni (1972) and Lillegraven and McKenna (1986) (table 16); however, Sahni (1972, p. 373) realized that these P4s were unusually large relative to the other teeth of C. clarki. Teeth of $C$. clarki are approximately $70 \%$ of the size of those of $C$. gracilis; however, the P4s assigned to C. clarki by Sahni (1972) and Lillegraven and McKenna (1986) are 25\% larger than those of C. gracilis and are very close to the size of ?Cimolomys sp. A described in Fox (1971). Fox (1971) considered the P4 of ?Cimolomys sp. A to be in the size range of C. trochuus (a conclusion shared by Archibald, 1982, p. 122) for which P 4 s have not been described. It seems most likely that P4s assigned to C. clarki by Sahni (1972) and Lillegraven and McKenna (1986) belong to another, larger species of Cimolomys, possibly a taxon similar in size to $C$. trochuus (also see discussion above under Cimolomys sp. B cf. C. clarki from the Kaiparowits Formation). For this reason, the P 4 s described here are considered to be closer to $C$. trochuus than to C. clarki, even though these are close to the size of P 4 s previously assigned to $C$. clarki. These P 4 s are also too large to belong to ?Cimolomys sp. A or B, described below.

## ?Cimolomys sp. A

table 16; figure 23D
Referred Specimen - MNA V5218, Rm1, Loc. 455-1 (?Cimolomyid, gen. \& sp. indet. in Eaton, 1987).

Description and Discussion - m1. MNA V5218 (figure 23D) has a cusp formula of $4: 4$. The tooth is broad relative to its width (LB:AP $=0.56$ ), and the anteromost cusps of each row are closely positioned immediately adjacent to the central valley. The first cusp of the external row is low, small, and shifted lingually and is a three-faced pyramidal cusp. It is well separated from the second pyramidal cusp, which is the tallest of the row. A wide valley separates cusps 2 and 3. The third cusp is pyramidal and leans posteriorly. The posteromost cusp is lower than cusps 2 and 3, but not as low as the first cusp. There is a slight hint of a posteroexternal shelf.

The central valley is straight and lined with shallow pits. The corners of the pyramidal cusps 2-4 of each row meet in the central valley and may have crossed the central valley as ridges prior to wear. The first cusp of the internal row is a small projection rising from an anteriorly directed crest originating from the second cusp. The second cusp is subpyramidal and the tallest of the row. A wide, deep valley separates cusps 2 and 3 . The third cusp is pyramidal and leans posteriorly. The fourth cusp is anteroposteriorly compressed.

The m1 (MNA V5218) is like those of Bryceomys in having cusp rows of equal width and having broad, U-shaped valleys separating the cusps of each row. The specimen is unlike Bryceomys in having a straight central valley and pyramidal cusps in both rows. The molar lacks the strongly crescentic cusps of Cimolomys gracilis, but is similar to the ml of C. clarki depicted by Lillegraven and McKenna (1986, figure 7A, UW 15535) in having broadly separated pyramidal cusps. The specimen is also similar to a molar described from the Kaiparowits Formation earlier in this paper as ?Cimolomys butleria sp. nov. The ml of ?C. butleria (UMNH 22837, figure 13A) is about the same size, has two more cusps in the external row, and is longer relative to width
(LB:AP $=0.50$ ) than MNA V5218. These two m1s are similar in having the anteromost cusps of each cusp row closely placed and in the shape and separation of the cusps. MNA 5218 (figure 23D) is also somewhat similar to ?Cimolomys sp. A described by Fox (1971) but appears to be more primitive in having two less cusps in the external row and less posterior protrusion of the external row.

It is likely that MNA 5218 represents a new genus intermediate between a taxon like Bryceomys and later crescenticcusped forms of Cimolomys. It may also be possible that ?Cimolomys butleria sp. nov., ?Cimolomys sp. A (Fox, 1971), and possibly $C$. trochuus should be included in this new genus as the m 1 s of these taxa all have pyramidal cusps separated by broad, open valleys, cusp rows of equal width, cusp formulae of 4-6:4, and the two anteromost cusps of each row closely appressed. The species from the Wahweap Formation appears to be the most primitive.

A formal genus is not established due to lack of knowledge of other tooth positions, m 1 s of $C$. trochuus are unknown, and taxonomic uncertainty about the m 1 attributed to C. clarki by Lillegraven and McKenna (1986) (see discussion above under ?Cimolomys butleria sp. nov. from the Kaiparowits Formation).

## ?Cimolomys sp. B

table 16; figures $22 \mathrm{E}-\mathrm{F}$
Referred Specimens - OMNH 23360, LP4 (part), Loc. 707-2; MNA V4529, LM2, Loc. 456-2 (Cimolomys n. sp. in Eaton, 1987); MNA 5206, LM2, Loc. 456-2 (Cimolomys n. sp. in Eaton, 1987); MNA V5320, RM2, Loc. 456-2 (Cimolomys n. sp. in Eaton, 1987); OMNH 20956, RM2, Loc. 455-2; UMNH VP7595, RM2, Loc. 77.

Description - P4. OMNH 23360 is the anterior part of a P4. The two striated cusps on the anteroexternal platform are closely appressed against the cusps of the medial cusp row and are only slight lower.

M2 - MNA V4529 (figure 23E) has a cusp formula of $2 ?: 3: 4$. The specimen is worn, but there appear to have been two or three distinct cusps on the anteroexternal ridge. The anteroexternal platform has several distinct pits. The anterior face of the first cusp of the medial row leans posterodorsally. The cusp is narrow and well separated from the ante-rior-leaning subpyramidal, second cusp. The third cusp leans less anteriorly than the second and has deep grooves on its lingual side. The central valley is deep and lined on both sides by grooves on the internal and medial cusp row walls. Cusps of the internal row decrease in height posteriorly and are separated apically and by grooves on the labial wall. The cusps appear to have been slightly better separated posteriorly prior to wear.

MNA V5320 (figure 23F) has a formula of Ri:3:4. The anteroexternal ridge hints at having had one or two small cusps prior to wear. The anteroexternal platform is deeply pitted. The first cusp of the medial row is low and, despite the great amount of wear on the tooth, it lacks occlusal wear. The second cusp is large and pyramidal and leans anteriorly. The central valley is lined with deep pits, and grooves descend into it from the face of both the medial and internal cusp rows. Cusps of the internal row become larger posteriorly and are separated apically.

Discussion - The partial P4 appears to represent Cimolomys, as the cusps of the anteroexternal platform can be closely appressed to the cusps of the medial row in that genus (e.g. C. gracilis, Archibald, 1982, figure 23c). By contrast, in Cimolodon the cusps of the external row are separated from those of the medial row by a distinct valley (e.g., $C$. nitidus, Clemens, 1973, figure 30; Archibald, 1982, figure 20). Striations are more commonly seen on Cimolodon but can be present on Cimolomys (e.g., C. clarki, Lillegraven and McKenna, 1986, figure 7e).

These M2s have complex pitting, which makes them appear closest to the illustrated M2s of Cimolodon electus (see Fox, 1971, figure 5a). However, in Cimolodon the internal and medial cusp rows tend to parallel each other at an angle oblique to the anteroposterior axis of the tooth, and the internal row cusps are relatively narrow compared to the medial row (e.g., C. electus, Fox, 1971, figure 5; C. nitidus, Lillegraven, 1969, figure 11-5b). The M2 illustrated by Sahni (1972, figure 11F) as C. clarki had deeply separated cusps in the internal cusp row (which appear to be deepest between the first two cusps), very unlike the condition seen in these M2s. Similarly, the highly crescentic cusps of the M2 of C. gracilis depicted by Clemens (1964, figure 38b) are deeply separated; however, the specimens of C. clarki shown by Lillegraven and McKenna (1986, figure 7D) and C. gracilis illustrated by Archibald (1982, figure 23d) have the first two cusps relatively weakly divided with deeper division of the cusps posteriorly. There is some hesitance in assigning these M2s to Cimolomys because of the shallow separation of the cusps of the internal row. These specimens appear to be in the possible size range (estimated from teeth in other positions, table 16) of Fox's (1971) ?Cimolomys sp. A or C. trochuus, for which no M2s have been described.

> ?Cimolomys sp. C (large) table 16 ; figure 23 G

Referred Specimen - MNA V4559, LM2; Loc. 456-2 (Cimolomys sp. near C. Clarki in Eaton, 1987).

Description - M2. MNA V4559 (figure 23G) has a cusp formula of Ri:3:4. There is a strong anteroexternal ridge, but no distinct cusps are evident on this worn specimen. The first cusp of the medial row is low and worn. The second cusp is larger, pyramidal in form, and the third cusp is taller but slightly smaller at its base than the second cusp. The central valley is deep, straight, and aligned with the anteroposterior axis of the molar. The cusps of the internal row are better separated posteriorly.

Discussion - The internal cusps are well separated in depicted M2s of Cimolomys clarki (see Sahni, 1972, figure 11F) and C. gracilis (see Clemens, 1964, figure 38b), which could be a character diagnostic of the genus (see discussion above under ?Cimolomys sp. B). The cusps of the internal cusp are not deeply divided on this worn specimen, but cusp separation appears to be more complete than on M2s of Cimolodon. M2s of Cimolodon also tend to have more cusps in the medial row, and these cusps are narrow, anteroposteriorly compressed crescentic cusps (Clemens, 1964, figure 31b; Lillegraven, 1969, figure 11-5b) unlike the broad second cusp on MNA V4559. The central valley tends to be oriented with the AP axis of the molar in Cimolomys and somewhat obliquely to it in the few illustrated M2s of Cimolodon.

Because of the weak separation of cusps of the internal row, this specimen is only tentatively referred to Cimolomys. It is within the size and cusp formula range for both Cimolomys clarki and Cimolodon electus.

Family indeterminate
Genus and species unknown
figures $23 \mathrm{H}-\mathrm{I}$
Referred Specimen - UMNH VP7599, Rp4 (partial), Loc. 77.

Description and Discussion - A single fragment (UMNH VP7599, figures $23 \mathrm{H}-\mathrm{I}$ ) of the posterior part of a large blade is present in the sample. The blade is distinctive in being very complex with striae oriented posteroventrally from the posteromost labial ridge. These striae terminate at the welldeveloped posterolabial cusp, which is positioned high on the labial wall. The p4 apparently has a high serration count, as this small portion of the blade has nine serrations.

The spacing of the serrations is similar to that of the p 4 s of Cimolodon sp. cf. C. nitidus described above (UMNH VP7978, figure 21G); however, the complex striated posterior wall of this specimen is different and is more similar to p4s of C. electus (see Fox, 1971, figure 3d-e). The posteroexternal cusp is relatively low compared to the crest of the tooth on all figured specimens of Cimolodon (e.g., Archibald, 1982, figure 18c; Fox, 1971, figure 3d, figure 5c). The posteroexternal cusp is positioned just below the last serration in Mesodma (e.g. Clemens, 1964, figure 10A), but the estimated size of this blade ( 5 mm ) exceeds that known for Mesodma. In complexity and size, this blade is most like the unidentified large blade (UCMP 118576-5.92 mm) shown in Montellano (1992, figure 11).

Cimexomys Sloan and Van Valen, 1965
Cimexomys sp. cf. C. antiquus Fox, 1971
table 17; figures 24A-B
Referred Specimens - MNA V5205, LM1, Loc. 456-2; MNA V5247, Rm1 (damaged), Loc. 456-2; MNA V5324, Lm1, Loc. 455-1.

Description - m1. MNA V5247 (figure 24A) is a small m 1 that narrows anteriorly and has a cusp formula of 5:4?. The cusps of the external row are separated by narrow valleys, and the last two cusps are poorly separated and ridgelike. The first cusp of the internal row is elongate. The last two (?) cusps of the internal row a re missing. Cusps on the specimen are worn but appear to be blocky. MNA V5324 was originally a better-preserved specimen than MNA V5247, but it was damaged while being prepared for illustration. MNA V5324 differs from MNA V5247 in having five or possibly six cusps on the external row and the first cusp of the external row is tiny and shifted lingually.

