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A NEW SPECIES AND ADDITIONAL MATERIAL OF *CATOPSALIS* (MAMMALIA, MULTITUBERCULATA) FROM THE WESTERN INTERIOR OF NORTH AMERICA

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ABSTRACT—The taeniolabidid multituberculate *Catopsalis* ranges from Late Cretaceous to late Paleocene in age. An early Paleocene locality in the Denver Formation of Colorado has produced well-preserved remains of a new species, *C. alexanderi*, which is intermediate in size, morphology and presumably age between the Lancian species, *C. joyneri*, and the Puercan species, *C. foliatus*. Additional specimens of *C. alexanderi* are known from Wyoming and Montana. Numerous teeth of *Catopsalis* from the late Torrejonian or early Tiffanian Shotgun local fauna of Wyoming are referred to *C. calgariensis*, the final species in the lineage. This new material shows the following chronological and presumably evolutionary trends within the North American species of *Catopsalis*: an increase in absolute size, an increase in relative size of the first molars, and an increase in enamel infolding, cuspules and cingula on the molars rather than a significant increase in cusp number.

INTRODUCTION

THE GENUS *Catopsalis* represents one of the better known lineages of multituberculate mammals. Kielan-Jaworowska and Sloan (1979), in their review of the genus, recognize seven species; two in the Late Cretaceous of Asia (*C. matthewi* and *C. catopsaloides*), one in the latest Cretaceous of North America (*C. joyneri*), and four in the Paleocene of North America (*C. foliatus*, *C. utahensis*, *C. fissidens* and *C. calgariensis*). They hypothesize that the genus originated in Asia and spread to North America in the Late Cretaceous (see also Kielan-Jaworowska, 1974). In general, species of the genus exhibit the following evolutionary trends: increase in body size, increase in molar cusp number, and a corresponding decrease in relative size of the lower fourth premolars (Kielan-Jaworowska and Sloan, 1979).

In the fall of 1973, a new fossil locality was discovered in the Denver Formation south of Littleton, Colorado. The locality (UCM locality 77267) is a leveled construction site in fine andesitic sands and silts, and the fossils are exposed by deflation. In addition to abundant remains of wood, leaves and seeds, and typical early Tertiary lower vertebrates (gars, amphibians, turtles, lizards and crocodylians), many well-preserved remains of mammals have been collected. The various species of multituberculates, insectivores, and condylarths, as well as a single species of marsupial, indicate an early Puercan age for the fauna. *Catopsalis* was one of the first-identified taxa, and the few

teeth then found were thought to belong to *C. foliatus*. Additional specimens have shown that the material, although obviously belonging to the genus, does not fit the description of any of the known species.

Isolated teeth of *Catopsalis* are known from a number of other sites of similar age. J. D. Archibald, while studying mammals of the Hell Creek and Tullock formations of Montana, identified a single M¹ fragment from the Tullock Formation as *Catopsalis* cf. *C. foliatus*, recognizing that it was considerably larger than *C. joyneri*, a common animal at some localities in the Hell Creek Formation (Archibald, written commun., 1980). Continued collecting at two localities in the Tullock Formation by W. A. Clemens has produced two more teeth; one unpacked and uncataloged, and an M². In addition, six isolated teeth of *Catopsalis* have been collected by Princeton University parties from the Mantua Lentil of the Polecat Bench Formation of Wyoming. Although identified as *C. foliatus* in the Princeton collections, these teeth are significantly smaller than the type of that species. Comparison of the above material with the abundant Denver *Catopsalis* specimens has shown the close similarity of all in size and morphology. Hence they are united here as a new species.

Catopsalis calgariensis is the youngest known species of the genus. It was named for an isolated M₂ from a late Torrejonian or early Tiffanian locality in the Porcupine Hills Formation of Alberta (Russell, 1926; see also Krause,

1978). Unfortunately, the type is lost but casts of it exist. This single tooth is still the only described specimen referred to this species. However, teeth of *Catopsalis* long known from the Shotgun local fauna of late Torrejonian or early Tiffanian age from the Shotgun Member of the Fort Union Formation of Wyoming are here referred to *C. calgariensis*. Originally identified by C. L. Gazin as *C. cf. fissidens* (Keefer, 1961), the near identity of a Shotgun M_2 to the type of *C. calgariensis* and the similarity in age of the two localities supports the referral of all the Shotgun *Catopsalis* teeth to *C. calgariensis*.

