Multituberculate mammals from near the Early–Late Cretaceous boundary, Cedar Mountain Formation, Utah

JEFFREY G. EATON and RICHARD L. CIFELLI

Herein we describe the oldest well-sampled multituberculate assemblage from the Cretaceous of North America. The fauna is dated at 98.37 Ma and thus approximates the Albian–Cenomanian (Early–Late Cretaceous) boundary. The multituberculate fauna is diverse. Two of the multituberculates (*Janumys erebos* gen. et sp. n. and an unidentified taxon) are provisionally placed among 'Plagiaulacida'. Another taxon, *Ameribaatar zofiae* gen. et sp. n., is of uncertain subordinal affinities. The remaining multituberculates appear to represent the advanced suborder Cimolodonta and fall within the '*Paracimexomys* group'. We rediagnose *Paracimexomys* on the basis of the type species, *P. priscus*, and refer to other species as cf. *Paracimexomys* (including cf. *P. perplexus* sp. n.). A revised diagnosis is also provided for Cenomanian *Dakotamys*. A previously-described species from the Cedar Mountain Formation is placed in *Cedaromys* gen. n. as *C. bestia*, together with *C. parvus* sp. n. *Bryceomys* is represented in the fauna by *B. intermedius* sp. n. Relationships of *Paracimexomys*-group to later taxa remain obscure. However, *Bryceomys* and *Cedaromys* share a number of features with Cimolodontidae. Given these resemblances, together with the fact that Cimolodontidae retain certain plesiomorphies (stout lower incisor, gigantoprismatic enamel) with respect to Ptilodontoidea (to which they are commonly referred), we suggest that Cimolodontidae may have arisen from a clade within the '*Paracimexomys* group', independent of ptilodontoids.

Key words: Multituberculata, 'Plagiaulacida', Cimolodonta, Cretaceous, Utah.

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Introduction

Multituberculata, which range from the Late or Middle Jurassic through the late Eocene, comprise the longest-lived order of mammals and, in North America, Europe, and Mongolia, at least, are both abundant and diverse elements of Cretaceous terrestrial faunas (Clemens & Kielan-Jaworowska 1979; Hahn & Hahn 1999; Kielan-

Jaworowska & Hurum 2001). Yet, despite spectacularly informative specimens for some taxa (e.g., Kielan-Jaworowska & Gambaryan 1994; Gambaryan & Kielan-Jaworowska 1995; Kielan-Jaworowska & Hurum 1997; Rougier *et al.* 1997, and references therein), many aspects of multituberculate history and relationships remain elusive (Simmons 1993). Uncertainty stems in part from an obviously high level of homoplasy in major anatomical systems (Kielan-Jaworowska & Hurum 2001), and in part due to gaps in the fossil record. One of the most troublesome of these is the late Early–early Late Cretaceous interval, for which very little was known until recently (Clemens *et al.* 1979). Earlier multituberculates are placed in the 'Plagiaulacida', a generally plesiomorphic and paraphyletic assemblage. Those of the Late Cretaceous onward, by contrast, are considered to represent a monophyletic group, Cimolodonta. A major problem in understanding of multituberculate phylogeny and biogeography is the origin of cimolodontans, which presumably arose from some 'plagiaulacidan' lineage late in the Early Cretaceous (Kielan-Jaworowska & Hurum 2001). In this context, virtually any substantial new fossils from this important time interval represent welcome additions to knowledge.

The Cedar Mountain Formation was named for terrigenous rocks lying above the Upper Jurassic Morrison Formation in central and eastern Utah; farther eastward, it is generally considered to be contiguous with the Burro Canyon Formation of western Colorado (see Stokes 1944, 1952; Tschudy *et al.* 1984). Long considered to generally be of Early Cretaceous age, the Cedar Mountain Formation has recently been divided into several members, collectively spanning the Upper–Lower Cretaceous boundary, downward to (perhaps) the Barremian (Kirkland, Britt, *et al.* 1997; Kirkland, Cifelli, *et al.* 1999). Several dinosaur assemblages have been found in the lower part of the Cedar Mountain Formation, but thus far, a substantial assemblage of mammals and other microvertebrates has been collected only from the uppermost, or Mussentuchit Member, west of the San Rafael Swell, Emery County, Utah (Fig. 1). Initial microvertebrate collecting in this member was undertaken independently by M. Nelson and JGE in the early 1980s (e.g., Nelson & Crooks 1987), resulting in a small sample of multituberculate fossils reported by Eaton & Nelson (1991). A large-scale recovery effort by RLC was conducted between 1990 and 1999, resulting in the recovery of a large, well-represented fauna from the Mussentuchit Member. The assemblage, termed the Mussentuchit local fauna, comes from closely spaced sites on the western side of the San Rafael Swell, in a restricted stratigraphic interval, 10–20 m below the contact with the overlying Dakota Formation (see stratigraphic sections in Cifelli *et al.* 1999). A volcanic ash associated with the fauna yielded a mean determination of 98.39±0.07 Ma (Cifelli *et al.* 1997), placing it at the Albian–Cenomanian (Early–Late Cretaceous) boundary as defined by Obradovich (1993) and Gradstein *et al.* (1994, 1995). As the Cretaceous includes only Early and Late epochs, this presents the conundrum of referring to the age of the Mussentuchit Member in a simple and precise manner. Herein we use the informal term 'medial Cretaceous' to refer to the age of the multituberculates from the Cedar Mountain Formation.

We report herein on the multituberculate mammals of the Mussentuchit local fauna. Although they are represented almost exclusively by isolated teeth, the sample is significant in its large size: more than 1,000 multituberculate specimens are known, thus permitting some tentative association of upper to lower dentitions, and evaluation

of variability, to an extent not possible among temporally comparable faunas from North America. The multituberculates of the Cedar Mountain Formation also merit attention because of their well-documented age that, as noted above, corresponds to an important but poorly known time in the history of the group. Finally, given the great and largely independent radiations of Late Cretaceous multituberculates in Asia and North America (Rougier *et al.* 1996; Kielan-Jaworowska & Hurum 1997; Kielan-Jaworowska & Hurum 2001), coupled with indications of mid-Cretaceous vertebrate dispersal between the two landmasses (Cifelli *et al.* 1997), the multituberculates of the Cedar Mountain Formation may eventually prove useful in deciphering the biogeographic history of the group. Our central purposes in this paper are morphological description, systematic treatment at the alpha taxonomic level, and discussion of character distributions and their possible significance. Given the equivocal results of recent analyses in resolving multituberculate relationships (Simmons 1993; Rougier *et al.* 1997; Kielan-Jaworowska & Hurum 2001) and the still scant nature of the fossil record for apparently critical taxa, we resist, for now, the temptation to place the new taxa into a comprehensive phylogenetic framework. Instead, we restrict our comments to the possible relationships of these taxa, based on distribution of certain dental characters, and again caution readers that association of dentitions presented herein is hypothetical and should be regarded as tentative.

Methods and conventions

The specimens described herein were collected from 10 sites in the Mussentuchit Member of the Cedar Mountain Formation. All are west of the San Rafael Swell, Emery County, Utah, with a cluster of the most productive sites occurring near the southernmost part of the local exposure (Fig. 1). One site (V695) yielded microvertebrate remains, including some multituberculate teeth and a few uninformative jaw fragments, through quarrying procedures, but the vast majority of specimens from this site, and all of those from the remaining 9 sites, were collected by underwater screenwashing and associated recovery techniques (Cifelli *et al.* 1996). Specimen measurements, to the 0.01 mm, were taken with a stereozoom microscope (using a single ocular) mounted on a two-stage measuring base equipped with Mitutoyo 0.005 mm micrometers. Descriptive statistics and scatterplots were generated by Microsoft Excel®. Inclusion of all data and resulting graphs in this paper would be impractical, but those critical to evaluating species distinctions are included, in order to provide a basis for our taxonomic assignments. Errors of association are always possible when a sample consists exclusively of isolated teeth and we caution that the reassignment of referred specimens proposed in our tentative associations could have a significant impact on taxonomic interpretation. In most cases, incisors and anterior upper premolars are described separately from the last premolars and molars. We discuss their possible association with taxa based on the posterior parts of the dentition, but these referrals must be regarded as highly tentative. We follow convention in identifying taxa that are probably paraphyletic by enclosing their names in quotes. The term 'crescentic' is applied only to cusps that are recurved posteriorly with a concave posterior face (lower molars) or recurved anteriorly with an anteriorly concave face (upper molars).
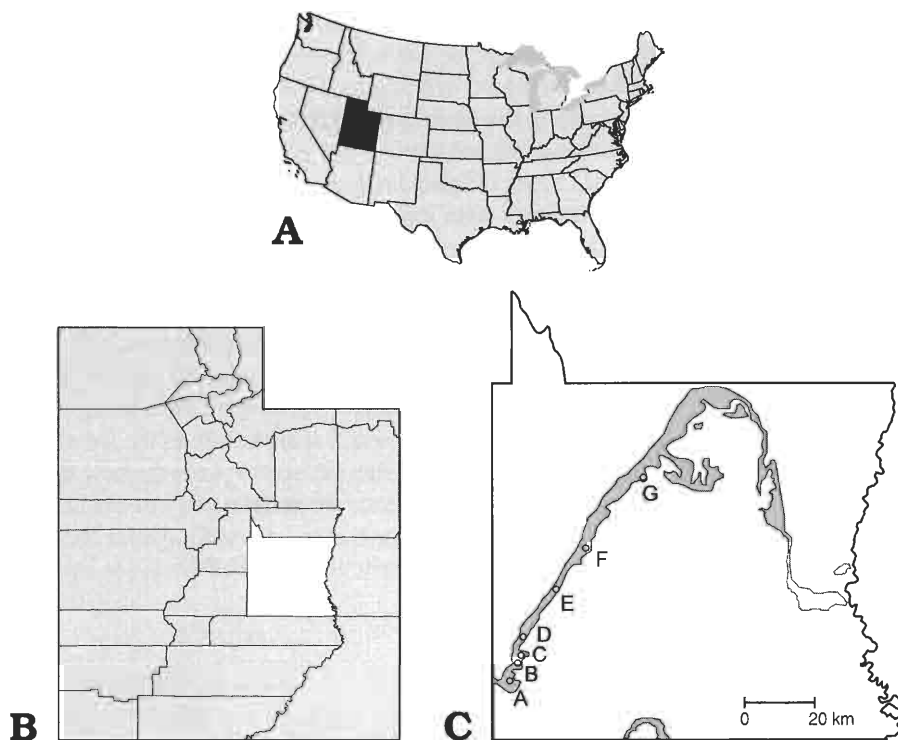
Fig. 1. Multituberculate-yielding sites in the Cedar Mountain Formation. **A**. Continental United States, showing the position of Utah (black). **B**. State of Utah, showing county lines and position of Emery County (white). **C**. Emery County, Utah, showing distribution of Cedar Mountain Formation (shaded) and approximate positions of sites (small A–G) yielding the specimens described herein. Site numbers: A, V235, V694, V695, V794; B, V236; C, V868; DE, V234; E, V239; F, V823; G, V801. See Cifelli *et al.* (1999) for details on stratigraphy.

All P4s, M1s, M2s, m1s, and m2 are figured with anterior margin up. Anterior upper premolars are figured in occlusal view, with inferred anterior margin up. Orientation of many anterior upper premolars cannot be unambiguously established, and the orientations shown should be regarded as hypothetical.

Institutional abbreviations. — AMNH, American Museum of Natural History, New York; FHSM, Sternberg Memorial Museum, Fort Hays State University, Hays, Kansas; MNA, Museum of Northern Arizona, Flagstaff; OMNH, Oklahoma Museum of Natural History, Norman (all fossils described in this paper are OMNH specimens and the acronym is thus not repeated in the listings of referred specimens); V (followed by three digits), OMNH fossil vertebrate locality number; UW, University of Wyoming, Laramie. Exact coordinates and other pertinent locality data are on file at OMNH and are available to qualified investigators upon request.

Morphology and statistics abbreviations. — Upper teeth are denoted with capital letters, lower teeth with lower case letters: I/i, incisor; P/p, premolar; M/m, molar. In case of deciduous teeth we use D/d as prefixes. Letters preceding tooth symbols: R, right; L, left. Details of dental terminology follows Eaton (1995: fig. 3). Numbers
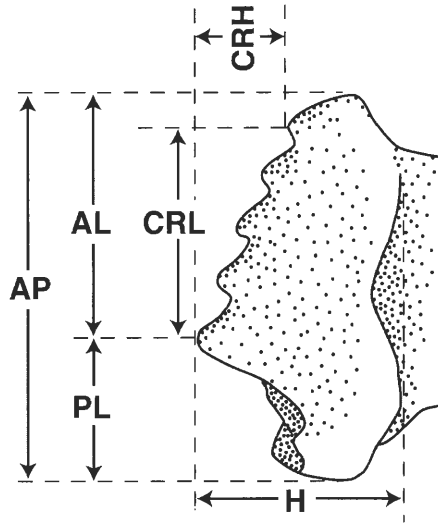
Fig. 2. Lingual view of P4 showing measurement of AP (anteroposterior length), H (crown height), PL (posterior length), AL (anterior length); CRL (climb rate length) and CRH (climb rate height). CR (climb rate) is calculated by dividing the CRH by the CRL.

separated by colons (e.g., 3:3:4), cusp formula, given from labial to lingual; Ri, a non-cuspidate ridge present anterolabially on M2; CV, coefficient of variation; SD, standard deviation. Measurements: AP, anteroposterior dimension (length); CR, climb rate of cusps of the central row of P4, measured by taking the anteroposterior distance (CRL), in lingual view, from the top of the first cusp to the point along the tooth where the maximum depth is reached, divided into the height (CRH), the distance measured between the lowest and highest cusp of the central row (Fig. 2); LB, lingual-labial dimension (width); PL, posterior length of P4 from highest point of the central row to the back of the tooth; PL:AP, ratio of the length of the posterior basin to the total length of P4. CW, cusp width, the distance between the apices of the posterior cusps of tricuspid anterior upper premolars; CL, cusp length, the anteroposterior distance between the line formed by the CW perpendicular to the anterior cusp of tricuspid anterior upper premolars. A '*' by a measurement indicates a damaged specimen.

Systematic paleontology

Order Multituberculata Cope, 1884
Suborder 'Plagiaulacida' Simpson, 1925
'Plagiaulacid line' of Kielan-Jaworowska & Hurum (2001)
Family ?Plagiaulacidae Gill, 1872
Genus and species indet.
Fig. 3.

Material. — p4: 33163, V695. P4: 25587, V235; 29727; 29726, V694; 29667, V696; 33981, V794.

Distribution. — Cedar Mountain Formation, near the Albian–Cenomanian stage boundary, San Rafael Swell, Utah.
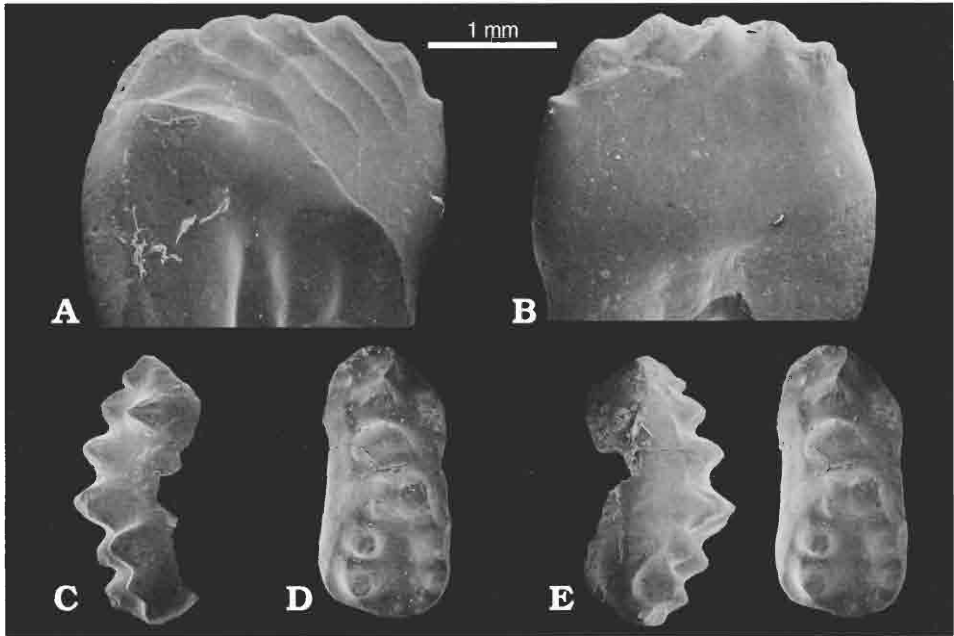
Fig. 3. Multituberculata, family and genus indet. **A**, **B**. Rp4 (33163). **C–E**. LP4 (29667). **A**, **C**, labial view; **B**, **E**, lingual view; **D**, occlusal stereopair.

Description. — **p4** (Fig. 3A, B): A single small p4 (OMNH 33163) with 6 serrations, 4 external and 3 internal ridges. The anterolabial lobe is absent as a result of breakage. The posterolabial cusp is prominent, about one-quarter the length of the tooth, and has an anteroposteriorly oriented groove worn into the occlusal surface.

The third serration is the highest; cusps 4, 5 and 6 are only slightly lower (although there is slight wear on these three cusps), forming an essentially flat-topped p4 that is rectangular in lateral view. The internal ridges are oriented anteroventrally on cusps 3, 4, and 5. There is a hint of a ridge on cusp 6. The specimen's dimensions are: AP = 2.66; LB = 1.19; H = 1.70; H:L = 0.64.

P4 (Fig. 3C–E): Cusp formula 1–2:4. The first cusp of the central cusp row of OMNH 29667 is very small and low. The second cusp is taller and larger. Both the first and second cusps are linguolabially compressed such that they bear a weak antero-posterior crest medially dividing the cusps, but the third and fourth cusps are broader than they are long.

There is a single cusp on the anteroexternal platform that is aligned laterally with the second cusp of the central row. The posterior basin is long (PL = 0.88) and is lined on each side by two well-developed cusps. The basin is deep and open posteriorly. The tooth's dimensions are: AP = 2.05; LB = 0.97; PL:AP = 0.43. Two other specimens have measurements as follows: OMNH 29727, AP = 2.15; LB = 0.98; OMNH 33981, AP = 2.02*; LB = 1.04, and two specimens are too damaged to measure.

Discussion. — The p4 is the most primitive recovered from the Cedar Mountain For-mation and in most respects is more plesiomorphic than any figured p4 of Cretaceous age. The p4 is very unlike the well-serrated and elongated p4 of *Arginbaatar*. The

broad base on the posterolabial cusp and the flat crest are similarities to the p4s of *Plagiaulax* (Kielan-Jaworowska *et al.* 1987: pl. 10–1b). However, the specimen from the Cedar Mountain Formation is much less elongate and has fewer serrations and ridges. A strong posterolabial cusp is present on *Eobaatar*, but the p4 of that taxon is much larger than the OMNH specimen, has a distinctly arched crest, and has many more serrations and ridges. In overall outline, the blade is similar to *Uzbekbaatar kizylkumensis* (see Kielan-Jaworowska & Nessov 1992) but that blade has more serrations and apparently lacks a posterolabial cusp.

The P4s appear to be very primitive for the Cretaceous, but they do not closely resemble any illustrated Jurassic or later Cretaceous P4. These might represent the P4 of *Ameribaatar* (new genus described later in this paper) but they lack the cusp depth necessary to represent that genus and the specimens do not fit well with any other M1 recovered as part of this fauna. These upper and lower fourth premolars may well belong to the same taxon: metric comparison of the two specimens yields a mean P4:p4 ratio of 0.79, which is within the range of some multituberculate taxa (see Table 1B; note however, that data for only a few cimolodontans are provided).

Family *incertae sedis*
Genus *Janumys* gen. n.

Type species by monotypy: *Janumys erebos* sp. n.

Derivation of the name: Latin – *Janus*, Roman god with two faces and god of gates and beginnings, in reference to presumed placement of this taxon near the base of cimolodontans; *mus*, mouse.

Diagnosis. — As for the species.

Janumys erebos sp. n.

Table 1A, B; Figs. 4, 5A–F.

Holotype: OMNH 26623, M1, V695.

Distribution: Cedar Mountain Formation, near the Albian–Cenomanian stage boundary, San Rafael Swell, Utah.

Derivation of the name: Greek – *Erebos*, a place of darkness in the nether world; an allusion to its morphological intermediacy between 'plagiaulacidans' and cimolodontans.

Material. — m1: 25592, V235; 27434, 27435, 27455, 27499, 29586, 29591, 33172, 33175, 33183, 33184, 34019, V695; 33987, V794; 29651, V801. m2: 33964, V868. P4: 33160, V695; 30530, V794; 32938 – partial, 32986, partial, V868. M1: 26619, 27565, 29589, 33173, V695; 30548, V794.

Diagnosis. — The new species is smaller than any other North American Cretaceous multituberculate. Cusp rows converge strongly on m1, there is no waist in occlusal view, and internal row cusps are conical unlike *Paracimexomys*; m1 most similar to *Eobaatar*, but has additional cusp in lingual row and third and fourth cusps of labial row better separated. P4 with little expansion of anteroexternal platform, very short, poorly developed posterior basin, and very low rate of cusp climb (CR = 0.26) unlike *Cedaromys, Bryceomys,* or *Dakotamys*. M1 lacks third cusp row, unlike *Eobaatar, Paracimexomys*, cf. *Paracimexomys, Bryceomys,* or *Dakotamys*, and is more elongate relative to width (LB:AP = 0.54) than *Cedaromys, Paracimexomys*, cf. *Paracimexomys, Dakotamys,* and *Bryceomys*. Cusp rows on M1 parallel, unlike *Paracimexomys*; m2s (and probably M2s)

Table 1A. Measurements (in mm) of lower teeth of *Cedaromys, Bryceomys, Janumys,* and cf. *Paracimexomys.*

Tooth		*C. bestia*	*C. parvus*	*B. intermedius*	*J. erebos*	cf. *P. perplexus*
p4	*n*	2	3	3		
	AP range	4.12–4.22	3.59–3.71	2.74–2.92		
	AP mean	4.19	3.66	2.84		
	H range	2.50–2.53	2.26–2.58	1.54–1.78		
	H mean	2.52	2.40	1.63		
	L:H	0.60	0.66	0.58		
m1	*n*	5	8	6	14	26
	AP range	2.42–2.64	2.03–2.28	1.79–1.93	1.14–1.46	1.52–1.82
	AP mean	2.49	2.06	1.88–6	1.26	1.65
	LB range	1.51–1.69	1.32–1.43	1.10–1.25	0.66–0.84	0.86–1.15
	LB mean	1.57	1.39	1.15	0.76	0.96
	LB:AP	0.63	0.67	0.62	0.60	0.58
	AP m1:p4	0.59	0.56	0.66		
m2	*n*	3	3	10	1	
	AP range	2.22–2.42	1.76–1.91	1.24–1.44	1.22	
	AP mean	2.33	1.82	1.33	1.22	
	LB range	2.02–2.36	1.58–1.88	1.05–1.30	0.97	
	LB mean	2.21	1.70	1.19	0.97	
	LB:AP	0.95	0.93	0.89	0.80	
	AP m2:m1	0.94	0.88	0.70	0.97	

Table 1B. Measurements (in mm) of upper teeth of *Cedaromys, Bryceomys, Janumys,* and cf. *Paracimexomys.*

Tooth		*C. bestia*	*C. parvus*	*B. intermedius*	*J. erebos*	cf. *P. perplexus*
P4	*n*	3	2	2	2	3
	AP range	2.60–2.72	2.51	2.26–2.30	1.54–1.71	1.60–1.87
	AP mean	2.67	2.51	2.28	1.63	1.72
	LB range	1.39–1.43	1.12–1.30	1.14	0.90	0.74–0.96
	LB mean	1.41	1.22	1.14	0.90	0.85
	LB:AP	0.53	0.49	0.50	0.55	0.49
	PL:AP	0.49	0.44	0.35	0.31	0.45
	CR	0.60	?	0.47	0.26	0.51
	AP P4:p4	0.64	0.69	0.80		
M1	*n*	4	6	2	6	14
	AP range	2.52–2.64	2.23–2.37	2.10	1.33–1.52	1.53–1.94
	AP mean	2.57	2.32	2.10	1.42	1.7
	LB range	1.55–1.63	1.39–1.48	1.37–1.48	0.65–0.85	0.97–1.20
	LB mean	1.59	1.45	1.43	0.76	1.06
	LB:AP	0.62	0.63	0.68	0.54	0.62
	AP M1:P4	0.96	0.92	0.92	0.87	0.99
M2	*n*	3	6	5		
	AP range	2.28–2.46	2.03–2.31	1.56–1.69		
	AP mean	2.38	2.17	1.61		
	LB range	1.95–2.12	1.71–1.92	1.29–1.42		
	LB mean	2.00	1.82	1.34		
	LB:AP	0.84	0.84	0.84		
	AP M2:M1	0.93	0.94	0.64		

almost as long as m1 (AP m2:m1 = 0.96). Molars lack pits and ribs as in *Paracimexomys,* but unlike *Eobaatar, Cedaromys, Bryceomys,* and *Dakotamys.*

Description. — **m1** (Fig. 4A, B): Cusp formula 4:3. The posterior margin of the tooth is directed strongly obliquely, the internal row being much shorter than the external.
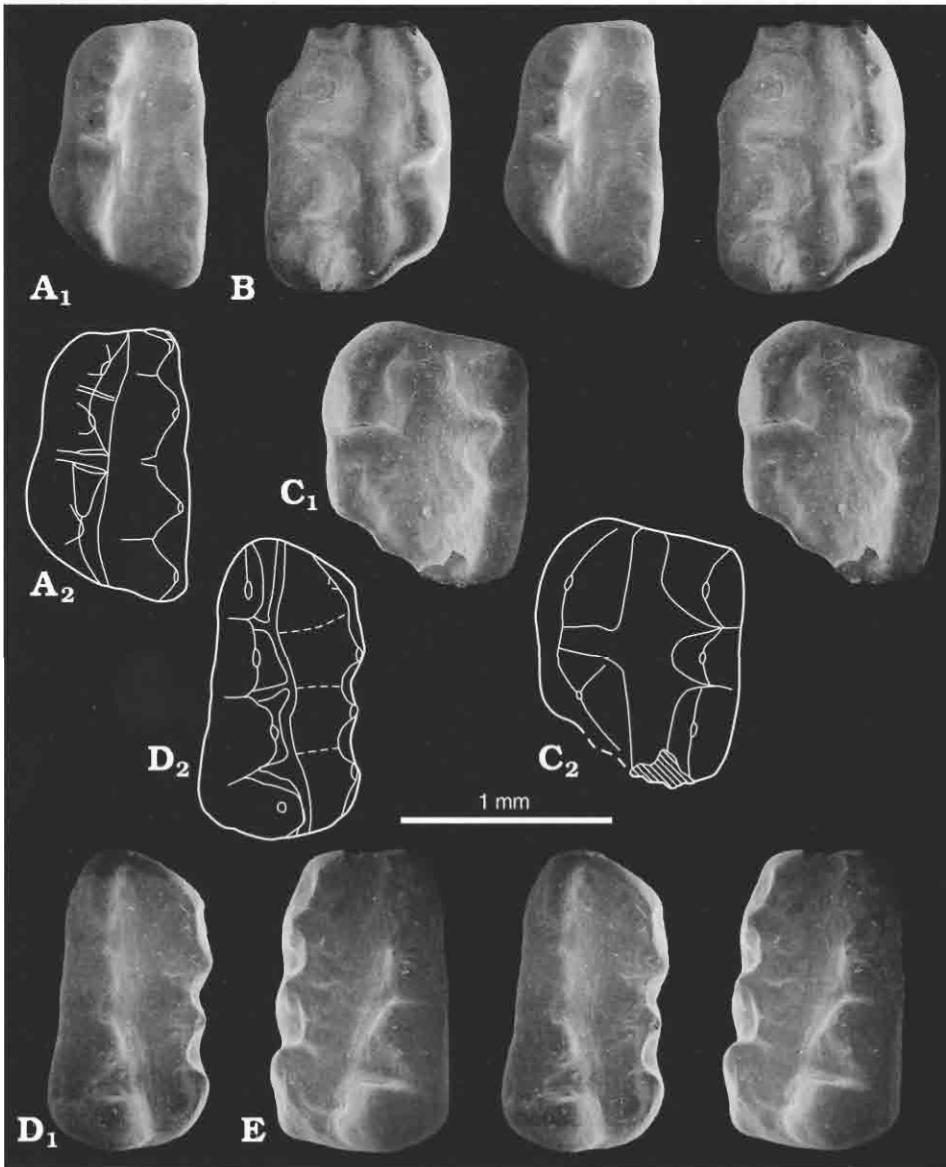
Fig. 4. *Janumys erebos* gen. et sp. n. **A**, Rm1 (29591); **B**, Lm1 (29586); **C**, Rm2 (33964); **D**, LM1 (26623, holotype); **E**, RM1 (29589). A_1, **B**, C_1, D_1, and **E**, stereopairs, occlusal view; A_2, C_2, and D_2, explanatory drawings of A_1, C_1, and D_1, respectively.