M1 - MNA V5205 (figure 24B) has a cusp formula of 4:6:2? (posteromost part of the tooth is missing). The cusps of the external row become markedly narrower posteriorly. There is a small cuspule (not counted in the formula) present along the anterior margin of the tooth in front of the first cusp. The first cusp is lower and smaller than the second cusp, and the two cusps are not deeply divided. The valley between cusps 2 and 3 is broader and deeper than the valley between the first two cusps, and it is deeper yet between


Figure 23. Cimolomys sp. cf. C. trochuus: A, (MNA V5326), LP4, stereo occlusal view; B, labial view; C, lingual view. ?Cimolomys sp. A: D, (MNA V5218), Rm1, stereo occlusal view. ?Cimolomys sp. B: E, (MNA V4529), LM2, stereo occlusal view; F, (MNA V5320), RM2, stereo occlusal view. ?Cimolomys sp. C (large): G, (MNA V4559), LM2, stereo occlusal view. Cimolodonta, Family indet., genus and species unknown: H, (UMNH VP7599), partial Rp4, labial view; I, lingual view. Scale bars $=1 \mathrm{~mm}$.
cusps 3 and 4 . The cusps have been worn to about the same height. The central valley is strongly oblique to the anteroposterior axis of the tooth. The cusps of the medial row are larger and broader posteriorly, and cusps 3-5 appear to have leaned anteriorly prior to wear. The internal row has two elongated cusps and joins the main body of the tooth between cusps 3 and 4 of the medial row.

Discussion - The M1 is similar to MOR 302 (Cimexomys judithae, Montellano and others, 2000, figure 1) in having a small first cusp on the external row, but the cusps are better divided on MOR 302 than on this specimen. The central valley is less oblique on MOR 302 but the cusps of the external row do narrow posteriorly and the cusps of the medial row broaden posteriorly as on this specimen. The cusps of MOR 302 are strongly aligned transversely, but UCMP 130504 (Cimexomys judithae, Montellano, 1992, figure 5) has cusps offset anteriorly and aligned posteriorly, with a strongly oblique central valley (as does C. minor, Archibald, 1982, figure 35). The MNA specimen is more like UCMP 130504.

The M1 (MNA V5205) is also similar in size to specimens referred to as cf. Cimexomys sp. by Montellano (1992). These specimens were identified on the basis of the length of the internal row being equal to or less than half the length of the tooth. This is probably not a certain diagnostic character of Cimexomys as it is not present on MOR 322, considered by Montellano (1992, figure 6) to represent C. judithae. Also, in M. primaeva (see Sahni, 1972, figure 10) the internal row of M1 is less than half the length of the tooth. One of the specimens (UCMP 131468) that Montellano (1992) referred to cf. Cimexomys sp. has a cusp formula (5:5:2?), close to that of the MNA M1 (4:6:2?). However, neither UCMP 131468 nor any of the other M1s referred to cf. Cimexomys sp. were illustrated by her.

MNA V5205 also was compared directly to the type of C. antiquus, UA 5640. The MNA specimen is similar in size and morphology except for having a more squared anterior margin and one less cusp in the external row. In cusp formula, size, and morphology, this specimen is closer to M1s of $C$. antiquus than to any other well-documented species of Cimexomys (this excludes cf. Cimexomys sp. of Montellano, 1992). In her differential diagnosis of C. judithae (see Montellano, 1992, p. 30), Montellano did not mention C. antiqu$u s$, and as such the assignment made here is not certain.

The m1s are of appropriate size to be included within either C. antiquus or $C$. judithae and are tentatively assigned here based on the M1. Both specimens are badly preserved, thus contributing to the uncertainty of their assignment.

Paracimexomys Archibald, 1982
cf. Paracimexomys sp. A
table 18; figures 24C-D
Referred Specimens - MNA V4567, Lm1, Loc. 456-2; MNA V4599, Lm1; Loc. 455-1; MNA V5233, LM2, Loc. 456-2; MNA V5240, RM1, Loc. 456-2; MNA V5325, Rm1, Loc. 455-1; OMNH 22544, LM2, Loc. V2; OMNH 24363, LM2, V11.

Description - m1. MNA V4599 has a cusp formula of $4: 3$. The specimen is very worn and poorly preserved (too poorly preserved to illustrate) as are many of the teeth in this sample of small multituberculates. The external cusp row is
worn almost to its base. The central valley is worn, forming a broad open valley. The internal cusp row is less worn than the external, and the first two cusps of the internal row are closely appressed and not deeply divided. The second and third cusps are deeply divided. The tooth is relatively broad compared to its length ( $\mathrm{LB}: \mathrm{AP}=0.66$ ).

M1 - MNA V5240 (figure 24C) is an incompletely preserved M1 with a cusp formula of $4: 4: 1$. The medial and internal cusp rows appear to be approximately parallel. The four cusps of the external row decrease in size posteriorly. A few of these cusps bear vertical striations, and more of them may have existed prior to wear. The central valley is deep and closed posteriorly and anteriorly. The cusps of the medial row increase in size and height posteriorly. The third cusp leans anteriorly. The internal row bears one small, low cusp. There is an indentation (seen in occlusal view) on the labial side of the tooth, but it is not determinable if there is one on the damaged lingual wall.

M2 - MNA V5233 (figure 24D) is a very worn specimen with a cusp formula of $1: 2: 3$. The external platform is complex and pitted. The medial row has two well-formed cusps with the anteromost leaning forward and merging with the ridge on the anterior face of the tooth. The posterior wall of the cusp is concave and slopes posteriorly to the base of the second cusp, which is the largest and tallest of the tooth. The central valley is sinuous with deep anteroposteriorly oriented pits. The first two cusps of the internal row form a high ridge. The posteromost cusp is distinct, but not deeply divided from the more anterior cusps.

Discussion - Indeterminable characteristics of the poorly preserved m 1 s include whether the central valley was sinuous, the molar cusps were ribbed, or if the valleys were pitted. The m1s are tentatively assigned here as their size and what can be seen of their morphology appears to be appropriate for association with the single M1.

The M1 (MNA V5240, figure 24C) is morphologically similar to those of Paracimexomys priscus (see Archibald, 1982, figure 39a), but $P$. priscus is much larger (table 18) and lacks any hint of ribbing on the cusps (see discussion and the revised diagnosis of Paracimexomys in Eaton and Cifelli, 2001). The M2 tapers strongly posteriorly, and the central valley is very sinuous as in P. priscus (see Archibald, 1982, figure 39b). However, the strong pitting in the central valley is not seen in P. priscus.

Eaton and Cifelli (2001) restricted Paracimexomys to taxa lacking complex ribs or pitting and referred the rather wide morphologic range of taxa previously assigned to Paracimexomys to cf. Paracimexomys. This species (cf. Paracimexomys sp. A) would be the smallest assigned either to Paracimexomys or cf. Paracimexomys except for the similarly sized cf. Paracimexomys perplexus from the Cedar Mountain Formation (Eaton and Cifelli, 2001) and cf. Paracimexomys sp. from the Dakota Formation (Eaton, 1995, table 18).

## cf. Paracimexomys sp. B table 18; figure 24 E

Referred Specimen - UMNH VP7982, Lm1-2, Loc. 130.
Description and Discussion - This specimen (figure 24 E ) is poorly preserved, and most of the molar enamel is missing. No cusp morphology is preserved, and the speci-
men is conferred to Paracimexomys based on the almost identical length of the m 1 and m 2 , a characteristic of Paracimexomys (see Eaton and Cifelli, 2001). The length of these molars is too great for this specimen to be included in cf. Paracimexomys sp. A, described above.

Bryceomys Eaton, 1995<br>Bryceomys sp. cf. B. fumosus Eaton, 1995<br>table 18; figure 24 F

Referred Specimen - MNA V7527, RM1, Loc. 455-1.
Description and Discussion - MNA V7527 (figure 24F) is a poorly preserved M1 with a cusp formula of 5?:4:2. The external and medial cusp rows are parallel and do not diverge anteriorly. The cusps of the external row descend in height posteriorly (the posteromost part of the tooth, possibly having a fifth cusp, is missing). The first cusp of the row is small and shifted lingually. The next three cusps are approximately equal in size and equally spaced, and they are all connected by a low ridge. The first two cusps of the medial row are elongate and poorly separated. The third cusp is more squared and deeply separated from both the second and fourth cusps. The last cusp of the medial row is the broadest and tallest of the tooth. The internal row is broad and has two distinct cusps on its lingual margin. The platform connects just posterior to the second cusp of the medial row.

The size (table 18) and morphology of this M1, particularly the very broadly expanded internal platform, are similar to that of the M1s of Bryceomys fumosus from the Smoky Hollow Member of the Straight Cliffs Formation (Turonian) described by Eaton (1995).

## Cedaromys Eaton and Cifelli, 2001 <br> Cedaromys sp. <br> table 18; figure 24 G

Referred Specimen - MNA V7534, Rm1, Loc. 455-1.
Description and Discussion - MNA V5734 (figure 24G) is a worn m 1 with a cusp formula of $4: 3$. The cusp rows converge anteriorly and the molar is strongly waisted in occlusal view. The first cusp of the external row is low and shallowly divided from the second cusp. The second and third cusps are larger than the first and a deep pit separates them. The third cusp is worn slightly lower than the second cusp. The fourth cusp is broad and flat. The central valley is sinuous. The first two cusps of the internal row are small, weakly divided, tall and conical cusps. Second and third cusps are well separated, but the separation does not reach the floor of the medial valley. The third cusp is larger and slightly taller than the first two cusps.

The robust appearance of this tooth is Bryceomys-like, but the molar cusps of Bryceomys are much better separated than those of Cedaromys. This molar is similar in morphology and size (table 18) to those of Cedaromys hutchisoni sp. nov., described from the Kaiparowits Formation earlier in this paper.
cf. Cedaromys sp.
table 18 ; figure 24 H
Referred Specimen - MNA V4627, Lm1, Loc. 455-1 (Paracimexomys sp. in Eaton, 1987).

Description and Discussion - MNA V4627 (figure 24H) is an ml with a cusp formula of $4: 3$. The cusps of the external row increase in height posteriorly. The first cusp is low and round. The second cusp is much larger and shallowly separated from the similar-sized third cusp, particularly along the labial wall. The fourth cusp is missing on this specimen. The central valley is only slightly sinuous. The cusps of the internal row decrease in height posteriorly. The first cusp is tall and essentially conical except for the worn flat surface facing the central valley. The first and second cusps are separated for about half their height. The second cusp is rounded anteriorly but is weakly squared at the posterior corners of the cusp. The third cusp is slightly elongated.

The cusps on this specimen are not as well separated as are those of m1s of Bryceomys, and the specimen lacks the pits separating the cusps in Dakotamys. The robust broad cusps of this specimen are closest to that seen on the m 1 s of Cedaromys, but they lack the closely paired first two cusps of the internal row that typifies Cedaromys (Eaton and Cifelli, 2001).

## Genus and species unknown table 18

Referred Specimens - MNA V5322, Rm2, Loc. 456-2 (Paracimexomys n. sp. in Eaton, 1987); OMNH 23362, Lm2, Loc. V16; UMNH VP7994, RM2, Loc. 130.

Description and Discussion - Three small second molars are present in the sample from the Wahweap Formation that are too small to fit with any of the taxa described earlier in this paper. MNA V5322 is small ( $\mathrm{AP}=1.12$; $\mathrm{LB}=0.94$ ), it has a cusp formula of 3:2 and an ovate shape. An attempt was made to associate this specimen with the m 1 s described as cf . Paracimexomys sp. A, but the resultant $\mathrm{m} 2: \mathrm{m} 1$ ratio would be 0.71 , too low for Paracimexomys (see Eaton and Cifelli, 2001) (table 18). If this specimen belongs with the m1s assigned to cf. Paracimexomys sp. A, then those m1s are incorrectly assigned.

Another small deeply worn m 2 is present, OMNH 23362. Its length $(\mathrm{AP}=1.34)$ would be appropriate for cf. Paracimexomys sp. A, but the molar is not wide enough ( $\mathrm{LB}=0.88$ ) to belong with the m 1 s of that species (table 18). This m2 and MNA V5322 do not represent the same species, but they hint at the presence of greater diversity of small multituberculates in the fauna than can be accounted for on the basis of first molars.