ABBREVIATIONS

The following abbreviations are used for measurements, statistics and institutions: L, length; W, width; CV, coefficient of variation; N, sample size; OR, observed range; SD, standard deviation; \bar{x} , mean; AMNH, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburgh; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; PU, Museum of Natural History, Princeton University, Princeton; UA, University of Alberta, Edmonton, Canada; UCM, University of Colorado Museum, Boulder; UCMP, University of California Museum of Paleontology, Berkeley; UMVP, University of Minnesota, Minneapolis; UW, Geological Museum, University of Wyoming, Laramie.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order MULTITUBERCULATA Cope, 1884
Family TAENIOLABIDIDAE Granger and Simpson, 1929

Genus CATOPSALIS Cope, 1882
CATOPSALIS ALEXANDERI n. sp.
Pl. 1, figs. 1–6

Catopsalis sp., ARCHIBALD, 1977, p. 149, fig. 24.
Catopsalis foliatus, KIELAN-JAWOROWSKA AND SLOAN, 1979, p. 192, fig. 2D.
Catopsalis foliatus (in part), SLOAN, 1981, p. 155.

Holotype.—UCM 34979, right lower jaw with I, P₄, M₁₋₂, collected by Carl Alexander in 1976 at the Alexander locality (UCM locality 77267), Denver Formation, Arapahoe County, Colorado.

Hypodigm.—UCM 34136–34143, 34176, 34331, 34332, 34568, 34578, 34596, 34598, 34600, 34603, 34608, 34934, 34940, 34946, 34948, 34949, 34963, 34979 (holotype), 34980–34984, 34995, 35002, 35006, 35026, 35028–35030, 35095, 36750, 38201, 38857, 39545, 39553, 40154, 43553, 43554; all from the Alexander locality. UCMP 116954 from Worm Coulee #1 (UCMP locality V74111) and UCMP 124404 from Hell's Hollow-Channel (UCMP locality V74110), Tullock Formation, Garfield County, Montana. PU 14550, 16647–16650, 18196; from the Mantua Lentil of the Polecat Bench Formation, Park County, Wyoming.

Diagnosis.—Intermediate in size and morphology between *Catopsalis joyneri* and *C. foliatus*. Most easily distinguished from both by size (see Tables 1, 2 and Text-figs. 1, 2). Differs from *C. joyneri* in being larger, in having a gliriform I² with enamel restricted to an anterodorsal band, and in having an inner row of cusps on M¹ extending the full length of the tooth, thus giving a higher cusp count. Differs from *C. foliatus* in having smaller molars, larger P₄ with a posteroexternal basal cusp, and in lacking the crenulations of the molar cusps seen on the type of *C. foliatus*.

EXPLANATION OF PLATE 1

FIGS. 1–6—*Catopsalis alexanderi* n. sp. All approx. $\times 1.4$ natural size. 1,2, UCM 34979 (holotype), right lower jaw in lingual and labial views. 3, stereophotograph of UCM 39553, partial palate in occlusal view. 4, stereophotograph of UCM 34979 (holotype), right lower jaw in occlusal view. 5, UCM 43553, proximal end of right tibia in posterior view. 6, UCM 43554, proximal end of left femur in posterior view.
7–12—*Catopsalis calgariensis*. All approx. $\times 2.2$ natural size. 7, stereophotograph of UW 6387, right P⁴ in occlusal view. 8, stereophotograph of UW 6407, right M¹ in occlusal view. 9, stereophotograph of UW 6388, right M₁ in occlusal view. 10, UW 14068, right lower incisor in posterolingual view. 11, stereophotograph of UW 14058, left M² in occlusal view. 12, stereophotograph of UW 14051, right M₂ in occlusal view.

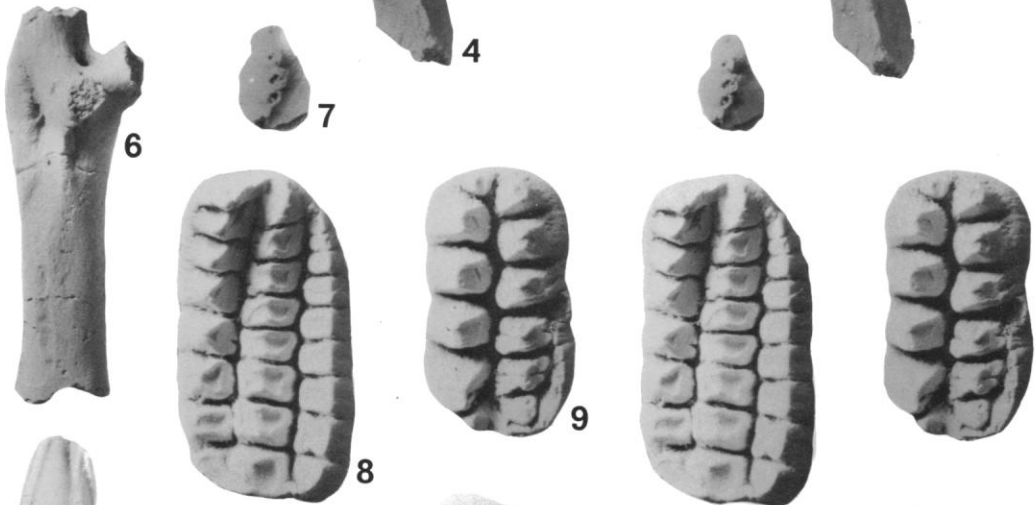


TABLE 1—Measurements (mm) of the upper dentition of *Catopsalis alexanderi*.

