

The multituberculate *Catopsalis* from the early Paleocene of the Crazy Mountains Basin in Montana

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A new species of the taeniolabidid multituberculate *Catopsalis* is described from the Simpson Quarry fauna of the Puercan age Bear Formation of the Crazy Mountains Basin, south-central Montana. The molars retain a conservative cusp formula, yet are distinct from those of other early members of the genus in their extremely large size, which is approximately the same as that of *C. calgariensis* from the late Torrejonian to early Tiffanian. The combination of apomorphic and plesiomorphic features in the new species indicates a greater degree of complexity in the evolution of the genus than previously recognized.

Key words: Multituberculata, Taeniolabididae, Puercan, Paleocene, Montana.

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Introduction

Systematic relationships within the family Taeniolabididae, particularly the genus *Catopsalis*, have been examined closely as new material and taxa have been described (Kielan-Jaworowska & Sloan 1979; Middleton 1982; Miao 1986; Simmons & Miao 1986). Although in these studies the conclusions concerning the systematics of *Catopsalis* differ somewhat, the conclusions about general evolutionary trends within the genus have been uniform, with species from younger localities tending to exhibit more derived character states. These trends include an increase in body size, molar cusp number and molar complexity (accessory cusps, cingulae, enamel infolding), and a decrease in size of P₄ and number of upper premolars.

Simmons & Miao (1986), in their cladistic analysis of *Catopsalis*, argued that the genus is paraphyletic, and suggested the removal of several of its taxa into monotypic genera. They demonstrated that two species, 'C.' (*Djadochtatherium*) *matthewi* Simpson 1925 and 'C.' (*Djadochtatherium*) *catopsaloides* Kielan-Jaworowska 1974, known only from the Late Cretaceous of Asia, are more primitive in a number of features than the currently recognized North American members of *Catopsalis*. They returned 'C.' (*Djadochtatherium*) *matthewi* to *Djadochtatherium*, and they made a strong case for the generic separation of 'C.' (*Djadochtatherium*) *catopsaloides*. Simmons (1993), in a more extensive cladistic treatment of the Multituberculata, supported this suggestion. Kielan-Jaworowska (1994), in response to the phylogenetic analysis of Simmons & Miao (1986), referred '*Catopsalis*' (*Djadochtatherium*) *catopsaloides* to the newly erected monospecific genus *Catopsbaatar*.

Simmons & Miao (1986) also recommended the removal of *C. joyneri* Sloan & Van Valen 1965 and *C. alexanderi* Middleton 1982 from *Catopsalis*. Relationships of the other members of the genus, as well as those between these species and other taeniolabidids, have not been resolved primarily because of the extremely limited material available for most taeniolabidid taxa, which results in inadequate character information.

Middleton (1983) suggested that *C. fissidens* Cope 1882 and *C. utahensis* Gazin 1939 are conspecific because of their similarity in molar size, M₁ cusp formulas (higher than other species of *Catopsalis*), and sympatric occurrence. Williamson & Lucas (1992) based their formal synonymy of *C. utahensis* with *C. fissidens* Cope 1884 on new material from Torrejonian deposits in the San Juan Basin. Williamson & Lucas (1993) also synonymized *C. johnstoni* with *C. foliatus* Cope 1882. Both referrals are followed here.

Previous workers have provided generic diagnoses of *Catopsalis* (Kielan-Jaworowska & Sloan 1979; Middleton 1983), but characters used to discriminate *Catopsalis* from *Taeniolabis* have since been found to be unreliable (size of individual molars), too poorly known for some of the species in question (dental formulas), or primitive for the group (cusp formulas) (Buckley 1989). In general, *Catopsalis* has been distinguished from *Taeniolabis* by the retention of plesiomorphic features, which, given the present taxonomy of the group, continue to be the criterion by which *Catopsalis* is recognized. A complete systematic revision for the family is necessary but must await additional material and a more thorough character analysis.