The tooth tapers strongly anteriorly so that the cusp rows converge anteriorly. There is an indentation labial to the third cusp of the external row, but no waist on some specimens (e.g., OMNH 29591, Fig. 4A) or a weakly developed waist on others (e.g., OMNH 29586, Fig. 4B). The first cusp of the external row is low and conical (OMNH 29586, Fig. 4B). The second cusp is shifted labially relative to the first cusp, and is the largest cusps of the row. It has a bulbous, conical shape (OMNH 29591, Fig. 4A).

A broad, deep valley separates the second and third cusps. The third and fourth cusps are close together and the fourth cusp is the tallest of the row. The fourth cusp of the longest specimen included here (OMNH 29651, AP = 1.46) shows incipient splitting of the fourth cusp. The central valley is sinuous and there is no evidence of pitting, but this may be the result of wear.

The cusps of the internal row are tall and conical; there is no shifting of the apices posteriorly. The first two cusps are only separated at their apices and together form a tall wall adjacent to the central valley. A much deeper valley, although not reaching the floor of the central valley, separates the second and third cusp. The second cusp is taller than the first or third if there is no apical wear (OMNH 29586, Fig. 4B). OMNH 29586 (Fig. 4B) is proportionally broader relative to length than OMNH 29591 (Fig. 4A). Third cusp of the internal row is almost as long as the two first. Cusps of the internal row are worn obliquely, sub-vertically along their labial side, leaving crescent-shaped wear surfaces facing towards the central valley.

m2 (Fig. 4C): A single m2, OMNH 33964, is tentatively included here. Cusp formula 3:2. The cusps of the labial row are coalesced peripherally; the first one is the lowest of the tooth. The second is weakly separated from the long third, ridge-like cusp that continues to the posterior margin of the tooth but does not close the central valley posteriorly. The central valley is broad, U-shaped, and open at both ends. The first cusp of the internal row is the longest and tallest of the tooth and is separated by a deep valley from the second cusp, but that valley is closed lingually. The second cusp is very thin and wall-like.

P4 (Fig. 5A–C): Cusp formula 1–3:4. On OMNH 33160 the anteroexternal platform is moderately expanded with the first cusp of the external row being larger and taller than the second. There is a well-developed notch for the posterior end of P3 at the anterior end of the central cusp row. The cusps of the central row climb at a low angle to the third cusp. The third and fourth cusps are about the same height. A ridge descends from the last cusp of the central row to the labial cusp of the open posterior basin. The lingual cusp of the posterior basin is weak and low. The posterior basin is weakly developed and relatively short (PL:AP = 0.34).

On OMNH 32986 (Fig. 5D–F) there is little expansion of the anteroexternal platform that bears 3 cusps. The first cusp is the largest and highest and the second and third cusps are smaller and lower. These cusps are formed almost as swellings of the striations descending labially from the second and third cusps of the central row. The cusps climb at a low angle and the third cusp of the row may be slightly taller than the fourth.

M1 (Fig. 4D, E): The cusp formula is 3–4:4. In occlusal outline the tooth is anteroposteriorly elongated and the anterior terminus of the tooth projects forward such that the internal row is much longer than the external row. There is no third cusp row on these upper molars. There is an unworn swelling of the labial anterior ridge that does not form a cusp in some specimens (OMNH 26623, holotype, Fig. 4D) or develops into a small cusp on other specimens (OMNH 29589, Fig. 4E). The first cusp of the external row (or the second cusp of specimens with 4 external cusps) is developed as a small conical point on a continuous anteroposteriorly oriented ridge. The second (or third) and third (or fourth) cusps of the row are similarly formed.

The central valley is broad and crosses the tooth obliquely. The external cusps maintain the same width along the row, but the cusps of the internal row broaden poste-
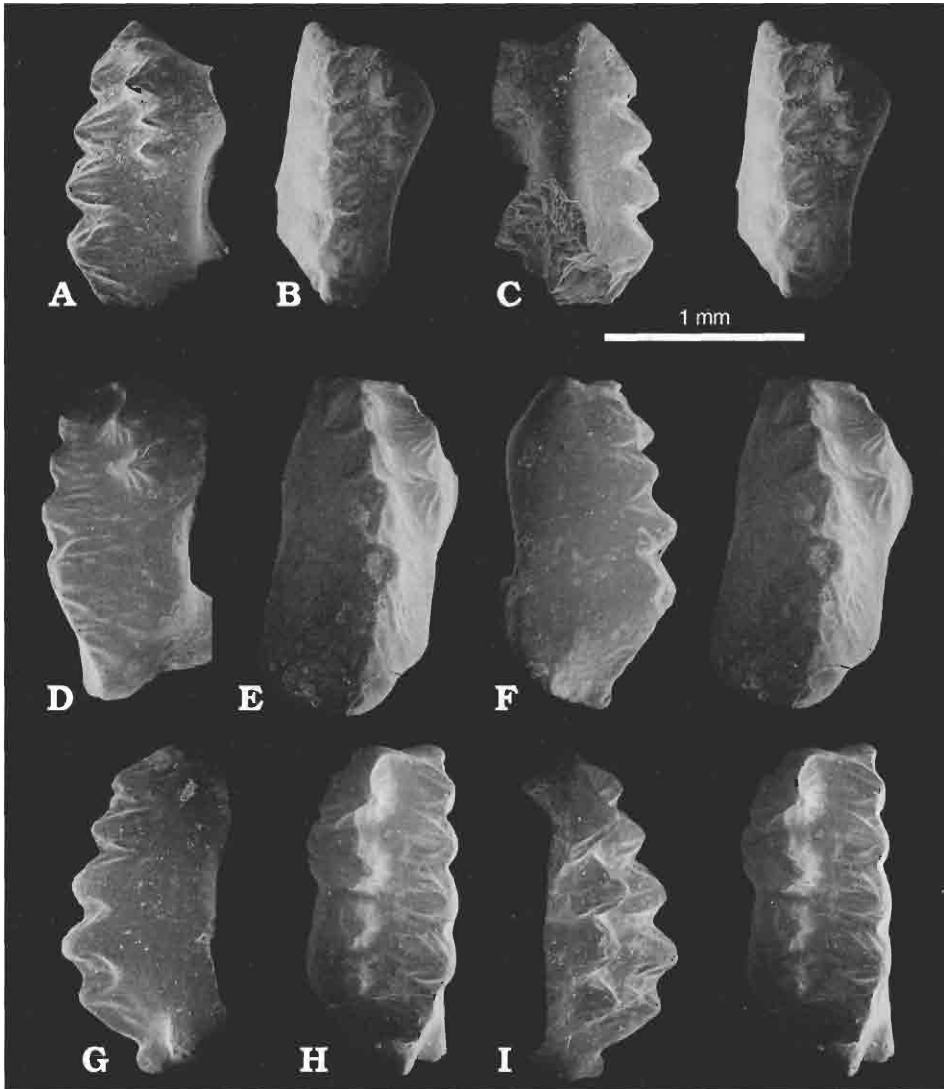
Fig. 5. *Janumys erebos* gen. et sp. n. (**A–F**) and cf. *Janumys erebos* (**G–I**). **A–C**, LP4 (33160); **D–F**, LP4 (32986); **G–I**, RP4 (26640). **A, D, I**, labial view; **B, E, H**, occlusal stereopairs; **C, F, G**, lingual view.

riorly. The cusp rows are essentially parallel on all specimens (OMNH 26623, Fig. 4D; OMNH 29589, Fig. 4E). The first cusp of the internal row is a low, broad cone. The second cusp is slightly more squared. The third cusp is weakly pyramidal. The apices of both cusps are shifted anteriorly. The fourth cusp is the broadest and tallest and is well separated from the third cusp.

Discussion. — Of the various informally recognized groups of 'Plagiaulacida', *Janumys* is morphologically closest to the 'plagiaulacid line' of Kielan-Jaworowska & Hurum (2001). The most notable similarities are to *Eobaatar*, especially in the structure of m1 (Kielan-Jaworowska *et al.* 1987). In both, the posterior margin of this molar is oblique

and the cusps of the lingual row face labially. However, m1 of *Janumys* differs from that of *Eobaatar* in having an additional cusp on the lingual row, better separation of the third and fourth cusps of the labial row, a sinuous rather than straight central valley, and very weak ornamentation, discernable only on unworn first molars (apparent differences in ornamentation may be due, in part, to state of preservation). A further difference between the two taxa is apparent on M1. *Janumys* lacks a true postero-lingual wing (incipient third row of cusps), having only a bulge in this region. In this respect, it resembles the incipient wing present in *Bolodon* (see Kielan-Jaworowska & Ensom 1992: pl. 3: 9). However, the overall tooth shape and cusp configuration of *Janumys* is quite different from M1 of either *Bolodon* or *Eobaatar*: cusps of the labial row are more connected, the tooth narrows rather than broadens anteriorly, the anterior margin is oblique rather than squared (Fig. 4D), and the cusps do not have a blocky appearance (see Kielan-Jaworowska *et al.* 1987: pl. 6: 3c) (also see Table 3). *Janumys* is more primitive than other multituberculates of the Cedar Mountain Formation (except *Cedaromys*) in lacking a third row of cusps on M1, and in having a particularly short, poorly developed posterior basin on P4 (Table 1A, B). However, the teeth are elongate relative to width, which is quite derived relative to the condition in members of the 'plagiaulacid line'. The teeth designated as P4 were identified as such because of their morphological similarity to P4 of taxa known from the North American Late Cretaceous. However, well-rooted 5–6 cusped upper anterior premolars described below are of the appropriate size for *J. erebos*, and they fit well against the strong recess in these P4s. There is no known P3 of this morphology that is preserved in a jaw, but complex P4s are known by specimens demonstrating association with P5 (e.g., *Bolodon*, see Kielan-Jaworowska *et al.* 1987; Kielan-Jaworowska & Ensom 1992). For this reason, we believe that the teeth herein designated P4 may actually represent P5. For the purposes of discussion, we tentatively consider *Janumys erebos* to retain the primitive condition of 5 upper premolars, but because homologies cannot be demonstrated with these isolated teeth, we continue to refer to them as P4. On the basis of this and other plesiomorphies, we tentatively associate *Janumys* with the 'plagiaulacid line' of the 'Plagiaulacida'. We consider present evidence insufficient to warrant even a tentative referral to family.

Morphology of p4 figures prominently in distinguishing 'plagiaulacidans' from cimolodontans (e.g., Simmons 1993; Kielan-Jaworowska & Hurum 2001: fig. 3), and it is unfortunate that no tooth of this locus can be referred to *J. erebos* with even remote confidence. We considered the possibility that the p4 described above, designated as gen. and sp. indet., could belong to *J. erebos*, as it evidently represents a 'plagiaulacidan'. However, measurements show that an extremely low m1:p4 ratio (0.47) would result. A ratio of this value is quite atypical of 'plagiaulacidans' (see Table 2A, B).

By comparison to 'plagiaulacidans', *Janumys erebos* appears to retain the greatest number of primitive characters among formally named taxa of the Cedar Mountain Formation. Most notable are the lack of a third cusp row on M1, a high m2:m1 length ratio (0.97), a low rate of cusp climb on P4, and, possibly, the presence of five upper premolars. In most regards, *Janumys* is more primitive than *Eobaatar* except that the P4 (which we believe may be P5) more closely approximates the morphology of other later Cretaceous North American multituberculates than does the P5 of *Eobaatar*, which is broad relative to length and lacks a posterior basin. Conceivably, future dis-

Table 2A. Tooth proportion data of selected North American multituberculate taxa. Boldface numbers indicate data based on associated teeth, '?' indicates an unusual value.

	m2:m1	m1:p4	M2:M1	M1:P4	Source
'Plagiaulacida'					
Allodontidae					
Ctenacodon serratus	**1.2**	**0.7**			Simpson 1929: p. 19
C. scindens	**1.0**	**0.8**			Simpson 1929: p. 20
C. laticeps			**1.0**	**0.7**	Simpson 1929: p. 25
?Psaladon marshi	**1.0**	**1.7**			Simpson 1925: p. 28
Family incertae sedis					
Janumys erebos	0.97			0.87	this paper: Tab. 1
Cimolodonta					
Paracimexomys group					4
cf. P. robisoni	0.8			0.9	Eaton & Nelson 1991
P. priscus	0.93		0.89		Archibald 1982: tab. 17
P. priscus	**0.92**	0.68			Lillegraven 1969: fig. 10
cf. P. perplexus				0.99	this paper: Tab. 1
Dakotamys malcolmi	0.86	0.72	0.80	0.82	Eaton 1995: tab. 3
Cedaromys bestia	0.94	0.59	0.93	0.96	this paper: Tab. 1
C. parvus	0.88	0.56	0.94	0.92	this paper: Tab. 1
Bryceomys intermedius	0.70	0.66	0.64	0.92	this paper: Tab. 1
B. fumosus	0.79	0.56	0.76	0.85	Eaton 1995: tab. 4
B. hadrosus	0.83		0.81		Eaton 1995: tab. 4
Cimexomys judithae	**0.62**	**0.62**	**0.67**	**1.11**	Montellano et al. 2000: tab. 1
C. gratus	**0.68**	**0.81**			Archibald 1982: tab. 16
C. gratus	0.65	0.84	0.70	1.03	Archibald 1982: tab. 16
Ptilodontoidea					
Cimolodontidae					
Cimolodon electus	0.9	0.6	0.8	0.9	Fox 1971: tab. 2
C. similis	0.7	0.7	0.8	0.8	Fox 1971: tab. 2
C. nitidus	0.63	0.78	0.60	1.09	Archibald 1982: tab. 8
C. nitidus	0.71	0.76	0.63	1.12	Lillegraven 1969: tab. 2
C. nitidus	0.7	0.7	0.7	0.7?	Clemens 1963: tab. 7
C. nitidus	**0.7**	**0.7**	**0.7**	**0.9**	Clemens 1963: tab. 8
Ptilodontidae					
Mesodma primaeva	0.7	0.7	0.5	1.0	Sahni 1972
M. hensleighi	0.57	0.67	0.50	1.24	Lillegraven 1969: tab. 1
M. garfieldensis	0.56	0.63	0.44	1.19	Archibald 1982: tab. 6
M. formosa	0.61	0.75	0.46	1.53?	Lillegraven 1969: tab. 1
M. formosa	**0.6**	**0.7**			Clemens 1963: p. 35
M. thompsoni	0.64	0.62	0.63	1.19	Archibald 1982: tab. 5
Taeniolabidoidea					
Taeniolabididae					
Catopsalis joyneri	0.8	2.2	0.6	2.5	Kielan-Jaworowska & Sloan 1979: tab. 1
C. joyneri	0.92		0.68	2.51	Lofgren 1995: tab. 14
Meniscoessus robustus	0.87	1.10	0.76	2.26	Lofgren 1995: tab. 17
Superfamily incertae sedis					
Family incertae sedis					
Essonodon browni	0.33		0.38	2.28	Archibald 1982: tab. 14
Cimolomyidae					
Cimolomys gracilis	0.7	1.1	0.7	1.6	Clemens 1963: tab. 9
Meniscoessus robustus	0.87	1.10	0.76	2.26	Lofgren 1995: tab. 17
Eucosmodontidae					
Stigymys gratus	0.5	0.9			Jepsen 1940: tab. 3
S. kuszmauli	0.64	0.90	0.55	1.47	Lofgren 1995: tab. 14
S. sp. aff. S. kuszmauli	0.59	0.94	0.57	1.33	Archibald 1982: tab. 9

Table 2B. Tooth proportion data of selected Eurasian multituberculate taxa. Boldface numbers indicate data based on associated teeth. '?' indicates an unusual value.

	m1:m2	m1:p4	M2:M1	M1:P4	Source
Superfamily *incertae sedis*					
Arginbaataridae					
Arginbaatar dimitrievae		0.4			Kielan-Jaworowska *et al.* 1987: tab. 1
'Plagiaulacida'					
Plagiaulacidae					
Bolodon osborni	1.1	0.6	**0.8**	**1.0**	Kielan-Jaworowska & Ensom 1992: fig. 3A
Eobaataridae					
Eobaatar magnus			**0.9**	**1.1**	Kielan-Jaworowska & Ensom 1992: fig. 3B
Cimolodonta					
Djadochtatherioidea					
Sloanbaataridae					
Sloanbaatar mirabilis		**0.6**	**0.6**	**1.1**	Kielan-Jaworowska 1970: tab. 2
Kamptobaatar kuczynskii		**0.8**	**0.6**	**1.1**	Kielan-Jaworowska 1970: tab. 2
Djadochtotheriidae					
Catopsbaatar					Kielan-Jaworowska & Sloan 1979:
catopsaloides	0.6	1.6	0.6	1.6	tab. 1
Djadochtatherium					Kielan-Jaworowska & Sloan 1979:
matthewi		1.5			tab. 1
Kryptobaatar					Kielan-Jaworowska & Dashzeveg
saichanensis	**0.8**	**0.8**	**0.9**	**1.3**	1978
Kryptobaatar dashzevegi	**0.8**	**0.8**	**0.8**	**1.2**	Kielan-Jaworowska 1970: tab. 2
Family *incertae sedis*					
Chulsanbaatar vulgaris	**0.5–0.6**	**1.0–1.1**	**0.4–0.5**	**1.3–2.2?**	Kielan-Jaworowska 1974: tab. 2
Bulganbaatar					
nemegtbaataroides			**0.5**	**1.2**	Kielan-Jaworowska 1974: tab. 2
Nemegtbaatar gobiensis			**0.5**	**1.8–1.9**	Kielan-Jaworowska & Sloan 1979: tab. 1
Superfamily *incertae sedis*					
Cimolomyidae					
Buginbaatar			**0.5**	**2.0**	Kielan-Jaworowska & Souchava
transaltaiensis					1969

covery of multituberculates from earlier in the Cretaceous of North America may reveal a group of post-'plagiaulacidan' North American multituberculates that are derived relative to known 'plagiaulacidans' in the structure of the last upper premolar, hence possibly requiring a new family designation. It is also possible that *Janumys erebos*, which lacks extensive development of pits and ribs, could represent a taxon from which certain species of *Paracimexomys* lacking ribbed cusps (e.g., *P. priscus*) could be derived (see discussion of *Paracimexomys* below).

cf. *Janumys erebos* gen. et sp. n.

Fig. 5G–I.

Material. — P4: 26640, 29573, V695.

Description and discussion. — OMNH 26640 (Fig. 5G–I) has a cusp formula of 4:5. The external cusp row consists of 4 cusps that are about the same height but which be-

come progressively smaller posteriorly. The cusps do not rest on a broadened antero-external platform but appear to rise directly from the labial sloping side of the tooth. The cusps are conical and deeply striated. There is a large notch at the anterior end of the central cusp row to accommodate the heel of P3. The cusps of the central row climb at a low angle with the fourth cusp being the tallest and the fifth cusp distinctly lower. There is no distinct posterior basin (PL:AP = 0.26), but there is a cusp at the posterior margin of the tooth in line with the central cusp row. There is a second posterior cusp lower and more lingually placed.

This P4 is clearly advanced over the condition seen in P5 of Jurassic 'plagiaulacidans', most notably in terms of its lateral compression, but the parallel cusp rows look very much like P4 and P5 of *Bolodon* (e.g., Kielan-Jaworowska & Ensom 1992: fig. 5 and pl. 5). Although OMNH 29573 is in the size range (AP = 1.57; LB = 0.73) of specimens included in *Janumys erebos*, it appears to represent either an extreme variant or another taxon.

OMNH 29573, an incomplete P4, has a lower cusp formula (2:4) than OMNH 26640 (4:5), but the two cusps of the external row are very large, exceeding the anterior cusps of the central row both in height and size. This tooth has a tiny posterior basin formed by a pit along the posterior margin of the tooth (PL:AP = 0.33). As with OMNH 26640, it is unclear if this represents variation within *Janumys erebos* or another taxon.

Suborder Cimolodonta McKenna, 1975
Family *incertae sedis*
Genus *Paracimexomys* Archibald, 1982

Species assigned: *Paracimexomys priscus* (Lillegraven, 1969), type species; *Cimexomys judithae* Sahni, 1972 (*partim*, at least one M1); and, tentatively, *P. magister* (Fox 1971).

Species removed from the genus, considered here as cf. *Paracimexomys*: *P. robisoni* Eaton & Nelson, 1991; *P. magnus* (Sahni, 1972); *?P. crossi* Cifelli, 1997; the M1 referred to *P. priscus* by Montellano (1992: fig. 5c); and many specimens referred to *Paracimexomys* sp. by Eaton & Nelson (1991) and Eaton (1995).

Revised diagnosis. — Molars with generally smooth enamel and lacking complex pitting and ribbing, although occasional pits may be present, unlike cf. *Paracimexomys* and *Eobaatar*. M1 (formula 4-5:4-5:1-2) with a short third cusp row (absent on *Cedaromys* or *Janumys*), better developed than on *Eobaatar*, and not as broadened as in *Bryceomys*; external and medial cusp rows of M1 diverge anteriorly unlike *Dakotamys*. Cusps of first molars alternate position (unlike *Cimexomys*) and are not crescentic but may slant anteriorly (M1) or posteriorly (m1). m1 (formula 4-5:3-4) has a waist in occlusal view unlike *Eobaatar* and *Dakotamys*; m2 relatively long compared to width (LB:AP = 0.77–0.81) as in *Eobaatar* and *Janumys*, but proportionally longer than in *Cedaromys* and *Bryceomys*; second to first molar length ratio is ~0.9, greater than in *Bryceomys*, but similar to *Dakotamys* and *Cedaromys*, and less than *Eobaatar* or *Janumys*.

Remarks. — Since initial recognition of *Paracimexomys* by Archibald (1982), this genus has become a frequent resting place for small, primitive species of North American, Cretaceous multituberculates lacking obvious affinities to more derived and better represented groups. As a result, the concept of the genus has been rather broad, and two taxa represented in the current sample are morphologically appropriate to fit this broad concept of *Paracimexomys*.

Resolution of these problems, together with formal systematic revision of *Paracimexomys* and similar taxa, are impossible based on the known fossil record: morphologically informative specimens, minimally including dentigerous jaws, are needed. Pending discovery and description of new material, we propose an interim solution whereby *Paracimexomys* is diagnosed on the basis of characters in which its type species, *P. priscus*, differs from other named genera. This presents the problem of taxonomic placement for the remaining species that have been referred to *Paracimexomys*: none of these clearly fits this diagnosis. These species are herein referred to cf. *Paracimexomys*, and we would anticipate that these would be placed in new genera in the future. To promote clarity and identify the most significant problems based on the current fossil record, we present a brief account of materials known for the various species, followed by an account of morphological variability seen among the fossils.

Taxa previously placed in *Paracimexomys*

The type species of *Paracimexomys*, *P. priscus* (Lillegraven, 1969), was described on the basis of Lancian fossils from Trochu, Alberta (Lillegraven 1969) and, subsequently, from the Lancian of Montana (Archibald 1982). A few isolated teeth are known from the Lancian localities of Wounded Knee (Fox 1989) and Gryde (Storer 1991). *P. priscus* has also been reported from two faunas of Judithian age: Wind River, Wyoming (Lillegraven & McKenna 1986); and Hill County, Montana (Montellano 1992). These Judithian specimens (both M1) differ somewhat from those of the Lancian (see below), and referral to the species should be regarded as uncertain.

Archibald (1982) also referred *Cimexomys magister* Fox, 1971 to *Paracimexomys*, a placement tentatively followed herein. Confident allocation to the genus will depend on better knowledge of the species, to include second molars. Archibald (1982: p. 112) considered placement in this genus probable for *Cimexomys judithae* Sahni, 1972. The M1 figured by Sahni (1972: fig. 10R) is very similar to M1 of *P. priscus* and we refer it to the genus. However, the holotype and most of the hypodigm should be retained in *Cimexomys* (Montellano 1992; Montellano *et al.* 2000). Archibald (1982) considered a referral to *Paracimexomys* possible for *C. magnus* Sahni, 1972. We formally exclude this species from *Paracimexomys* because the M1 of *C. magnus* does not have anteriorly diverging cusp rows and is deeply ribbed. Work in progress by JGE (manuscript in preparation) will result in transferal of *C. magnus* to another genus.

Eaton & Nelson (1991) referred two then-new species from the Cedar Mountain Formation, Utah, to *Paracimexomys*: *P. bestia* and *P. robisoni*. *P. bestia* is herein transferred to *Cedaromys* gen. n., described below. We formally exclude *P. robisoni* from *Paracimexomys*. The hypodigm of cf. *P. robisoni* includes one to a few of each major cheek tooth except p4 and M2; herein we describe two additional M1s that are questionably referable to the species. It should be noted that referral of P4 to the species was based on 'fit' with M1s in the sample, rather than morphological comparisons with other taxa. The cusp rows of the M1 in cf. *P. robisoni* do not diverge anteriorly and the specimens are heavily ribbed and pitted, unlike *Paracimexomys*. Other cf. *Paracimexomys* taxa in Eaton & Nelson (1991) and Eaton (1995) appear to have second to first molar length ratios that are significantly different from either cf. *P. robisoni* or *P. priscus*.

A final named species that has been tentatively referred to *Paracimexomys* is ?*P. crossi*, from the Aptian–Albian Antlers Formation of Oklahoma (Cifelli 1997). The

species is based on a single, somewhat abraded p4; additional specimens, currently under study by C.L. Gordon and colleagues, may eventually prove to be referable to the species; however, referral to this genus is doubtful. In the interim, we refer to the species as cf. *P. crossi*.

Aspects of variation in *Paracimexomys* and cf. *Paracimexomys*

Upper and lower fourth premolars. — Few ultimate premolars have been assigned to species (named or not) of *Paracimexomys* and cf. *Paracimexomys*. The p4 of *P. priscus* illustrated in Lillegraven (1969: fig. 3a, b) has a crest that is high relative to the deep anteroexternal lobe, but of moderate height in lingual view (estimated H:L = 0.65). The maximum height of the crest is reached posterior to the mid-point of the tooth (although this may reflect wear); ?8–10 serrations are present. The p4 referred to *P. magister* (see Fox 1971: fig. 2b) is somewhat different. Here, the anterior face is more vertical and the first serration is very strong, with a flattened crest as seen in labial view (no lingual view was presented). The single referred p4 has ?11 serrations. The p4 of cf. *P. crossi* differs from both those of *P. priscus* and cf. *P. magister* in a number of respects: it has fewer serrations (only seven appear to have been present), a less arcuate, more rectilinear profile in labial view; and the crown does not overhang the posterior root (Cifelli 1997).