Specimen number	I ² max	I ² min	I ³ max	I ³ min	P ⁴ L	P ⁴ W	M ¹ L	M ¹ W	M ² L	M ² W
UCM 34139								6.5		
34140									6.9*	6.3*
34143							10.5*	5.6*		
34331								5.5		
34568								5.2	6.2	5.7
34596									6.6	5.9
34600									6.0	5.5
34608									6.8	6.0
34940	7.8	4.3								
34946	6.5	3.8								
34949							9.9	5.5		
34982									6.2	5.7
34983							10.4*			
35006			2.6	2.0						
35030	6.5	3.1								
36750									6.8	6.2
38201							10.0*	5.2		
lt. 39553	6.7	3.0*			4.1	3.6	10.7	5.9	6.7*	6.2
rt. 39553	6.4	2.8	2.6	2.0	4.5	3.4	10.5*	6.0	6.6	6.2
PU 14550					4.3	2.8				
16647							10.0	5.1		
16648									7.2	5.9
UCMP 116954								5.4*		
124404									6.0	5.4
N	5	5	2	2	3	3	7	10	11	11
OR	6.4–7.8	2.8–4.3	2.6	2.0	4.1–4.5	2.8–3.6	9.9–10.7	5.1–6.5	6.0–7.2	5.4–6.3
	6.8	3.4	2.6	2.0	4.3	3.3	10.3	5.6	6.5	5.9
SD	.58	.63	—	—	.2	.42	.31	.43	.39	.30
CV	8.6	18.5	—	—	4.7	12.6	3.0	7.7	6.1	5.2

* Estimated.

Etymology.—Name given in honor of Carl Alexander, discoverer of the Alexander locality and collector of the holotype.

Age and distribution.—Known from the early Puercan (Mantuan of Van Valen, 1978) of Colorado, Wyoming and Montana.

Description.—The upper dentition of *Catopsalis alexanderi* is of particular interest in being the most complete known for a North American species of the genus. UCM 39553, a well-preserved partial palate with both tooth rows, shows quite clearly the morphology of the teeth (Pl. 1, fig. 3). I² is large, robust and gliriform, with a long root constricted at the end. The enamel is restricted to an anterodorsal band. It resembles closely the same tooth in *Taeniolabis* (see Granger and Simpson, 1929). None of the six specimens preserve the morphology of the unworn tip. However, on less worn teeth, the enamel wraps around onto the posterior surface near the tip, indicating the unworn tip was enamel covered. It is likely the tip was multi-cusped, but with use was quickly worn down to a single chisel-like blade.

A suggestion of an accessory cusp is often seen low on the lateral edge, in the form of an enamel pillar fused onto the main body of the tooth.

The small I³ is situated directly posterior and close to I². It is on the margin of the palate as in *Taeniolabis*; not in a more posteromedial position as in the earlier, Asian species of *Catopsalis* (Clemens and Kielan-Jaworowska, 1979). Its morphology is almost identical to that of *Taeniolabis* as well.

The number of upper premolars is unknown, although it is possible that only P⁴ remained. In *Catopsalis joyneri*, P³ is present as a small single rooted peg, separated by a diastema from P⁴, and situated opposite the anterior edge of zygoma (UMVP 1642). Unfortunately, that part of the maxilla is not preserved in any specimens of *C. alexanderi*. P⁴ is only preserved on UCM 39553 and PU 14550. It is similar to the P⁴ of *C. joyneri* (see Sloan and Van Valen, 1965), with a cusp formula of 1–3:5:2. The cusp position and formula varies on the left and right sides of UCM

TABLE 2—Measurements (mm) of the lower dentition of *Catopsalis alexanderi*.