UMNH VP7994 is a small M2 ( $\mathrm{AP}=1.08^{*}$; $\mathrm{LB}=0.97^{*}$ ) with an unexpanded external platform expressed only by a narrow ridge. The external row has a narrow, sharp ridge anteriorly, but the ridge is too low to count as a cusp. The tooth is dominated by the first cusp of the external row, which is ribbed and the tallest and largest of the tooth. The second cusp is widely separated from, and smaller than, the first cusp. The central valley is slightly sinuous, unpitted, and open at both ends. The internal row has four cusps. The first is small, low, and closely joined to the larger second cusp. The second, third, and fourth cusps are separated by wide valleys formed by concave surfaces on the anterior and posterior faces of the cusps. The third cusp is the largest, and the apical separation between the third and fourth cusps is the deepest of the row. The large central cusp of the external row and the lack of an expanded external platform are similar to


Figure 24. Cimexomys sp. cf. C. antiquus: A, (MNA V5247), Rm1, stereo occlusal view; B, (MNA V5205), incomplete LM1, stereo occlusal view. cf. Paracimexomys sp. A: C, (MNA V5240), RM1, stereo occlusal view; D, (MNA V5233), LM2, stereo occlusal view. cf. Paracimexomys sp. B: E, (UMNH VP7982), Lm1-2, stereo occlusal view. Bryceomys sp. cf. B. fumosus: F, (MNA V7527), incomplete RM1, stereo occlusal view. Cedaromys sp.: G, (MNA V5734), Rm1, stereo occlusal view. cf. Cedaromys sp.: H, (MNA V4627), incomplete Lm1, stereo occlusal view. Scale bars = 1 mm.
the condition seen in M2s of Paracimexomys priscus (see Archibald, 1982, 39b). This tooth possibly represents Paracimexomys or cf. Paracimexomys, and it is similar in size and proportions to MNA V5322 (m2). This supports the presence of a smaller species of Paracimexomys or cf. Paracimexomys in the fauna.

## BIOSTRATIGRAPHIC IMPLICATIONS OF FAUNAS

Only two taxa from the Kaiparowits Formation described here are conspecific with previously described taxa (tables 19, 20). These include Dakotamys magnus, which was originally described by Sahni (1972) from the Judith River Formation and Mesodma archibaldi, which is the same taxon described by Montellano (1992) as Mesodma sp., also from the Judith River Formation. Dakotamys magnus was considered a unique occurrence in the Judithian by Lillegraven and McKenna (1986), as are most of the species to which taxa are conferred here: Cimexomys sp. cf. C. judithae; Cimolomys sp. A and B cf. C. Clarki; Meniscoessus sp. cf. M. intermedius; and Meniscoessus sp. cf. M. major. Only one conferred species, Cimolodon sp. cf. C. nitidus, is known from younger "Edmontonian" (and Lancian) localities, but the species described here appears to be morphologically more primitive than that species. Mesodma sp. (large) is most similar to M. senecta from the Aquilan, but the equivalency is difficult to establish as that species is poorly known. Both Cimolodon foxi and Cimolodon sp. cf. C. similis are closest to C. similis, an Aquilan taxon.

There is little doubt of the Judithian affinities of this multituberculate fauna, and this is consistent with data derived from therian mammals (Cifelli, 1994). Within the Judithian, this fauna may be slightly older than those from the type Judith River Formation based on some occurrences of taxa closer to Aquilan than to Judithian faunas and the sharing of four possibly conspecific taxa with the underlying Wahweap Formation (Aquilan) (see tables 18 and 19). The only taxon unique to a stratigraphic horizon is Dakotamys magnus from the stratigraphically highest well-sampled locality (TB8, MNA Loc. 1004-1; OMNH V5) in the Kaiparowits Formation ( 640 m above the base of the formation, Eaton, 1991). This may suggest a late immigration event of Dakotamys magnus into the area and perhaps indicate a basis on which to establish an approximate correlation with this part of the Kaiparowits Formation to the type Judithian.

Taxa described from the Wahweap Formation (tables 19, 20) include only two species identified with certainty, Cimolodon electus and C. similis, both of which are known from the Aquilan. One conferred species (Cimexomys sp. cf. C. antiquus) is close to an Aquilan taxon, as are two species questionably assigned to ?Cimolomys (sp. A and B). One conferred species (Meniscoessus sp. cf. M. intermedius) is closer to a Judithian member of the genus, and another conferred species (Cimolodon sp. cf. C. nitidus) is closest to an "Edmontonian" (and Lancian) species. Two other conferred species (Cimolomys sp. cf. C. trochuus and Mesodma sp. cf. M. formosa) are closest to Lancian species. Although there is little doubt of the Aquilan age of the Wahweap Formation, it contains a fauna significantly different from that of the Milk River Formation of Canada, the type fauna for the Aquilan. This may reflect latitudinal differences and/or the fauna from the Wahweap Formation may be somewhat older than the Milk River fauna based on some of the primitive characters present in species of both Mesodma (presence of pitting on molars) and Cimolodon (both C. electus and $C$. similis appear slightly more primitive than those species recovered from the Milk River Formation).

Refinement of North American Land Mammal "Ages" so that estimates of relative positions of faunas to the type "ages" can be achieved will require better sampling of mammalian faunas, more continuous latitudinal sampling, and the integration of data from other fossil groups (palynomorphs, ostracodes, lower vertebrates).

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Table 1. Comparison of measurements, ratios, and cusp formulae of fourth premolars of Kaiparowits Formation species of Mesodma to other species. Boldface specimen numbers indicate specimens described in this paper; "*" indicates damaged specimen; "e" indicates measurement estimated from a depicted specimen; "?" indicates an uncertain value; "!" indicates an unusual value.

| Tooth | Taxon | Source | S:ER:IR | AP | H | H:AP | AL:AP | p4:m1 | P4:p4 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| p4 | M. hensleighi | Lillegraven, 1969 | 11:8:9 | 2.70 |  |  |  | 1.50 | 0.66 |
|  | " | Archibald, 1982 | 9-10:7:7 | 2.66-2.89 | 1.04-1.39 | 0.45 | 0.47 | 1.49 | 0.64 |
|  | M. archibaldi | MNA V7533 | 9:6:7 | 2.90 | 1.52 | 0.52 | 0.48 | 1.57 |  |
|  | M. formosa | Lillegraven, 1969 |  | 3.05-3.10 |  |  |  | 1.34 | 0.67 |
|  | " | Archibald, 1982 | 11:8:7 | 3.09 | 1.44 | 0.47 |  |  | 0.74 |
|  | M. thompsoni | Lillegraven, 1969 |  | 4.3 |  |  |  | 1.51 |  |
|  | " | Archibald, 1982 | 12-13:10:9 | 4.55-4.61 | 1.96-2.21 | 0.45 | 0.43 | 1.67 | 0.56 |
|  | M. garfieldensis | Archibald, 1982 | 11-14:9-10:10 | 3.50-4.57 | 1.64-2.13 | 0.48 | 0.43 | 1.59 | 0.71 |
|  | M. primaeva | Sahni, 1972 | 11:?:? | 4.7e |  | 0.5 e |  |  |  |
|  | " | Novacek \& C., 1977 |  | 4.59-4.81 |  | 0.42 |  |  |  |
|  | M. "primaeva" | Lilleg. \& McK., 1986 |  | 3.48-3.47? |  |  |  |  | 1.00 ! |
|  | " | Montellano, 1992 | 11:??? | 3.71 ? |  |  |  |  | 1.16 ! |
|  | M. sp. (large) | UMNH VP7642 | 10:7:7 | 3.70 | 2.17 | 0.59 | 0.53* | 1.47 | 0.7 |
|  | M. senecta | Fox, 1971 | 15:13:13 | 4.6 |  | 0.46 e |  |  | 0.6 |
|  | " | Novacek \& C., 1977 |  | 4.18-4.54 |  | 0.44 |  |  |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | H:AP | PL:AP | P4:M1 |
| P4 | M. hensleighi | Lillegraven, 1969 | 1:6 | 1.60-1.90 | 0.70-0.90 | 0.45 | 0.48 e | 0.39 e | 0.81 |
|  | " | Archibald, 1982 | 1-2:6 | 1.73-1.79 | 1.07-1.10 | 0.61 |  |  | 0.81 |
|  | M. formosa | Lillegraven, 1969 | 2:6 | 2.05 | 1.01 | 0.49 | 0.48 e | 0.31e | 0.66 |
|  | " | Archibald, 1982 | 1-2:6-7 | 2.18-2.42 | 1.19-1.28 | 0.55 |  |  | 0.90 |
|  | M. thompsoni | Clemens, 1964 | 1-6:5-8 | 2.3-3.2 | 1.0-1.5 | 0.4 | 0.5 e | 0.54 e |  |
|  | " | Archibald, 1982 | 2-5:6-7 | 2.51-2.56 | 1.36-1.58 | 0.57 |  |  | 0.78 |
|  | M. garfieldensis | Archibald, 1982 | 1-4:7-8 | 2.42-3.23 | 1.63-2.27 | 0.50 | 0.4-0.5e | 0.32-0.35e | 0.84 |
|  | M. senecta | Fox, 1971 | 1-2:6 | 2.7 |  |  | 0.5 e | 0.35 e |  |
|  | M. sp. (large) | MNA V5315 | 2:6 | 2.79 | 1.47 | 0.53 | 0.63 | 0.37 |  |
|  | " | OMNH 20351 | 1:6 | 2.38 | 1.15 | 0.48 | 0.55 | 0.34 |  |
|  | " | OMNH 20366 | 3:6 | 2.62 | 1.32 | 0.50 | 0.55 | 0.34 |  |
|  | " | means | 1-3:6 | 2.60 | 1.32 | 0.51 | 0.58 | 0.35 |  |
|  | M. primaeva | Sahni, 1972 | 2:6 | 4.0 |  |  |  |  |  |
|  | " | Montellano, 1992 | 1-2:6-7 | 4.10-4.43 |  |  |  | 0.28 e |  |
|  | M. "primaeva" | Lilleg. \& McK., 1986 | 1:7 | 3.39-3.60 | 1.77-1.89 | 0.52 | 0.54 e | 0.28 e |  |
|  | Mesodma sp. | Montellano, 1992 | 3-4:6-7 | 2.38-2.74 |  |  |  | 0.32 e | 1.05 ! |

Table 2. Comparison of measurements, ratios, and cusp formulae of lower molars of Kaiparowits Formation species of Mesodma to other species. Boldface specimen numbers indicate specimens described in this paper; " e " indicates measurement estimated from a depicted specimen.

| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | M1:m1 | m2:m1 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| m1 | Mesodma minor | UMNH VP5606 | 6:4 | 1.56 | 0.80 | 0.53 |  |  |
|  | " | MNA V7538 | 6:4 | 1.54 | 0.82 | 0.53 |  |  |
|  | " | means | 6:4 | 1.55 | 0.81 | 0.53 | 1.30 |  |
|  | M. hensleighi | Lillegraven, 1969 | 6:5 | 1.70-1.95 | 0.75-0.85 | 0.43 | 1.22 | 0.57 |
|  | " | Archibald, 1982 | 6:4 | 1.70-1.97 | 0.72-1.00 | 0.43-0.50 | 1.22-1.31 | 0.57-0.60 |
|  | M. archibaldi | MNA V5343 | 6:4 | 1.79 | 0.84 | 0.47 |  |  |
|  | " | MNA V7531 | 6:4 | 1.89 | 0.88 | 0.47 |  |  |
|  | " | MNA V7536 | 6:4 | 1.70 | 0.86 | 0.51 |  |  |
|  | " | OMNH 20764 | 6:5 | 1.87 | 0.85 | 0.46 |  |  |
|  | " | OMNH 22298 | 6:5 | 1.80 | 0.80 | 0.44 |  |  |
|  | " | OMNH 22300 | 6:4 | 1.88 | 0.92 | 0.49 |  |  |
|  | " | OMNH 22835 | 6:4 | 1.99 | 0.97 | 0.49 |  |  |
|  | ${ }^{\prime}$ | OMNH 24056 | 6:4 | 1.85 | 0.86 | 0.47 |  |  |
|  | ${ }^{\prime}$ | means | 6:4-5 | 1.85 | 0.87 | 0.48 | 1.35 | 0.63 |
|  | M. formosa | Lillegraven, 1969 | 6-7:4-5 | 2.10-2.50 | 1.00-1.40 | 0.47 | 1.36 | 0.61 |
|  | " | Archibald, 1982 | 6:4-5 | 2.05-2.55 | 0.90-1.35 | 0.44-0.47 | 1.24-1.36 | 0.58-0.61 |
|  | M. sp. (large) | MNA V5338 | 6:4 | 2.55 | 1.15 | 0.45 |  |  |
|  | " | OMNH 20356 | 6:4 | 2.48 | 1.23 | 0.50 |  |  |
|  | " | means | 6:4 | 2.52 | 1.19 | 0.48 |  |  |
|  | M. garfieldensis | Archibald, 1982 | 6-7:4-5 | 2.27-2.76 | 0.88-1.22 | 0.44 | 1.34 | 0.56 |
|  | M. thompsoni | Lillegraven, 1969 | 7:4 | 2.85 | 1.25 | 0.44 |  | 0.68 |
|  | " | Archibald, 1982 | 6-7:5 | 2.65-2.90 | 1.05-1.30 | 0.44 | 1.29 | 0.75 |
|  | M. primaeva | Sahni, 1972 | 5-6:4 | 3.15-3.60 |  | 0.4 e | 1.2 | 0.7 |
| m2 | M. archibaldi | MNA V4502 | 4:2 | 1.13 | 1.00 | 0.89 |  |  |
|  | " | MNA V5230 | 3:2 | 1.09 | 0.98 | 0.90 |  |  |
|  | " | MNA V5303 | 4:2 | 1.14 | 0.99 | 0.87 |  |  |
|  | " | MNA V7531 | 4:2 | 1.23 | 0.94 | 0.76 |  |  |
|  | " | UMNH VP7643 | 4:2 | 1.10 | 0.98 | 0.89 |  |  |
|  | " | OMNH 20518 | 4:2 | 1.20 | 0.98 | 0.79 |  |  |
|  | " | OMNH 22868 | 3?:2 | 1.27 | 1.10 | 0.80 |  |  |
|  | " | means | 3-4:2 | 1.17 | 1.00 | 0.84 |  |  |
|  | M. hensleighi | Lillegraven, 1969 | 3:2 | 0.95-1.10 | 0.80-0.90 | 0.83 |  |  |
|  | " | Archibald, 1982 | 3-4:2 | 0.95-1.23 | 0.80-1.07 | 0.83-0.86 |  |  |
|  | M. formosa | Lillegraven, 1969 | 3-4:2 | 1.25-1.60 | 1.00-1.40 | 0.84 |  |  |
|  | " | Archibald, 1982 | 3:02 | 1.25-1.60 | 1.00-1.40 | 0.84-0.88 |  |  |
|  | M. sp. large | MNA V5267 | 4:2 | 1.64 | 1.33 | 0.81 |  |  |
|  | M. thompsoni | Lillegraven, 1969 | 3-4:2 | 1.90-2.00 | 1.50-1.60 | 0.80 |  |  |
|  | " | Archibald, 1982 | 4?:2 | 1.75-2.15 | 1.35-1.60 | 0.77-0.80 |  |  |
|  | M. garfieldensis | Archibald, 1982 | 3-4:2 | 1.81 | 1.64 | 0.91 |  |  |
|  | M. primaeva | Sahni, 1972 | 4:2 | 2.4 | 1.7 e | 0.8 e |  |  |