The P4 has not been described for *P. priscus* and only a few teeth from this locus have previously been assigned to cf. *Paracimexomys* in general. Eaton & Nelson (1991: fig. 2D, E) figured P4s they referred to *P. robisoni*. Eaton (1995: fig. 6D, I) illustrated two P4s he assigned to *Paracimexomys* (as *P.* sp. cf. *P. robisoni* and *P.* sp. indet.). Each of these P4s has a cusp formula of 1:5, with a broadly expanded anteroexternal platform, a moderately well developed posterior basin (range of PL:AP = 0.37–0.47), and a moderate rate of climb for the cusps of the central row (range of CR = 0.50–0.55). No comparative statements can be made at this time, and, lacking P4 for *P. priscus*, characterization for the tooth cannot be made for *Paracimexomys*.

Cusp rows on M1. — The M1 of *Paracimexomys priscus* figured by Archibald (1982: fig. 39a) has both cusp rows clearly diverging anteriorly. The external cusp row is oriented along the anteroposterior axis of the tooth, while the medial cusp row narrows anteriorly such that it is oblique to the anteroposterior axis. Also, there appears to be distinct separation of the posteriormost cusp of the external row from the adjacent anterior cusp in unworn specimens. Both of these features (divergence of cusp rows, separation of posteriormost cusp) are also seen on M1 of *P. priscus* illustrated in Lillegraven (1969: fig. 10). However, the M1 illustrated as *P. priscus* in Montellano (1992: fig. 5c) has parallel cusp rows, with the external cusp row being very narrow and crest-like, so that the cusps of the external row form a continuous ridge. This specimen is of Judithian age, whereas the others are of Lancian age.

Similar variability is encountered among other M1s referred to species of *Paracimexomys*. Those of *P. magister* (Fox 1971: fig. 2c) and *Paracimexomys* sp. (Sahni 1972: fig. 10R, AMNH 77100; described as *Cimexomys judithae*, the type and other specimens are retained in *Cimexomys*; we follow Archibald 1982 in referring this specimen to *Paracimexomys*) are similar to Lancian M1s of *P. priscus* in that the cusp rows clearly diverge anteriorly and the last cusp of the external row is well separated. On the other hand, parallel cusp rows are seen in cf. *P. magnus* (Sahni 1972: fig. 10U,

AMNH 77120). Specimens of cf. *P. robisoni* illustrated by Eaton & Nelson (1991: fig. 2F–G) also have parallel cusp rows, both oblique to the molar axis. To further complicate matters, both variations are seen in specimens referred to cf. *Paracimexomys* from the Dakota Formation: several M1s of cf. *P.* sp. cf. *P. robisoni* (e.g., Eaton 1995: fig. 6E) have cusp rows diverging anteriorly, while others, referred to cf. *Paracimexomys* sp. indet. (e.g., Eaton 1995: fig. 6K), have parallel cusp rows.

Ornamentation on molars. — It is not certain whether ornamentation, in the form of complex ribbing and pitting, is a primitive character among cimolodontans, as the condition is seen among 'Plagiaulacida' in the 'plagiaulacid line' and in some members of the 'paulchoffatiid line', but absent in the 'allodontid lin e' (Kielan-Jaworowska & Hurum 2001). Such ornamentation is lacking from M1s of *Paracimexomys priscus* from the Trochu fauna (Lancian), described by Lillegraven (1969), and from molars referred to this species from the Hell Creek Formation (also Lancian) of Montana (Archibald 1982). An M1 referred to *P. priscus* from the Judithian of Wyoming does, however, show a few pits (Lillegraven & McKenna 1986: fig. 7I). In Judithian cf. *P. magnus*, complex pitting and ribbing is present (see Sahni 1972: fig. 10U), and this is also the case for molars of cf. *Paracimexomys robisoni* and cf. *P.* cf. *P. robisoni* previously described from the Cedar Mountain and Dakota formations (Eaton & Nelson 1991; Eaton 1995).

Waisting of first molars. — Waisting on the M1 consists of a constriction on both sides of the molar, near or posterior to the middle of the tooth. This feature is present on the Lancian specimens of *P. priscus* illustrated by Archibald (1982: fig. 39a) and Lillegraven (1969: fig. 10–1c). The waist on m1 of this species consists mostly of an indentation along the external side of the tooth, as the m1 illustrated by Archibald (1982: fig. 39c) shows no clear indentation on the lingual side. However, the waist appears better developed on the specimen illustrated by Lillegraven (1969: fig. 10-2b).

However, a medial constriction or waist is absent on many other first molars referred to species of *Paracimexomys*. Examples include M1 referred to *P. priscus* from the Judithian of Montana (Montellano 1992: fig. 5c), both m1 and M1 of *P. magister* (see Fox 1971: figs. 2c–d); and M1 of cf. *Paracimexomys* sp. (Eaton 1995: fig. 6J).

Proportions and relative length of second molars. — Lower second molars assigned to *Paracimexomys priscus* are distinctive in being (1) relatively long compared to their width (LB:AP = 0.81 based on Archibald 1982: table 1; LB:AP = 0.77 based on Lillegraven 1969: fig. 10); and (2) long relative to m1 (AP ratio of m2:m1 = 0.9, see Table 2A; also see Krause *et al.* 1992 for similar data). Other m2s referred to *Paracimexomys* by Eaton & Nelson (1991) are more squared (cf. *P. robisoni*, LB:AP = 0.88; cf. *P.* sp. n. A, LB:AP = 0.94; cf. *P.* sp. n. B, LB:AP = 1.0), as are those referred to that genus by Eaton 1995 (cf. *P.* sp. cf. *P. robisoni*, LB:AP = 0.91; cf. *Paracimexomys* sp., LB:AP = 0.97). The m2:m1 length ratios of specimens assigned to cf. *P.* sp. cf. *P. robisoni* in Eaton (1995) are appropriate for *Paracimexomys* (m2:m1 = 0.97); however, other of the cf. *Paracimexomys* taxa in Eaton & Nelson (1991) (cf. *P. robisoni*, m2:m1 = 0.78; cf. *P.* sp. n. B, m2:m1 = 0.81) and Eaton (1995) (cf. *P.* sp., m2:m1 = 0.79) are lower than for *P. priscus*.

Upper second molars assigned to *P. priscus* are similar in proportions to the lower second molars (LB:AP = 0.82; M2:M1 = 0.9). No upper second molars were assigned to *Paracimexomys* in Eaton & Nelson (1991). The M2s assigned to *Paracimexomys* in Eaton (1995) are, as in the case of the m2s, more squared than in *P. priscus* (cf. *P.* sp. cf.

P. robisoni, LB:AP = 0.91; cf. *P.* sp., LB:AP = 0.92). The M2:M1 length ratio (0.92) for cf. *P.* sp. cf. *P. robisoni* in Eaton (1995) is appropriate for *Paracimexomys*, but the M2:M1 of cf. *P.* sp. is only 0.74.

This suggests there are some significant and consistent proportional differences in second molars of cf. *Paracimexomys* taxa relative to *P. priscus.* No second molars were assigned to *P. magister* (Fox 1971), cf. *P. magnus* (Sahni 1972), or cf. *P. perplexus* (this paper) so it is not possible to assess these features in those taxa.

It should also be noted that the M2 of *P. priscus* illustrated by Archibald (1982: fig. 39b) has a constriction on both sides of the molar posterior to the midpoint of the tooth and this has not been observed on any of the M2s assigned to various species of cf. *Paracimexomys.*

cf. *Paracimexomys perplexus* sp. n.

Table 1A, B; Figs. 6, 7.

Holotype: OMNH 27615, M1, V794.

Distribution: Cedar Mountain Formation, near the Albian–Cenomanian stage boundary, San Rafael Swell, Utah.

Derivation of the name: Latin, *perplexus* – perplex, in reference to the debatable affinities of the species.

Material. — m1: 25590, 25591, 29759, 29760, 32933, V235; 25665, 25748, 27241, 29705, V239; 26615, 26616, 29592, 29594, 29596, 33176, 33179, 33181, V695; 29664, V696; 27623, 27624, 27625, 27626, 30542, 30543, 30547, 30549, 30555, 33988, 33989, 33990, 33991, V794; 33002, 33007, V868. P4: 29755, 32926, V235; 26642, V695; 30529, V794. M1: 26399, 26400, 32932, 32934, V235; 25751, V239; 29728, 29729, V694; 26624, 26674, 27450, 27451, 27516, 27517, 29574, V695; 27580, 27615, 30531, 33982, 33983, V794 (also specimens referred to ?*Paracimexomys* sp. n. B in Eaton & Nelson 1991).

Diagnosis. — Cusp rows of M1 diverge anteriorly as in *Paracimexomys priscus.* Smaller than cf. *Paracimexomys robisoni* and *P. priscus.* First molars with more external cusps than most specimens of *Paracimexomys and cf. Paracimexomys* (m1 – 5:3; M1 – 5:4:1). Pits present in molar valleys, more than in *P. priscus* but not as common or well-developed as in *Cedaromys* and *Bryceomys.* Molar cusps ribbed as in *Dakotamys* but unlike *P. priscus.* Upper molar cusps lean anteriorly unlike *Cedaromys* and *Bryceomys* but as in *Paracimexomys* and cf. *Paracimexomys.* P4 (?) cusp formula 1–2:4, less than in *Bryceomys* (2:5) or *Dakotamys* (3:6); high rate of cusp climb (CR = 0.51), greater than in *Dakotamys* and *Janumys*, but less than in *Cedaromys.*

Description. — **m1** (Fig. 6A–C): Cusp formula 5:3. Some specimens show an indentation ('waist') on the labial side of the tooth in the position of the third cusp of the external row (OMNH 33988, Fig. 6A). The first cusp of the external row is low and small. A pit is present low on the labial side of the tooth below the first cusp (OMNH 25748, Fig. 6B). The second and third cusps are conical anteriorly and concave posteriorly. The valley separating the first and second cusp is open into the central valley but is not as low as the valley on some specimens (OMNH 25748, Fig. 6B), though it does reach the floor in others (OMNH 33988, Fig. 6A). The valley between the second and third cusps is very deep and is closed both lingually and labially. When worn deeply these valleys tend to extend into the central valley but remain closed labially. The fourth cusp is small and the
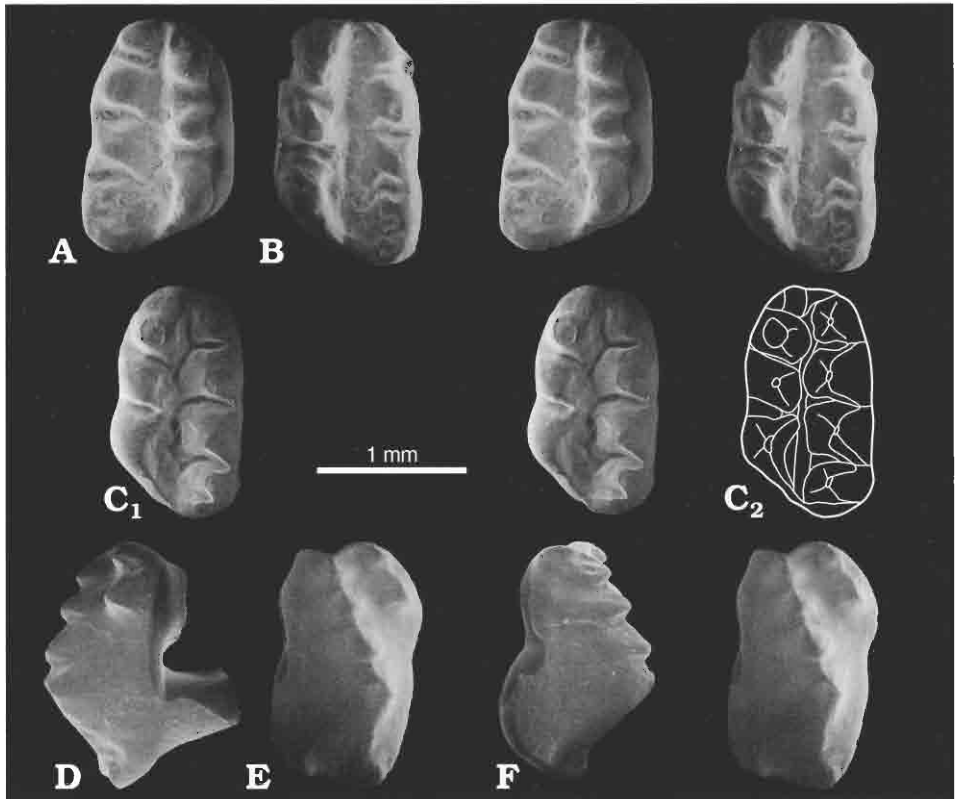
Fig. 6. cf. *Paracimexomys perplexus* sp. n. **A**, Lm1 (33988); **B**, Rm1 (25748); **C**, Rm1 (29760); **D–F**, LP4 (29755). **A–C₁**, **E**, occlusal stereopairs; **C₂** explanatory drawing for C₁; **D**, labial view; **F**, lingual view.

fifth cusp is formed by a slight elevation of the ridge just posterior to the fourth cusp. They are clearly distinguished as two separate cusps on OMNH 25748 (Fig. 6B) by the presence of two distinct wear surfaces that appear to be formed as a subdivision of the posterior cusp. On other specimens, such as OMNH 33988 (Fig. 6A), the fourth and fifth cusps are the same size and are clearly separated. There is wear on the labial side of cusps 3–5 suggesting the presence of a third cusp row on the upper first molar. The first cusp is the lowest of the row, the second and third cusps are worn to approximately the same height, and the fifth cusp is the tallest of the row (OMNH 25748, Fig. 6B) or beveled to the same level as cusps 2–4 (OMNH 33988, Fig. 6A).

The central valley is slightly sinuous on some specimens (e.g., OMNH 25748, Fig. 6B; OMNH 33988, Fig. 6A) but is more strongly sinuous on other specimens (OMNH 29760, Fig. 6C, and there is evidence of pitting and ribs OMNH 33988, Fig. 6A). On well worn teeth the central valley appears to be straight (OMNH 26616). The first cusp of the internal row is conical and has an anteromedially directed ridge that connects to the central valley. The valley between the first and second cusp is shallow on OMNH 25748 (Fig. 6B) but is much deeper on OMNH 29760 (Fig. 6C). The second cusp is rounded anteriorly and is concave on its posterior face. The cusp apices are shifted posteriorly on both the first and second cusp. The first and second cusps have crenulations

or ribs on their labial side. The valley separating the second and third cusps is as deep or deeper than that separating the first and second cusp. The valleys are closed off from the central valley but are open lingually. The third cusp is somewhat blade-like. In an unworn state the second cusp is slightly taller than the other two (OMNH 33988, Fig. 6A), but with apical wear all three cusps are of equal height.

P4 (Fig. 6D–F): Cusp formula 1–2:4. On OMNH 29755 the anteroexternal platform is expanded labially and bears a small first cusp and a larger second cusp. The apices of the cusps are weakly striated. A strong notch is present at the anterior end of the central cusp row for the posterior end of the preceding premolar. A low ridge connects this invagination to the first cusp of the external row. The central cusp row climbs steeply, with the third and fourth cusps closely approximated and of about the same height. A ridge descends from the last cusp of the central row into the open posterior basin. The posterior basin comprises 46% of the tooth length. OMNH 29755 is broad relative to its length (LB:AP = 0.57). OMNH 32926 is not as broad relative to length as OMNH 29755 (LB:AP = 0.46) and has a broadly expanded anteroexternal platform bearing a single cusp.

M1 (Fig. 7A–E): Cusp formula 5:4:1–2?. The first cusp of the external row is small and low, shifted slightly lingual of the other cusps of the row, and has a ridge originating near its apex that descends lingually across the front of the central valley. Another ridge connects posteriorly to the low, conical second cusp that may bear many fine ribs (OMNH 26624, Fig. 7A). Anteroposteriorly oriented ribs form ridges that connect the cusps of the row. On some specimens (e.g., OMNH 26400, Fig. 7B), there is a deep pit present labial of the ridge connecting the first and second cusps. The second cusp is less worn lingually than the three more posterior cusps. This sharp ridge continues posteriorly linking the conical cusp 3 and the smaller cusp 4 on most specimens, but on OMNH 27580 (Fig. 7C) the valley is deep and opens into the central valley. The fourth and fifth cusps are formed by the subdivision of the posterolingual ridge. The cusps of the external row are small and narrow relative to the surface area of the tooth and are formed more as a series of small cusps connected by a low sharp ridge, than as a series of cusps divided by valleys. These cusps may bear ribs on their labial side (OMNH 29729, Fig. 7D). The third (middle) cusp of the row is the lowest, as the overall shape of the tooth in side view is concave (OMNH 27615, holotype, Fig. 7E) with relatively little wear; with greater wear the row can be beveled progressively lower posteriorly (OMNH 26624, Fig. 7A; OMNH 26400, Fig. 7B). The external row forms a high, continuous wall that closes off the central valley.

The central valley is essentially straight, somewhat oblique to the anteroposterior axis of the tooth. It is broad, with crenulated enamel and occasional deep pitting (OMNH 29729, Fig. 7D). The valley is closed posteriorly and only opens after considerable wear, in which case it exits at the posterolabial corner of the tooth where the fifth cusp of the external row is obliterated by wear (OMNH 26400, Fig. 7B). Cusps of the internal and external row diverge slightly anteriorly, particularly if the first cusp of the external row is ignored, as it is shifted lingually. Cusps are offset and alternate position from row to row.

The cusps of the medial row form anteroposteriorly elongated pyramids, with cusp apices shifted anteriorly. The valleys separating them are narrow, deep, and closed labially (OMNH 26400, Fig. 7B). The first three cusps of the central row are of about the same length but broaden posteriorly. The cusps bear many vertical ribs. The first cusp is the lowest and is conical; the remaining cusps increase in height posteriorly. The sec-

ond cusp is subpyramidal and the apex of the cusp is shifted anteriorly such that there is a broad separation between the apices of the second cusp and the very similar but larger third cusp (OMNH 26624, Fig. 7A). The valley separating cusps 3 and 4 extends to the lingual margin of the tooth. The fourth cusp has a smaller base than the third, is the tallest cusp of the tooth, and forms a distinct point on the posterior wall of the tooth. The first, third and fourth cusps are taller than the second (OMNH 29729, Fig. 7D) due to the concave shape of the tooth.

The internal cusp row is represented by a small but distinct platform, developed as a lingual expansion of the posterior wall of the tooth on some specimens (OMNH 27615, Fig. 7E). On one specimen there is a slight swelling that has not been fully formed into a platform (OMNH 26624, Fig. 7A), but the enamel along that side of the tooth suggests the possibility of abrasion due to post mortem transport. The platform may also be separated from the main body of the tooth by a series of deep pits (OMNH 29729, Fig. 7D). The number of cusps present on the platform (on specimens where it is developed) is probably one, but all that remains after wear is the platform itself. On some specimens the adjacent internal cusp is beveled to the level of the platform, but on more moderately worn specimens the single conical cusp shows no wear (OMNH 27580, Fig. 7C). It may be that the internal cusp does not come into occlusal contact until there has been substantial wear.

Discussion. — The lack of p4, m2, or M2 is puzzling considering the size of the sample; however, p4s are in general very rare among the smaller specimens in this collection and we ignored the large number of worn second molars. No specimens were assigned to this taxon solely on the basis of size; appropriate morphology was also required. Among the m1s, the largest specimens (OMNH 33002, 33006, 33007, 33008) are all from locality V868, perhaps suggesting that a sub-population of larger individuals is represented there.

The m1s are smaller than specimens assigned to cf. *P. robisoni* (Eaton & Nelson 1991: table 1, size range of cf. *P. robisoni*: AP = 2.0–2.1; LB = 1.2–1.3; the mean of cf. *P. perplexus*: AP = 1.64; LB = 0.96) and are in the size range of ?*Paracimexomys* new sp. B (Eaton & Nelson 1991: AP = 1.6; LB = 1.1).

The referred P4s have a very strong anterior recess for the preceding premolar and fit well with five- to six-cusped permanent (?) premolars described below. If these five- to six-cusped premolars do belong with this taxon, it is unlikely that they represent P3 (see discussion with the anterior upper premolars below). Hence, the teeth termed P4 here (due to their morphologic similarity with P4s of Late Cretaceous taxa and uncertainties surrounding identification of isolated anterior upper premolars in general) may actually represent P5. As for *Janumys erebos*, data in hand suggest the possibility that five upper premolars may have been present in cf. *Paracimexomys perplexus*. The upper premolar formula cannot be established for any species previously referred to *Paracimexomys*.

The M1s of this taxon are markedly different from those of *Cedaromys parvus* gen. et sp. n. Proportionally, they are narrower relative to length (cf. *P. perplexus*, LB:AP = 0.62; for *Cedaromys parvus*, LB:AP = 0.63, but there is no third cusp row on *Cedaromys*). The molars of cf. *P. perplexus* consistently have a waist in occlusal view, distinct divergence of cusp rows, well ribbed molar cusps but unpitted central valleys, a third cusp row, and they are somewhat concave in side view. These M1s are smaller
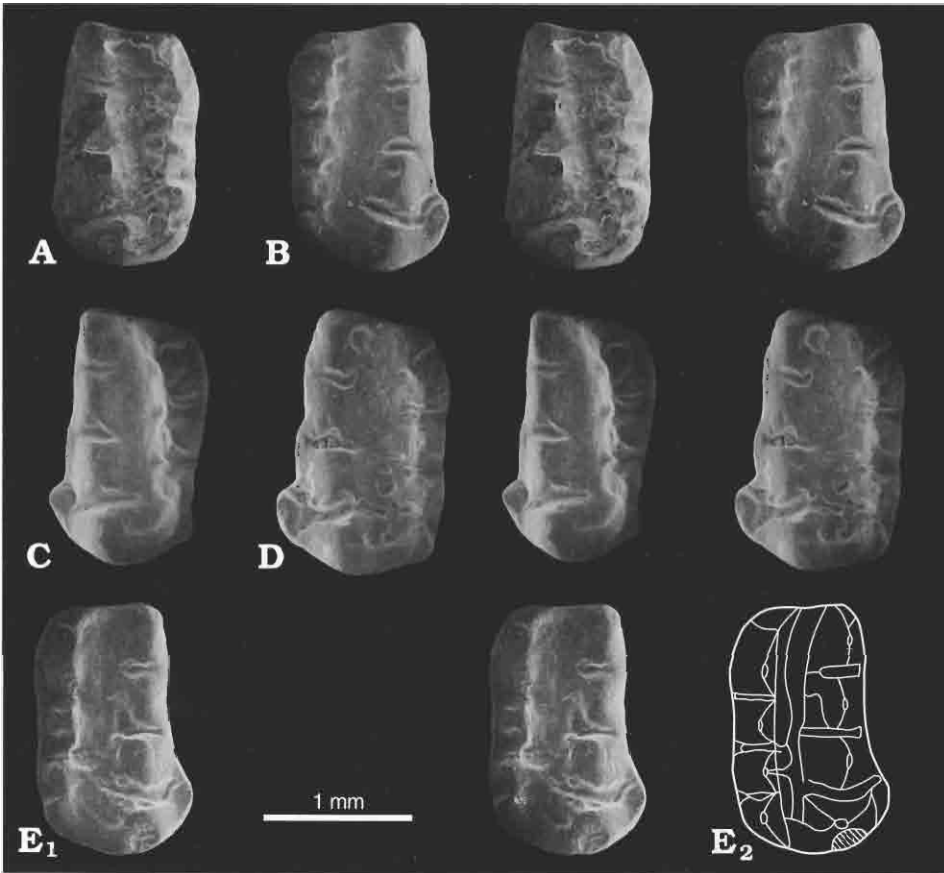
Fig. 7. cf. *Paracimexomys perplexus* sp. n. **A**, LM1 (26624); **B**, RM1 (26400); **C**, LM1 (27580); **D**, LM1 (29729); **E**, RM1 (27615, holotype). Occlusal stereopairs except E_2, which is explanatory drawing for E_1.

than those assigned to cf. *P. robisoni* (Eaton & Nelson 1991: table 1, AP = 2.1–2.3, LB = 1.3; mean values for cf. *P. perplexus*: AP = 1.71; LB = 1.06). The known M1s of cf. *P. robisoni* have a cusp formula of 4:4:1 and there appears to be an additional external cusp in this species. The slight shift of apices of the second and third cusp of the medial row appears to foreshadow the eventual development of crescentic cusps. No such tendency is evident on the molars of *Cedaromys*.

Overall, cf. *P. perplexus* is morphologically most similar to species currently referred to *Paracimexomys* (see Table 3). Pending resolution of the affinities among these taxa, which we believe is not possible with available fossils, we provisionally refer this species to cf. *Paracimexomys*, as explained in the foregoing account of the genus. We note, however, that this referral is problematic for several reasons above and beyond those previously mentioned in connection with the status of this 'genus' in general. The cusp formula for the external row of first molars is slightly greater (5 as opposed to 4) than illustrated specimens of *Paracimexomys* and cf. *Paracimexomys*. Conversely, the P4 formula is less than for specimens assigned to cf. *Paracimexomys* (Eaton 1995). Unfortunately, no second molars included in the available sample can be

Table 3. Morphologic comparisons of mid-Cretaceous North American multituberculates to *Eobaatar* and *Paracimexomys priscus* (*P. = Paracimexomys*).

Tooth	Character	Eobaatar	Janumys	Cedaromys	Bryceomys	Dakotamys	cf. P. perplexus	P. priscus
I	enamel	restricted	covered?	covered	covered	covered		covered
p4	height of blade, H:L	0.66		0.60–0.66	0.58	0.53–0.58		0.65
	number of serrations	9–10		9–10	8–11	9–10		8?–10
m1	cusp formula	4:3	4:3	4:3	4:3	4:3	5:3	4–5:3–4
	shape of central valley	straight	sinuous	sinuous	sinuous	straight	sinuous	sinuous
	pits and ribs	ribs	none	both	both	ribs	both	rare pits
	width relative to length, LB:AP	0.72	0.60	0.64–0.65	0.60–0.62	0.58	0.58	0.61
	waist in occlusal view	no	none-slight	none-slight	none-slight	no	yes	yes
	length m1:p4	0.52	0.63	0.56–0.59	0.56–0.66	0.72		0.68
m2	width relative to length, LB:AP	0.76	0.80	0.94–0.95	0.89–0.91	0.84		0.77–0.81
m2:m1	AP length ratio	1.16	0.96	0.88–0.94	0.70?–0.78	0.86		0.93
Ps	number of upper premolars	5	5?	4	4?	4?	5?	?
P4 (P5)	cusp formula	(P5) 2:4	1–3:4	2:4	2:5	3:6	1–2:4	
	rate medial cusp row climb, CR		0.26	0.58–0.60	0.47	0.38	0.51	
	Ant. width < or > post. width	(P5) A>P	A>P	P>A	A>P	A>P	A=P	
	swelling of anteroext. platform	strong	slight	slight	moderate	strong	strong	
	posterior basin, PL:AP length	0	0.31	0.34–0.49?	0.35	0.35	0.45	
	width relative to length, LB:AP	(P5) 0.7	0.55	0.49–0.53	0.50	0.50	0.49	
M1	orientation of cusp rows	parallel	parallel	parallel	parallel	parallel	diverge	diverge
	cusp formula	3:4	3–4:4	3:4	3–4:4:2–3	4–5:4:2	5:4:1–2?	4–5:4–5:1–2
	development internal cusp row	slight	none-slight	none	strong	moderate	moderate	moderate
	pit at anterolabial corner	no	no	yes	yes	yes	yes	no
	pitting and ribs	ribs	none	both	both	strong ribs	ribbed	rare pits
	width relative to length, LB:AP	0.64	0.54	0.62	0.65–0.68	0.58	0.62	0.60
M2	width relative to length, LB:AP	0.9		0.84	0.84	0.84		0.82
	expansion of labial ridge area	moderate		moderate	broad	broad		moderate
M2:M1	AP length ratio	0.94		0.93–0.94	0.76–0.81	0.80		0.89

confidently referred to cf. *P. perplexus*. Thus, determination of the ratio between lengths of second and first molars, an important diagnostic character (see above), is impossible. Three morphologically appropriate M2s are described below under the heading cf. *Paracimexomys* sp. cf. *P. perplexus*. Comparison of these teeth to the M1s formally assigned to cf. *P. perplexus* yields an M2:M1 length ratio that is extremely low (0.71) compared to that of *P. priscus* (0.90, see Table 2A). These results suggest two alternative possibilities: (1) the M2s in question do not belong to cf. *P. perplexus*; or (2) cf. *P. perplexus* differs significantly in this respect from *P. priscus*, a difference probably warranting generic separation. A defensible selection between these alternatives cannot be made on the basis of available data.