Specimen number	I Max	I min	P ₄ L	P ₄ W	M ₁ L	M ₁ W	M ₂ L	M ₂ W
UCM 34136			4.0	2.9	8.8	5.1	5.9	4.9
34137	5.5	3.9						
34141					9.0	4.9		
34142	5.9	4.0						
34332					9.0	4.8		
34578							7.1	5.3*
34603	5.3	3.9						
34934							6.5	4.9*
34948					8.2	4.6	5.7*	4.6
34979	4.9	3.4	4.2	2.5	8.3	4.3	6.1	4.8
34980	5.0	3.5						
34984						5.0*		
35095	5.0	3.5	4.6*	2.5*	9.3*	4.7*	6.4*	5.0*
38857	5.7	3.6	4.5	2.7	8.6	5.2	7.2	5.2
40154					9.0	4.9		
PU 16649					8.4*	4.5		
16650							7.1	5.3
N	7	7	4	4	9	10	8	8
OR	4.9–5.9	3.4–4.0	4.0–4.6*	2.5–2.9	8.2–9.3*	4.3–5.2	5.7*–7.2	4.6–5.3
\bar{x}	5.3	3.7	4.3	2.65	8.7	4.8	6.5	5.0
SD	.39	.24	.28	.19	.38	.28	.58	.25
CV	7.3	6.5	6.4	7.2	4.3	5.8	9.0	5.0

* Estimated.

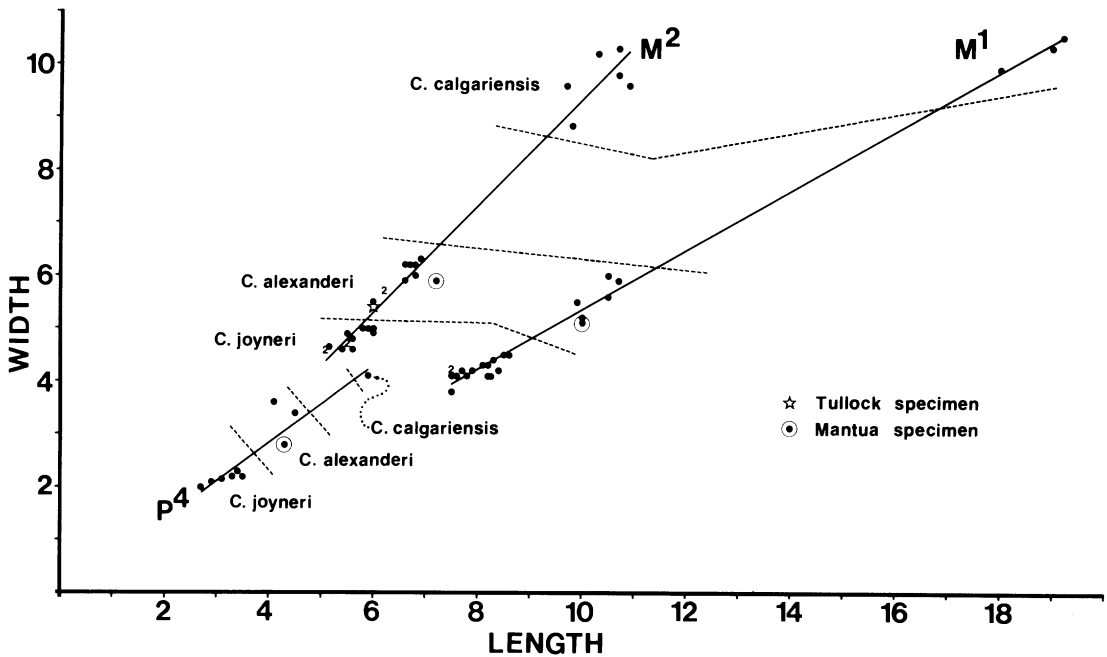
39553; the right P⁴ has an anteroexternal accessory cusp not present on the left. The external row otherwise is composed of one (UCM 39553) or two (PU 14550) small posterobasal cusps. The medial row consists of a small anterobasal cuspule and four large closely-spaced cusps, the second or third of which is the highest. The two internal cusps lie along a small cingulum which forms a pocket on the postero-internal rim of the tooth. On all three specimens, those cusps are largely removed by a posterointernal wear facet.

The upper molars are variable, M² more so than M¹. M¹ has a cusp formula of 7:7:9. One M¹, UCM 34983, has an additional transverse cuspidate ridge anterior to the two outer rows, making its formula 8:8:9. The inner row narrows and its cusps decrease in size anteriorly, making an exact count difficult. This row extends the full length of the tooth, or nearly so. M² has a cusp formula of 1–2:3:3–4. The external row may have a single cusp, a cusp with a ridge extending from it posteriorly, or two cusps. The first cusp of the medial row is often simply a ridge connected to the anteroexternal cusp. The inner row may have three cusps, three cusps and a posterior ridge, or a fourth cusp posteriorly. The fourth cusp, when present, is slightly medial in position relative to

the other three. Those teeth that have a high cusp formula (2:3:4) are also largest in size.