Table 3. Comparison of measurements, ratios, and cusp formulae of upper molars of Kaiparowits Formation species of Mesodma to other species. Boldface specimen numbers indicate specimens described in this paper; "e" indicates measurements estimated from a depicted specimen; "?" indicates uncertain value.

| Tooth | Taxon | Source | Formula | AP | LB | LB:AP |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| M1 | M. archibaldi | MNA V7524 | 5:6:4 | 2.41 | 1.26 | 0.53 |  |  |
|  | " | OMNH 20511 | 5:6:4 | 2.42 | 1.24 | 0.51 |  |  |
|  | " | OMNH 24039 | 5:6:4 | 2.64 | 1.27 | 0.48 |  |  |
|  | " | means | 5:6:4 | 2.49 | 1.26 | 0.51 |  |  |
|  | Mesodma sp. | Montellano, 1992 | 5-6:6-7:3-5 | 2.30-2.81 | 1.17-1.41 | 0.52 |  |  |
|  | M. cf. archibaldi | MNA V5291 | 5:6:5 | 2.21 | 1.39 | 0.63 |  |  |
|  | Mesodma sp. | Lillegr. \& M.,1986 | 5:6:3-5 | 2.36-2.43 | 1.41-1.44 | 0.59-0.61 |  |  |
|  | ?Mesodma sp. | Fox, 1971 | 6:7:5 | 2.3 | 1.1 | 0.5 |  |  |
|  | M. primaeva | Sahni, 1972 | 6:7:5 | 4.0 e | 2.0 e | 0.5 e |  |  |
|  | M. minor | MNA V4503 |  | 2.22 | 1.22 | 0.55 |  |  |
|  | " | MNA V5294 |  |  | 1.08 |  |  |  |
|  | " | MNA V7525 | 6:6:4 | 1.90 | 1.05 | 0.55 |  |  |
|  | " | UMNH VP7635 | 5:6:5? | 1.90 | 1.05 | 0.55 |  |  |
|  | " | OMNH 20369 | 5:6:4 | 2.04 | 1.10 | 0.54 |  |  |
|  | " | OMNH 24045 | 4:6?:4 | 2.03 | 1.24 | 0.61 |  |  |
|  | " | means | 4-6:6:4-5? | 2.02 | 1.12 | 0.56 |  |  |
|  | M. hensleighi | Lillegraven, 1969 | 6-7:8-9:4-5 | 2.10-2.30 | 1.00-1.10 | 0.46 |  |  |
|  | " | Archibald, 1982 | 6:8:5 | 2.10-2.60 | 1.00-1.30 | 0.46-0.49 |  |  |
|  | M. formosa | Lillegraven, 1969 | 8-9:9:6-7 | 3.10-3.15 | 1.25-1.40 | 0.44 |  |  |
|  | " | Archibald, 1982 |  | 2.53-3.25 | 1.21-1.45 | 0.44-0.46 |  |  |
|  | M. thompsoni | Archibald, 1982 | 7-8:9:4-6 | 3.15-3.70 | 1.35-3.70 | 0.44-0.49 |  |  |
|  | M. garfieldensis | Archibald, 1982 | 6-8:8-11:4-5 | 3.09-3.65 | 1.31-1.65 | 0.45 |  |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | M2:M1 | M2:m2 |
| M2 | M. minor | MNA V7529 | Ri:3:3 | 1.25 | 1.13 | 0.95 |  |  |
|  | " | OMNH 20011 | Ri:3:3 | 1.30 | 1.16 | 0.89 |  |  |
|  | " | OMNH 20364 | Ri:3:3 | 1.26 | 1.14 | 0.91 |  |  |
|  | " | OMNH 22296 | Ri:3:3 | 1.18 | 1.10 | 0.93 |  |  |
|  | " | OMNH 22302 | Ri:3:3 | 1.15 | 1.13 | 0.98 |  |  |
|  | " | means | Ri:3:3 | 1.23 | 1.13 | 0.92 | 0.61 |  |
|  | M. hensleighi | Lillegraven, 1969 | 1:3:3 | 1.00-1.15 | 1.00-1.15 | 0.99 | 0.50 | 1.07 |
|  | " | Archibald, 1982 |  | 1.00-1.22 | 0.97-1.17 | 0.97-0.99 | 0.50-0.53 | 1.02-1.06 |
|  | M. formosa | Lillegraven, 1969 | 1:3:3 | 1.30-1.60 | 1.25-1.50 | 0.95 | 0.46 | 1.02 |
|  | " | Archibald, 1982 |  | 1.21-1.75 | 1.23-1.65 | 0.95-0.98 | 0.46-0.56 | 1.02-1.12 |
|  | M. sp. (large) | OMNH 24041 | 2:3:4 | 1.65 | 1.63 | 0.99 |  | 1.01 |
|  | M. thompsoni | Lillegraven, 1969 | 1:3:3-4 | 1.85-1.90 | 1.65-1.80 | 0.92 |  | 0.96 |
|  | " | Archibald, 1982 |  | 1.85-2.15 | 1.60-1.80 | 0.85-0.92 | 0.61 | 0.96-1.14 |
|  | M. garfieldensis | Archibald, 1982 | 1:3:4 | 2.00 | 1.79 | 0.90 | 0.63 | 1.11 |
|  | M. primaeva | Sahni, 1972 | 1:3:4 | 2.1 | 1.6 | 0.8 | 0.5 | 0.9 |
|  | " | Montellano, 1992 | 1:3:4 | 2.24-2.36 | 1.86-1.95 | 0.83 |  |  |
|  | Mesodma sp. | Montellano, 1992 | 1:3:3-4 | 1.31-1.69 | 0.94-1.40 | 0.86 | 0.63 |  |

Table 4. Comparison of measurements, ratios, and cusp formulae of upper teeth of Kaiparowits Formation species of Cimolodon to other species Boldface specimen numbers indicate specimens described in this paper; "*" indicates a damaged specimen; "e" indicates measurement estimated from a depicted specimen; "?" indicates uncertain value; "!" indicates an unusual value.

| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | PL:AP | H:AP |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| P4 | C. foxi | UMNH VP7630 | 4:5 | 3.18 | 1.48 | 0.47 | 0.31 | 0.46* |
|  | " | MNA V5270 | 4:5 | 2.99 | 1.42 | 0.48 | 0.35 | 0.41* |
|  | " | MNA V5302 | 4:6 | 2.98 | 1.32 | 0.44 | 0.34 | 0.44 |
|  | " | MNA V5339 | 4:6 | 3.22 | 1.65 | 0.51 | 0.41* | 0.41* |
|  | " | means | 4:5-6 | 3.09 | 1.47 | 0.48 | 0.35 | 0.43 |
|  | C. cf. nitidus | MNA V5337 | 3:7 | 3.88 | 2.07 | 0.53 | 0.31 | 0.44 |
|  | C. nitidus | Clemens, 1964 | 3-6:5-8 | 3.7-5.3 | 1.75-2.6 | 0.48 | 0.7 e |  |
|  | " | Lillegraven, 1969 | 3-4:5-7 | 4.35-5.00 | 1.85-2.70 | 0.50 | 0.5 e | 0.5 e |
|  | " | Archibald, 1982 | 3-4:5-?7 | 3.40-4.56 | 2.20-2.87 | 0.63 | 0.4 e | 0.34e |
|  | C. similis | Fox, 1971 | 1:8-9 | 4.1 | 1.8-1.9 | 0.45 |  |  |
|  | C. electus | Fox, 1971 | 1:7-9 | 4.3-4.5 | 1.8-2.0 | 0.43 | 0.3 e | 0.5 e |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | P4:M1 |  |
| M1 | C. foxi | MNA V4638 | ?:??4 |  | 1.62 |  |  |  |
|  | " | OMNH 24038 | 5:7:4 | 2.60 | 1.58 | 0.61 |  |  |
|  | " | OMNH 24040 | 5:7:6 | 2.66 |  |  |  |  |
|  | " | OMNH 24326 | 5:6:5 | 2.44 | 1.55 | 0.64 |  |  |
|  | " | means | 5-6:7:4-6 | 2.57 | 1.59 | 0.62 | 1.2 |  |
|  | C. cf. nitidus | OMNH 20477 | 6:7:5 | 5.13 | 2.60 | 0.49 | 0.76 ! |  |
|  | C. nitidus | Clemens, 1964 | 5-7:7-8:3-5 | 3.1-5.1 | 1.7-2.7 | 0.56 | 1.1 |  |
|  | " | Lillegraven, 1969 | 3-4:5-7 | 4.70-6.15 | 2.80-3.20 | 0.56 | 0.89 |  |
|  | " | Archibald, 1982 | 5-6:?7-8:?4-6 | 4.31-4.66 | 1.88-2.64 | 0.57 | 0.91 |  |
|  | C. electus | Fox, 1971 | 7:8:7 | 3.9-4.0 | 2.3-2.5 | 0.6 | 1.1 |  |
|  | C. similis | Fox, 1971 | 5:7:4-5 | 3.3-3.4 | 2.1 | 0.6 | 1.2 |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | M2:M1 |  |
| M2 | C. foxi | MNA V4635 | Ri:3:4? | 1.75 | 1.72 | 0.98 |  |  |
|  | " | OMNH 22316 | Ri:2:5 | 1.78 | 1.58 | 0.89 |  |  |
|  | " | OMNH 24043 | Ri:2:4? | 1.54 | 1.41 | 0.92 |  |  |
|  | " | OMNH 24044 | Ri:2:5 | 1.78 | 1.64 | 0.92 |  |  |
|  | " | means | Ri:2-3:4?-5 | 1.71 | 1.59 | 0.93 | 0.67 |  |
|  | C. cf. nitidus | OMNH 20477 | 3:3:2 | 2.98 | 2.62 | 0.95 | 0.58 |  |
|  | C. nitidus | Clemens, 1964 | 1-5:3-4:4-6 | 2.3-3.4 | 2.0-3.1 | 1.1 | 0.7 |  |
|  | " | Lillegraven, 1969 |  | 3.00-3.60 | 2.80-3.15 | 0.9 | 0.63 |  |
|  | " | Archibald, 1982 | 1-3:4:4-6 | 2.42-3.57 | 2.02-2.64 | 0.97 | 0.61 |  |
|  | C. electus | Fox, 1971 | 1-2:3:5-6 | 2.9-3.3 | 2.8-3.0 | 0.9 | 0.8 |  |
|  | C. similis | Fox, 1971 | 1:3:4-5 | 2.6-2.7 | 2.2-2.6 | 0.9 | 0.8 |  |