Another complexity in generic placement is the presence of strong ribbing and pitting on the first molars of cf. *P. perplexus*. This character state is presumed to be primitive; it is present, for example, in all Plagiaulacidae (see family diagnosis, Kielan-Jaworowska & Ensom 1992). Unsurprisingly, ribbing and pitting on M1 is a common feature among many early Late Cretaceous multituberculates (Eaton 1995). However, such ornamentation is lacking (presumed to represent the derived condition) in other relevant taxa, most notably the type species of *Paracimexomys*, *P. priscus*. The intrageneric variation implied by formal referral of cf. *P. perplexus* to *Paracimexomys* is unsettling, to say the least, if molar ornamentation is viewed as an important diagnostic trait in interpreting the higher-level phylogeny of Multituberculata (see discussion below).

cf. *Paracimexomys* sp. cf. *P. perplexus* sp. n.
Fig. 8A, B.

Material. — M2: 29758, 32936, V235; 27561, V695.

Description and discussion. — **M2** (Fig. 8A, B): Cusp formula Ri:2:3.The width (mean LB = 1.00) and morphology of these M2s appear to be appropriate for cf. *Paracimexomys perplexus*; however, the length of these M2s (mean AP = 1.21) implies an M2:M1 length ratio (0.71) that differs substantially from that of *P. priscus* (0.89) (see Table 2A) and casts doubt on potential referral of these specimens to cf. *P. perplexus*. OMNH 27561 (Fig. 8A) has a small inset on the anterior face to accommodate the posterior part of M1. There is a moderately developed anteroexternal platform with a weak cusp at its corner on OMNH 27561 (Fig. 8A). The platform is less broadly expanded, with a more distinct cusp at the corner, on OMNH 32936 (Fig. 8B). The first cusp of the external row is essentially conical and merges with the anterior wall of the tooth. This cusp is the largest of the tooth and is strongly ribbed. These ribs extend into the central valley, but wear in the central valley precludes observation of whether these ribs crossed the valley. No other evidence of ribbing or pitting is present on the tooth. The first cusp is widely separated from the second cusp of the external row. The central valley is broad, straight, and smooth. The first two cusps of the internal row are shorter than the third. The cusps are divided labially by equal-sized valleys, and the apices of all three cusps are distinctly, but only slightly separated.

The ribs on the first cusp of the external row of M2 may have crossed the central valley, as is the case in *Bryceomys*. If so, however, the character is less well developed than in *Bryceomys*, from which these M2s differ further in lacking the distinct pit anterolabial of the first cusp of the internal row, as seen on M2 of *Bryceomys*. The teeth are similar to those of *Paracimexomys* and cf. *Paracimexomys* in having a narrow
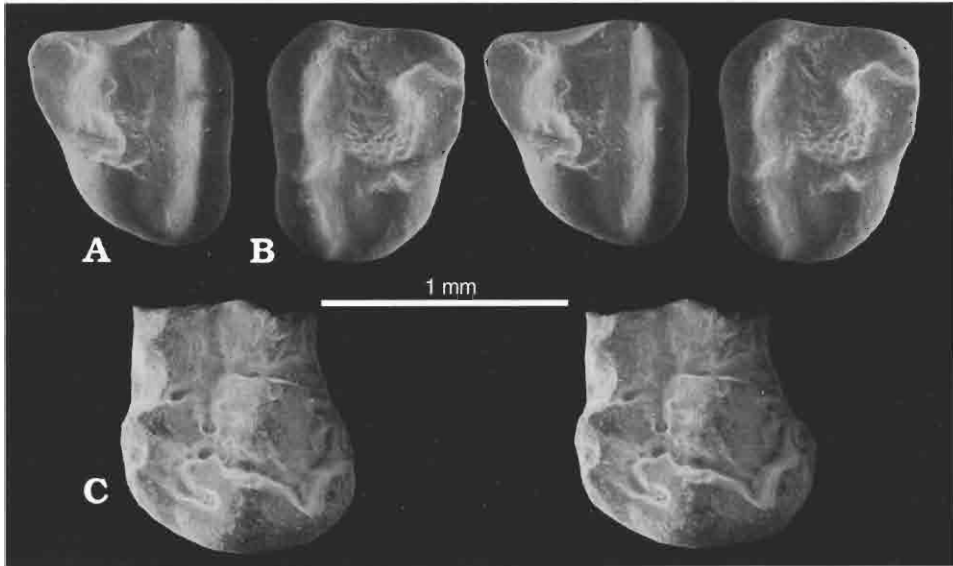
Fig. 8. cf. *Paracimexomys* sp. cf. *P. perplexus* sp. n. (**A, B**), and cf. *P.* sp. cf. *robisoni* (**C**). **A**, RM2 (27561); **B**, LM2 (32936); **C**, RM1 (25733). Occlusal view, stereopairs.

anteroexternal platform, in lacking a robust central cusp (first cusp of external row), and in the tapering (rather than square) posterior margin. The specimens appear to be too small to belong to cf. *Paracimexomys robisoni*. Direct comparison is not possible, however, because no M2s were included in the hypodigm by Eaton & Nelson (1991).

cf. *Paracimexomys* cf. *P. robisoni* Eaton & Nelson, 1991
Fig. 8C.

Material. — M1: 25733 (partial), V239; 27660, V823; 33959, V868.

Description and discussion. — **M1** (Fig. 8C): Three incomplete M1s are included here largely on the basis of their width (range of 1.17–1.28, mean = 1.25; range for cf. *P. robisoni* in Eaton & Nelson 1991: 1.2–1.3) and the presence of a distinct but short third row of cusps developed at the posterolingual corner of the tooth. On OMNH 25733 (Fig. 8C) the third row bears two cusps, the first is small and low and the second is tall and well developed. The molars bear complex pitting and ribbing, unlike *P. priscus*.

cf. *Paracimexomys robisoni*, described by Eaton & Nelson (1991), was based on 12 specimens. In the larger collection now at hand, few additional specimens are morphologically close to those originally described. It seems likely that the occurrence of this species is restricted geographically (as appears to be the case for other mammals known from the unit, Cifelli & Madsen 1999) or stratigraphically. These M2s are similar to those included in cf. *P. robisoni* by Eaton & Nelson (1991), but are not sufficiently complete to be formally referred to the species.

Bryceomys Eaton, 1995
Bryceomys intermedius sp. n.
Table 1A, B; Figs. 9, 10.

Holotype: OMNH 33001, V868, m1.

Distribution: Cedar Mountain Formation, near the Albian–Cenomanian stage boundary, San Rafael Swell, Utah.

Derivation of the name: In reference to its morphological intermediacy between *Cedaromys* and *Bryceomys* spp.

Material. — p4: 32929, V235; 34004, 34005, V794. m1: 33174, V695; 27661, V823; 33004, 33006, 33961, V868. m2: 32942, V235; 26626, 26632, 33190, 33192, V695; 30563, 30564, 30566, 30569, V794. P4s: 32985, 33958, V868. M1: 25735, V235; 27553, V695. M2: 29756, V235; 27242, V239; 26679, 27453, V695; 30532, V794 (as well as MNA V5816, P4 (partial), originally described as *Paracimexomys* sp. n. A in Eaton & Nelson (1991).

Diagnosis. — Intermediate in size between *Bryceomys fumosus* and *B. hadrosus*, and morphologically between *Cedaromys* and other species of *Bryceomys*; p4 with a distinct and widely separated first serration as in *Cedaromys*, but not later species of *Bryceomys*, and H:L (0.58) ratio closer to later species of *Bryceomys* (0.56) than in *Cedaromys* (≥0.60). P4 with large anterior notch for P3, as in *Cedaromys*, but with a cusp formula (2:5) as in *Bryceomys*. Molars narrower relative to width than in *Cedaromys*, but not as narrow as later species of *Bryceomys*. M1 with wide, long (~50% of tooth length) internal (3rd) cusp row, unlike species of *Cedaromys*, *Paracimexomys*, cf. *Paracimexomys*, or *Dakotamys*.

Description. — **p4** (Fig. 9A, B): Relatively high crowned, arcuate, with 8?–10 serrations, 5–6 internal ridges, and 6 external ridges. The H:L ratio on the two measured specimens ranges from 0.56–0.62. On OMNH 34405 (Fig. 9A, B) the first cusp is very strong and is placed anteriorly, just above the short anterior face of the blade. The first and second cusps are widely separated and cusps 2, 3, and 4 are about equally separated. The maximum height of the blade is reached at the fourth cusp on all specimens. The posterior crest of the blade is worn flat by apical wear making the total number of cusps uncertain (estimated at 8 on OMNH 34405). There is a weak posteroexternal cusp below the strong worn face of the blade that slopes anteroventrally. Ridges on both side of the blade are widely spaced with their separations increasing ventrally.

   m1 (Fig. 9C, D): Morphologically very similar to m1 of *Cedaromys parvus* sp. n., but shorter and narrower. Cusp formula of 4:3. The first cusp of the external row is low, the lowest of the tooth, and is completely separated from the second cusp by a deep transverse valley at the level of the central valley. This transverse valley terminates labially in a small depression (OMNH 33001, holotype, Fig. 9C) that can form a protruding basin (OMNH 27661, Fig. 9D). The second cusp is rounded anteriorly, exhibits no wear on the lingual side of the cusp, and is concave posteriorly (OMNH 33001, Fig. 9C). The second cusp is the largest of the row in all specimens referred to this species, as is the condition in *Cedaromys parvus* sp. n. The valley separating the second and third cusps is broad and deep, but is not open labially as is the valley between the first and second cusps. The third cusp is smaller than the second or fourth cusp and is separated from the fourth cusp by a deep, closed pit that is not open to the central valley. The third cusp is pyramidal with a concave posterior wall and is connected labially to the fourth cusp by a ridge. The fourth cusp of OMNH 33001 (Fig. 9C) is low and indistinct but the less worn cusp of OMNH 27661 (Fig. 9D) is complexly pitted and ribbed. The second cusp of the row is
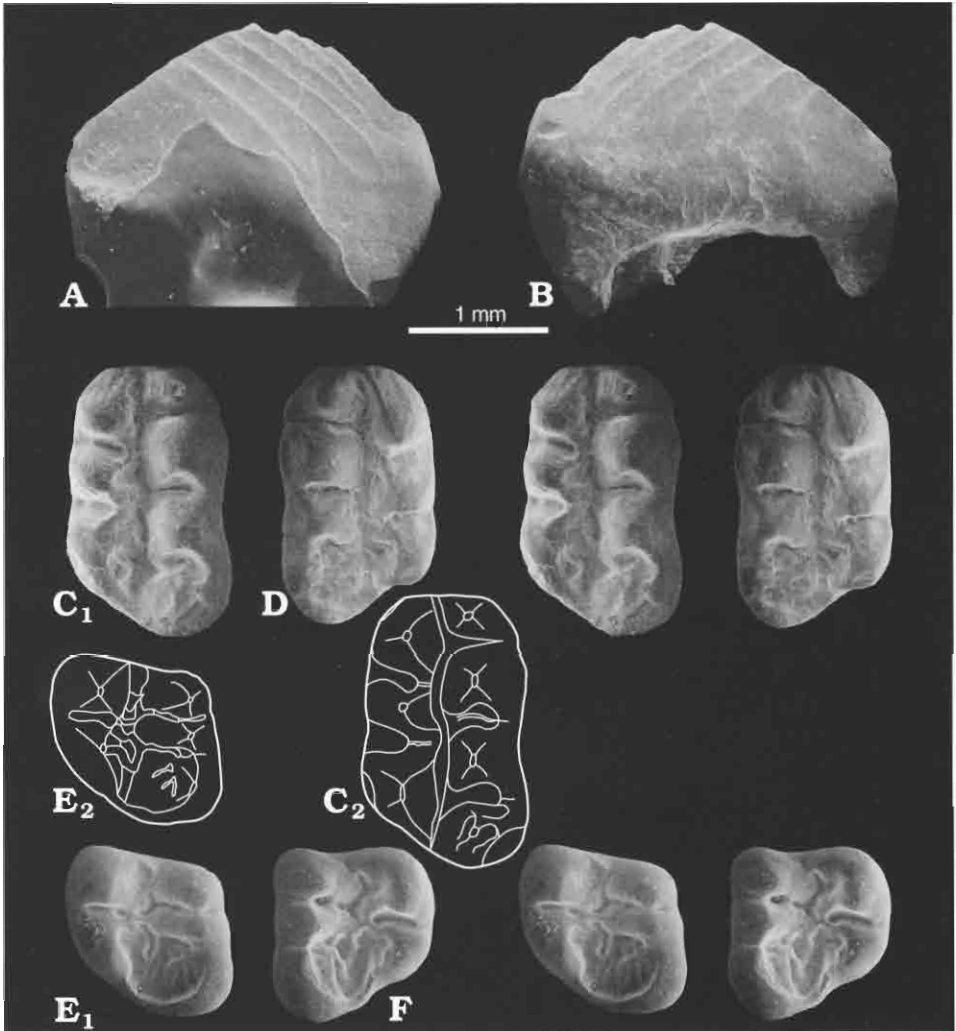
Fig. 9. *Bryceomys intermedius* sp. n., lower dentition. **A**, **B**, Rp4 (34405); **C**, Rm1 (33001, holotype); **D**, Lm1 (27661); **E**, Rm2 (26626); **F**. Lm2 (26632). **A**, labial view; **B**, lingual view; **C₁**, **D**, **E₁**, **F**, occlusal stereopairs; **C₂**, **E₂**, explanatory drawings for C_1 and E_1, respectively.

the tallest and the third and fourth cusps are worn progressively lower posteriorly. The central valley is sinuous and is deeply pitted posteriorly.

The cusps of the internal row have vertically oriented ribs on their labial sides. The first cusp is tall and divided by a deep valley from the second cusp, but it does not open into the floor of the central valley, as the valley is closed off by ribs at the labial corners of the adjacent cusps. The second cusp is slightly taller than the first cusp and is rounded on the anterolingual corner but squared on the other three corners. The cusp has a concave posterior face. The third cusp is the tallest and longest cusp of the tooth on OMNH 33001 (Fig. 9C), but the second cusp is slightly taller on OMNH 27661 (Fig. 9D). It is separated from the second cusp by a deep valley that is open lingually

but is closed to the central valley. A posterior wall closes off the central basin on OMNH 27661 (Fig. 9D) and there is a distinct notch on the posterior wall just lingual of the central valley.

One m1 (OMNH 33174) of the sample is similar in length to the others, but differs in being relatively broader (AP = 1.83; LB = 1.25; LB:AP = 0.68). It is proportionally similar to those of *Cedaromys parvus* sp. n. but is smaller, and differs in having a distinct indentation at the anterior end of the tooth, between the first cusp of each row.

m2 (Fig. 9E, F): Cusp formula 3:2. The first cusp of the external row (OMNH 26626, Fig. 9E) is relatively wide and anteroposteriorly narrow; it is poorly separated from the slightly taller second cusp. The valley separating the two cusps slopes into the central valley and can be formed by deep pits (OMNH 26632, Fig. 9F). Posterior to the second cusp is a long ridge, slightly lower than the apex of the second cusp, with no indication of a distinct cusp. The ridge is complexly crenulated, closes the posterior end of the tooth, and connects to the back of the second cusp of the internal row. The central valley is complex with deep pits and ribs crossing it. On OMNH 26626 (Fig. 9E) the connection between the first cusp of the internal row to the second cusp of the external row is weak, but on OMNH 26632 (Fig. 9F) it is strongly developed.

The first cusp of the internal row is broad, rounded anteriorly, and squared posteriorly, with the apex of the cusp shifted posteriorly. The first cusp may be anteroposteriorly shorter (OMNH 26626, Fig. 9E) but is always taller than the second cusp and the valley separating it from the second cusp is deeper lingually than the valley separating the first two cusps of the external row, but is still higher than the floor of the central valley.

P4 (Fig. 10A–C): Cusp formula 2:5. There is a distinct recess at the anterior end of the tooth, immediately in front of the central cusp row, allowing for a posterior projection of the P3. The anteroexternal platform is moderately expanded (OMNH 33958, Fig. 10A–C). There is also a swelling on the opposite (lingual) side of the tooth such that the anterior of the tooth is broader than the posterior. The cusps of the external row are well striated and the first cusp is smaller than the second. The cusps of the central row are striated, climb steeply, and increase in size posteriorly. A sharp ridge descends from the last cusp of the central row, connecting it to the labial cusp of the posterior basin. A low but distinct wall closes the posterior basin and the enamel in the basin is crenulated.

M1 (Fig. 10D): Only two M1s potentially belonging to this taxon were identified. Both specimens are very worn and one (OMNH 27553) is incomplete. Characteristic of both specimens is a broad third internal cusp row with 2–3 cusps. On OMNH 25735 (Fig. 10D) the internal cusp row bears 3 distinct cusps. The row extends slightly less (45%) than the total length of the tooth, where it connects to the second cusp of the medial row. The internal platform is separated from the main body of the tooth by deep pits.

The cusps of the external row are not divided to the depth of the central valley. In this very worn specimen the row is worn lower posteriorly such that the first cusp of the row is the tallest of the tooth. The central valley is broad and the internal and external cusp rows are parallel.

M2 (Fig. 10E–G): Cusp formula Ri:2–3:3–4. A ridge completely surrounds the anterolabial part of the tooth (OMNH 26679, Fig. 10F). Although the ridge is broadly separated from the first cusp of the external row, there are two small crests
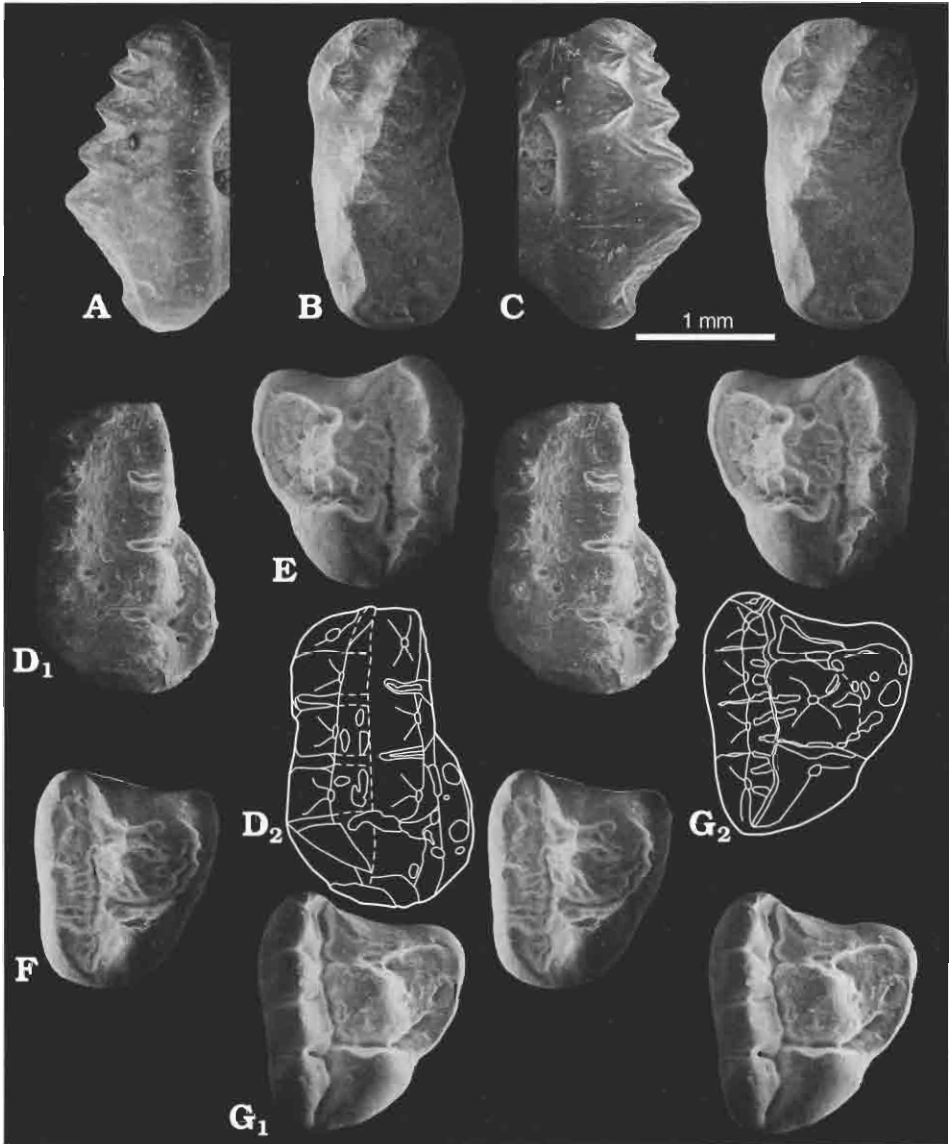
Fig. 10. *Bryceomys intermedius* sp. n., upper dentition. **A–C**, RP4 (33958); **D**, RM1 (25735); **E**, RM2 (29756); **F**, LM2 (26679); **G**, LM2 (27242). **A**, lingual view; **B**, **D₁**, **F**, **G₁**, occlusal stereopairs; **C**, labial view; **D₂**, **G₂**, explanatory drawings for D₁ and G₁, respectively.

that descend lingually toward the first cusp. The ridge may also be cuspate along the labial side of the tooth (OMNH 27242, Fig. 10G). The ridge crosses the front of the tooth but is not elevated enough to have occluded with lower molars until the tooth was very deeply worn, so the anterior ridge is not counted as a cusp on most specimens. On one specimen (OMNH 27453), however, the anterior cusp appears to be distinct and is connected to the larger second cusp by a ridge. The first cusp of the external row (if it is not formed by the anterior wall) is the largest of the tooth and is

subpyramidal in form. It has deeply crenulated enamel (OMNH 29756, Fig. 10E) and can be surrounded by a series of pits (OMNH 30532). The second cusp is of about the same elevation; however, if the first cusp is deeply worn there is little wear on the second and it can be taller than the first (OMNH 29756, Fig. 10E). Lingually, the second cusp has a deeply concave surface that descends into a deep pit at the posterior end of the central valley.

The central valley is slightly sinuous. The valley is closed both anteriorly and posteriorly because of the presence of deep pits. The four cusps of the internal row form a slight arch in lateral view but all are lower than those of the external row. The cusps are of about the same size and progressively more deeply separated posteriorly.

Discussion. — The poor condition of the single complete M1 (OMNH 25735) precluded its designation as the holotype, and an m1 (OMNH 33001) was therefore chosen.

The p4s, with their short anterior face and arch accompanied by a weak postero-external sloping cusp, resemble figured specimens of *Bryceomys* (Eaton 1995: fig. 8G–H) and *Cimexomys* (Archibald 1982: fig. 37). The markedly strong and well-separated first cusp appears to be unique to this species. The m1s are very similar to those illustrated for *Bryceomys* in Eaton (1995) and are slightly larger, with more robust cusps, than those of *B. fumosus*. The connection of the first cusp of the internal row to the second cusp of the external row is characteristic of m2 of *Bryceomys* but is not as consistently developed in this species as in later species of this genus.

The m2 is similar to previously described species of *Bryceomys* (Eaton 1995) in that there is a distinct pit on the inside of the first cusp of the internal row; there is a ridge connecting the first cusp of the internal row to the second cusp of the external row; and the first two cusps of the external row are cylindrical in shape. The m2 of *B. intermedius* differs from those belonging to previously described species of *Bryceomys* in that the first two cusps of the internal row are more deeply divided lingually, the first cusp of the internal row is proportionally larger than the second, and the posterior wall is not cuspate. The cylindrical cusps and strong ridges crossing the tooth basin are different from what is seen in cf. *Paracimexomys*. This suggests that a specimen figured by Eaton (1995: fig. 6B) as *Paracimexomys* belongs instead to *Bryceomys*.

The low cusp formula (2:5) and the broader anterior than posterior end of P4 of *B. intermedius* are characters shared by later species of *Bryceomys* (Eaton 1995: p. 776). There is a deep pit or some degree of closure by a posterior wall in P4 of *Bryceomys* that differs from the condition seen in P4 of *Cedaromys* where the posterior basin is open posteriorly.

The referral of M1s to *B. intermedius* is made difficult by the poor condition of available specimens, although their assignment is critical for the placement of this species within *Bryceomys*. The single complete molar occludes reasonably well with m1 and fits the posterior margin of the P4s included here. The length of the internal row is similar to that of *Cimexomys* but in almost all other regards, such as the alternation of cusp positions between rows, these molars are unlike those of *Cimexomys*. The internal row is broader and better developed than in either cf. *Paracimexomys* or *Dakotamys*. The molars most closely approximate those of *Bryceomys* of described taxa, but they clearly have a broader external cusp row than do later species of *Bryceomys*.

Bryceomys sp. cf. *B. intermedius* sp. n.
Fig. 11A–C.

Material. — m2: 25593, V235; 33015, V868; 26579, V695. M1: 25734, V239.

Description and discussion. — **m2** (Fig. 11A, B): Morphologically similar to those of *Bryceomys intermedius* sp. n. but with significantly different proportions. It is unclear if this represents intraspecific variation or another taxon in the sample.

OMNH 33015 (Fig. 11A) has a cusp formula 3:2 if the posterior ridge of the external row is counted as a cusp. The first two cusps of the external cusp row are about equal in size and are cylindrically shaped. A shallow valley descends into the central valley, dividing the cusps; in turn, these are closed off labially such that they (and the posterior ridge) are only slightly separated. Posterior to the second cusp is a continuous ridge, with no marked cusp development, that connects to the posterior margin of the second cusp of the internal row. The central valley is complex and pitted. On the lingual side of the second cusp of the external row there is a ridge that crosses the central valley; on the lingual side of the valley it splits into two ribs, one connecting to the posterolabial corner of the first cusp of the internal row, and the other to the anterolabial corner of the second cusp.

The first and second cusps of the internal row are about the same size, and apical wear has reduced the height of both cusps to about equal height. The valley separating the two cusps is deep and arcuate in occlusal view. A pit is present on the labial wall of both cusps. This specimen is larger and slightly broader relative to length (AP = 1.55; LB = 1.44, LB:AP = 0.93) than other specimens included in *Bryceomys intermedius*.

OMNH 25593 (Fig. 11B) is relatively long as compared to its width (AP = 1.54; LB = 1.25; LB:AP = 0.81; mean LB:AP for *B. intermedius* is 0.89). The tooth has a cusp formula of 3:2. As on other m2s of *Bryceomys*, the first two cusps of the external row are cylindrical in shape and slope into the central valley. A distinct wear facet is present on the posterior ridge (cusp 3). The central valley is complex and pitted, and is crossed by a ridge from the first cusp of the internal row to the second cusp of the external row as in other m2s of *Bryceomys*. The first cusp of the internal row is the largest and tallest of the tooth, whereas these cusps are more or less equal sized in *B. intermedius*. The apices of both cusps of this row are shifted posteriorly. A deep pit is present on the labial side of the first cusp. The internal row projects much further anteriorly than does the external row, unlike any described species of *Bryceomys*.

M1 (Fig. 11C): OMNH 25734 (Fig. 11C) is morphologically similar to OMNH 25735 (Fig. 10D), an M1 of *B. intermedius*, but it is smaller (AP = 1.90; LB = 1.19). Also, the third cusp of the medial cusp row is proportionally broader based than in OMNH 25735 and the internal cusp row is less expanded lingually than in other M1s of *Bryceomys*. Another specimen, OMNH 26579, is the posterior portion of an M1 that is very similar to OMNH 25734 but is even smaller (LB = 1.12). This M1 suggests that a smaller species of *Bryceomys* may be present in this sample.

Genus *Cedaromys* gen. n.

Type species: *Cedaromys bestia* (Eaton & Nelson, 1991).

Other assigned species: *C. parvus* sp. n.