The mandible is well-preserved in the holotype, UCM 34979 (Pl. 1, figs. 1, 2, 4). Comparison with other species of *Catopsalis* is difficult, since none of the North American species have well-preserved lower jaws, and the Asian species are considerably more primitive in jaw morphology and dentition. However, Granger and Simpson's (1929, p. 611) description of the mandible of *Taeniolabis* would serve equally well for *C. alexanderi*. The jaw is not quite as robust; the masseteric fossa not as sharply defined anteriorly.

The lower dentition of *Catopsalis alexanderi* closely resembles *C. joyneri* (see Sloan and Van Valen, 1965) except in the larger size of the teeth. The lower incisor is gliriform, with enamel largely restricted to an anteroventral band and extending for a short distance inside the alveolus. The morphology of the unworn tip can be seen on PU 18196. It is enamel-capped, although the enamel quickly thins on the dorsal surface. The tip is composed of three anteroposteriorly flattened cusps, the largest one internal. P₄ has three small cusps on its anterior slope. The third is most distinct. The first two are quickly removed by an external wear facet, and only a shallow groove in the



TEXT-FIG. 1—Bivariate plot of length and width of upper cheek teeth of North American species of *Catopsalis*. Solid lines are regression lines. Dashed lines separate species. Scale in mm. Equations for the regression lines are as follows: P⁴, $Y = -0.06 + 0.73X$, $r^2 = .86$, $N = 10$; M¹, $Y = -0.23 + 0.56X$, $r^2 = .99$, $N = 25$; M², $Y = -0.75 + 1.01X$, $r^2 = .98$, $N = 30$.

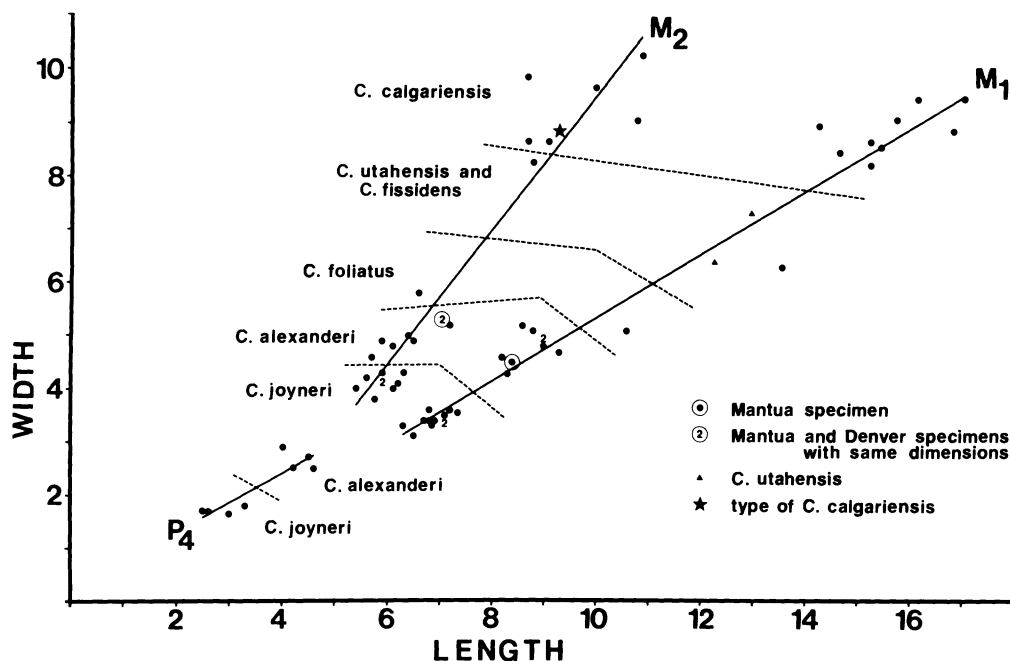
enamel on the side of the tooth indicates their presence. All three are relatively smaller than in *C. joyneri*. A basal cusp is situated on the posteroexternal margin of the tooth.

As in *Catopsalis joyneri* and *C. foliatus*, M₁ has a cusp formula of 5:4. On less worn teeth, a sixth small posteroexternal cusp lies on the ridge connecting the last cusps of both rows, but with wear that cusp loses its distinctiveness and merges with the fifth. Small anterior cusps may be present either externally or internally. On one tooth (UCM 38857), two small cusps are located midway along the tooth on the internal side. The enamel on the medial side of the cusps of M₁ and M₂ is never as infolded as in *C. foliatus*. M₂ has a cusp formula of 3:2. Ridges extend toward each other from the last cusps of both rows, but are separated by the medial groove. The ridges may also be separated from the last cusps by a small notch.