Material

Mammalian fossils were discovered at Simpson Quarry in the Bear Formation of the Crazy Mountains Basin in south-central Montana in 1985 (Fig. 1).

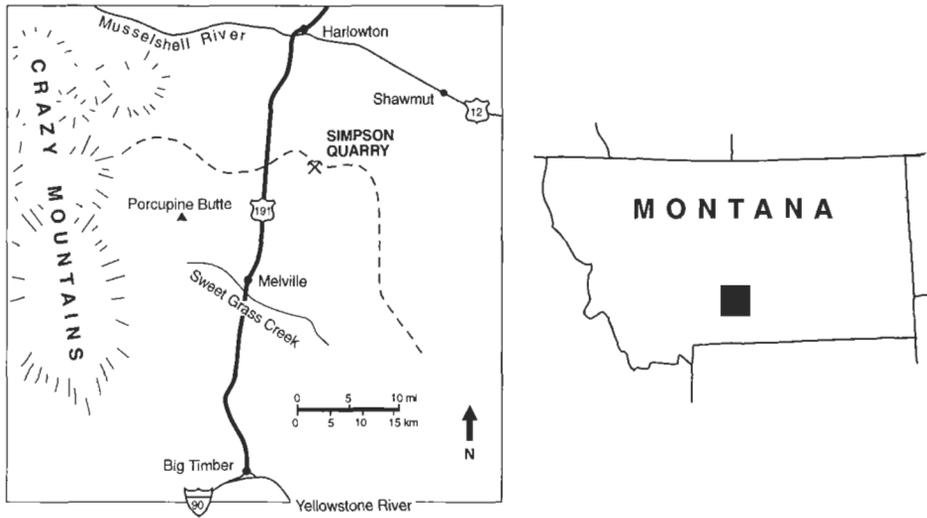


Fig. 1. Map showing the location of Simpson Quarry in Wheatland County, Montana. Dashed line indicates the approximate contact between the Bear Formation and underlying Cretaceous units to the north and east. Adapted from Alt & Hyndman (1986).

Biostratigraphic and magnetostratigraphic analyses (Buckley & Krause 1987; Hartman *et al.* 1989; Buckley 1993) indicate that the quarry assemblage is early Paleocene in age and is correlative with other faunas belonging to the middle-late Puercan North American Land Mammal Age (Pu2/3). Several field seasons of collecting at Simpson Quarry have resulted in one of the largest known samples of Puercan mammals in the world. Important mammalian groups composing the fauna include multituberculates, marsupials, palaeoryctid 'insectivores', plesiadapiform 'primates', and primitive ungulates or 'condylarths'. In addition to the approximately 600 specimens representing 33 different species of fossil mammals recovered from the quarry, pollen, leaves, mollusks, and lower vertebrates have also been collected. Included in the fossil mammal assemblage are three teeth of a new species of *Catopsalis*.

The new species comprises an extremely sparse element of the mammalian assemblage at Simpson Quarry. It is known from only three specimens, an M^2 and two M_1 's, one of which is incomplete. Morphological distinctions between the new species and other species of *Catopsalis* and *Taeniolabis* are substantial and indicate that the Simpson Quarry form is a previously unknown species. A combination of plesiomorphic and apomorphic features in the dental morphology of the new species also indicates a greater degree of complexity in the evolution of the family Taeniolabidae than was previously recognized.

Material of the new species is housed at the Museum of Paleontology, University of Michigan, abbreviated UM. Other abbreviations used are Carter County Museum, Ekalaka, Montana (CCM), Carnegie Museum, Pittsburgh, Pennsylvania (CM), and University of Wyoming (UW).

Descriptions

Class Mammalia Linnaeus 1758

Order Multituberculata Cope 1884

Family Taeniolabididae Granger & Simpson 1929

Genus *Catopsalis* Cope 1882

Type species: *Catopsalis foliatus* Cope 1882.

Catopsalis waddleae sp. n.

Holotype: UM 90042, left M_1 (Fig. 2A).