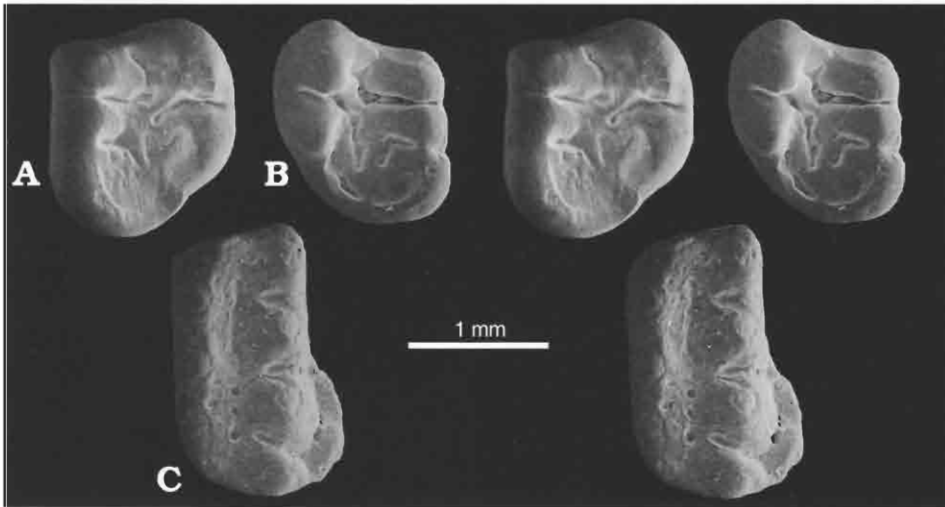Distribution: Near the Albian–Cenomanian stage boundary, Cedar Mountain Formation, San Rafael Swell, Utah.

Fig. 11. *Bryceomys* sp. cf. *B. intermedius*. **A**, Lm2 (33015); **B**, Rm2 (25593); **C**, RM1 (25734). All occlusal stereopairs.

Derivation of the name: After Cedar Mountain and Latin *mus* – a mouse.

Diagnosis. — Most similar to *Bryceomys*. Lower incisor covered with enamel, oval in cross section, slightly curved, with a spatulate wear facet. p4 is highly and symmetrically arched (H:L $\geq$ 0.60), more arched than *Bryceomys*, with first serration strong and well-separated from the second. Shares with *Eobaatar*, *Janumys*, and *Bryceomys* asymmetric lower molars, with internal row shorter than external, and cusps of the internal row on m1 worn obliquely towards the central valley. Tendency for lower molar cusps to coalesce, particularly labial cusp row of m2. Lower molars broader relative to length than in *Bryceomys*. Cusps of the molars are more robust, proportionally less tall, and not as deeply divided as those of *Bryceomys*, particularly internal cusp rows of first molar. P4 with cusp formula 2:4, less than in *Bryceomys*, and higher rate of cusp climb (0.58–0.60) than *Bryceomys, Dakotamys,* and *Janumys*. Shares with *Janumys* lack of internal (3rd) cusp row on M1, and differs in this respect from *Bryceomys*, *Paracimexomys*, cf. *Paracimexomys*, or *Dakotamys*.

Cedaromys bestia (Eaton & Nelson, 1991)
Table 1A–B; Figs. 12, 13.

Paracimexomys bestia Eaton & Nelson, 1991

Holotype: MNA V5658 (Eaton & Nelson 1991), MNA Loc. 1072. Cedar Mountain Formation, San Rafael Swell, Utah.

Distribution: Cedar Mountain Formation, close to the Albian–Cenomanian stage boundary, San Rafael Swell, Utah.

Material. — lower incisor: 28505, 28512, V695; 27604, V794. p4: 26636, 29582, V695. m1: 25752, V239; 26617 (partial); 26620, 26622 (partial), 27498, 29587, 33178, V695; 34010, V794; 33962, 32992, V868. m2: 32943, V235; 33186, V695; 34009, V794. P4: 30634, 33159, V695; 27440, V696; M1: 27564, 33178, 33180, V695; 29676, V696. M2: 25736, V239; 27538, 29576, V695 (also material included in

the hypodigm of *Paracimexomys bestia* in Eaton and Nelson, 1991, as well as FHSM 10357, m1, originally described as *Paracimexomys* sp. n. A).

Revised diagnosis. — The larger (17–20%) of the two species referred to the genus. Differs from *C. parvus* sp. n. in having lower arched p4.

Description. — **Lower incisor** (Fig. 12C): These incisors are assigned to *C. bestia* due to their large size, which is a distinctive feature of *C. bestia* among multi-tuberculates of the Cedar Mountain Formation. They are ovate to subcircular in cross section. They are only slightly curved (OMNH 27604, Fig. 12C), and terminate anteriorly in a spatulate wear facet. The incisors are completely covered in enamel.

p4 (Fig. 12A, B): OMNH 26636 (Fig. 12A, B) has 10 serrations with 7 internal and 7(?) external ridges (OMNH 29582 has 8 external ridges). The two blades highly arched and have a mean H:L ratio of 0.60. The anterior face of the blade is curved and the first cusp is very large and separated widely from the second cusp, as in *Cedaromys* and *Bryceomys intermedius* but unlike the condition in p4 of younger species of *Bryceomys*. The apex of the crest is reached at the fourth cusp. The posteroexternal cusp slopes anteroventrally and the enamel dorsal to the cusp is crenulated, as it is in both *Cedaromys* and *Bryceomys intermedius*.

m1 (Fig. 12D, E): Cusp formula 4:3. The molars taper slightly anteriorly. Some have no distinct waist in occlusal view (OMNH 25752, Fig. 12D); on other specimens, a weakly developed waist is formed by an indentation labial of the third cusp of the external row and a less distinct lingual indentation in about the same position, adjacent to the internal row (OMNH 27498, Fig. 12E). The first cusp of the external row is low, worn, and weakly pyramidal (OMNH 27498, Fig. 12E). It is divided from the second cusp by a broad, shallow valley (OMNH 25752, Fig. 12D). The second cusp is pyramidal and worn apically, and is much taller than the first cusp. A broad, deep valley separates cusps 2 and 3 and the valley forms slightly concave walls on the sides of the cusps that face each other. The fourth cusp is deeply worn and separated from the third cusp by a broad valley. The valleys separating the cusps of the internal row can extend to the floor of the central valley or can even be deeper (e.g., OMNH 26617). The first cusp is the lowest of the row, the second and fourth cusps are about the same height, and the third cusp is slightly lowest than cusp 2 and 4 (OMNH 25752, Fig. 12D) or about the same height (OMNH 27498, Fig. 12E).

The central valley is sinuous. The first and second cusps of each row alternate positions but the valleys separating the second and third cusps of both rows are only slightly offset. There is some indication of ribbing and deep pits in the central valley (OMNH 25752, Fig. 12D). The central valley of OMNH 27498 (Fig. 12E) has a more strongly sinuous valley than OMNH 25752 and the cusps alternate position the entire length of the tooth.

All of the cusps of the internal row are taller than those of the external row. The first cusp is conical, elongated anteriorly, and lacks a ridge connecting it to the second cusp (OMNH 25752, Fig. 12D), although in some specimens (e.g., OMNH 26617) a low, sharp crest connects these cusps. The valley separating the two cusps does not reach the floor of the central valley. The second cusp is essentially conical except for a somewhat flattened posterior wall or slight squaring of the antero- and posterolabial corners (OMNH 27498, Fig. 12E). The valley between it and the third cusp is broad and deep,
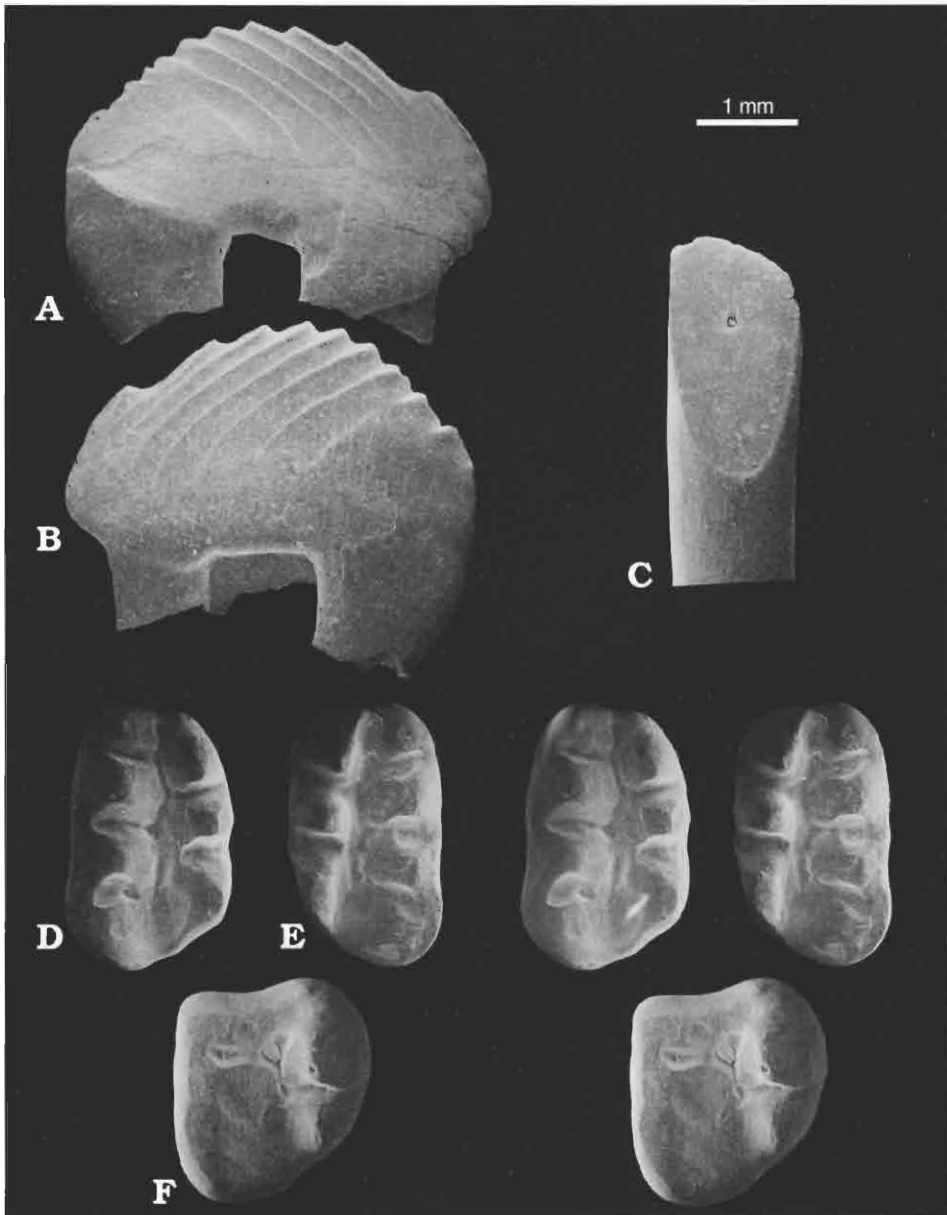
Fig. 12. *Cedaromys bestia*, lower dentition. **A**, **B**, Rp4 (26636); **C**, Ri1 (27604); **D**, Lm1 (25752); **E**, Lm1 (27498); **F**, Lm2 (33186). **A**, labial view; **B**, lingual view; **C**, dorsal view; **D–F**, occlusal stereopairs.

and a low ridge connects the cusps labially along the lingual wall of the central valley. Cusps of this row are approximately the same height.

m2 (Fig. 12F): The specimens assigned here are well worn and are associated principally due to their size and fit with the posterior ends of m1s assigned to this species. They appear to have a cusp formula of 2:3. The first cusp of the external row is larger

and much taller than the second (OMNH 33186, Fig. 12F). The cusps of the external row are weakly separated and are taller posteriorly.

P4 (Fig. 13A–C): Cusp formula 2:4. There is no to slight swelling of the antero-external platform. The external cusps rise out of the sloping labial sides of the tooth. The cusps of the external row are strongly striated (OMNH 33159, Fig. 13A–C). The first cusp has a slightly broader base than the second, but the second is slightly taller. There is a deep notch at the anterior end of the tooth, suggesting the presence of a strong posterior projection on the P3. On one specimen (OMNH 27440) there is a cuspule anterior to the first cusp.

The central four cusps climb steeply and are more strongly worn posteriorly. One specimen (OMNH 27440) has a small cuspule anterior to the first cusp. All the cusps of the central row are striated, but wear has obliterated most of the striations on the lingual face. A groove descends posteriorly from the last cusp of the central row to the unworn and well-developed labial cusp of the elongate posterior basin (mean PL:AP = 0.49). The lingual cusp of the posterior basin is lower and well worn. The posterior basin is deep but not closed posteriorly. The tooth swells labially (in occlusal view) above the last cusp of the central row and also on the lingual side, posterior to the fourth cusp.

M1 (Fig. 13D): Cusp formula 3(4?):4. There is no hint of a third (lingual) cusp row, although there may be a slight expansion at the posterolingual corner of these molars. At the anterior margin of the external cusp row there is a small cuspule (not counted as a cusp here, but might be by other workers) connected to the first cusp by a low, sharp-edged crest (OMNH 29676, Fig. 13D). A deep, broad pit is present labial to the crest. This depression continues up the anterior face of the first cusp, forming a slightly concave surface. Deep, pit-like valleys separate the first from the second and the second from the third cusps. These valleys are closed off labially from the central valley by ridges that connect the cusps. The lingual sides of the cusps are well worn but there is no apical wear.

The cusps of the two rows alternate position. The apices of the two rows are parallel and do not diverge anteriorly (at least when worn; no unworn examples are present in the sample). Because only the lingual sides of the cusps of the external row are worn, they are taller than the anteriormost two cusps of the internal row, which are worn across their apices.

M2 (Fig. 13E): Cusp formula Ri:3:4?. The first two or three cusps of the internal row form a continuous ridge with wear (OMNH 25736, Fig. 13E). The last cusp of the row is the most distinct and least worn. The central valley is deep, sinuous, and formed by a series of pits. The first and second cusps of the external row are not well divided, but a deep, narrow, pitted valley separates the second and third cusps. The first cusp of the external row is squared. The anterolabial platform is worn and it cannot be determined if distinct cusps were present.

Discussion. — The most notable features of p4 of *Cedaromys bestia* are the vertical anterior face and the strong degree of arching (H:L = 0.60). These high crowned, arched blades are most similar to those of *Cimolodon* and *Meniscoessus*, as is the curved face of the blade. A further similarity is the distinctness of the first serration, and its relatively great separation from the second.

The m1 is very similar to that of *Bryceomys hadrosus* (see Eaton 1995: fig. 9J) but the valleys separating the cusps in each row on the specimens from the Cedar Mountain For-
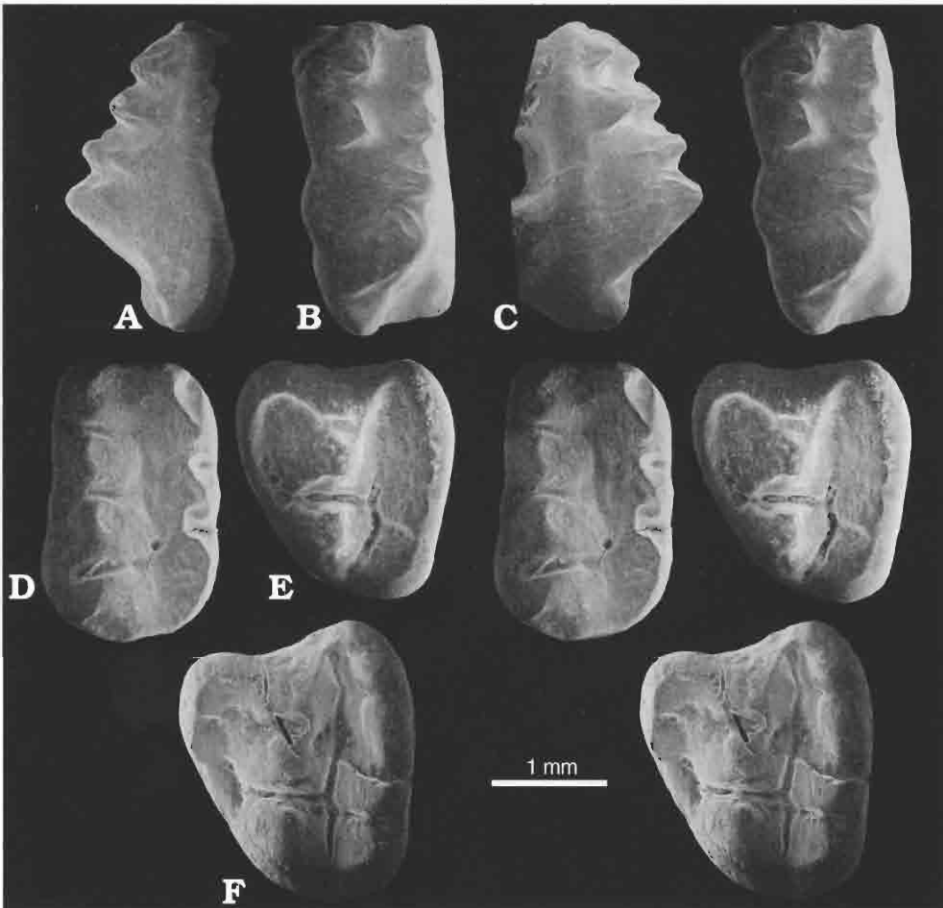
Fig. 13. **A–E.** *Cedaromys bestia*, upper dentition. **A–C**, RP4 (33159); **D**, LM1 (29676); **E**, RM2 (25736). **F.** *Cedaromys* sp. cf. *C. bestia*, RM2 (34007). **A**, lingual view; **B, D, E, F**, occlusal stereopairs; **C**, labial view.

mation are not as wide or as deep as those from the younger (Turonian) Smoky Hollow Member of the Straight Cliffs Formation. The specimens from the Cedar Mountain Formation are also slightly more robust, have less height differential between the valleys of the internal and external cusp rows, and a more distinct indentation ('waist') on the external wall of the tooth labial to the third cusp. The anteriormost two cusps of each row in *Eobataar* are not offset, and the central valley of m1 in *Eobataar* is straight, (Kielan-Jaworowska *et al.* 1987: pl. 2: 2b) not sinuous as in *Cedaromys*.

The P4 has a central cusp row that climbs steeply, as seen in *Mesodma*, but these specimens have far fewer cusps, a less swollen anteroexternal platform, and a much longer posterior basin relative to the total length of the tooth. These premolars are similar to those of cf. *Paracimexomys magnus* illustrated in Sahni (1972), but the specimens from the Cedar Mountain Formation have fewer cusps and are smaller. Fox (1971: fig. 7) illustrated a P4 designated as ?*Cimolomys* sp. B from the upper Santonian or lower Campanian Milk River Formation. Archibald (1982: p. 122) suggested that the P4 might be referable to *Paracimexomys magister*. If this is the case, then at

least the P4 of *Paracimexomys magister* may be closer to *Cedaromys* than to *Para-cimexomys*, part of our reason for tentative inclusion of *P. magister* in the genus. The P4 of *Cedaromys bestia* is similar to ?*Cimolomys* sp. B (Fox 1971) in having a low cusp formula (?*Cimolomys* sp. B, 1:4; *C. bestia* 2:4), well-striated faces, strong and deep posterior basin, and in being relatively broad compared to length (?*Cimolomys* sp. B mean LB:AP = 0.46; *C. bestia* mean LB:AP = 0.53).

The lack of a third cusp row on the upper molars is clearly a retained primitive feature. The only anterior premolars in the collection that are of the appropriate size for this taxon (see below) are simple, tricusped teeth. The lack of permanent anterior premolars of this size with more than three cusps suggests that *Cedaromys* has four anterior upper premolars, of which the first three are tricusped. Multituberculate taxa retaining five premolars have tricusped P1-3, but a more cuspate P4 (e.g., *Bolodon*, Kielan-Jaworowska *et al.* 1987: pl. 12: 1).

Cedaromys sp. cf. *C. bestia*

Fig. 13F.

Material. — M2: 34007, V794.

Description and discussion. — A large M2 (AP = 2.79; LB = 2.30), OMNH 34007 (Fig. 13F) has a formula of 1(?):3:4 and is anteroposteriorly elongate. The central valley is oblique to the AP axis. In the area of the anteroexternal ridge there is an elevated, cusp-like region. The specimen is worn, but this elevated area does not appear to be continuous with the third cusp of the external row. The first cusp of the external row is narrow and shallowly divided from the more robust second cusp. The valley separating cusps 2 and 3 is better developed. The third cusp is slightly smaller but is equal in height to the second. The central valley is slightly sinuous and is open posteriorly. The cusps of the internal row are weakly divided.

This specimen is morphologically similar to those described for *Cedaromys bestia* but falls somewhat outside the observed size range of that species (AP = 2.28–2.46), suggesting the possibility of the presence of an additional taxon, larger than *Cedaromys bestia*, in the fauna.

Cedaromys parvus sp. n.

Table 1A, B; Figs. 14–16.

Holotype: OMNH 25747, V239, M1.

Distribution: Cedar Mountain Formation, near the Albian–Cenomanian stage boundary, San Rafael Swell, Utah.

Derivation of the name: Latin, *parvus* – in reference to the small size of the species.

Material. — p4: 27497, V695; 29650, V801; 32987, V868. m1: 29761, V235; 25747, 25750, 25755, 29702, V239; 26628, 26683, 29583, 30633, V695. m2: 25759, 25760, V239; 26627, V695. P4: 29692, 29693, V239. M1: 25620, V234; 25731, 25747, 29701, V239; 33185, V695; 34008, V794. M2s: 32937, V235; 25742, 27240, 29695, 29698, V239; 26678, V695 (as well as FHSM 10358, p4, described as *Paracimexomys* sp. n. A, and the specimens referred to Suborder Ptilodontoidea, *incertae sedis*, in Eaton & Nelson 1991).
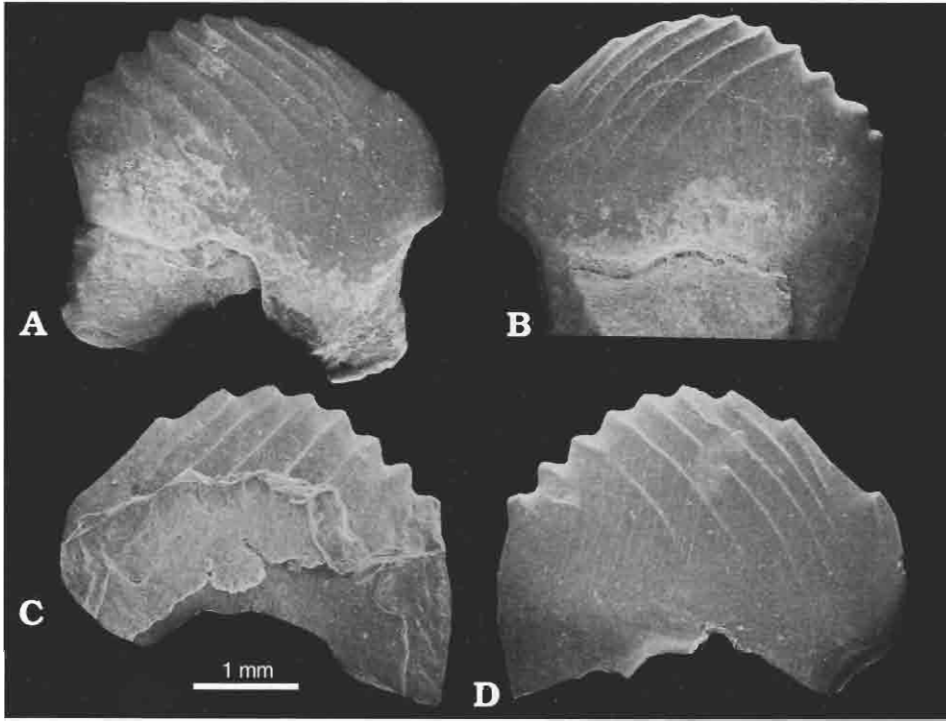
Fig. 14. *Cedaromys parvus* sp. n. **A, B**, Rp4 (32987); **C, D**, Lp4 (27497). **A, C**, labial view; **B, D**, lingual view.

Diagnosis. — Smaller than *C. bestia* (AP means about 15% less), with higher crested p4s (L:H = 0.66).

Description. — **p4** (Fig. 14A–D): Formula 9–10 serrations, 7 lingual ridges, and 6–7 labial ridges. OMNH 32987 (Fig. 14A, B) has a vertical anterior face, with the anteriormost serration oriented dorsally and a large gap between the first and second serrations, a characteristic particularly accentuated on OMNH 27497 (Fig. 14C, D). The blade is symmetrically and highly arched (H:L range 0.63–0.70), reaching its apex at or near the fourth serration (OMNH 32987; on OMNH 27497 the third serration; on OMNH 29650 the fifth serration). The serrations become larger and broader posteriorly. There is complex crenulation of the enamel on the labial wall of the tooth above the well-developed posteroexternal cusp. There is a deep anterior notch high on the front of the tooth to accommodate what must have been a relatively large p3, although none were recovered in the sample. Although OMNH 29650 is morphologically very similar to the other p4s included here, it has a higher H:L ratio (0.70) than the other two specimens (mean = 0.65).

   m1 (Fig. 15A, B): Cusp formula 4:3; cusps of the two rows alternate positions. OMNH 25750 (Fig. 15A) is slightly waisted in occlusal view, just posterior to the anteroposterior midpoint of the tooth. The cusps of the external row show marked apical wear. The first cusp is low and well worn. The second cusp is much larger, the largest of the row, and is pyramidal. A valley that is not quite as deep as the central valley separates it from the first cusp. A valley that is as deep as the central valley separates
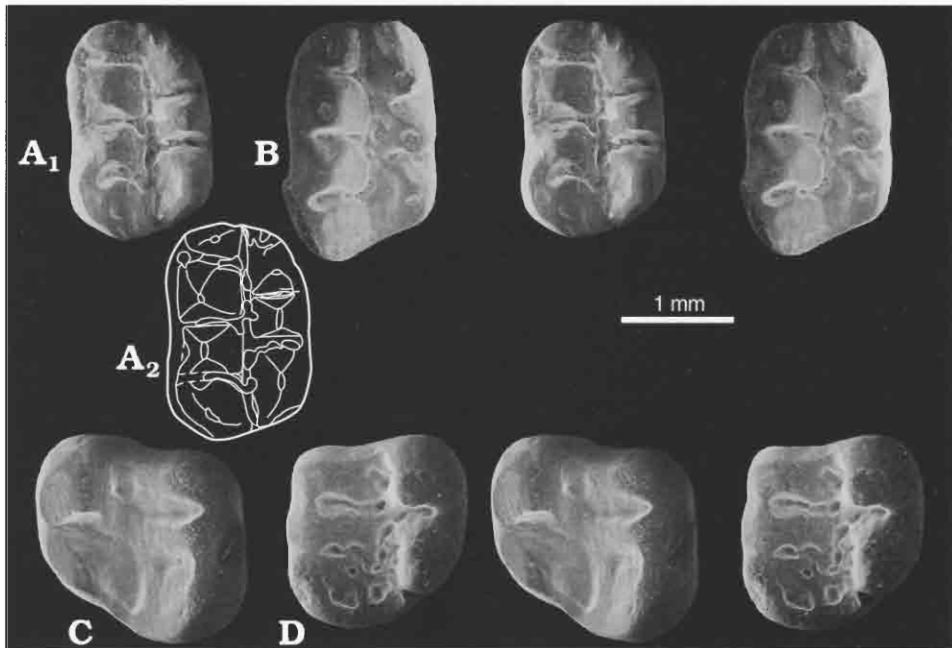
Fig. 15. *Cedaromys parvus* sp. n., lower molars. A_1, Lm1 (25750); **B**, Lm1 (25755); **C**, Rm2 (25760); **D**, Lm2 (26227). All occlusal stereopairs. A_2, explanatory drawing for A_1.

the second cusp from the smaller third cusp. The cusps are well worn apically and the cusps increase slightly in height posteriorly. On very worn specimens (e.g., OMNH 30635) the second cusp is still the tallest in the row, with progressively deeper wear posteriorly, such that the fourth cusp is worn to the level of the central valley. The central valley ranges from sinuous to almost straight on very worn specimens. Deep pitting is present in the central valley.