Two postcranial bones from the Alexander locality, a proximal femoral fragment (UCM 43554) and a proximal tibial fragment (UCM 43553) almost certainly belong to *Catopsalis alexanderi* (Pl. 1, figs. 5, 6). *C. alexanderi* is

the only large multituberculate known from the Alexander locality; from the size of its lower jaw it was slightly smaller than a modern woodchuck (*Marmota monax*). These two bones are also slightly smaller than the homologous bones of a woodchuck. They both have characteristic multituberculate features (see Clemens and Kielan-Jaworowska, 1979). The femoral head and the ends of both the greater and lesser trochanters are broken off the femur. Nevertheless, the greater trochanter is large and extends well above the femoral head. The lesser trochanter is robust and situated in the middle of the posterior surface of the femur. The deep, elongate fossa lateral to the lesser trochanter, known only in multituberculates, is well developed. The tibial fragment is from a young individual, judging from the incomplete fusion of the proximal epiphysis and the shaft. The lateral tuberosity is largely broken off. The posteroproximal surface of the shaft is deeply excavated; a feature found only in multituberculates. The cnemial crest is sharp; the lateral surface of the shaft concave.

Discussion.—*Catopsalis alexanderi* is inter-



TEXT-FIG. 2—Bivariate plot of length and width of lower cheek teeth of North American species of *Catopsalis*. Solid lines are regression lines. Dashed lines separate species. Scale in mm. Equations for the regression lines are as follows: P₄, $Y = 0.23 + 0.54X$, $r^2 = .78$, $N = 8$; M₁, $Y = -0.61 + 0.59X$, $r^2 = .96$, $N = 34$; M₂, $Y = -3.13 + 1.27X$, $r^2 = .91$, $N = 26$.

mediate in size and morphology between *C. joyneri* from the Late Cretaceous (Lancian) Hell Creek Formation of Montana and *C. foliatus* from the early Paleocene (Puercan) of the Nacimiento Formation, San Juan Basin, New Mexico. *C. alexanderi* shows a number of apomorphic (derived) characters not seen in *C. joyneri*: gliriform I², relatively more reduced P₄, larger absolute size and a more complete inner row of cusps on M¹. Separation of *C. alexanderi* from *C. foliatus* has proved more difficult. Only a single dentulous specimen of *C. foliatus* is known, a lower jaw with a fragment of P₄ and M₁₋₂ (AMNH 3035). The six Mantua teeth (representing at least three individuals based on stages of wear), although in the Princeton collections for some time, were not separated as a new species because there was not enough material known to show they were distinct. They were simply considered small individuals of *C. foliatus*. When the numerous Denver Formation *Catopsalis* teeth were collected (minimum number of individuals = 7), it soon became evident that the type of *C. foliatus* was well outside the range of

variation seen in those teeth (Text-figs. 1, 2). On the other hand, both the Mantua and Tullock teeth are within the range of variation in size and morphology seen in teeth from the Alexander locality. For that reason they are here included in *C. alexanderi*. However, the possibility exists that with further collecting of more complete material, the Mantua or Tullock *Catopsalis* may prove to be distinct.

Three isolated teeth (UA 16056–16058) from the Long Fall locality in the Ravenscrag Formation of Saskatchewan, Canada, have recently been referred to *Catopsalis* cf. *C. foliatus* by Paul Johnston (written commun., 1980). He states that the teeth are intermediate in size between *C. joyneri* and *C. foliatus*, and may be conspecific with the Tullock and Denver Formation species (*C. alexanderi*). I have not included them here for a number of reasons. One of the teeth, a fragment of a lower incisor, is not diagnostic. Another, an I², is very small and may represent a different taxon (similar in size and morphology to the same tooth in *C. joyneri*). The third, an M₁, is longer than any *C. alexanderi* specimens. For

TABLE 3—Measurements (mm) of the dentition of *Catopsalis calgariensis* (UW, CM and MCZ specimens) from the Shotgun Local Fauna, Fremont Co., Wyoming.

	N	OR	\bar{x}	SD	CV
P ⁴ L	1	—	5.9	—	—
P ⁴ W	1	—	4.1	—	—
M ¹ L	4	18.0–19.2	18.8	.54	2.9
M ¹ W	3	9.9–10.5	10.2	.31	3.0
M ² L	6	9.7–10.9	10.4	.50	4.9
M ² W	6	8.9–10.3	9.7	.52	5.4
M ₁ L	10	14.3–17.1	15.7	.88	5.6
M ₁ W	10	8.3–9.5	8.9	.40	4.5
M ₂ L	6	8.7–10.9	9.7	1.01	10.4
M ₂ W	6	8.7–10.3	9.4	.67	7.1

these reasons additional material is necessary for positive identification. Johnston feels the Long Fall locality is of latest Cretaceous age, even though he recognizes its closest affinities are to the earliest Paleocene Hell's Hollow localities in the Tullock Formation of Montana.