Table 5. Comparison of measurements, ratios, and cusp formulae for lower teeth of Kaiparowits Formation species of Cimolodon to other species. Boldface specimen numbers indicate specimens described in this paper; "*" indicates damaged specimen; "e" indicates measurement estimated from a depicted specimen; "?" indicates an uncertain value.

| Tooth | Taxon | Source | S:ER:IR | AP | H:AP | p4:m1 | AL:AP |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| p4 | C. foxi | OMNH 20483 | 12:10:9 | 3.70 | 0.61 |  | 0.40 |
|  | C. sp. cf. similis | OMNH 20347 | 12:9:9 | 4.30 | 0.55* |  | 0.51* |
|  | " | OMNH 20484 | 12:7:12 | 3.92 | 0.64 |  | 0.57* |
|  | " | OMNH 22313 | 11:9:10 | 4.30 | 0.56 |  | 0.46 |
|  | " | MNA V7532 | 12:8:9 | 4.26 | 0.57 |  | 0.55 |
|  | " | means | 11-12:7-9:9-12 | 4.20 | 0.58 |  | 0.52 |
|  | C. similis | Fox, 1971 | 12:9?:8? | 3.9-4.6 | 0.6 e | 1.4 | 0.5 e |
|  | C. electus | Fox, 1971 | 15:9?:9? | 5.8-6.2 | 0.6 e | 1.8 |  |
|  | C. nitidus | Clemens, 1964 | 12-14:??? | 5.0-7.1 |  | 1.5 | 0.52 e |
|  | " | Lillegraven, 1969 |  | 6.00-6.88 | 0.6 e |  |  |
|  | " | Archibald, 1982 | 12-14:?:? | 5.11-6.30 | 0.55-0.60 | 1.28 |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP |  |
| m 2 | C. foxi | OMNH 20005 | 4:2 | 1.94 | 1.64 | 0.85 |  |
|  | " | OMNH 20492 | ?4:2 | 1.64 | 1.5 | 0.92 |  |
|  | C. foxi? | MNA V7540 | 3?:2 | 1.75 | 1.48 | 0.85 |  |
|  | C. similis | Fox, 1971 | 4:2 | 2.3 | 2 | 0.9 |  |
|  | C. electus | Fox, 1971 | 4-6:2-3 | 2.5-3.2 | 2.2-2.5 | 0.8 |  |
|  | C. nitidus | Clemens, 1964 | 4-6:2 | 2.3-3.5 | 1.7-2.6 | 0.7 |  |
|  | " | Lillegraven, 1969 |  | 3.10-3.80 | 2.20-2.85 | 0.74 |  |
|  | " | Archibald, 1982 | 4:2 | 2.49-3.11 | 1.74-2.38 | 0.75 |  |

Table 6. Comparison of measurements, ratios, and cusp formulae of molars of Kaiparomys cifellii from the Kaiparowits Formation to selected species of Mesodma and Cimolodon. Boldface specimen numbers indicate specimens described in this paper.

| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | m2:m1 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| m1 | Kaiparomys cifellii | UCM 50420 | 7:4 | 3.04 | 1.48 | 0.49 | 0.65 |
|  | Mesodma thompsoni | Lillegraven, 1969 | 7:4 | 2.85 | 1.25 | 0.44 | 0.68 |
|  | " | Archibald, 1982 | 6-7:4-5 | 2.65-2.90 | 1.05-1.30 | 0.44 | 0.75 |
|  | Cimolodon similis | Fox, 1971 | 6-7:4 | 3.0-3.2 | 1.6-1.8 | 0.6 | 0.7 |
|  | C. nitidus | Lillegraven, 1969 |  | 4.70-5.05 | 2.10-2.40 | 0.45 | 0.71 |
|  | " | Archibald, 1982 | 6-7:4 | 4.48-4.53 | 1.97-2.11 | 0.45 | 0.63 |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP |  |
| m2 | Kaiparomys cifellii | UCM 50420 | 4:2 | 1.96 | 1.66 | 0.85 |  |
|  | " | UCM 50384 | 5:2 | 2.00 | 1.57 | 0.79 |  |
|  | " | OMNH 22842 | 4:2 | 1.80* | 1.53 | 0.85 |  |
|  | " | MNA V5264 | 4:2 | 1.82 | 1.48 | 0.81 |  |
|  | " | means | 4-5:2 | 1.87 | 1.53 | 0.82 |  |
|  | Mesodma thompsoni | Lillegraven, 1969 | 3-4:2 | 1.90-2.00 | 1.50-1.60 | 0.80 |  |
|  | " | Archibald, 1982 | 4?:2 | 1.75-2.15 | 1.35-1.60 | 0.77-0.80 |  |
|  | Cimolodon similis | Fox, 1971 | 4:2 | 2.3 | 2 | 0.90 |  |
|  | C. nitidus | Lillegraven, 1969 |  | 3.10-3.80 | 2.20-2.85 | 0.74 |  |
|  | " | Archibald, 1982 | 4:2 | 2.49-3.11 | 1.74-2.38 | 0.76 |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP |  |
| M2 | Kaiparomys cifellii | MNA V7530 | Ri:3:4 | 1.75 | 1.60 | 0.91 |  |
|  | " | OMNH 20362 | 3:3:3 | 1.55 | 1.52 | 0.98 |  |
|  | " | OMNH 22325 | 4:3:3 | 1.62 | 1.61 | 0.99 |  |
|  | " | means | R-3-4:3:3-4 | 1.63 | 1.58 | 0.96 |  |
|  | Mesodma thompsoni | Lillegraven, 1969 | 1:3:3-4 | 1.85-1.90 | 1.65-1.80 | 0.92 |  |
|  | " | Archibald, 1982 | 1:3:4 | 1.85-2.15 | 1.60-1.80 | 0.85-0.92 |  |
|  | Cimolodon similis | Fox, 1971 | 1:3:3-4 | 2.6-2.7 | 2.2-2.6 | 0.9 |  |
|  | C. nitidus | Lillegraven, 1969 |  | 3.00-3.60 | 2.80-3.15 | 0.90 |  |
|  | " | Archibald, 1982 | 1-3:4:4-6 | 2.42-3.57 | 2.02-2.70 | 0.82 |  |

Table 7. Comparison of measurements, ratios, and cusp formulae of first molars of Kaiparowits Formation species of Meniscoessus to other species. Boldface specimen numbers indicate specimens described in this paper; "e" indicates measurements estimated from a depicted specimen; "?" indicates uncertain value.

| Tooth | Taxon | Source | Formula | AP | LB | LB:AP |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| m1 | M. cf. intermedius | OMNH 20507 | $6: 4$ | 4.67 | 2.12 | 0.45 |
|  | M. intermedius | Fox, 1976 | $7: 4$ | 5.3 e | 2.1 e | 0.4 e |
|  | M. major | Sahni, 1972 | $8: 6$ | 5.1 e | 2.5 e | 0.5 e |
|  | M. major | Fox, 1980 | $7: 5$ | $6.0-6.5$ | $2.5-4.0$ | 0.5 |
| M1 | M. robustus | Clemens, 1964 | $5: 4$ | $7.1-9.8$ | $3.3-4.7$ | 0.5 |
|  | M. cf. intermedius | OMNH 20481 | $?: ?: 6 ?$ |  | 2.88 |  |

Table 8. Comparison of measurements, ratios, and cusp formulae of teeth of Kaiparowits Formation species of Cimolomys and ?Cimolomys to other species. Boldface specimen numbers indicate specimens described in this paper, "e" indicates measurements estimated from a depicted specimen; "?" indicates uncertain value.

| Tooth | Taxon | Source | Formula | AP | LB | LB:AP |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| m1 | ?C. butleria | OMNH 22837 | 6:4 | 2.85 | 1.42 | 0.50 |  |  |
|  | ?Cimolomys sp. A | Fox, 1971 | 6:4 | 3.9-4.1 | 2.0-2.3 | 0.5 |  |  |
|  | C. clarki | Lillegraven \& M., 1986 | 6-7:4 | 4.24-4.35 | 1.76-2.22 | 0.46 |  |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | H:AP | PL:AL |
| P4 | C. sp. B cf. clarki | MNA V4586 | 1:5 | 4.28 | 2.06 | 0.48 | 0.51 | 0.53 |
|  | " | MNA V7526 | 1:5 | 4.12 | 2.1 | 0.51 | 0.54 | 0.52 |
|  | C. "clarki" | Sahni, 1972 | 2:5-6 | 4.0 | 1.5 e | 0.4 e |  | 0.63 |
|  | " | Lillegraven \& M., 1986 | 3:6 | 3.99 | 1.56 | 0.39 | 0.53 e | 0.38 |
|  | ?Cimolomys sp. A | Fox, 1971 | 1:5 | 4.2 | 1.7 | 0.4 | 0.58 e | 0.47 |
|  | C. gracilis | Clemens, 1964 | 1-2:5-6 | 2.9-3.1 | 1.3-1.4 | 0.4 |  | 0.67 |
|  | " | Archibald, 1982 | 1-2:5-6 | 2.68-2.88 | 1.46-1.50 | 0.53 | 0.42 e | 0.38 |
|  | ?C. butleria | MNA V5341 | 1:5 | 2.63 | 1.23 | 0.47 | 0.48 | 0.34 |
|  | " | OMNH 20010 | 1:5 | 2.67 | 1.00 | 0.38 | 0.49 | 0.33 |
|  | " | OMNH 22306 | 1:5 | 2.70 | 1.20 | 0.44 | 0.44 | 0.30 |
|  | " | means | 1:5 | 2.67 | 1.14 | 0.43 | 0.47 | 0.32 |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | P4:M1 |  |
| M1 | ?C. butleria | MNA V5226 | 4:6:5? | 3.13 | 1.87 | 0.60 | 0.85 |  |
|  | C. sp. A cf. clarki | OMNH 24037 | 5:6:7 | 3.22 | 2.01 | 0.62 |  |  |
|  | C. sp. B. cf. clarki | OMNH 24327 |  |  | 1.88 |  |  |  |
|  | C. clarki | Sahni, 1972 | 5:6:6 | 3.5 e | 2.0 e | 0.6 e | 1.1e? |  |
|  | " | Lillegraven \& M., 1986 | 7:7:5 | 4.20-4.36 | 2.34-2.73 | 0.59 | 0.94 ? |  |
|  | C. trochuus | Lillegraven, 1969 | 5:6:7 | 4.70-4.80 | 2.90 | 0.62 |  |  |
|  | C. gracilis | Clemens, 1964 | 5-8:7-10:4-6 | 4.3-6.0 | 2.1-3.1 | 0.7 | 0.6 |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | M2:M1 |  |
| M2 | C. sp. A cf. clarki | OMNH 24324 | 3:3:4 | 2.24 | 2.26 | 1.01 | 0.70 |  |
|  | C. clarki | Sahni, 1972 | 2:3:4 | 2.7 e | 2.7 e | 1.0 e | 0.8 e |  |
|  | " | Lillegraven \& M., 1986 | 1:3:3-4 | 2.74-3.30 | 2.60-2.90 | 0.93 | 0.71 |  |
|  | C. gracilis | Clemens, 1964 | 2-3:3-4:4-7 | 3.1-3.8 | 2.7-3.0 | 0.8 | 0.7 |  |
|  | " | Archibald, 1982 | 2:3:4 | 3.38-3.73 | 2.95-3.25 | 0.87 |  |  |

Table 9. Comparison of measurements, ratios, and cusp formulae of fourth premolars of Kaiparowits Formation species of Cimexomys to other species. Boldface specimen numbers indicate specimens described in this paper; "e" indicates estimates made from a depicted specimen; "?" indicates uncertain value.