The cusps of the internal row are tall and there is little evidence of apical wear on OMNH 25750 (Fig. 15A) but some apical wear is evident on OMNH 25755 (Fig. 15B) and other specimens. The posterior cusps receive the most wear, so that in very worn specimens (e.g., OMNH 29583) the unworn first cusp is the tallest of the tooth. The first cusp of the row is elongated anteriorly, conical in shape lingually, and flattened by wear labially. On some specimens a valley that is deeper labially than lingually separates the first from the second cusp, while in others it can be poorly separated by a pit present labial to the valley (OMNH 25755, Fig. 15B). There is no distinct ridge connecting these cusps. The second cusp is the narrowest of the row and has squared corners resulting from the shape of the valley that borders it anteriorly and posteriorly. The valley that separates the second and third cusps is deep and is comprised of two pits that are deeper than the central valley. The third cusp is elongate posteriorly.

m2 (Fig. 15C, D): Cusp formula 2-3?:2. Specimens in sample are well worn. On the external cusp row of OMNH 25760 (Fig. 15C) the entire top of the row is worn such that it forms a continuous ridge. The height of the row increases slightly posteriorly. The central valley has strong ribs and deep pits (OMNH 26627, Fig. 15D). The first cusp of the internal row is the largest of the tooth and is longer than the second cusp.

The first cusp connects with a ridge or ridges across the central valley to the second cusp of the external row, as it does in m2 of *Bryceomys*. Most of the wear on the cusps of the internal row is on the lingual side and the posterior part of the row is more deeply worn than the anterior. There is a distinct notch on the posterior wall of the tooth behind the second cusp of the internal row.

P4 (Fig. 16A–C): Cusp formula 2:4. There is only a slight expansion of the anteroexternal platform (OMNH 29692, Fig. 16A–C). The first cusp of the external row is smaller and lower than the second. The central cusp row has a relatively steep angle of climb, reduced somewhat by apical wear on the sub-equal sized third and fourth cusps. Both sides of the central cusp row appear to have crenulated enamel rather than distinct striae. The crest ascends posteriorly from the last cusp of the central row. A concave surface (groove) develops at the upper end of the crest, just anterior to the labial cusp of the posterior basin. The lingual and labial cusps of the posterior basin are about the same size and height. The basin is open posteriorly. The tooth is slightly constricted in occlusal view, just anterior to the midpoint of the tooth.

M1 (Fig. 16D, E): Cusp formula 3:4. These molars are broad relative to their length (average LB:AP ratio of 63%) and a third lingual row of cusps on a separated platform is not developed on any of these specimens. However, on one specimen (OMNH 25620, Fig. 16D), there is a distinct cuspule low on the posterolingual side of the tooth in the position where the third cusp row is developed on M1 of other multituberculate taxa. On the external cusp row there is a tiny cuspule present anterolingual to the first cusp. The cuspule is connected to the first cusp by a low ridge. On some specimens (e.g., OMNH 25620, Fig. 16D), there is a deep, broad pit labial to this ridge. The pit continues up the anterior face of the second cusp, making the anterior wall of the cusp slightly concave. The first cusp is conical labially but is flattened lingually as the result of wear, and is connected to the second cusp by a low, anteroposteriorly oriented ridge. The second cusp is formed of three almost flat surfaces labially (forming half of a hexagon, OMNH 25747, holotype, Fig. 16E), which reflect the presence of widely spaced vertical ribs. The lingual side of the cusp is worn but is not as flattened as the lingual surface of the first cusp. A low, rounded ridge connects the second and third cusps of the row. A deep pit is present on one specimen (OMNH 25747, Fig. 16E) labial to the valley between the second and third cusps. Posteriorly, the third cusp of the external row is connected to the terminal cusp of the internal row by a broad wall.

The central valley tends to be well worn but is sinuous, and the cusps of the internal and external rows are offset such that they alternate positions (they are not aligned linguolabially). However, with sufficient wear the sinuosity of the central valley is obliterated. The central valley divides the anterior part of the tooth approximately in equal halves, but the valley shifts posterolabially due to the large size of the third cusp of the internal row. The cusp apices (after wear) of the two rows are approximately parallel and do not diverge anteriorly, unlike the cusp rows diagnostic of Lancian *Paracimexomys priscus* (see Archibald 1982: p. 111). The cusps apices of the internal row may even form a gentle arc that is convex lingually (OMNH 25620, Fig. 16D). The first two cusps of the external row are taller (after wear) that the first two cusps of the internal row. The third cusps of both rows are worn to approximately the same height. The fourth cusp of the internal row is the tallest cusp of the tooth. Because of the elevated ridges that connect the cusps of the external row and the wear that flattens the lin-
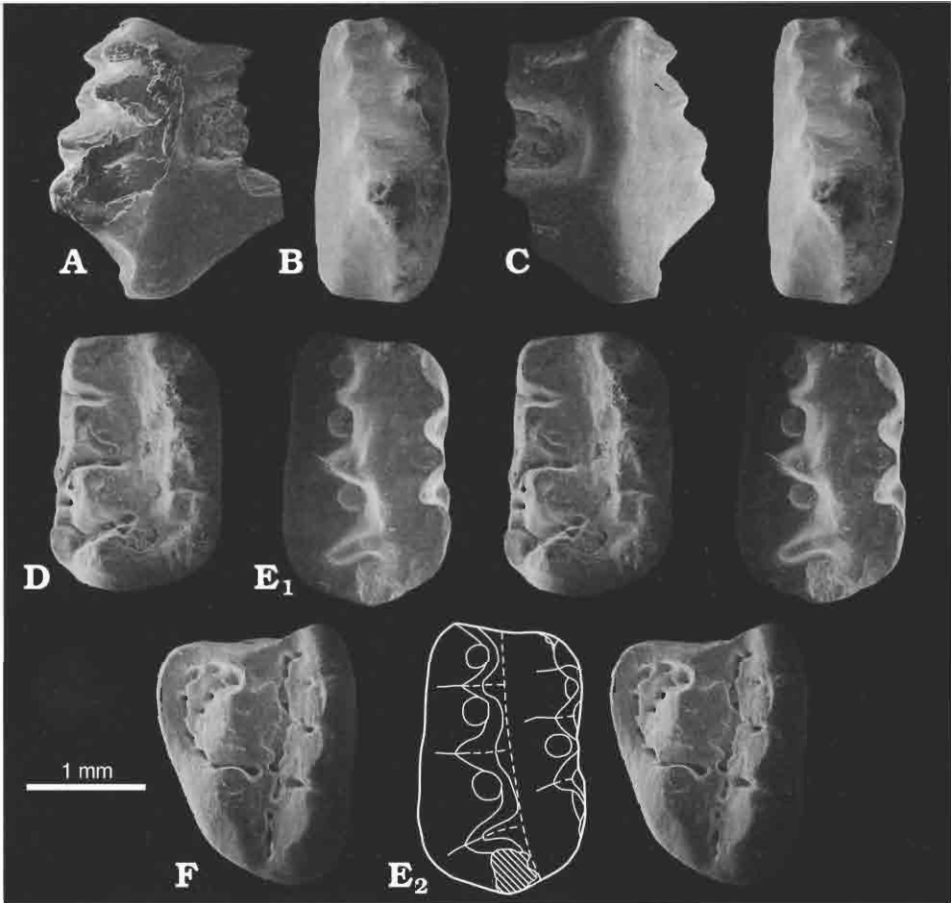
Fig. 16. *Cedaromys parvus* sp. n., upper dentition. **A–C**, LP4 (29692); **D**, LM1 (25620); **E**, LM1 (25747, holotype); **F**, RM2 (26678). **A**, labial view; **B**, **D**, **E₁**, **F**, occlusal stereopairs; **E₂**, explanatory drawing for E_1; **C**, lingual view.

gual side of the row, it forms a closed wall along the labial margin of the central valley, whereas the internal cusp row does not.

The first cusp of the internal row is the smallest cusp of the row and is not well separated from the pyramidal second cusp. A distinct valley separates cusp two from the broad and pyramidal third cusp, which can bear well developed vertically oriented ribs on its lingual wall (OMNH 25620, Fig. 16D). The first and second cusps become flattened by apical wear. A distinct but somewhat narrower and posterolingually oriented valley separates the third and fourth cusps. There is a well-developed wear facet on the anterolingual side of the tooth.

M2 (Fig. 16F): Cusp formula Ri:3:4. These molars are relatively elongate. The first cusp of the external row is an elevated area on the anterior ridge and is connected by a narrow, sharp crest to the second cusp. Both cusps may have apices oriented anteriorly (OMNH 26678, Fig. 16F). The second cusp is separated from the surrounding ridge by a series of deep pits. The second and third cusps are deeply separated except near the floor of the central valley. The cusps of the external row increase slightly in height pos-
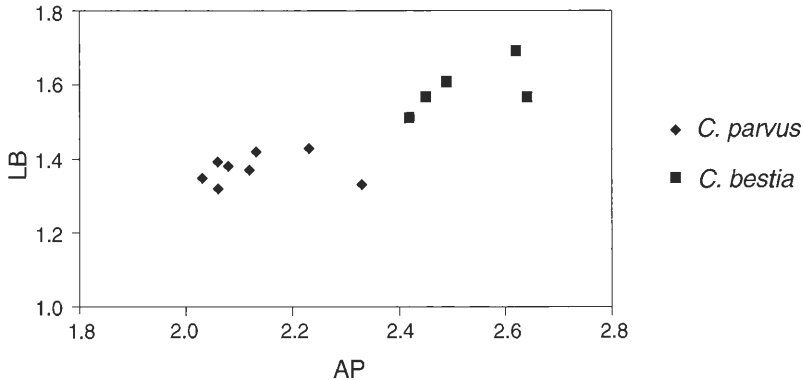
Fig. 17. Size distribution of m1s referred to *Cedaromys* spp.

teriorly. The central valley is deep and straight and is deepened by a continuous series of pits. The valley is closed by a low ridge anteriorly but is open posteriorly in most specimens. In one specimen (OMNH 29698) there is a low posterior wall, resulting in slight closure of the valley.

The internal cusp row is longer than the external. The first two cusps of the row are poorly separated, but the more posterior cusps are more deeply divided. The cusps appear to be taller posteriorly relative to the valley floor, but relative to the enamel line on the lingual side of the tooth the row is worn slightly lower posteriorly.

Discussion. — This species is morphologically similar to *Cedaromys bestia*. Recognition of *C. parvus* as a distinct species is supported by the lack of overlap in size range of specimens between it and *C. bestia* (Table 1) for most teeth; lower teeth appear more distinct in size than do the uppers. The clustering of the separate samples of m1s (Fig. 17) supports the presence of two distinct species. The sample of m1 of *C. bestia* yields a CV (for the AP dimension) of 4.0 and those of *C. parvus* a value of 4.6. By combining the values for the AP dimension for the m1 of both species, the CV rises to 9.8, well beyond the value for living or fossils species reported in Gingerich (1974). Recognizing that caution must be exercised in interpretation based on small samples, available data support recognition of two species of *Cedaromys* in the Cedar Mountain Formation, based on both morphologic and morphometric criteria.

Cedaromys sp. cf. *C. parvus* sp. n.
Fig. 18A–E.

Material. — m1: 27247, 25749, V239; 30551, V794. P4: 33161, V695.

Description and discussion. — Several additional specimens in the sample may well belong to the taxon described above. Available evidence is insufficient to determine whether the specimens are simply intraspecific variants, or whether, they reflect the presence of an additional taxon (or taxa) in the fauna.

m1 (Fig. 18A, B): Two of the specimens (OMNH 27247 and 30551) appear proportionally longer relative to width than in *C. parvus* (only OMNH 27247, Fig. 18B, is a measurable specimen: AP = 2.23; LB = 1.33; LB:AB = 0.57; LB:AP ratio for *Cedaromys parvus* = 0.66). This difference may seem small but tooth widths are criti-

cal in multituberculates if molars are to occlude and wear properly. These specimens do not occlude well with any of the M1s of *C. parvus*, described above, but only with a partial M1 described below. There are also some morphological distinctions. The first cusp of the external row is better developed than on the m1s referred to *C. parvus*, is weakly pyramidal, and is separated from the second cusp by a broad valley that is as deep as the central valley. The second and third cusps are both pyramidal, about equal in size (the second cusp is not larger than the third cusp as in *C. parvus*), and they are divided by a deep valley. The fourth cusp hints at being subdivided. The central valley is more clearly sinuous and shows no sign of pitting. The first two cusps of the internal row are not as deeply divided as they are in *C. parvus*.

Another m1, OMNH 25749 (Fig. 18A), has a cusp formula of 4:3. The first cusp of the external row is missing due to breakage. The third cusp is the largest of the row. The fourth cusp is developed on the posterolabial ridge and does not form a distinct cusp. The central valley is sinuous and well pitted. The first cusp of the internal row is conical and separated from the more squared second cusp by a valley that is closed lingually but opens into the central valley. The second and third cusps are separated by a deep valley that is not pitted and that does not quite reach the level of the central valley. There is strong wear on the lingual side of the third cusp, indicating the presence of a third row on the occluding upper molar. This tooth is similar in size (LB = 1.39; mean LB for *Cedaromys parvus* = 1.38) to those of *C. parvus* but differs morphologically in that: 1) the valleys separating the cusps of the internal row are open to the central valley; 2) the third cusp of the external row is larger than the second; and 3) there is strong wear on the lingual side of the third cusp of the internal row. It is unclear if this simply represents variation within *C. parvus* or a different taxon.

P4 (Fig. 18C–E): A P4 (OMNH 33161) is of appropriate size (AP = 2.51; LB = 1.12) for *C. parvus* described above, but has some distinctive characteristics. It has a cusp formula of 2:5 where the formula is 2:4 for P4s assigned to *C. parvus* above. The central cusp row climbs (CR = 0.55 measured to the fourth cusp) more shallowly than on P4s of *C. bestia* (CR = 0.60). The single measurable P4 assigned to *C. parvus* is too worn to determine the CR but it appears to be similar in this respect to the P4s assigned to *C. bestia*. The central row reaches its apex at the fourth cusp and the fifth cusp is distinctly lower and is not worn on this specimen. The additional cusp has the effect of shortening the posterior basin such that the PL:AP is 0.34, much lower than otherwise seen in *Cedaromys* (range of PL:AP = 0.42–0.49). The posterolingual cusp is very well developed and bulbous on this specimen, as it is on P4s of *Cedaromys*. This specimen may represent a variant of *C. parvus*, with different proportions resulting from the addition of another cusp on the central cusp row. On the other hand, it may represent another taxon, perhaps not even one that is closely related.

Genus *Dakotamys* Eaton, 1995

Type species by monotypy: *Dakotamys malcolmi* Eaton, 1995.
Distribution: Dakota Formation (Cenomanian), southern Utah.

Revised diagnosis. — p4 with lower H:L than in *Cedaromys*, *Paracimexomys* or cf. *Paracimexomys*. First molars with low cusp formulae (m1 – 4:3; M1 – 4–5:4:1-2); less than cf. *Paracimexomys perplexus* but similar to *Paracimexomys priscus*. Short internal row present on M1, unlike *Cedaromys* or *Janumys*. Cusps of external and medial
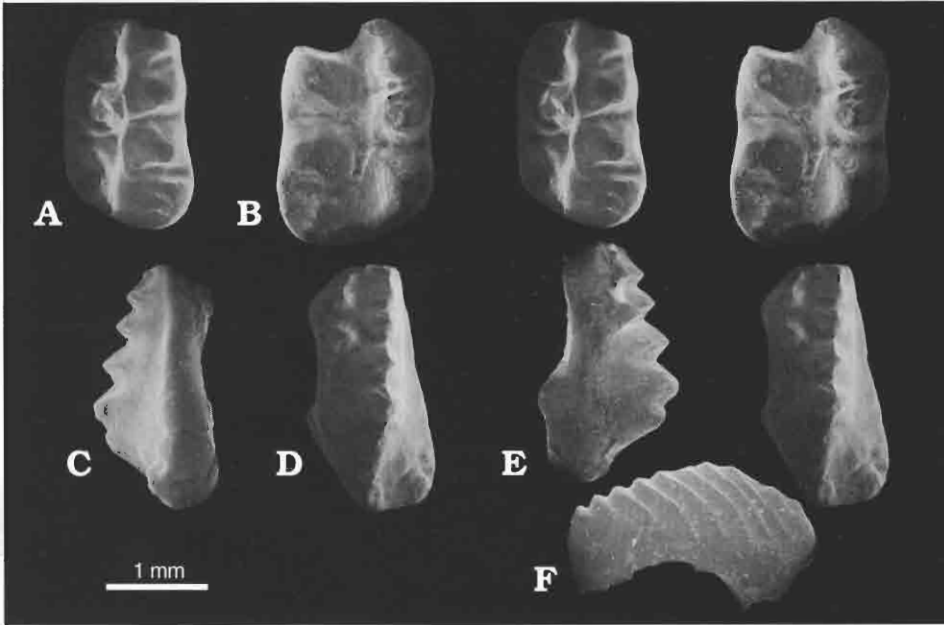
Fig. 18. **A–E.** *Cedaromys* sp. cf. *C. parvus.* **A,** Lm1 (25749); **B,** Rm1 (27247); **C–E,** RP4 (33161); **F.** *?Mesodma* sp., Lp4 (27563). **A, B, D,** occlusal stereopairs; **C, F,** lingual view; **E,** labial view.

rows on M1 offset (not aligned transversely), unlike *Cimexomys*. Second to first molar length ratios (0.85) less than in *Paracimexomys*, cf. *Paracimexomys*, *Janumys*, and *Cedaromys* but greater than in *Bryceomys*. Differs from *Paracimexomys priscus* in having strongly ribbed molar cusps, cusp rows on M1 not diverging anteriorly, and central valley on m1 straight rather than sinuous. P4s with labial expanded antero-external platform, unlike *Cedaromys*, *Bryceomys*, and *Janumys*, and with rate of cusp climb (CR = 0.38) higher than in *Janumys* but lower than in *Cedaromys*, *Bryceomys*, and cf. *Paracimexomys perplexus*.

Remarks. — *Dakotamys* is not present in the Cedar Mountain Formation, but a revised diagnosis is given here in order facilitate distinction among the primitive cimolodontans (*Paracimexomys* group) described herein.

Suborder ?Ptilodontoidea Sloan & Van Valen, 1965
Family ?Neoplagiaulacidae Ameghino, 1890
Genus ?*Mesodma* Jepsen, 1940
?*Mesodma* sp. indet.
Fig. 18G.

Material. — 27563, V695, p4.

Description and discussion. — This single p4, OMNH 27563 (Fig. 18G) is moderately sized (AP = 2.67; H = 1.42) and has a low H:L ratio (0.53). The specimen has 10 serrations and 8 internal ridges (the external side is missing). The low, relatively flat-crested blade reaches its maximum height at serrations 3 and 4. The anterior face

of the blade leans posteriorly. The first two serrations are closer together than are serrations 2 and 3. Serrations 4–10 are almost linearly aligned, with the cusps increasing in size posteriorly.

In being rather flat-crested, this p4 is very similar to those of *Mesodma*. OMNH 27563 lacks the vertical anterior face seen on most figured specimens of *Mesodma*; however, some figured specimens have a posteriorly recumbent leading edge (*Mesodma formosa*, Clemens 1963: fig. 7a; *M. primaeva*, Montellano 1992: fig. 4), as seen on this specimen. It is unlikely that *Mesodma* is present in this fauna, but this p4 is unique in the sample and, among illustrated p4s, its lack of broad arch is most similar to those of *Mesodma*. The low crest and high serration number are suggestive, perhaps, of a non-rotating *Arginbaatar* blade, in turn suggesting possible referral to *Ameribaatar*, which resembles *Arginbaatar* in molar structure (see above). However, this blade is low-crested and of delicate construction, and is unlikely to belong to *Ameribaatar*, which has large and very deep cusped molars (see below).

Suborder and Family *incertae sedis*
Genus *Ameribaatar* gen. n.

Type species by monotypy: *Ameribaatar zofiae* sp. n.

Diagnosis: As for the species.

Derivation of the name: 'Ameri' in reference to North America; and 'baatar', Mongolian for a hero (a suffix commonly given to Asian multituberculates by Dr. Zofia Kielan-Jaworowska), in reference to a superficial similarity of this taxon to *Arginbaatar* (from the Early Cretaceous of Mongolia).

Ameribaatar zofiae sp. n.
Fig. 19.

Holotype: OMNH 33984, V794, M2.

Distribution: Cedar Mountain Formation, near the Albian–Cenomanian stage boundary, San Rafael Swell, Utah.

Derivation of the name: For Zofia Kielan-Jaworowska, in recognition of her remarkable contributions to our understanding of Eurasian multituberculates.

Material. — m1: 32990 (partial), V868. m2: 26397, V235; 33992, V794; 32939, V235, 29734, V694; 33167, V695; 32993, V868. M1: 33177 (partial), V695. M2: 26398, V235; 27583, 27616 (anterior portion), 33984, V794; 32989 (posterior fragment), 32991 (partial), V868; 33165, V695 (and FHSM 10350, m1 (partial), described in Eaton & Nelson 1991, as *incertae sedis*).

Diagnosis. — Molar cusps relatively small and conical, very widely spaced. The apomorphy of this genus is a unique type of molar wear, resulting in the development of U-shaped transverse valleys, delimited by sharp ridges, between cusps; the faces of the cusps adjacent to U-shaped valleys remains concave. On m1 (incompletely known) the central valley is narrow and sigmoid; m2 is broad with straight anterior and rounded posterior margins and wide central valley, cusp formula 3:2. M1 incompletely known. M2 long relatively to width with strongly oblique anterior margin (internal cusp row much longer than external), narrow and deep central valley, cusp formula 2:3. No ornamentation.

Description. — **m1** (Fig. 19A): On OMNH 32990, a partial molar, the anterior lingual cusps are taller than the labial cusps. Cusps of each row are broadly separated by
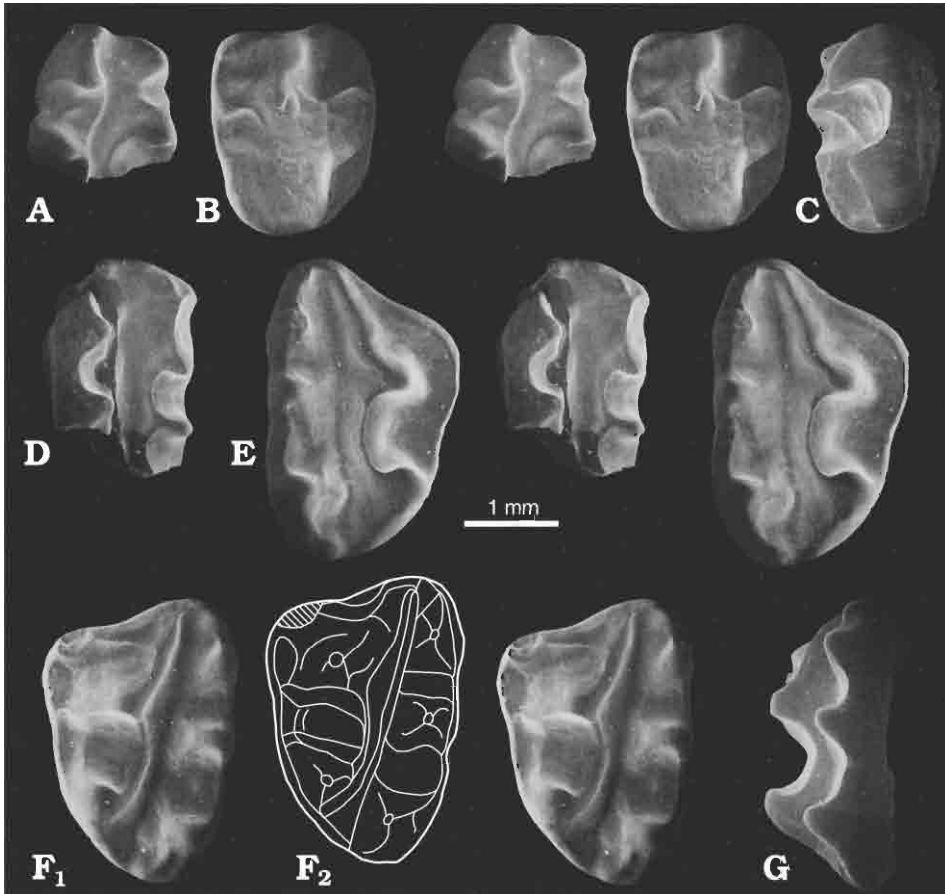
Fig. 19. *Ameribaatar zofiae* gen. et sp. n. **A**, partial Rm1 (32990); **B, C**, Lm2 (33167); **D**, LM1 (33177); **E**, LM2 (26398); **F, G**, RM2 (33984, holotype). **A, B, D, F_1**, occlusal stereopairs; **F_2**, explanatory drawing for F_1; **C, G**, lingual view.

U-shaped valleys. The central valley is strongly sinuous, such that cusps of one row are opposite the valleys of the other row (alternating position of cusps).

The tooth is considered to be an m1 because of a flattened surface high on the anterolingual corner of the tooth, which appears to represent the interstitial facet of a strongly offset p4 (see Kielan-Jaworowska *et al.* 1987: pl. 14–1c).

m2 (Fig. 19B, C): OMNH 33167 has a cusp formula of 3:2 and is relatively large (AP range 2.30–2.62; LB range 1.65–1.86). The external cusp row has a small, low, conical first cusp. The second cusp is widely separated from both cusps 1 and 3. Valleys between the cusps are deep lingually, but labially the separation is not deep, so that there is a continuous labial wall along the side of the tooth. Cusp 3 forms a continuous crest when worn. The central valley is straight and broadens posteriorly. An interstitial facet for m1 is present at the anterior end of the central valley.

The anterior cusp of the internal row is deeply excavated posteriorly, forming a broad, deep valley that continues past the labial wall of cusp 2. The second cusp forms a ridge along the lingual margin of the tooth.

M1 (Fig. 19D): OMNH 33177 is an anterior portion of a possible ?LM1. The tooth is considered to represent an M1 due to its blunt anterior end; also, it shows evidence of wear along the occlusal surface, as on M1s assigned to an unidentified taxon by Kielan-Jaworowska *et al.* 1987 (pl. 6: 1, 2).

M2 (Fig. 19E–G): OMNH 33984 (Fig. 19F, G), the holotype, has a cusp formula of 2:3 and is large for M2s in the Cedar Mountain sample (AP range 2.48–4.10; LB range 1.69–1.92). The internal cusp row is much longer than the external cusp row and it extends beyond the external cusp row both anteriorly and posteriorly. It bears three conical cusps separated by broad U-shaped valleys (in side view) that do not reach the valley floor and that are deeper labially than lingually (Fig. 19G). The walls on the anterior and posterior faces of the cusps are concave except for the anterior face of cusp 1 and the posterior face of cusp 3. A small cuspule is present anterior of cusp 1; it is not counted in the formula. The cusps are both taller and broader posteriorly. The central valley is deep, can be slightly sinuous (OMNH 26398, Fig. 19E), and can be open at both ends (OMNH 33984, Fig. 19F) or slightly closed (OMNH 26398, Fig. 19E).

The external cusp row has an isolated first cusp surrounded by a basin on all sides except the side interrupted by the central valley, which forms a ridge that cuts across to anterolingual margin of the tooth. The second cusp is subequal in height to the first, but is built on a smaller base. It is separated from the first cusp by a wide U-shaped valley.

The molar is anteroposteriorly elongate and rounded at the posterior end. The anterior margin of the tooth bears an interstitial facet for M1 labial of the central valley.

On OMNH 27583 the central valley projects anteriorly on a strong, sharp projection. There is no evidence of an interstitial facet posteriorly, but there is a distinct interstitial facet labial of the anterior projection. The tooth deepens and the cusps become progressively taller posteriorly.