Since *Catopsalis alexanderi* is intermediate in size and morphology between the Lancian and Puercan species of *Catopsalis*, it is not surprising that it is intermediate in age as well. The Mantuan age was defined by Van Valen (1978) for the local fauna from the Mantua Lentil of the Polecat Bench Formation. According to Sloan (written commun., 1980), it is the earliest Paleocene land mammal age, immediately postdating dinosaur extinction. Whether or not the term "Mantuan" gains general acceptance, mammals of approximately this age are known from the Mantua and Leidy Quarries of the Polecat Bench Formation in Wyoming (Van Valen, 1978), the Hell's Hollow local fauna of the Tullock Formation in Montana (Archibald, written commun., 1980), and now from the Alexander locality in the Denver Formation of Colorado. From the composition of the entire mammalian fauna, it appears that the Hell's Hollow local fauna may be slightly older than the Mantua local fauna (Archibald, written commun., 1980), while the Alexander locality is younger.

CATOPSALIS CALGARIENSIS Russell, 1926

Pl. 1, figs. 7–12

Catopsalis cf. *C. fissidens*, KEEFER, 1961, p. 1315.

Referred specimens.—UW 6387, 6388, 6407, 14046–14070, 15100–15102. CM 15940–15942. UCM 25337. A number of uncataloged MCZ specimens. All from the Shotgun (Twin Buttes)

localities (UW localities V-60014 and V-60016), Shotgun Member of the Fort Union Formation, Fremont Co., Wyoming.

Revised diagnosis.—Largest and youngest known species of the genus. Slightly smaller than *Taeniolabis taoensis*, with a lower cusp count on the molars. Distinguished from earlier members of the genus *Catopsalis* by its larger size (see Table 3 and Text-figs. 1, 2), strong posteroexternal cingulum on M₁, crenulation of enamel on the cheek teeth, and single-rooted P⁴ without external cusps.

Age and distribution.—Known from the late Torrejonian or early Tiffanian of Alberta and Wyoming (see Krause, 1978, for review of the age assignment).

Description.—Unfortunately, *Catopsalis calgariensis* is still known only from isolated teeth. In most respects, the dentition is extremely similar to *C. alexanderi*, except for its larger size.

I² is known from two fragments, both of which preserve the unworn tip of the tooth. The tip is composed of two anteroposteriorly flattened cusps separated by a small groove. The cusps themselves have shallow, broad longitudinal grooves which extend a short distance down the anterior face of the tooth. The enamel wraps around onto the posterior surface only very close to the tip. One of the specimens, UW 14063, shows three transverse growth lines in the enamel further down the tooth. I³ is very similar to the same tooth in *Taeniolabis taoensis* and *Catopsalis alexanderi*. On less worn specimens, the tip is enamel-capped, and a small lateral accessory cusp is closely appressed to the main cusp. The smaller cusp quickly disappears with wear.

The anterior premolars, if present, are unknown. Only one P⁴ has been found in the collections (UW 6387; Pl. 1, fig. 7). Its cusp formula is 0:5:cingulum. The external row has been lost. The medial row consists of five cusps as in *Catopsalis joyneri* and *C. alexanderi*. There is a small basal anterior cusp, followed by four closely-spaced cusps, the penultimate being the highest. Only a small posteroexternal cingulum remains of the internal row. Much of the enamel has been broken off low along the internal flank, but it is unlikely that any cusps were situated there. In contrast to the P⁴ of *C. joyneri* and *C. alexanderi*, this tooth is single-rooted.

M^1 has a cusp formula of 7:7-8:7-10. A transverse cuspidate ridge is located on the anteroexternal corner of the crown, connecting with the first cusp of the medial row. On some teeth this ridge functions as an additional cusp on the external row. As in *Catopsalis alexanderi*, the inner row extends the full length of the tooth, or nearly so. One tooth, UW 14054, has a small accessory cusp midway along its internal side. The unworn enamel is marked by fine vertical striations, and shallow infolding may occur in the enamel of the cusps. The larger posterior and smaller anterior roots are connected by a low interradicular crest, with a number of accessory roots on both sides.