Type horizon and locality: Early Paleocene (Puercan NALMA, Pu2/3) of the Bear Formation, Crazy Mountains Basin, Simpson Quarry, SW 1/4 SW 1/4 NW 1/4 NW 1/4 of section 24, T. 6N., R. 15E., Ten O'clock Gate 7 1/2' quadrangle map, Wheatland Co., Montana.

Referred specimens: UM 90212, fragmentary right M_1 ; UM 90215, left M^2 .

Etymology: Named for Dr. Diane Waddle, collector of the holotype in 1986.

Diagnosis. — M_1 very large with a cusp formula of 5–6? : 4–5?, subquadrangular to subcrenate cusps with slight enamel infolding, and no distobuccal accessory cusps or cingulum. M^2 very large with a cusp formula of 1 : 3 : 4. Distinguished symplesiomorphically from *Taeniolabis* by low molar cusp formulas. Distinguished synapomorphically from all species of *Catopsalis* except *C. calgariensis* Middleton 1982 in large size of M_1 . Distinguished autapomorphically from all species of *Catopsalis* in large size of M^2 . Distinguished symplesiomorphically from *C. calgariensis* and *C. fissidens* in absence of distobuccal cingulid on M_1 .

Description. — Two lower first molars of *Catopsalis waddleae* are known; a complete left M_1 (UM 90042) and a fragmentary right M_1 (UM 90212) (Fig. 2A, B). In the type, UM 90042, the cusp formula is 5 : 4 (L = 16.4 mm, W = 9.3 mm), with a very small sixth distobuccal cusp present. The cusps are distally inclined and are subquadrangular to subcrenate, with well-developed wear facets on the lingual and buccal sides of the cusp apices. UM 90042 (M_1) evidently belonged to a young individual, as indicated by the lack of wear on the cusp apices tips, similar to the condition seen in UW 6388, a specimen of *C. calgariensis* from the Shotgun Member of the Fort Union Formation of Wyoming (Middleton 1982). UM 90042 is waisted, with shallow flexus at the third buccal cusp and between the second and third lingual cusps. There is no development of cingulae or accessory cusps, although there is a slight development of enamel infolding on the medial side of the distal cusps. Infolding is less than in *C. calgariensis*, however. There is also no development of enamel wrinkling.

UM 90212 is a mesial fragment of an M_1 , with a buccolingual width (9.0 mm) similar to that of UM 90042. Expansion of the mesiolingual margin indicates that it is from the right side of the dentition. UM 90212 differs from UM 90042 in possessing an additional mesial cusp in the lingual row. This cusp is moderately well developed, although it is smaller than the other lingual cusp and two buccal cusps preserved in the specimen. The outline of the tooth in occlusal view is similar to that of UM 90042, with