Discussion. — The type of wear observed in *Ameribaatar* appears to be unique among multituberculates. Certain similarity may be found with m1 of *Arginbaatar* (Kielan-Jaworowska *et al.* 1987: pl. 14: 1a, b) in which m1, when observed in side view, shows U-shaped valleys between the widely spaced cusps. However, the same specimen in occlusal view (pl. 14: 1c of the same paper) shows tooth shape and cusp structure different from *Ameribaatar*. The type of wear characteristic of *Ameribaatar* has not been observed among Asian multituberculates (Zofia Kielan-Jaworowska personal communication).

Another genus which invites comparison is *Essonodon*, from the latest Cretaceous of North America (see Archibald 1982: figs. 31–34), in which there are also deep U-shaped valleys (in side view) between molar cusps. *Essonodon* lacks any known morphological antecedents in earlier faunas (Cifelli *et al.* in press), though a relationship has been suggested with the Late Cretaceous taxa *Cimolomys* and *Meniscoessus* (Weil 1999). Molar structure of *Ameribaatar* is not otherwise closely comparable to that of *Essonodon*, however, so that the significance of their U-shaped transverse valleys is uncertain, as is also the case for *Arginbaatar*.

Isolated anterior teeth

Incisors. — Considering the size of the sample, incisors are rare. A few very large lower incisors were assigned to *Cedaromys bestia* because of their size. The remaining lower incisors are all smaller than those assigned to *C. bestia* and cannot be reliably as-

signed based on size. They are all covered in enamel and have a strongly developed linguoventral cingulum (e.g., OMNH 26381, V235; OMNH 29674, V696). These are similar to the incisors figured in Eaton & Nelson (1991: fig. 3F) and Eaton (1995: fig. 10G–H). All upper incisors in the sample are bicusped I2s.

Anterior upper premolars. — There are enormous numbers of anterior premolars in the sample from the Cedar Mountain Formation. The lack of any specimens demonstrating direct association of these teeth with fourth premolars or molars makes taxonomic assignment a most difficult task. We could have decided to simply ignore these premolars, but they represent an enormous amount of data and it was thought that their analysis might lead to an initial estimate of the changes in the anterior upper premolar series between Jurassic–earliest Cretaceous 'Plagiaulacida' and the Cimolodonta, which presumably originated later. This could provide useful data in terms of familial assignments. We acknowledge that this is a first attempt at such a premolar analysis and only the subsequent discoveries of dentigerous maxillae can be used to fully evaluate this approach. Although we suggest taxonomic affiliations for some specimens, the basis for taxonomic assignment is weak. Accordingly, the anterior upper premolars have been omitted from formal inclusion in species hypodigms, and they are described separately below.

Bicusped premolars. — In the entire sample there are only two bicusped premolars. OMNH 33954 (V868), Fig. 20A, B, is small (AP = 0.70; LB = 0.52). The two cusps are arranged anteroposteriorly and are of equal size and height. The cusps do not rise far from the upper surface of the tooth and are weakly striated. The cusps are shifted slightly to one end, so that the cuspate region of the crown is shifted posteriorly (?). The apices of the cusps lean slightly to one side of the tooth (lingual?). The tooth is single rooted and swells below the base of the enameled part of the tooth.

A larger (AP = 0.85; LB = 0.68) bicusped upper premolar, OMNH 33125 (V695), Fig. 20C–D, has cusps of different size. Based on the vertical orientation of the front and the posterior lean of the back of the root, we have interpreted the smaller cusp to be the more anterior. The premolar flares slightly on one side. If this represents the pattern seen in tricusped anterior premolars, this would be the labial side of the tooth, making this a left premolar. The root is initially single, but splits into two at its base. The cusps bear radial striations and there is a possible wear facet on the labial (?) side of the posterior (?) cusp.

Bicusped upper premolars are rare and the only Cretaceous report of them is from the Densuş-Ciula Formation of Romania (Csiki & Grigorescu 2000). In general appearance, the Cedar Mountain and Densuş-Ciula premolars are similar, but the Densuş-Ciula specimens are elongate perpendicular to the axis formed by the two cusps, whereas the Cedar Mountain specimens are elongate parallel to the axis as formed by the two cusps.

Neither of these specimens appears to be large enough to be appropriate to fit with the largest of the tricusped premolars that probably belong to *Cedaromys bestia*. As such, there is no basis for taxonomic assignment.

Tricusped premolars. — Tricusped premolars described here are all interpreted to be part of the permanent dentition, as most show distinct roots. However, roots are lacking from some specimens, and the mounting process has commonly obscured crown bases. For these specimens, it cannot be determined whether root absence is due to resorption or breakage, and the possibility that they are deciduous cannot be excluded.
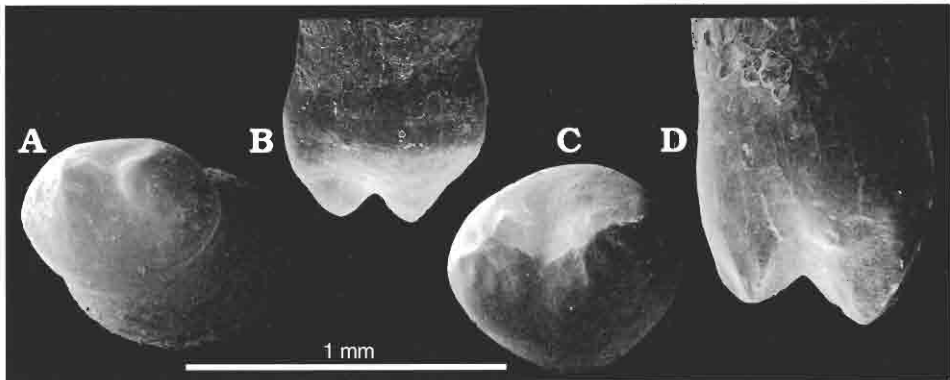
Fig. 20. Bicusped upper premolars. **A**, **B**, 33954; **C**, **D**, 33125. **A**, **C**, occlusal view; **B**, **D**, ?lingual view.

There is a large range of size among tricusped upper premolars in this sample. They are divided into groups below based on their size. The size data for these specimens are presented in Table 4. These data include two measurements not used elsewhere. CW (cusp width) is the distance between the apices of the two posterior cusps; CL (cusp length) is the distance measured perpendicular to the line formed by the CW to the apex of the anterior cusp. These measurements were undertaken to assess variability in the relationship between tooth size and cusp position, hence providing a basis for assessing which would be the most useful measurement of upper premolars, or would be of most utility in sorting out premolar position. We also made an attempt to estimate tooth position based on previously figured tricusped upper premolars. On illustrated P1 (*Cimolodon nitidus* in Clemens 1963: fig. 27b; Lillegraven 1969: fig. 11–2a; *Bolodon crassidens*, Kielan-Jaworowska & Ensom 1992: pl. 5: 7) the anteriormost cusp is positioned medially, with the posterior two cusps aligned transverse to the maxillary tooth row. P2 (Lillegraven 1969: fig. 11–3b) has the anteriormost cusp shifted lingually, such that there is a lingual cusp row and the labial cusp is shifted slightly anterior to the posteriormost lingual cusp, with a small posterolingual shelf commonly present. On many of the specimens examined it was difficult to clearly assign specimens to either the P1 or P2 morph and we emphasize that the designations in the text and in Table 4 are provisional. The interpretation of isolated teeth as P3 is based on a dentigerous maxillary fragment, described below. On that specimen (OMNH 33118, V695, Fig. 21K, L) the internal cusp row of P3 is elongated, with a posteriorly directed lobe that would fit the notch in the anterior face of P4. The labial cusp is placed just posterior to the middle of the crown.

Group 1: These are the largest tricusped premolars in the sample (Table 4). OMNH 29680 (Fig. 21A, V794) is interpreted as a left P1. The tooth is triangular in occlusal outline and only slightly anteroposteriorly elongated. The three cusps are evenly spaced, are the same size and height, and are all strongly striated. There is a very slight posterior shelf and the apex of the posteriormost cusp shows some apical wear. OMNH 27658 (Fig. 21B, V823) is interpreted as a left P2. The anteriormost cusp is shifted lingually. The tooth has a marked, centrally placed posterior shelf. OMNH 32978 (Fig. 21C, V868) is interpreted as a right P3. The labial cusp is medially placed and there is a strong posteriorly oriented ridge descending from the posterolingual cusp. If this is a

Table 4. Size data (in mm) for tricusped anterior upper premolars. Standard deviation (SD) provided for larger samples.

Tooth	Dimension	Group 1	Group 2	SD	Group 3	Group 4	SD	Group 5
P1?	sample *n*	2	11		5	12		3
	range AP	1.43–1.58	1.10–1.42	0.10	1.00–1.15	0.73–0.84	0.03	0.65–0.70
	mean AP	1.51	1.22		1.05	0.78		0.68
	range LB	1.33–1.39	0.99–1.14	0.05	0.89–0.93	0.59–0.79	0.05	0.54–0.62
	mean LB	1.36	1.07		0.90	0.70		0.58
	LB:AP	0.90	0.88		0.90	0.90		0.85
	range CW	0.59–0.70	0.52–0.82	0.08	0.53–0.62	0.36–0.47	0.03	0.28–0.32
	mean CW	0.65	0.62		0.56	0.42		0.3
	range CL	.65–0.70	0.47–0.62	0.05	0.40–0.54	0.29–0.40	0.04	0.26–0.28
	mean CL	0.68	0.54		0.48	0.34		0.27
	CW:CL	0.96	1.15		1.17	1.24		1.11
P2?	sample *n*	3	12		6	16		3
	range AP	1.44–1.56	1.12–1.29	0.05	0.99–1.12	0.71–0.90	0.05	0.66–0.73
	mean AP	1.52	1.20		1.05	0.84		0.69
	range LB	1.12–1.39	0.97–1.16	0.06	0.89–0.93	0.65–0.83	0.05	0.56–0.63
	mean LB	1.27	1.07		0.9	0.76		0.59
	LB:AP	0.84	0.89		0.86	0.90		0.85
	range CW	0.60–0.65	0.53–0.68	0.05	0.48–0.60	0.40–0.54	0.04	0.28–0.31
	mean CW	0.63	0.62		0.54	0.46		0.3
	range CL	0.59–0.79	0.44–0.57	0.04	0.38–0.54	0.27–0.43	0.04	0.23
	mean CL	0.69	0.51		0.43	0.35		0.23
	CW:CL	0.91	1.22		1.26	1.31		1.3
P3?	sample *n*	6	9		9	17		
	range AP	1.41–1.61	1.20–1.40	0.07	1.08–1.29	0.77–0.99	0.04	
	mean AP	1.53	1.29		1.15	0.86		
	range LB	1.11–1.33	0.86–1.14		0.82–0.97	0.62–0.84	0.06	
	mean LB	1.22	1.00		0.90	0.72		
	LB:AP	0.80	0.78		0.78	0.84		
	range CW	0.64–0.76	0.52–0.67	0.05	0.42–0.60	0.40–0.50	0.03	
	mean CW	0.69	0.59		0.53	0.44		
	range CL	0.61–0.72	0.48–0.68	0.07	0.43–0.64	0.31–0.45	0.04	
	mean CL	0.67	0.58		0.51	0.39		
	CW:CL	0.97	1.02		1.04	1.13		

P3, then it is less anteroposteriorly elongated than in some other taxa. One feature suggesting that the tooth represents a P3 is the fact that the strongly sloping posterolingual ridge would fit into the notch at the anterior margin of a P4. Another tooth interpreted to be a P3, OMNH 27493 (Fig. 21D, V695), also has the medially placed labial cusp. Most of the P3s in the sample are double rooted, but on some specimens such as OMNH 27493, the root splits only in its lower part. There is a slight shelf behind the posterolingual cusp and that cusp appears to have apical wear.

There are no premolars with larger numbers of cusps that approach the size of these tricusped molars. For this reason, and given the large sample size, we suggest that each of the first three premolars were tricusped in this taxon. It is likely that these specimens belong to the largest taxon described in this paper, *Cedaromys bestia*. The presence of apical wear does not suggest occlusal wear, but rather abrasion from ingested material, probably vegetation, moved across the upper premolars during mastication (see Krause 1982). It is also possible that some of these large tricusped premolars may belong to *Ameribaatar*, which presumably has some tricusped premolars.
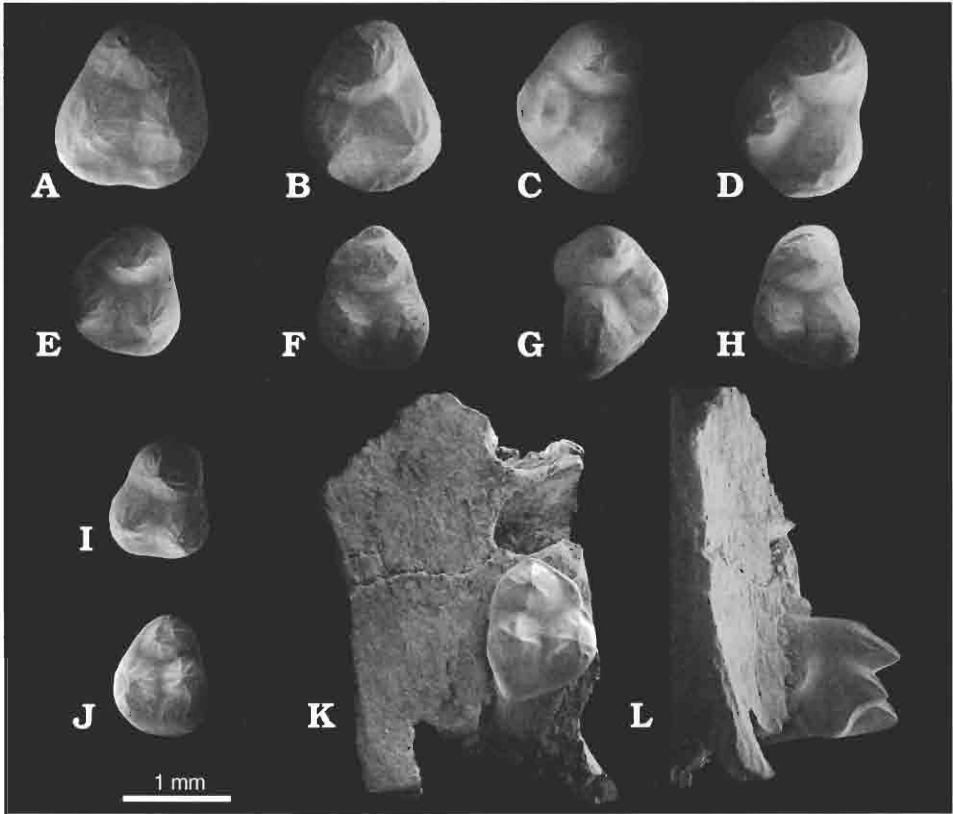
Fig. 21. Tricusped upper premolars, groups 1–3. **A–D**. Group 1 (*?Cedaromys bestia*). **E–H**. Group 2 (*?Cedaromys parvus* n. sp.). **I–L**. Group 3 (*?Bryceomys intermedius* sp. n.). **A**, ?LP1 (29680); **B**, ?LP2 (27658); **C**, ?RP3 (32978); **D**, ?RP3 (27493); **E**, ?RP2 (33157); **F**, ?RP1 (29689); **G**, ?LP3 (25727); **H**, ?RP3 (33141); **I**, ?RP1 (27655); **J**, ?RP2 (27657); **K**, **L**, maxillary fragment with L?P3 (33118). **A–K**, occlusal view; **L**, lingual view.

Group 2: These specimens comprise the next largest group of tricusped upper premolars. Typical of these is OMNH 33157 (Fig. 21E, V695), a P2, which has the anteriormost cusp shifted lingually. The cusps are well-striated. The labial cusp is larger than the two lingual cusps. The posterior shelf consists only of a slight swelling. Some of the teeth included here have some odd features. OMNH 29689 (Fig. 21F, V239), a P1, has the anteriormost cusp in a median position. This cusp has a broader base than the other two cusps and is worn apically. There is a small cuspule anterior to the first cusp, and the tooth is more anteroposteriorly elongate compared to most P1s. The tooth has a slight posterior shelf with a tiny, U-shaped basin.

There is also a wide range of morphological variation among presumed P3s. OMNH 25727 (Fig. 21G, V239), a P3, has the two lingual cusp aligned anteroposteriorly, with a labial cusp in an intermediate position. The posteriormost cusp is well separated from the labial cusp and has the broadest base. The lingual cusps are slightly taller than the labial cusp. A very different P3, OMNH 33141 (Fig. 21H, V695), has the anteriormost cusp isolated such that the anterior part of the tooth is con-

stricted posterior to it. The lingual cusp is the most posterior of the tooth and there is a strong, posteriorly oriented shelf behind this cusp. The labial cusp is positioned slightly more anterior than the posterolingual cusp.

There are no other premolars of this size in the sample, suggesting that the first three premolars of the taxa (or taxon) these belong to were tricusped premolars resembling, for example, the premolar configuration in *Bolodon* (see Kielan-Jaworowska & Ensom 1992: pls. 5–7). Most of these premolars are double-rooted. As with the Group 1 sample, the frequent presence of apical wear on cusps suggests that these teeth did not occlude with counterparts in the lower jaw. It seems likely, based on size, that at least some of the premolars of Group 2 belong to *Cedaromys parvus*.

It is interesting to note (Table 4) that the LB:AP data are very similar for Group 1 and 2, and that for both, the P3 gave the lowest LB:AP value. Also interesting is the fact that the CW:CL of Group 1 was consistently below 1.00, but in Group 2 the CW:CL consistently exceeded 1, particularly in P1 and P2. This could indicate a taxonomic difference. Also, in both groups the P3 had a low LB:AP value (0.78–0.80) but the CW:CL values (0.97–1.02) did not reflect the elongation of the tooth base. This suggests that the position of the three cusps may be functionally unrelated to the size of the tooth base. The standard deviation of AP, LB, CW, and CL measurements do not indicate that the distances between cusp apices is any less variable than overall tooth dimensions.

Group 3: These tricusped premolars are slightly smaller than those of Group 2. OMNH 27655 (V823, Fig. 21I) is characteristic of P1. The anteriormost cusp is the largest cusp (although cusp size is variable in the sample) and is placed in a medial position. The lingual side of the tooth is slightly longer than the labial side. The apices of the cusps form an almost equilateral triangle. OMNH 27657 (V823, Fig. 21J), interpreted as a P2, has the anteriormost cusp shifted lingually, while the posterolabial cusp is positioned posterior to the second lingual cusp and is the largest of the tooth. The posterolingual shelf is variably developed. OMNH 33118 (V695, Fig. 21K, L) is interpreted as a P3, and is preserved in a maxillary fragment. The anterior root is almost vertical and the posterior root leans posteriorly. The much larger and deeper root cavity posterior to this tooth suggests that the succeeding tooth was a P4. The cusps of the lingual row are closely connected. The larger posterolabial cusp is positioned more posteriorly than are the lingual cusps. A small but distinct crest descends posteriorly from the second cusp of the lingual row into a small, low posterior shelf. Presumably this crest would have fitted into the notch on the anterior face of the P4.

It is possible that these teeth represent the anterior premolars of *Bryceomys intermedius*, which is somewhat smaller than *Cedaromys parvus* (Table 1A, B). Both the Group 3 premolars and specimens formally assigned to *B. intermedius* are present in relatively small numbers in the sample, which would be consistent with their representing the same species. On the other hand, the size ranges of Groups 2 and 3 overlap and it is conceivable that they represent the same taxon. However, we tentatively recognize them as distinct, primarily on the basis of the distinctive posterior position of the labial cusp on both P2 and P3 assigned to Group 3. These premolars have proportions very similar to those of Groups 2 and 4 (Table 4).

Group 4: Specimens of Group 4 are smaller than those of Groups 1–3. They are also morphologically similar, particularly to those of Group 2. A sample P1, OMNH 30509 (V794), is shown in Fig. 22A. The anteriormost cusp is placed slightly lingual to the
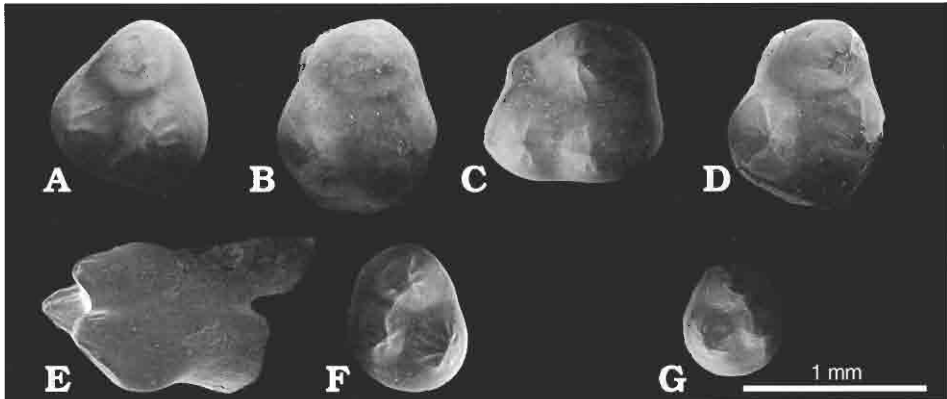
Fig. 22. Tricusped upper premolars, groups 4–5. **A–D**. Group 4 (?cf. *Paracimexomys perplexus* sp. n.). **E–G**. Group 5 (?*Janumys erebos* gen. n. et sp.). **A**, ?RP1 (30509); **B**, ?RP2 (27490); **C**, ?RP2 (30490); **D**, ?RP3 (30480); **E, F**, ?LP1 (27536); **G**, ?RP2 (29749). A–D, F, G, occlusal view; E, lingual view.

middle of the tooth such that it is more closely positioned to the posterolingual cusp than to the labial cusp. The cusp apices form an almost equilateral triangle. There is no posterior shelf. The anteriormost cusp appears to have some wear on its anteroventral surface.

OMNH 27490 (V695, Fig. 22B) is typical of P2 included in Group 2. OMNH 30490 (V794, Fig. 22C) differs from Group 2 P2 in having a small cusp present on the anterolabial side of the tooth and the posterolingual shelf is moderately developed. The posterior margin of the tooth is squared such that the lingual side of the tooth is not more posteriorly elongated than the labial side. This tooth is somewhat like those of *Bolodon* (Kielan-Jaworowska & Ensom 1992: pl. 4: 4).

P3 (e.g., 30480, V794, Fig. 22D) is similar to those of Groups 1–3. However, the CW:CL values are consistently higher among these specimens than in the other groups, whereas the LB:AP values are remarkably similar across Groups 1–4 (Table 4). This suggests that cusp position is somewhat independent of molar size and that it appears to vary taxonomically. These 3-cusped premolars are of appropriate size and align properly with the possible P4 (see below) of cf. *Paracimexomys perplexus*.

Group 5: These specimens are the smallest tricusped premolars in the sample (Table 4). Differentiation of tooth position was very difficult among these specimens. The presumed P1 morphology is shown in OMNH 27536 (V695, Fig. 22E, F). The tooth is clearly double rooted. The anteriormost cusp is shifted lingually and is smaller than the posterolingual cusp, from which it is not deeply separated. The labial cusp is in about the same position posteriorly as the posterolingual cusp, unlike the case of the P2.

OMNH 29749 (V235, Fig. 22G) is considered to represent P2. Small cusps project from a relatively large tooth crown. The anterior cusp is placed in a median position and is connected to the posterolingual cusp by a slight crest. The labial cusp is the most posteriorly positioned of the tooth. The posterior margin of the posterolingual cusp forms a sharp crest. These premolars have LB:AP and CW:CL ratios similar to those of P1 and P2 of the other groups (except the CW:CLs of Group 1). No tooth is present that clearly has a morphology like that of P3 among the Group 5 premolars, and it may be that these teeth belong to a taxon that has posterior premolars with more than 3 cusps. The Group 5 premolars are in the size range anticipated for *Janumys erebos*.

Four-cusped premolars. — OMNH 30507 (V794, Fig. 23A, B) is interpreted as a small (AP = 0.80; LB = 0.74) right P2 or P3. The tooth is double-rooted. The lingual two cusps are of about the same size and height and are anteroposteriorly connected by a striation. Behind the second lingual cusp there is a posteriorly directed lobe. The anterolabial cusp is small and the lowest of the tooth, yet it appears to have undergone apical wear. The posterolabial cusp is the largest and tallest of the tooth and is well striated. In form this premolar looks like a slightly modified tricusped form, one to which an anterolabial cusp has been added. Another similar specimen, OMNH 32925 (V234) is about the same size (AP = 0.78; LB = 0.72), is double-rooted, has cusps of about equal size, and has weak striae (partly removed by abrasion?). Two very similar-sized, four-cusped premolars in the sample are clearly deciduous. OMNH 27235 (V239, AP = 0.79; LB = 0.60, Fig. 23C) is a possible right DP2. The two cusps of the lingual row are of about the same size, but they are widely separated and the row extends farther posteriorly than does the labial cusp row. The anterolabial cusp is small but distinct. The posterolabial cusp is as large as the lingual cusps, but is lower. The posterolabial cusp is weakly striated. OMNH 25598 (V235, AP = 0.84; LB = 0.60) is interpreted as a left DP2 or 3 and has only a few striae on the cusps. The cusp apices form a rectangle and, lacking roots, the specimen is difficult to orient. These premolars appear to fit in about the size range of cf. *Paracimexomys perplexus*.

There is also a group of larger four-cusped premolars in the sample. OMNH 25597 (V235, AP = 1.10; LB = 0.92, Fig. 23D) is possibly a left P2 or 3. The specimen is double-rooted. The two lingual cusps are about the same size and are less deeply separated than the other cusps. There is a posteriorly projecting lobe behind the lingual cusp row. The posterolabial cusp is the largest and tallest of the tooth and the anterolabial cusp is the smallest and lowest. The cusps are well striated and their apices approximate a square in shape. OMNH 25701 (V239; AP = 1.10; LB = 0.98) is a very similar tooth.

OMNH 25639 (V236, AP = 1.20; LB = 0.85, Fig. 23E) is a possible left (?) DP2 or 3. The tooth is waisted and essentially divided across its middle. It is difficult to determine anterior and posterior and the smallest cusp is interpreted here to be the posterolingual one. The cusp apices are offset so that they form a parallelogram. Two other specimens also appear to be deciduous four-cusped premolars of about the same size (OMNH 27494, V695, AP = 1.14; LB = 0.85; OMNH 33127, V695, AP = 1.23*; LB = 0.76*). These premolars fall in the expected size range of *Bryceomys intermedius*.

Deciduous five-, six-, and seven-cusped premolars. — There is a large number of specimens interpreted as deciduous anterior upper premolars. They have a large number of cusps (5 or more), lack roots, and often (but not always) have translucent enamel. The majority of these (72% of 76 specimens) have five cusps (26% have six cusps; 1% have seven cusps). Most of these five-cusped specimens are anteroposteriorly elongate and have four principal cusps of similar size, arranged with apices forming a parallelogram (or some less orderly arrangement) and an additional posterolingual cusp of variable size. OMNH 27614 (V794, AP = 1.17; LB = 0.80, Fig. 23F) is typical of these. Some of the five-cusped deciduous premolars are small, with a bulbous crown bearing relatively small cusps projecting from the crown surface. OMNH 30484 (V794, AP = 0.90; LB = 0.59, Fig. 23G) is such a premolar, with three cusps in the internal row (if oriented correctly) and two in the labial cusp row.
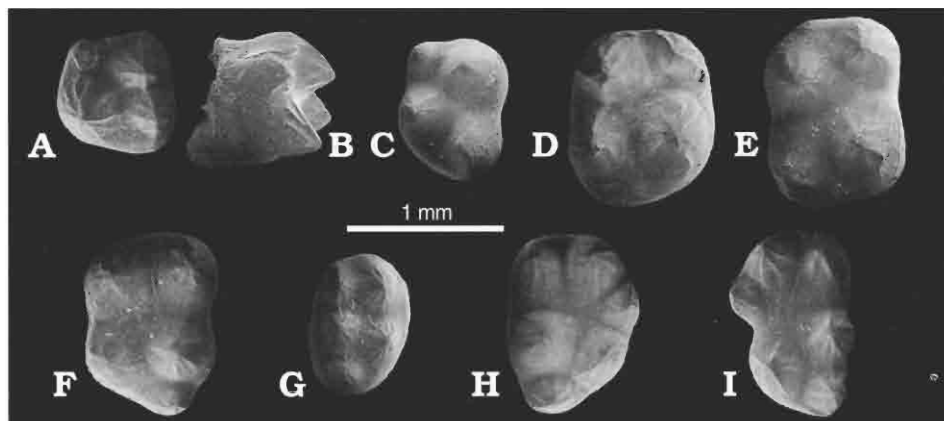
Fig. 23. Four-cusped upper premolars and 5–7-cusped deciduous upper premolars. **A–C.** ?cf. *Paracimexomys perplexus.* **D, E.** *?Bryceomys intermedius.* **A, B,** ?RP2 or 3 (30507); **C,** ?RDP2 (27235); **D,** ?LP2 or 3 (25597); **E,** ?LDP2 or 3 (25639); **F,** ?RDPx (27614); **G,** ?LDPx (30484); **H,** ?LDPx (25641); **I,** ?RDPx (27534). **A, C–I,** occlusal view; **B,** labial view.