| Tooth | Taxon | Source | S:ER:IR | AP | H:AP | AL:AP |  |  | p4:m1 |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| p4 | C. cf. judithae | MNA V5312 | 9:8:7 | 3.10 | 0.50 | 0.47 |  |  |  |  |
|  | " | OMNH 22315 | 10:6:7 | 3.02 | 0.51 | 0.46 |  |  |  |  |
|  | " | means | 9-10:6-8:7 | 3.06 | 0.51 | 0.47 |  |  |  |  |
|  | C. judithae | Sahni, 1972 | 9:?:? | 3.0 |  |  |  |  |  |  |
|  | " | Montellano, 1992 | 9:6:5 | 3.18 | 0.51 e | 0.46 |  |  |  |  |
|  | C. minor | Archibald, 1982 | 8-9:6:6 | 2.66-2.74 | 0.59 | 0.52 |  |  | 1.08 |  |
|  | " | Lofgren, 1995 |  | 2.70-2.77 |  |  |  |  | 1.06 |  |
|  | C. gratus | Archibald, 1982 | 9-10?:6:6 | 3.72-4.26 | 0.52 | 0.54 |  |  | 1.19 |  |
|  | " | Lofgren, 1995 |  | 3.56-4.24 |  |  |  |  | 1.16-1.24 |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | H:AP | PL:AP | P4:M1 | P4:p4 |
| P4 | C. cf. judithae | MNA V4639 | 2:5 | 2.34 | 1.11 | 0.47 | 0.44 | 0.36 |  |  |
|  | " | OMNH 20190 | 4:6 | 2.25 | 1.03 | 0.46 | 0.41 | 0.36 |  |  |
|  | " | means | 2-4:5-6 | 2.30 | 1.07 | 0.47 | 0.43 | 0.36 |  | 0.75 |
|  | C. antiquus | Fox, 1971 | 2:5 | 2.1-2.2 | 0.7-1.0 | 0.4 | 0.52e | 0.43 | 0.9 |  |
|  | C. judithae | Sahni, 1972 | 3:5 | 2.4 |  |  | 0.4 e |  | 1.0 | 0.8 |
|  | " | Montellano, 1992 | 2:5 | 2.15 | 1.00 | 0.47 | 0.47e | 0.37e | 0.90 |  |
|  | " | Montel. et al., 2000 | 3:5 | 2.21 | 0.63 | 0.29 | 0.56e | 0.42e | 0.97 | 0.7 |
|  | C. minor | Archibald, 1982 | 3:5 | 2.30-2.32 | 1.22-1.26 | 0.54 | 0.52e | 0.39e | 0.94 | 0.87 |
|  | " | Lofgren, 1995 | 3:5 | 2.09-2.25 | 1.13-1.25 | 0.55 |  |  | 0.87 | 0.80 |
|  | C. gratus | Archibald, 1982 | 3-4:5-6 | 3.05-3.44 | 1.65-1.73 | 0.52 | 0.41e | 0.35 e | 0.97 | 0.80 |
|  | ${ }^{\prime}$ | Lofgren, 1995 | 3-4:5-6 | 2.77-3.38 | 1.31-1.91 | 0.53-0.55 |  |  | 0.93-0.96 | 0.77-0.81 |

Table 10. Comparison of measurements, ratios, and cusp formulae of m 1 s and M2s of Cimexomys or Mesodma sp. from the Kaiparowits Formation to species of Cimexomys. Boldface specimen numbers indicate specimens described here; "*" indicates a damaged specimen; "?" indicates an uncertain value.

| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | M1:M2 |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| m1 | Cimexomys or Mesodma sp. | UMNH VP5604 | $6: 4$ | 2.37 | 1.13 | 0.48 |  |
|  | $"$ | UMNH VP5611 | $7: 4$ | 2.55 | 1.16 | 0.46 |  |
|  | $"$ | UMNH VP7640 | $7: 4$ | 2.17 | 1.09 | 0.5 |  |
|  | $"$ | MNA V5269 | $6: 4$ | 2.31 | 1.18 | 0.51 |  |
|  | $"$ | OMNH 20006 | $6: 4$ | 2.26 | 1.08 | $0.48^{*}$ |  |
|  | $"$ | OMNH 20359 | $6: 4$ | 2.37 | 1.18 | 0.50 |  |
|  | $"$ | OMNH 20494 | $6: 4$ | 2.21 | 1.10 | 0.50 |  |
|  | $"$ | OMNH 22314 | $6: 4$ | 2.37 | 1.25 | 0.53 |  |
|  | $"$ | OMNH 22847 | $6: 4$ | 2.17 | 1.18 | 0.54 |  |
|  | $"$ | OMNH 24053 | $7: 4$ | 2.38 | 1.19 | 0.50 |  |
|  | " | OMNH 24055 | $6: 4$ | 2.22 | 1.14 | 0.51 |  |
|  | " | means | $6-7: 4$ | 2.31 | 1.15 | 0.50 |  |
|  | Cimexomys gratus | Lofgren, 1995 |  | $2.94-3.99$ | $1.37-1.97$ | 0.47 |  |
|  | C. gratus | Archibald, 1982 | $6-7: 4$ | $3.35-3.58$ | $1.46-1.62$ | 0.46 |  |
|  | C. antiquus | Fox, 1971 | $6: 4-5$ | $2.1-2.2$ | 1.1 | 0.51 |  |
|  | C. judithae | Montellano et al., 2000 | $6: 4$ | 1.97 | 0.88 | 0.45 | 0.62 |
|  | Oimexomys judithae | Montellano et al., 2000 | $1: 3: 3$ | $1.30-1.59$ | $1.34-1.35$ | $0.96-1.03$ |  |
|  | Cimexomys or Mesodma sp. | OMNH 20343 | Ri:3:4? | 1.72 | 1.59 | 0.92 | 1.55 |

Table 11. Comparison of measurements, ratios, and cusp formulae of m 1 s of Cedaromys hutchisoni from the Kaiparowits Formation to m 1 s of Eobaatar, Dakotamys, Paracimexomys, Janumys, Bryceomys, and other species of Cedaromys. Boldface specimen numbers indicate specimens described in this paper; "*" indicates a damaged specimen; "!" indicates an unusual value.

| Taxon | Source | Formula | AP | LB | LB:AP | p4:m1 | m2:m1 | M1:m1 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Eobaatar magnus | Kielan-J. et al., 1987 | 4:2? | 1.6-1.8 | 1.1 | 0.7 | 1.94 | 1.0 | 1.1 |
| Cedaromys hutchisoni | MNA V4657 | 4:3 | 1.82 | 1.16 | 0.64 |  |  |  |
| " | MNA V5260 | 4:3 | 1.80 | 1.17 | 0.65 |  |  |  |
| " | MNA V5266 | 4:3 | 1.75 | 1.08 | 0.62 |  |  |  |
| " | MNA V5306 | 4:3 | 1.70 | 1.07 | 0.63 |  |  |  |
| " | MNA V7535 | 4:3 | 1.82 | 1.17 | 0.64 |  |  |  |
| " | MNA V7537 | 5:3 | 1.95 | 1.25 | 0.64 |  |  |  |
| " | OMNH 20008 | 5:3 | 2.06 | 1.27 | 0.62 |  |  |  |
| " | OMNH 20350 | 4:3 | 1.90 | 1.23 | 0.65 |  |  |  |
| " | OMNH 22318 | 4:3 | 2.06 | 1.34 | 0.65 |  |  |  |
| " | UMNH VP5608 | 4:3 | 1.84 | 1.23 | 0.67 |  |  |  |
| " | UMNH VP7631 | 4:3 | 2.10 | 1.34 | 0.64 |  |  |  |
| " | means | 4-5:3 | 1.89 | 1.21 | 0.64 |  |  | 1.01 |
| Cedaromys parvus | Eaton \& Cifelli, 2001 | 4:3 | 2.02-2.28 | 1.32-1.43 | 0.68 | 1.78 | 0.93 | 1.13 |
| Cedaromys bestia | Eaton \& Cifelli, 2001 | 4:3 | 2.42-2.64 | 1.51-1.69 | 0.64 | 1.68 | 0.94 | 1.03 |
| Bryceomys fumosus | Eaton, 1995 | 4:3 | 1.32-1.88 | 0.81-1.18 | 0.61 | 1.79 | 0.79 | 1.12 |
| B. hadrosus | Eaton, 1995 | 5:3 | 2.64-2.71 | 1.60-1.61 | 0.61 |  | 0.79 | 1.01 |
| B. intermedius | Eaton \& Cifelli, 2001 | 4:3 | 1.79-1.93 | 1.10-1.25 | 0.62 | 1.51 | 0.71 | 1.12 |
| Dakotamys malcolmi | Eaton, 1995 | 4:3 | 1.82-2.02 | 1.03-1.23 | 0.58 | 1.38 | 0.86 | 1.04 |
| Janumys erebos | Eaton \& Cifelli, 2001 | 4:3 | 1.14-1.46 | 0.66-0.84 | 0.60 |  | 0.97 | 1.13 |
| Paracimexomys priscus | Lillegraven, 1969 | 4:3 | 2.60 | 1.60 | 0.61 | 1.46 | 0.92 | 1.23 |
| " | Archibald, 1982 | 4:3 | 2.06*-2.31 | 1.30-1.41 | 0.61 |  | 0.93 | 1.08 |
| cf. P. robisoni | Eaton \& Nelson, 1991 | 4:3 | 2.0-2.1 | 1.2-1.3 | 0.6 |  | 0.78 ! | 1.07 |

Table 12. Comparison of measurements, ratios, and cusp formulae of M1s of Kaiparowits Formation species of Cedaromys and Dakotamys to M1s of species of Eobaatar, Janumys, Paracimexomys, Bryceomys, and other species of Cedaromys and Dakotamys. Boldface specimen numbers indicate specimens described in this paper; "e" indicates measurement estimated from a depicted specimen; "?" indicates uncertain value.

| Taxon | Source | Formula | AP | LB | LB:AP | M2:M1 | P4:M1 | M1:m1 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Eobaatar magnus | Kielan-J. et al., 1987 | 3:4:1 | 1.7-1.9 | 1.0-1.3 | 0.64 | 0.9 | 0.9 | 1.1 |
| Janumys erebos | Eaton \& Cifelli, 2001 | 3-4:4 | 1.33-1.52 | 0.65-0.85 | 0.54 |  | 1.15 | 1.13 |
| Paracimexomys priscus | Lillegraven, 1969 | 4:4:2 | 2.60 | 1.60 | 0.62 |  |  | 1.00 |
| " | Archibald, 1982 | 4:4:2 | 2.21-2.58 | 1.34-1.60 | 0.60 | 0.89 |  | 1.08 |
| " | Lillegraven \& M., 1986 | 4:4:1 | 2.24 | 1.40 | 0.63 |  |  |  |
| " | Montellano, 1992 | 4:4:2 | 2.4 | 1.86 | 0.78 e |  |  |  |
| P. robisoni | Eaton \& Nelson, 1991 | 4:4:1 | 2.1-2.3 | 1.3 | 0.6 |  | 0.9 | 1.1 |
| Dakotamys malcolmi | Eaton, 1995 | 4:4:1-2 | 1.82-2.18 | 1.06-1.30 | 0.58 | 0.80 | 1.22 | 1.04 |
| Dakotamys magnus | MNA V5301 | 5:5:2 or 3 | 4.03 | 2.62 | 0.65 |  |  |  |
| ${ }^{\prime}$ | OMNH 20354 | 5:5:2 | 4.02* | 2.59 | 0.64* |  |  |  |
| Cedaromys bestia | Eaton \& Cifelli, 2001 | 3:4 | 2.52-2.64 | 1.55-1.63 | 0.62 | 0.93 | 1.04 | 1.03 |
| Cedaromys parvus | Eaton \& Cifelli, 2001 | 3:4 | 2.32 | 1.39-1.48 | 0.63 | 0.94 | 1.08 | 1.13 |
| Cedaromys hutchisoni | MNA V4583 | 3:4:1 |  |  |  |  |  |  |
| " | MNA V5274 | 3:4:1 | 1.77 | 1.19 | 0.67 |  |  |  |
| " | MNA V5288 | 3:4:1 |  |  |  |  |  |  |
| " | MNA V5316 | 3:4:0 | 1.90 |  |  |  |  |  |
| " | MNA V5340 | 4:4:1 | 1.80 | 1.17 | 0.65 |  |  |  |
| " | MNA V5342 | 3:4:1 | 2.15 | 1.35 | 0.63 |  |  |  |
| " | OMNH 20009 | 3:4:1 | 1.87 | 1.23 | 0.66 |  |  |  |
| " | OMNH 20340 | 3:4:1 | 2.03 | 1.28 | 0.63 |  |  |  |
| " | OMNH 22861 | 3:4:1 | 1.95 | 1.18 | 0.61 |  |  |  |
| " | OMNH 22295 | 3:4:0 | 1.65 | 1.07 | 0.65 |  |  |  |
| " | OMNH 22834 | 3:4:0 | 1.95 | 1.31 | 0.67 |  |  |  |
| " | OMNH 24054 | 3?:4:1 | 2.07 | 1.30 | 0.63 |  |  |  |
| ${ }^{\prime}$ | means | 3-4:4:0-1 | 1.91 | 1.23 | 0.64 |  |  |  |
| Bryceomys fumosus | Eaton, 1995 | 3-5:4:2-3 | 1.52-2.10 | 1.05-1.39 | 0.68 | 0.77 | 1.20 | 1.12 |
| B. hadrosus | Eaton, 1995 | 3-5:4:2-3 | 2.68 | 1.63-1.87 | 0.65 | 0.83 |  | 1.01 |
| B. intermedius | Eaton \& Cifelli, 2001 | 3-4:4:2-3 | 2.10 | 1.43 | 0.68 | 0.64 | 1.09 | 1.12 |