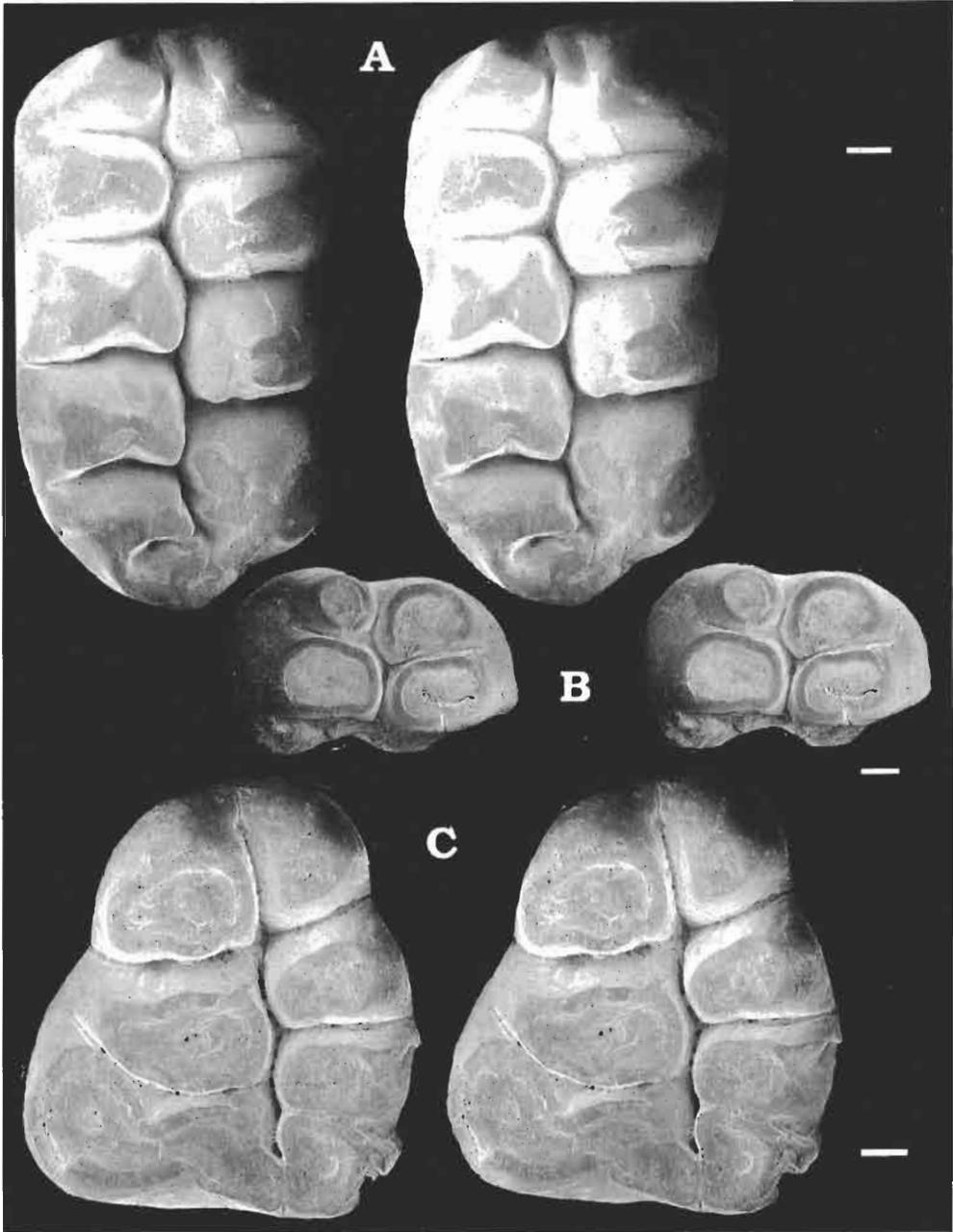


Fig. 2. *Catopsalis waddleae* sp. n. □A. Stereophotographic pair of the holotype, left M_1 UM 90042 in occlusal view. □B. Stereophotographic pair of right M_1 UM 90212 in occlusal view. □C. Stereophotographic pair of left M_2 UM 90215 in occlusal view. For all specimens, anterior is towards the top of the page. Bar scale — 1 mm.