M^2 has a cusp formula of 1:3:3. The first cusp of the medial row is simply a widening of a transverse ridge connecting the first cusps of the inner and outer rows. The slight infolding of the enamel seen on M^1 cusps is more pronounced on M^2 .

The unworn tip of the lower incisor is composed of two small anteroposteriorly flattened cusps (Pl. 1, fig. 10). A vestige of a third cusp slightly lower on the lateral edge is indicated by a slight bump and a shallow groove in the enamel of the anterior surface (UW 14068). A very thin enamel film is present on the posterior face near the tip. The enamel band of the tooth is covered by fine longitudinal wrinkles with occasional transverse growth lines.

A P_4 referable to this species has not been found, although a small concave wear surface on the anterior face of M_1 attests to its presence. M_1 has a cusp formula of 5-6:4-5. The most distinctive aspect of M_1 is the strong posteroexternal cingulum seen on all specimens (a similar but less well-developed cingulum occurs on M_1 of *Catopsalis utahensis*). The cingulum starts at the medial valley as a transverse ridge along the posterior margin of the tooth, then wraps around the posteroexternal corner and continues to the middle of the external side. It is high and cuspidate, and with moderate wear begins to coalesce with the posterior cusps of the external row. The sixth cusp of the external row, if present, is smaller than the other cusps and closely appressed to the cingulum. One tooth (UW 15101) has a small accessory cusplule anterior to the external row. Accessory cusps are often found anterior to and almost always posterior to the internal row. The anterior accessory cusp may be large

enough to be considered a fifth cusp of the internal row. Again, the enamel is covered with fine vertical striations. Strong enamel infolding is seen on the medial side of the more posterior cusps.

M_2 has a cusp formula of 3-4:2. Its morphology is quite variable. The internal row is composed of two large cusps. The external row may have three moderately-sized cusps or four small cusps. The fourth, when present, is an enlargement of the ridge extending across the posterior margin of the tooth to the last cusp of the internal row. The external cusps may be conical, as in the type specimen (see Russell, 1926 or Simpson, 1927) or anteroposteriorly compressed and quite transverse, especially when four cusps are present. The enamel is often strongly crenulated and infolded on the medial side of the cusps.

Discussion.—*Catopsalis calgariensis* was named by Russell (1926) for an isolated M_2 from the late Torrejonian or early Tiffanian Calgary site 2E in the Porcupine Hills Formation of Alberta (formerly included in the Paskapoo Formation; see Krause, 1978). Until now, this single tooth was the only described specimen referred to this species. The Shotgun *Catopsalis* was originally identified by C. L. Gazin as *C. cf. fissidens* (Keefer, 1961), but the much larger sample now known (minimum number of individuals = 8) permits a more accurate identification. The Shotgun *Catopsalis* can be distinguished from *C. fissidens* (AMNH 3044) by its larger and proportionately wider M_1 with a prominent posteroexternal cingulum and lower cusp formula, and an M_2 lacking an accessory internal cusp row. The near identity in size and morphology of a number of Shotgun M_2 's to the type of *C. calgariensis* and the similarity in age of the two localities supports the referral of the Shotgun *Catopsalis* teeth to *C. calgariensis*.

EVOLUTIONARY TRENDS

Kielan-Jaworowska and Sloan (1979) have pointed out that certain evolutionary trends become evident when the species of *Catopsalis* are viewed in ascending chronologic order. These trends can be seen despite incomplete knowledge of some species and an oversimplified view of the entire lineage. The new material of *C. alexanderi* and *C. calgariensis* has filled gaps in the record of the lineage and

added significantly to our knowledge of its evolution.

Catopsalis calgariensis is the youngest known species of the genus. In many respects it represents the culmination of the evolutionary trends seen in the lineage. Bivariate plots of length and width of upper and lower cheek teeth of all North American species of *Catopsalis* (Text-figs. 1, 2) show the gradual increase in size from the earliest species, *C. joyneri*, to the latest, *C. calgariensis*, the second largest multituberculate known. While both molars increase approximately equally in width, M_1^1 becomes proportionately longer than M_2^2 . This is shown by an increasing M_1/M_2 length ratio (*C. joyneri*, 1.15; *C. alexanderi*, 1.34; *C. calgariensis*, 1.62). Upper molars show the same trend (*C. joyneri*, 1.45; *C. alexanderi*, 1.58; *C. calgariensis*, 1.81). The trend toward reduction of P_4^4 proceeded until the P^4 of *C. calgariensis* had been reduced to a single-rooted tooth with only two cusp rows (P_4^4 is unknown in this species). Only a very small increase in molar cusp number occurred in Paleocene species of the genus. Instead, there was an increase in molar cuspules, cingula and enamel infolding, presumably for increased grinding efficiency.

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