The wide range of size and morphology among these five-cusped teeth defy categorization. This may suggest that multituberculate deciduous premolars are more variable than the permanent equivalents.

The six-cusped deciduous premolars appear to be only slight variations on the five-cusped form. The teeth are rootless and lack any sign of wear. Two large cusps anteriorly with one smaller posterior (?) cusp form the lingual (?) row. Two cusps of about the same size as those of the anterior two cusps of the lingual row form the labial row. A smaller cusp is in a median position and labial of the two cusps of the labial row (e.g., OMNH 25641, V236, left? DPx; AP = 1.10; LB = 0.79; Fig. 23H). Like the specimens with five cusps, the six-cusped premolars vary in size, presence or absence of cusp striations, and in relative position of the cusps. As with the five-cusped forms, some of these specimens are constricted in occlusal view (e.g., they have a waist). The constriction separates the three anterior cusps, arranged in an arc, from the three posterior cusps, which are arranged such that they form a triangle (e.g., OMNH 27534, V695, right? DPx; AP = 1.20; LB = 0.77, Fig. 23I).

There is only one seven-cusped deciduous upper premolar. It (OMNH 25719, V239, left DP?, AP = 1.14; LB = 0.84) is similar to the six-cusped deciduous premolars but has an additional posterolabial (?) cusp such that there are two small posterior cusps. The enamel is smooth on this specimen but there appears to be some wear on the anteriormost labial cusp, which is unique among these specimens.

Five- to six-cusped permanent (?) premolars. — The cusp number in the five- and six-cusped permanent (at least well-rooted) upper premolars appears to represent variation among otherwise very similar teeth. We place these premolars into three size groups (Table 5) and these are described separately below. Of described anterior upper premolars, these teeth are most similar to ?P5s of *Sunnyodon notleyi*. We have oriented them as implied by text-figure 5F (a right ?P5) in Kielan-Jaworowska & Ensom (1992); however, they label the same specimen elsewhere (pl. 5: 3) as being from the

Table 5. Measurements (in mm) of five- six-cusped anterior upper premolars.

Group	1	2	3
n	9	10	8
AP range	0.81–1.00	1.09–1.22	1.26–1.35
AP mean	0.91	1.17	1.32
LB range	0.57–0.65	0.70–0.87	0.85–0.96
LB mean	0.61	0.78	0.90
LB:AP	0.67	0.67	0.68

right side, with an opposite orientation. We have assumed that the negative was reversed in this latter instance.

Group 1: These are the smallest of the five- to six-cusped permanent (?) premolars (Table 5). OMNH 29568 (V695, Fig. 24A, B) clearly has strong, unresorbed roots and bears six cusps (as do OMNH 26669, 29568, 33140, V695; 27627, V794; 32924, V235). It is possibly a right P4 (see discussion below). The four cusps of the lingual (?) row are all connected and the cusps are all anteriorly recumbent. The anteriormost cusp is the tallest and the cusps decrease in height but increase slightly in size posteriorly. Two similar but widely spaced and unconnected cusps form the labial cusp row. Of illustrated teeth, this is most similar to the ?P5 of *Sunnyodon notleyi*, a paulchoffatiid illustrated in Kielan-Jaworowska & Ensom (1992: pl. 5: 3), but OMNH 29568 lacks the development of an incipient lingual ridge. This specimen is also very close in size to that of *S. notleyi*. The ?P5 of *Eobaatar* also has the same number of cusps (Hahn & Hahn 1992: fig. 5A), but differs morphologically, with the two labial cusps placed anteriorly.

OMNH 27627 (V794, Fig. 24C) is very similar to OMNH 29568 in size and cusp morphology but is more weakly striated and there is no distinct evidence of permanent roots. If this is a deciduous premolar, morphology will provide little guidance in distinguishing permanent from deciduous premolars in these forms. OMNH 26662 (V695, Fig. 24D, E), interpreted to be a right P4, is a five-cusped variant, of which there are four other specimens in the sample (OMNH 27600, 33978, V794; 32923, V235; 33129, V695). The tooth consists of a large platform with small cusps. The two cusps of the labial row are widely separated by a broad, U-shaped valley. The posterior two cusps of the lingual row are positioned closely together and far from the anteriormost lingual cusp. A small ridge crosses the tooth anteriorly. These teeth are well rooted and are very similar to the six-cusped forms. They may present a variation in cusp number.

All of these premolars are in the appropriate size range of *Janumys erebos*. Several teeth were formally referred to that taxon as P4s. Those P4s have anterior faces with a large recess that is obvious in occlusal view, and as such did not (in life) overhang the preceding tooth. This recess is also present in the P4s assigned to cf. *Paracimexomys perplexus*, but it is lacking in those of *Bryceomys* and *Cedaromys*. P4s of *Janumys erebos* fit well with the posterior margins of these five- and six-cusped premolars (particularly OMNH 29658, a right (?) premolar with OMNH 29573, a right P4 of *J. erebos*, both from V695). It seems unlikely that these represent five- or six-cusped P3. In virtually all illustrated maxillae of 'plagiaulacidans' (e.g., *Bolodon*, Kielan-Jaworowska *et al.* 1987: pl. 12: 1; Kielan-Jaworowska & Ensom 1992: pl. 4: 9), P1–P3 are tricusped but P4–P5 can be quite complex, with parallel cusp rows. Of figured permanent anterior upper premolars from the North American Late Cretaceous, P1–P3 range in form from triangular, tricusped teeth to four-cusped, squared teeth (see various fig-
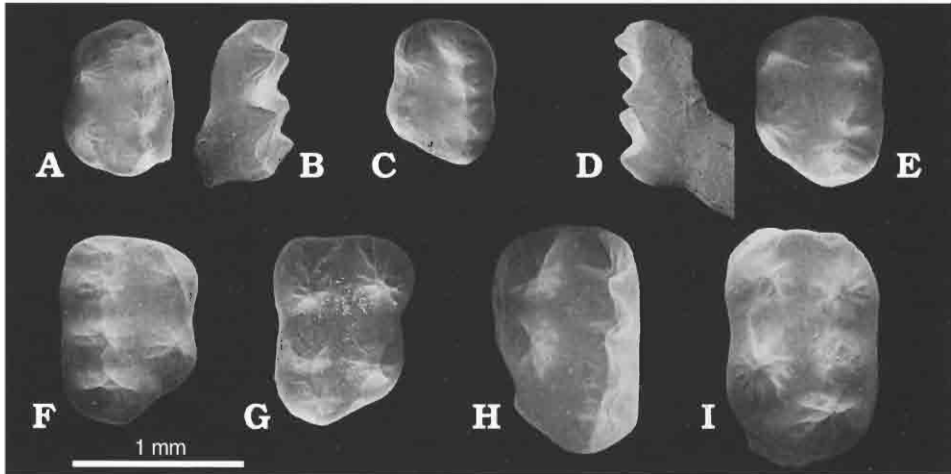
Fig. 24. Five- to six-cusped permanent upper premolars, groups 1–3. **A–E.** Group 1 (*?Janumys erebos*). **F, G.** Group 2 (*?cf. Paracimexomys perplexus*). **H, I.** Group 3 (*?Bryceomys intermedius*). **A, B,** ?RP4 (29568); **C,** ?RP4 or DP4 (27627); **D, E,** ?RP4 (26662); **F,** ?LP4 (32979); **G,** ?LP4 (32973); **H.** ?RP4 (29550); **I,** ?RP4 (25704). **A, C, E–I,** occlusal view; **B, D,** labial view.

ures in Clemens 1963, Lillegraven 1969). The only exceptions are the triangular, five-cusped P2 of *Cimolodon nitidus* (Clemens 1963: fig. 27b), which is very unlike any of the premolars described herein, and a complex premolar Lillegraven (1969: fig. 12-2) considered to be a ?P3 and assigned only to the family level (Ptilodontidae). Interestingly, that premolar is morphologically similar to P4 of *Bolodon osborni* (see Kielan-Jaworowska & Ensom 1992: pl. 4: 9) but is proportionally broader. Taeniolabidoid P1–P3 have three to four cusps, but the P4 of *Kryptobaatar* has five cusps (Kielan-Jaworowska 1970). On present evidence, we consider it likely that these five- to six-cusped premolars represent P4 and that those teeth considered as P4 in the description of *Janumys erebos* are actually P5. These conclusions must be considered as tentative, pending recovery of jaws.

Group 2: This group of five- to six-cusped premolars is intermediate in size (Table 5). OMNH 32979 (V868, Fig. 24F) is double-rooted and is typical of the six-cusped specimens in this group (also including OMNH 25725, V295; 27227, V239; 27445, 29563, V695; 32980, V868). Following the interpretation adopted here, the longest cusp row is on the lingual side of the tooth; this row has four cusps. The anterolingual (?) cusp is very small and the posterior three cusps are of about equal size; the last extends well posterior of the labial (?) cusp row. The 2 cusps of the labial (?) row are widely separated by a U-shaped valley, and an emargination on the labial face of the tooth is present between the two cusps. These cusps are about the same size as those of the lingual cusp row. The central valley of the tooth is closed anteriorly by a ridge that connects the anterior cusps of both rows.

The five-cusped premolars are similar to those with six cusps. OMNH 32973 (V868, Fig. 24G) is typical of these premolars (also OMNH 27232, V239; 29562 [deciduous?], V695; 33000, V868). The tooth is double-rooted and short. The anteriormost four cusps form a rectangle, with broad U-shaped basins separating the cusps

from each other. A single posterior cusp is present posterolingually (?). The tooth has a distinct 'waist' in occlusal view.

These premolars are in the appropriate size range for cf. *Paracimexomys perplexus*, to which four P4s were assigned. P4 has a strong recess at the anterior part of the tooth that is clearly evident in occlusal view. This recess could have accommodated the posterior end of one of these premolars, and suggests the likelihood (as with *Janumys erebos*) that these P4s are really P5s and that the five- to six-cusped premolars described here represent P4.

Group 3: These are the largest of the five- to six-cusped permanent premolars. OMNH 29550 (V695, Fig. 24H) is double rooted and typical of the remaining six-cusped specimens (OMNH 26389, V235; 26658, 27567 [deciduous?], 33126, 33137, 33170, V695). The two central cusps of the lingual row are taller than the postero- and anteriormost cusps. The lingual cusp row is longer than the labial row, which bears two cusps. The tooth is similar to that figured for *Sunnyodon* (Kielan-Jaworowska & Ensom 1992: pl. 5: 3, ?P5), but although the lingual margin of this tooth is broad it does not form a distinct ridge as in *Sunnyodon*, and these specimens are clearly larger than those referred to *Sunnyodon*.

OMNH 25704 (V239, Fig. 24I) is typical of the five-cusped specimens (including OMNH 27579, 30501, V794) and is almost identical to the six-cusped forms, but has one fewer cusp in the lingual row. The teeth in this group have well-developed pairs of roots.

These specimens are appropriate in size for *Bryceomys intermedius* but the single assigned P4 for which the anterior end is present (OMNH 33958, Fig. 10A–C) lacks the large notch seen in P4? of *Janumys erebos* and cf. *Paracimexomys perplexus*. The formula for anterior upper premolars is unknown for *Bryceomys* and the data presented here are inadequate to suggest one.

Possible relationships of the multituberculates from the Cedar Mountain Formation

As might be suspected on the basis of its medial Cretaceous age, the multituberculate fauna of the Cedar Mountain Formation appears to be transitional between older (Late Jurassic) and younger (Late Cretaceous) assemblages of North America. Two taxa (*Janumys erebos* and an unnamed taxon, Fig. 3A–E), as far as known, are characterized mainly by primitive morphology with respect to Cimolodonta and, as such, are placed in the 'Plagiaulacida'. *Janumys* is notable in lacking any trace of a third cusp row on M1, having P4 with a central cusp row that has a very low climb rate and small posterior basin, and lower molars that are nearly equal in length (length ratio of m2:m1 = 0.96). Based on the existing sample, the balance of evidence suggests that *Janumys* retained the primitive count (among multituberculates) of five anterior upper premolars. Unfortunately, the lower premolars of this taxon remain unknown.

One element of the multituberculate fauna from the Cedar Mountain Formation, *Ameribaatar*, is characterized by a distinctive pattern of molar crowns, with widely separated, U-shaped transverse valleys, and ridge-like cusps. These features make *Ameribaatar* unique among multituberculates of the fauna and, for that matter, those of the early Late Cretaceous of North America. The molar pattern is vaguely similar to

what is seen in *Arginbaatar*, from the Early Cretaceous of Mongolia. U-shaped valleys are also present on molars of *Essonodon*, from the latest Cretaceous of North America, but otherwise the molars are quite different. Regardless, the affinities of *Ameribaatar,* even at the subordinal level, are unknown.

The vast majority of multituberculates from the Cedar Mountain Formation appear to be referable to the advanced suborder Cimolodonta (see reviews by Simmons 1993, Weil 1999, and Kielan-Jaworowska & Hurum 2001). A major difference from multituberculate assemblages from the Late Cretaceous of North America is that few, if any, of these taxa can be referred to families or genera that form the bulk of later assemblages. The only possible exception is a p4 that appears to be similar to that of *Mesodma*; lacking other information about the taxon represented, however, nothing can be said about its identity or relationships.

Sloan & Van Valen (1965) recognized two suborders (Taeniolabidoidea and Ptilodontoidea) for then-known Late Cretaceous–Tertiary multituberculates. McKenna (1975) assigned them the rank of parvorders and united them into the infraorder Cimolodonta. Kielan-Jaworowska & Hurum (1997) erected the new suborder Djadochtatheria; subsequently these authors (2001) divided Multituberculata into the paraphyletic suborder 'Plagiaulacida' and the apparently monophyletic suborder Cimolodonta. They divided Cimolodonta into an informal *Paracimexomys* group; three superfamilies, Ptilodontoidea, Djadochtatheroidea, and Taeniolabidoidea (restricted to Taeniolabididae, also see Fox 1999); and five families of uncertain affinities within the suborder (Eucosmodontidae, Microcosmodontidae, Cimolodontidae, Boffiidae, and Kogaionidae); several additional genera were left *incertae sedis*.

Primitive cimolodontans from the Cedar Mountain Formation, cf. *Paracimexomys*, *Cedaromys*, and *Bryceomys*, cannot be placed with confidence in any of the superfamilies mentioned above. For present purposes, we relegate these genera to a taxonomic nether world, the '*Paracimexomys* group', following Kielan-Jaworowska & Hurum (2001). These authors also included *Barbatodon* and *Cimexomys* in the *Paracimexomys* group. Romanian *Barbatodon* is too poorly known to comment on. *Cimexomys*, though often placed near the base of Cimolodonta in phylogenetic analyses, includes a heterogeneous assemblage of species (Montellano *et al.* 2000), most of which differ in significant ways from the remainder of the *Paracimexomys* group (e.g., the lingual-labial alignment of cusps on M1).

Table 3 provides a comparison of morphologic characteristics of *Janumys*, *Paracimexomys*-group taxa from the medial and early Late Cretaceous of North America, *Paracimexomys priscus*, and Eurasian *Eobaatar* (a 'plagiaulacidan'). The *Paracimexomys* group has been characterized as sharing primitive molar structure (e.g., presence of ornamentation and coalescing cusps, low number of cusps on M1 with little to no development of third row) and gigantoprismatic enamel with 'Plagiaulacida', while having a cimolodontan dental formula (loss of anterior premolars) and an arcuate p4, as seen in cimolodontans (Kielan-Jaworowska & Hurum 2001). The cheektooth formula cannot be established with certainty for any taxon in the *Paracimexomys* group. Based on evidence presented above, however, it is possible that at least two species, cf. *Paracimexomys perplexus* and *Bryceomys intermedius*, may have retained five upper premolars. Molar ornamentation (ribbing, pitting) is quite variable within the group (Table 3). In addition to being arcuate (a difference from 'Plagiaulacida'),

the p4 of known taxa in the *Paracimexomys* group differs from that of most remaining Cimolodonta in having fewer serrations. Where known, the p4 of *Paracimexomys*-group taxa resembles that of Ptilodontoidea in being large and protruding strongly above the level of the molars: this appears to be the case, at least, for *Cedaromys* (Fig. 13A–C), *Dakotamys* (Eaton 1995: fig. 7A–D), *Bryceomys* (Eaton 1995: fig. 8E–H), and, possibly, *Paracimexomys priscus* (Lillegraven 1969: fig. 10-3a–b) and *P. magister* (Fox 1971: fig. 2b). But *Paracimexomys*-group taxa lack other ptilodontoid apomorphies (see Kielan-Jaworowska & Hurum 2001). Except for *Cimolodon* (see below), enamel ultrastructure in Ptilodontoidea is microprismatic. Thus far, enamel ultrastructure is known only for one species included in the *Paracimexomys* group, *P. magister* (see Carlson & Krause 1985), in which it is gigantoprismatic. Ptilodontoids are also characterized by a slender lower incisor (see illustrations in Jepsen 1940).

Among the *Paracimexomys*-group multituberculates from the Cedar Mountain Formation, *Cedaromys* and *Bryceomys* are quite similar and may be closely related. *Cedaromys* is more primitive in having p4 with a somewhat lower profile in lateral view, and a much higher second to first molar length ratio; and in lacking a third cusp row on M1. In other features, such as tooth proportions, robust shape of the molar cusps, and the presence of broad U-shaped separations between the cusps, these taxa are closely comparable. The m1, in particular, is very similar. Of all genera of the *Paracimexomys* group, *Cedaromys* and *Bryceomys* warrant special discussion because their morphology suggests the possibility that they may be related to one or more groups of later multituberculates.

Cimolodontidae, particularly *Cimolodon* itself, provide the most intriguing comparisons with *Bryceomys* and *Cedaromys*. The p4 of *Bryceomys* and *Cedaromys* are highly arched and symmetrical, as seen in Cimolodontidae, though they have fewer serrations (12–14 for cimolodontids; 9–11 in *Cedaromys* and *Bryceomys*). Cimolodontids (e.g., *Cimolodon electus*, Fox 1971: fig. 4c), *Bryceomys*, and *Cedaromys* have pyramidal cusps on the external row and slightly more conical cusps on the internal row of m1. An additional point of similarity on m1 is the presence of a posterior wall that closes off the central valley. This is clearly seen in *Cimolodon electus* (see Fox 1971: fig. 4c), *Bryceomys,* and *Cedaromys*. The medial cusp row on M1 of *Cimolodon* is pyramidal and cusps show no tendency to become crescentic but apices do lean anteriorly; the cusp rows are parallel but transverse to the tooth axis such that the labial cusp row broadens anteriorly while the medial cusp row narrows anteriorly; and the cusps commonly bear ribs (Clemens 1963: fig. 29c; Fox 1971: fig. 4d). These are characteristics shared with *Cedaromys*, but less so with *Bryceomys* (see discussion below). Tooth proportions for *Cedaromys* are not very different from those of the most primitive species of cimolodontid, *Cimolodon electus*. Were these taxa included in the Cimolodontidae, the diagnosis of the family would change little except for broadening the range of p4 serrations and molar cusps (p4: 8–14 serrations; m1: 4–8, 3–6; m2: 3–6, 2; P4 2–6, 4–8; M1: 3–7; 4–8; 0–5; M2: 1–5, 3–4, 3–6). However, this would have the result of including a rather broad range of morphology within the family, particularly as *Cedaromys* lacks an internal cusp row on M1.

Cimolodontidae are generally placed among the Ptilodontoidea, but Kielan-Jaworowska & Hurum (2001: p. 406) stated: '*Cimolodon* differs from other cimolodontid genera in retaining gigantoprismatic enamel, which is a more plesiomorphic character

than the microprismatic (Carlson & Krause 1985). We suggest that Ptilodontoidea acquired microprismatic enamel […] after separation of *Cimolodon* (which we tentatively assign to Ptilodontoidea) from the main ptilodontoidean line.' Cimolodontidae also differ from Ptilodontoidea in the lack of a slender lower incisor (see Lillegraven 1969: fig. 11-7); as far as enamel microstructure is concerned, *Cimolodon* and *Paracimexomys magister* share almost identically-sized gigantoprismatic enamel.

We agree with Kielan-Jaworowska & Hurum (2001), but we go a step further and suggest that an alternative hypothesis should be entertained for the relationships of Cimolodontidae: that they are not Ptilodontoidea, but represent a group that originated independently from basal cimolodontans, perhaps a clade including *Bryceomys* and *Cedaromys*. In this case, the extremely high-arched p4 seen in *Cimolodon* (e.g., Archibald 1982: fig. 18) would have developed independently from that seen among various advanced ptilodontoids.

Cimolomyidae include Late Cretaceous, North American multituberculates of uncertain subordinal affinities. Because the relationships of sometimes-included genera are disputed (see Simmons 1993, Rougier *et al.* 1997, and discussion in Weil 1999: pp. 67–68), we limit comparisons to *Cimolomys* itself. *Cimolomys* is atypical (but not unique, note *Mesodma*) among later Cretaceous North American taxa in having M1 with parallel cusp rows and anteroposterior valleys oriented with the anteroposterior axis of the tooth, such that the rows do not broaden or narrow anteriorly (Lillegraven 1969: fig. 4a–c; Sahni 1972: fig. 11G; Clemens 1963: fig. 37a–b)[1]. This character is consistent among all figured M1s of *Cimolomys*. However, Anne Weil (personal communication) has observed wide variation in cusp row obliquity among specimens assigned to *C. clarki* by Sahni (1972). As we have not studied these specimens, it is unclear whether Sahni incorrectly assigned some specimens to the species, or if there is more variability in this character than figured specimens indicate.

The central valley is quite oblique to the anteroposterior axis on M1 of *Cedaromys* (see Fig. 13D), but is much less so on M1 of *Bryceomys intermedius* (see Fig. 10D). M1 among later species of *Bryceomys* have central valleys that are slightly oblique to the anteroposterior axis (Eaton 1995: *B. fumosus*, fig. 9A–F; *B. hadrosus*, fig. 9L) and are therefore closer to the condition seen on M1 of *Cimolomys* than to that of *Janumys*, *Paracimexomys* (and similar taxa), or *Dakotamys*.

More intriguing with respect to the possibility of a relationship among *Cedaromys*, *Bryceomys* and *Cimolomys* is the morphology of m1. Molars of *Bryceomys* and *Cedaromys* have broadly separated, pyramidal cusps. In a revised diagnosis of *Cimolomys* (based on Lancian *C. gracilis*), Clemens (1963: p. 76) noted that the cusps of m1 are strongly crescentic. However, the specimen illustrated by Lillegraven & McKenna (1986: UW 15535, fig. 7A) as *Cimolomys clarki* (Judithian, and therefore older than *C. gracilis*) has broadly separated cusps that appear to be far less crescentic in form than those of *C. gracilis*, and only slightly more crescentic than the cusps of *Bryceomys*. The m1 illustrated by Lillegraven & McKenna (1986: fig. 7A) is remarkably similar

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[1] We note that a specimen assigned to *Cimolomys clarki* and illustrated in McKenna & Lillegraven (1986: AMNH 88485, fig. 7C), has strongly ribbed pyramidal cusps (and lacks the crescentic cusps of the medial row present both in *C. clarki* and *C. gracilis*) with cusps rows oblique to the tooth axis, such that the external row broadens anteriorly and the medial row broadens posteriorly. It appears that this tooth should be referred to *Cimolodon*.

to, but has more cusps than, *Bryceomys hadrosus* (see Eaton 1995: fig. 9J), and if it is correctly assigned to *C. clarki*, it may represent a morphologic intermediate between *Bryceomys* and *C. gracilis*. Alternately, UW 15535 might also represent an advanced form of *Bryceomys* rather than *Cimolomys*.

Cimolomys and *Cimolodon* are consistently paired on the cladograms of Rougier *et al.* (1997) (however, see Simmons 1993, in which the taxa are widely separated) and *Cimolomys*, *Cimolodon*, and cf. *Paracimexomys magister* share gigantoprismtic enamel (Krause & Carlson 1987). It may be that *Cimolomys* also had its origin within a group that includes cf. *Paracimexomys* group and (as suggested herein) *Cimolodon*.

Based on the foregoing considerations *Mesodma* (which first occurs in the Santonian of North America; JGE manuscript in preparation) currently appears to represent the oldest, morphologically basal member of Ptilodontoidea. Notable features of *Mesodma* include dominantly small enamel prisms, elongate p4, and reduction of the relative length of second to first molars. Beyond the tantalizing record of a much older (Albian–Cenomanian) *Mesodma*-like p4, the fauna described here sheds no obvious light on *Mesodma*'s origin or, following our interpretation, the Ptilodontoidea.

Acknowledgements

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Wieloguzkowce z formacji Cedar Mountain w stanie Utah, z przełomu wczesnej i późnej kredy

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Streszczenie

W pracy opisano najstarszy dobrze opróbowany zespół zębów wieloguzkowców (Multituberculata) z kredy Ameryki Północnej. Fauna formacji Cedar Mountain jest datowana na 98,37 mln lat temu, a więc pochodzi mniej więcej z granicy albu i cenomanu (a więc przełomu wczesnej i późnej kredy). Fauna wieloguzkowców jest zróżnicowana. Dwa z nich (*Janumys erebos* gen. et sp. n. oraz nieoznaczony takson) tymczasowo zaliczono do „Plagiaulacida". Kolejny takson, *Ameribaatar zofiae* gen. et sp. n., ma niejasną przynależność na szczeblu podrzędu. Wydaje się, że pozostałe wieloguzkowce reprezentują zaawansowany podrząd Cimolodonta i należałoby je umieścić w „grupie *Paracimexomys*". Diagnoza *Paracimexomys* została zrewidowana na podstawie gatunku typowego, *P. priscus*, toteż inne gatunki potraktowano jako cf. *Paracimexomys* (w tym cf. *P. perplexus* sp. n.). Zrewidowaną diagnozę uzyskał także cenomański *Dakotamys*. Opisany już wcześniej z formacji Cedar Mountain gatunek umieszczony został w nowym rdzoaju *Cedaromys* jako *C. bestia*, obok *C. parvus* sp. n. *Bryceomys* reprezentowany jest w opisywanej faunie przez *B. intermedius* sp. n. Niejasne pozostają pokrewieństwa między grupą *Paracimexomys* a późniejszymi taksonami. *Bryceomys* i *Cedaromys* mają jednak wiele cech wspólnych z rodziną Cimolodontidae. Ze względu na owe podobieństwa, a także na zachowanie przez Cimolodontidae pewnych plezjomorfii (masywny dolny siekacz, gigantopryzmatczne szkliwo) nieobecnych u Ptilodontoidea (do których się je zwykle zalicza), sugerujemy, że Cimolodontidae mogły się wyodrębnić z kladu w obrębie „grupy *Paracimexomys*", niezależnie od ptilodontoidów.