Table 13. Comparison of measurements, ratios, and cusp formulae of $\mathrm{m} 1 \mathrm{~s}, \mathrm{~m} 2 \mathrm{~s}, \mathrm{P} 4 \mathrm{~s}$, and M2s of Wahweap Formation species of Mesodma to other species. Boldface specimen numbers indicate specimens described in this paper; "e" indicates measurement estimated from a depicted specimen; "?" indicates an uncertain value.

| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | m2:m1 |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| m1 | Mesodma sp. cf. M. formosa | UMNH VP7989 | 6:5 | 2.27 | 1.26 | 0.56 |  |  |
|  | M. formosa | Lillegraven, 1969 | 6-7:4-5 | 2.10-2.50 | 1.00-1.40 | 0.47 | 0.61 |  |
|  | M. formosa | Archibald, 1982 |  | 2.05-2.55 | 0.90-1.35 |  | 0.58-0.61 |  |
|  | M. garfieldensis | Archibald, 1982 | 6-7:4-5 | 2.27-2.76 | 0.88-1.22 | 0.44 | 0.56 |  |
| m2 | M. sp. cf. M. formosa | MNA V4571 | 4:2 | 1.29 | 1.08 | 0.84 |  |  |
|  | " | MNA V5241 | $4: 2$ | 1.47 | 1.21 | 0.83 |  |  |
|  | " | OMNH 23340 | 4:2 | 1.29 | 1.12 | 0.87 |  |  |
|  | " | means | 4:2 | 1.35 | 1.14 | 0.84 | 0.59 |  |
|  | M. formosa | Lillegraven, 1969 |  | 1.25-1.60 | 1.00-1.40 | 0.84 | 0.61 |  |
|  | M. garfieldensis | Archibald, 1982 | 3-4:2 | 1.22-1.66 | 1.03-1.39 | 0.84 | 0.56 |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | H:AP | PL:AP |
| P4 | Mesodma sp. cf. M. formosa | MNA V5254 | 2:5 | 2.22 | 1.13 | 0.51 | 0.49 | 0.39 |
|  | M. formosa | Clemens, 1964 | 1-4:5-7 | 1.90-2.80 | 0.85-1.20 |  |  |  |
|  | " | Lillegraven, 1969 |  | 2.05 | 0.80-1.25 | 0.49 | 0.48 e | 0.31 e |
|  | M. garfieldensis | Archibald, 1982 | 1-4:7-8 | 2.42-3.23 | 1.63-2.27 | 0.5 | 0.4-0.5e | 0.32-0.35e |
| M2 | Mesodma sp. cf. M. formosa | MNA V5244 | Ri:3:3? | 1.40 | 1.27 | 0.91 |  |  |
|  | " | MNA V5250 | Ri:3:4 | 1.41 | 1.35 | 0.96 |  |  |
|  | " | OMNH 20782 | Ri:3:4 | 1.45 | 1.38 | 0.95 |  |  |
|  | " | means | Ri:3:3?-4 | 1.42 | 1.33 | 0.94 |  |  |
|  | M. formosa | Lillegraven, 1969 |  | 1.30-1.60 | 1.25-1.50 | 0.95 |  |  |
|  | M. garfieldensis | Archibald, 1982 | 1:3:4 | 1.28-1.60 | 1.32-1.57 | 0.97 |  |  |

Table 14. Comparison of measurements, ratios, and cusp formulae of teeth of Wahweap Formation species of Cimolodon to other species of Cimolodon and Cimexomys (for p 4 ). Boldface specimen numbers indicate specimens described in this paper, "*" indicates a damaged specimen; "e" indicates measurement estimated from a depicted specimen; "?" indicates an uncertain value.

| Tooth | Taxon | Source | S:ER:IR | AP | H:AP | AL:AP |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| p4 | Cimolodon similis | UMNH VP7592 | 11:8:10 | 3.46 | 0.63 | 0.52 |  |  |  |
|  | " | Fox, 1971 | 12:8?:9: | 3.9-4.6 | 0.6e | 0.5 e |  |  |  |
|  | C. sp. cf. C. nitidus | UMNH VP7978 | 11:9:10 | 5.19 | 0.61 | 0.51 |  |  |  |
|  | " | UMNH VP7988 | 11:9:10 | 5.18 | 0.60 | 0.47 |  |  |  |
|  | C. nitidus | Archibald. 1982 | 12-14:?:? | 5.11-6.30 | 0.55-0.60 |  |  |  |  |
|  | C. sp. (small) | MNA V4525 | 10:6:6 | 2.99 | 0.65 | 0.48 |  |  |  |
|  | C. foxi | this paper | 12:10:9 | 3.70 | 0.61 | 0.4 |  |  |  |
|  | Cimexomys judithae | Montellano, 1992 | 9:?:? | 3.18 | 0.51 e | 0.46 e |  |  |  |
|  | " | Mont. et al., 2000 | 9:7:7 | 3.18 | 0.43 e | 0.56e |  |  |  |
|  | Cimexomys gratus | Archibald, 1982 | 9-10:6-5:5-6 | 3.72-4.26 | 0.52 |  |  |  |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP |  |  |  |
| m1 | Cimolodon electus | MNA V4613 | 7:4 | 3.52 | 1.95 | 0.55 |  |  |  |
|  | " | UMNH VP7562 | 6:4 | 3.76 | 1.89 | 0.50 |  |  |  |
|  | " | Fox, 1971 | 6-8:4 | 3.3-3.5 | 1.7-2.2 | 0.57 |  |  |  |
|  | Cimolodon similis | MNA V5245 | 6:4 | 3.20 | 1.72 | 0.54 |  |  |  |
|  | " | UMNH VP7980 | 6:4 | 2.80 | 1.56 | 0.56 |  |  |  |
|  | " | UMNH VP7987 | 6:3 | 2.72 | 1.54 | 0.57 |  |  |  |
|  | " | UMNH VP7989 | ?:4 | 2.84 |  |  |  |  |  |
|  | " | Fox, 1971 | 6-7:4 | 3.0-3.2 | 1.6-1.7 | 0.55 |  |  |  |
| m 2 | Cimolodon electus | MNA V5200 | 5:2 | 2.60 | 2.38 | 0.92 |  |  |  |
|  | " | MNA V5273 | 5:2 | 2.56 | 2.12* |  |  |  |  |
|  | Cimolodon electus | Fox, 1971 | 2-3:4-6 | 2.5-3.2 | 2.2-2.5 | 0.8 |  |  |  |
|  | Cimolodon similis | UMNH VP7990 | 4:2 | 2.20 | 1.93 | 0.88 |  |  |  |
|  | " | Fox, 1971 | 4:2 | 2.3 | 2.0 | 0.87 |  |  |  |
|  | Cimolomys clarki | Lill. \& McK., 1986 | 5:2 | 2.92 | 2.11 | 0.72 |  |  |  |
|  | Cimolomys gracilis | Clemens, 1964 | 4-6:2-3 | 3.2-4.2 | 2.1-2.9 | 0.6-0.7 |  |  |  |
|  | Cimolodon sp. (small) | MNA V4537 | 4:2 | 1.89 | 1.59 | 0.84 |  |  |  |
|  | Cimolodon foxi | this paper | 4:2 | 1.79 | 1.57 | 0.89 |  |  |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | PL:AP | H:AP | CR |
| P4 | Cimolodon similis | MNA V4595 | 1:8 | 3.93 | 1.72 | 0.44 | 0.28 | 0.45* |  |
|  | " | MNA V5217 | 2:6 | 3.62 | 1.75 | 0.48 | 0.30 | 0.53 | 0.27 |
|  | " | MNA V5221 | 2:7 | 3.71 |  |  | 0.32 | 0.44 | 0.32 |
|  | " | means | 1-2:6-8 | 3.75 | 1.74 | 0.46 | 0.30 | 0.49 | 0.30 |
|  | " | Fox, 1971 | 1:8-9 | 4.1 | 1.8-1.9 | 0.45 |  |  |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP |  |  |  |
| M1 | Cimolodon electus | MNA V5234 | 6:7:5 | 3.76 | 2.43 | 0.65 |  |  |  |
|  | " | Fox, 1971 | 7:8:7 | 3.9-4.0 | 2.3-2.5 | 0.61 |  |  |  |
|  | Cimolodon. similis | Fox, 1971 | 5:7:4 | 3.3-3.4 | 2.1 | 0.63 |  |  |  |
|  | C. sp. cf. C. nitidus | UMNH VP7981 | 6?:7:5? | 4.58 e | 2.61 e | 0.60e |  |  |  |
|  | Cimolodon nitidus | Clemens, 1964 | 5-7:7-8:3-5 | 3.1-5.1 | 1.7-2.7 | 0.56 |  |  |  |
|  | " | Lillegraven, 1969 | 6-7:7-8:6-8 | 4.70-6.15 | 2.80-3.20 | 0.56 |  |  |  |
|  | " | Archibald, 1982 | 5-6:?7-8:?4-6 | 4.31-4.66 | 1.88-2.64 | 0.57 |  |  |  |

Table 15. Comparison of measurements, ratios, and numbers of medial row cusps (P4) and internal row cusps (M1) of Meniscoessus sp. cf. M. intermedius from the Wahweap Formation to other species of Meniscoessus. Boldface specimen numbers indicate specimens described in this paper; "*" indicates a damaged specimen; "e" indicates a measurement estimated from a figured specimen.

| Tooth | Taxon | Source | Medial Cusps | AP | H:AP | PL:AP |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| P4 | M. sp. cf. M. intermedius | MNA V5287 | 5 | $2.11^{*}$ | $0.8^{*}$ | $0.48^{*}$ |
|  | Meniscoessus major | Sahni, 1972 | 4 or 5 | 3.3 e |  |  |
|  | Meniscoessus robustus | Archibald, 1982 | $3-4$ | $3.60-4.40$ |  |  |
|  | Meniscoessus ferox | Fox, 1971 | 4 | 4.5 |  |  |
| Tooth | Taxon | Source | Internal Cusps | LB |  |  |
| M1 | M. sp. cf. M. intermedius | MNA V5281 | 5 | 2.63 |  |  |
|  | Meniscoessus intermedius | Fox, 1976 | 5 | 3.2 |  |  |
|  | Meniscoessus major | Montellano, 1992 | 6 | $3.36-4.40$ |  |  |
|  | Meniscoessus robustus | Archibald, 1982 | $6-7$ | $4.77-5.71$ |  |  |

Table 16. Comparison of measurements, ratios, and cusp formulae of teeth of Wahweap Formation species of Cimolomys and ?Cimolomys to other species. Boldface specimen numbers indicate specimens described in this paper; "?" indicates an uncertain value; "*" indicates a damaged specimen; "e" indicates a measurement estimated from a figured specimen.

| Tooth | Taxon | Source | Formula | AP | LB | LB:AP |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| m1 | ?Cimolomys sp. A | MNA V5218 | 4:4 | 2.77 | 1.55 | 0.56 |  |  |  |
|  | ?Cimolomys butleria | this paper | 6:4 | 2.85 | 1.42 | 0.50 |  |  |  |
|  | ?Cimolomys sp. A | Fox, 1971 | 6:4 | 3.9-4.1 | 2.0-2.3 | 0.50 |  |  |  |
|  | Cimolomys clarki | Sahni, 1972 | 5-6:4 | 3.15?-3.6? |  |  |  |  |  |
|  | Cimolomys "clarki" | Lill. \& McK., 1986 | 6-7:4 | 4.24-4.35 | 1.76-2.22 | 0.46 |  |  |  |
|  | Cimolomys gracilis | Clemens, 1964 | 7-8:5-7 | 4.3-5.5 | 1.8-2.5 | 0.40 |  |  |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | H:AP | PL:AL | CR |
| P4 | C. sp. cf. C. trochuus | MNA V5326 | 1:5 | 3.85 | 1.71* | 0.44* | 0.55 | 0.34 | 0.58 |
|  | " | OMNH 23350 | 1:5 | 4.16 | 1.74 | 0.42 | 0.50* | 0.33* | 0.44* |
|  | " | means | 1:5 | 4 | 1.73 | 0.43 | 0.53 | 0.34 | 0.51 |
|  | ?Cimolomys sp. A | Fox, 1971 | 1:5 | 4.2 | 1.7 | 0.4 | 0.58 e | 0.47 |  |
|  | Cimolomys "clarki" | Sahni, 1972 | 2:5-6 | 4 | 1.5 e | 0.4 e |  | 0.63 |  |
|  | " | Lill. \& McK., 1986 | 3:6 | 3.99 | 1.56 | 0.39 | 0.53 | 0.38 |  |
|  | Cimolomys gracilis | Clemens, 1964 | 1-2:5-6 | 2.9-3.1 | 1.3-1.4 | 0.4 |  | 0.67 |  |
|  | " | Archibald, 1982 | 1-2:5-6 | 2.68-2.88 | 1.45-1.50 | 0.53 | 0.42 e | 0.38 |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP |  |  |  |
| M2 | ?Cimolomys sp. C (large) | MNA V4559 | Ri:3:4 | 3.16 | 3.08 | 0.98 |  |  |  |
|  | Cimolomys clarki | Lill. \& McK., 1986 | 1:3:3-4 | 2.74-3.30 | 2.60-2.90 | 0.93 |  |  |  |
|  | Cimolodon electus | Fox, 1971 | 1-5:3-4:4-6 | 2.9-3.3 | 2.8-3.0 | 0.9 |  |  |  |
|  | ?Cimolomys sp. B | MNA V4529 | 2?:3:4 | 2.58 | 2.47 | 0.96 |  |  |  |
|  | " | MNA V5206 | 1:3:4 | 2.33 | 2.48 | 1.06 |  |  |  |
|  | " | MNA V5320 | 1?:3:4 | 2.36 | 2.20 | 0.93 |  |  |  |
|  | " | OMNH 20956 | 3:3:4? | 2.64 | 2.37 | 0.90 |  |  |  |
|  | " | UMNH VP7595 | ? | 2.53 | 2.19 | 0.87 |  |  |  |
|  | " | means | 1-3:3:4? | 2.49 | 2.34 | 0.91 |  |  |  |
|  | Cimolodon similis | Fox, 1971 | 1:3:4 | 2.6-2.7 | 2.4-2.6 | 0.91 |  |  |  |

Table 17. Comparison of measurements, ratios, and cusp formulae of first molars of Wahweap Formation species of Cimexomys to other species. Boldface specimen numbers indicate specimens described in this paper; "?" indicates and uncertain value; "*" indicates a damaged specimen.

| Tooth | Taxon | Source | Formula | AP | LB | LB:AP |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| m1 | Cimexomys sp. cf. antiquus | MNA V5247 | $5: 4 ?$ | 1.72 | 0.92 | 0.54 |
|  | $"$ | MNA V5324 | $? 5: 4$ | 1.95 | 1.1 | 0.56 |
|  | Cimexomys antiquus | Fox, 1971 | $6: 4-5$ | $2.1-2.2$ | 1.1 | 0.51 |
|  | Cimexomys judithae | Montellano et al., 2000 | $6: 4$ | 1.97 | 0.88 | 0.45 |
|  | Cimexomys gratus | Archibald, 1982 | $6-7: 4$ | $3.35-3.58$ | $1.45-1.62$ | 0.46 |
| M1 | Cimexomys sp. cf. antiquus | MNA V5205 | $4: 6: 2 ?$ | $2.05^{*}$ | 1.29 | $0.63^{*}$ |
|  | Cimexomys antiquus | Fox, 1971 | $5: 6: 3-4$ | $2.2-2.6$ | $1.2-1.5$ | 0.56 |
|  | Cimexomys judithae | Montellano et al., 2000 | $5: 6: 1+$ | $2.29-2.39$ | $1.12-1.20$ | 0.50 |
|  | cf. Cimexomys sp. | Montellano, 1992 | $5-6: 5-7: 2$ | $1.95-2.20$ | $0.98-1.40$ | 0.53 |

Table 18. Comparison of measurements, ratios, and cusp formulae of molars of Wahweap Formation species of cf. Paracimexomys, Cedaromys, cf. Cedaromys, Bryceomys, and genus and species unknown to other species. Boldface specimen numbers indicate specimens described in this paper; "*" indicates damaged specimen.

| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | m2:m1 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| m1 | cf. Paracimexomys sp. A | MNA V4599 | 4:3 | 1.57 | 1.03 | 0.66 |  |
|  | " | MNA V4567 | 4:3 | 1.50* | 1.01 | 0.67* |  |
|  | " | MNA V5325 | 4:3 | 1.63 | 1.05 | 0.64 |  |
|  | " | means | 4:3 | 1.57 | 1.03 | 0.66 |  |
|  | cf. Paracimexomys perplexus | Eaton \& Cifelli, 2001 | 5:3 | 1.52-1.82 | 0.86-1.15 | 0.58 |  |
|  | Paracimexomys priscus | Archibald, 1982 | 4:3 | 2.06-2.31 | 1.20-1.41 | 0.61 |  |
|  | cf. Paracimexomys sp. | Eaton, 1995 | 4:3 | 1.32 | 0.98 | 0.74 |  |
|  | cf. Paracimexomys sp. B | UMNH VP7982 |  | 2.05* | 1.02* | 0.50* | 1.02* |
|  | Cedaromys sp. | MNA V7534 | 4:3 | 1.73 | 1.09 | 0.63 |  |
|  | Cedaromys hutchisoni | this paper | 4-5:3 | 1.70-2.06 | 1.07-1.34 | 0.64 |  |
|  | cf. Cedaromys sp. | MNA V4627 | 4:3 | 2.11* | 1.28 | 0.61* |  |
| m2 | cf. Paracimexomys sp. B | UMNH VP7982 |  | 2.10* | 1.38* | 0.66* | 1.02* |
|  | genus \& sp. unknown | MNA V5322 | 3:2 | 1.12 | 0.94 | 0.84 |  |
|  | " | OMNH 23362 | ? | 1.32 | 0.88 | 0.67 |  |
| Tooth | Taxon | Source | Formula | AP | LB | LB:AP | M2:M1 |
| M1 | cf. Paracimexomys sp. A | MNA V5240 | 4:4:1 | 1.73 | 0.91* | 0.53* | 0.88 |
|  | cf. Paracimexomys perplexus | Eaton \& Cifelli, 2001 | 5:4:1-2 | 1.53-1.94 | 0.97-1.20 | 0.62 |  |
|  | Paracimexomys priscus | Archibald, 1982 | 4:4:2 | 2.21-2.58 | 1.34-1.60 | 0.60 | 0.89 |
|  | cf. Paracimexomys sp. | Eaton, 1995 | 4:4:1 | 1.51-1.72 | 0.92-0.99 | 0.61 | 0.74 |
|  | Bryceomys sp. cf. B. fumosus | MNA V7527 | 5?:4:2 | 1.77 | 1.18 | 0.67 |  |
|  | Bryceomys fumosus | Eaton, 1995 | 3-5:4:2-4 | 1.52-2.10 | 1.05-1.39 | 0.68 |  |
| M2 | cf. Paracimexomys sp. A | MNA V5233 | Ri:2:3 | 1.52 | 1.29 | 0.85 |  |
|  | " | OMNH 22544 | Ri:2:3 | 1.55 | 1.38 | 0.89 |  |
|  | " | OMNH 24363 | Ri:2:3 | 1.48 | 1.27 | 0.86 |  |
|  | " | means | Ri:2:3 | 1.52 | 1.31 | 0.86 | 0.88 |

Table 19. Comparison of Wahweap and Kaiparowits Formation multituberculate species to those of the Aquilan, Judithian, "Edmontonian," and Lancian North American Land Mammal "Ages." Land Mammal "Age" faunas based on Lillegraven and McKenna (1986), Lofgren (1995), and Weil (1999). "X"- indicates conspecific occurrence; "cf." indicates conferred occurrence of species, and "?" indicates a possible conspecific occurence. Taxa with a "*" after them were considered unique occurrences within that "age" by Lillegraven and McKenna (1986).

| Aquilan multituberculate taxa | Wahweap Formation | Kaiparowits Formation |
| :---: | :---: | :---: |
| Mesodma senecta* |  |  |
| Cimexomys antiquus* | cf. |  |
| Paracimexomys magister* |  |  |
| Cimolodon electus* | X |  |
| Cimolodon similis* | X | cf. |
| ?Cimolomys sp. A* (Fox, 1971) | ? |  |
| ?Cimolomys sp. B* (Fox, 1971) |  |  |
| Meniscoessus ferox* |  |  |
| Judithian multituberculate taxa |  |  |
| Mesodma primaeva* |  |  |
| Mesodma archibaldi sp. nov. |  | X |
| Cimexomys judithae* |  | cf. |
| Dakotamys magnus* |  | X |
| Cimolomys clarki* |  | cf. |
| Meniscoessus intermedius* | cf. | cf. |
| Meniscoessus major* |  | cf. |
| Paracimexomys priscus |  |  |
| "Edmontonian" multituberculate taxa |  |  |
| Mesodma cf. M. thompsoni |  |  |
| Cimexomys sp. cf. C. judithae |  |  |
| Kimbethohia campi |  |  |
| Cimolodon nitidus | cf. | cf. |
| Cimolomys gracilis |  |  |
| Meniscoessus robustus |  |  |
| Lancian multituberculate taxa |  |  |
| Mesodma formosa | cf. |  |
| Mesodma hensleighi* |  |  |
| Mesodma thompsoni |  |  |
| Cimolodon nitidus | cf. | cf. |
| ?Neoplagiaulax burgessi |  |  |
| Cimexomys minor* |  |  |
| Cimolomys trochuus* | cf. |  |
| Essonodon browni * |  |  |

Table 20. Multituberculate faunas from the Wahweap and Kaiparowits formations with known occurrences of similar species of North American Land Mammal "Ages." "X" indicates the occurrence of similar species and "?" indicates the presence of a possibly similar species. The "*" after some taxonomic names indicate that a similar species is shared by both the Wahweap and Kaiparowits formations.

|  | Aquilan | Judithian | "Edmontonian" | Lancian |
| :---: | :---: | :---: | :---: | :---: |
| Wahweap Formation |  |  |  |  |
| Mesodma sp. cf. M. formosa |  |  |  | X |
| Cimolodon electus | X |  |  |  |
| Cimolodon similis* | X |  |  |  |
| Cimolodon sp. cf. C. nitidus* |  |  | X | X |
| Cimolodon sp. (small)* |  |  |  |  |
| Meniscoessus sp. cf. M. intermedius* |  | X |  |  |
| Cimolomys sp. cf. C. trochuus |  |  |  | X |
| ?Cimolomys sp. A | ? |  |  |  |
| ?Cimolomys sp. B | ? |  |  |  |
| ?Cimolomys sp. C (large) |  |  |  |  |
| Family indeterminate |  | ? |  |  |
| Cimexomys sp. cf. C. antiquus | X |  |  |  |
| cf. Paracimexomys sp. A |  |  |  |  |
| cf. Paracimexomys sp. B |  |  |  |  |
| Bryceomys sp. cf. B. fumosus |  |  |  |  |
| Cedaromys sp. |  |  |  |  |
| cf. Cedaromys sp. |  |  |  |  |
| Genus and species unknown |  |  |  |  |
| Kaiparowits Formation |  |  |  |  |
| Mesodma archibaldi, sp. nov. |  | X |  |  |
| Mesodma sp. cf. M. archibaldi, sp. nov. |  | ? |  |  |
| Mesodma minor, sp. nov. |  |  |  |  |
| Mesodma sp. (large) | ? |  |  |  |
| Cimolodon foxi, sp. nov.* |  |  |  |  |
| Cimolodon sp. cf. C. nitidus* |  |  | X | X |
| Cimolodon sp. cf. C. similis* | X |  |  |  |
| Kaiparomys cifellii, gen. \& sp. nov. |  |  |  |  |
| Meniscoessus sp. cf. M. intermedius* |  | X |  |  |
| Meniscoessus sp. cf. M. major |  | X |  |  |
| Cimolomys sp. A cf. C. clarki |  | X |  |  |
| Cimolomys sp. B cf. C. clarki |  | X |  |  |
| ?Cimolomys butleria, sp. nov. | ? | ? |  |  |
| Cimexomys sp. cf. C. judithae |  | X | ? |  |
| Cedaromys hutchisoni, sp. nov. |  |  |  |  |
| cf. Cedaromys sp. |  |  |  |  |
| Dakotamys magnus |  | X |  |  |