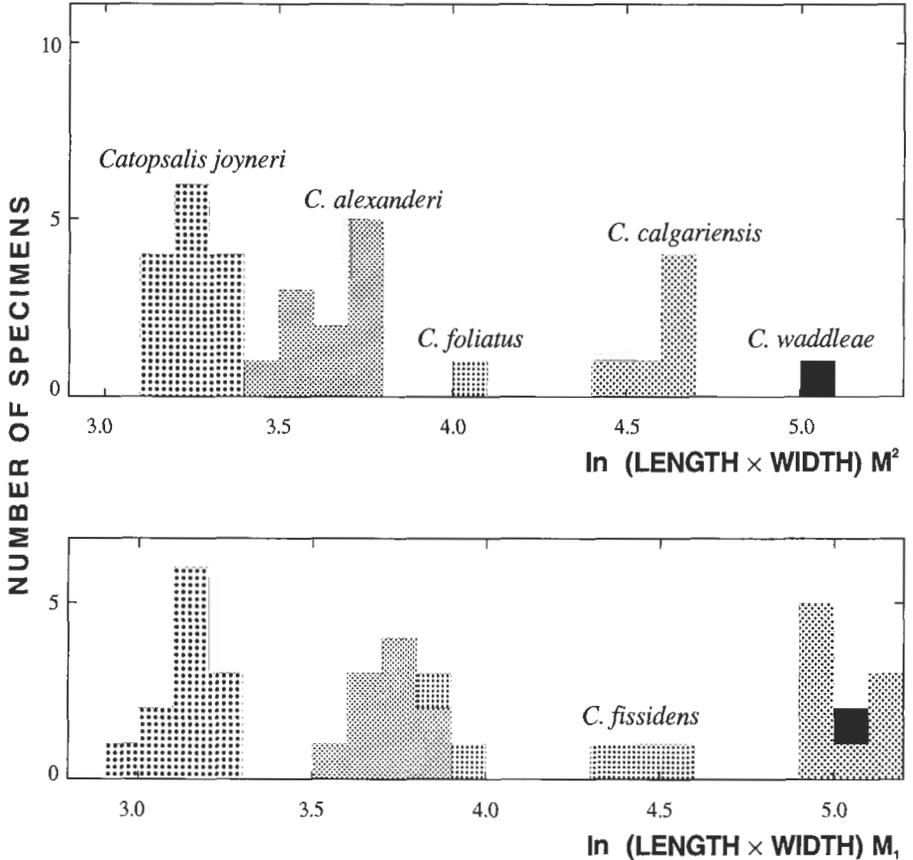


Fig. 3. Size ranges of *Catopsalis* M₁'s and M₂'s. Measurements (except for *C. waddleae*) from Middleton (1982).

the mesiolingual margin only slightly more expanded as a result of the additional cusp. Apical wear has reduced the cusps to low rings of enamel surrounding dentine islands, as in CM 15940, a specimen of *C. calgariensis*, indicating that it came from an older individual than UM 90042.

A single left M₂ (UM 90215) has a cusp formula of 1 : 3 : 4 (L = 12.9 mm, W = 11.8 mm) (Fig. 2). The buccal cusp is much larger in proportion to the rest of the tooth than in *C. calgariensis*. The three medial cusps and the buccal cusp are nearly equal in size. The four lingual cusps are smaller than those of the other two rows, with the distalmost cusp the smallest of the four. This cusp is slightly offset distobuccally from the rest of the cusp row.

Although the enamel is not crenulated, as in *C. calgariensis*, the cusp outlines in occlusal view are irregular and slightly infolded, although not to the degree seen in *Taeniolabis*. UM 90215 (M₂) exhibits a wear pattern similar to that of UM 90212 (M₁), in which apical wear has reduced the cusps to low rings of enamel surrounding dentine islands.

Distribution. — Type locality in Montana and possibly the Ravenscrag Formation in Saskatchewan.

Discussion. — The additional lingual cusp on UM 90212 suggests that the M_1 cusp formula for *C. waddleae* may be the same as that for *C. calgariensis* (5-6 : 4-5), which also variably develops the same additional lingual cusp (Middleton 1982). The pattern of wear is similar to that seen in other species of *Catopsalis* as well as in *Taeniolabis*, in which cusp wear, originally confined to the buccal and lingual sides of the cusps (as in UM 90042), changes to apical wear (as in UM 90212) through ontogeny (Granger & Simpson 1929; Clemens & Kielan-Jaworowska 1979).

Assignment of UM 90215 to *Catopsalis* was initially tenuous because of the large size of the specimen. It falls well above the M^2 size range of *C. calgariensis* (Fig. 3) and within the known size range of *Taeniolabis taoensis*, the largest known multituberculate. It was expected that the M^2 of *C. waddleae* would be approximately the same size as that of *C. calgariensis* because of the similarity in sizes of their lower first molars (Fig. 3). A comparison of the areal ratios of these two teeth in other taeniolabidids (Fig. 4) indicates that *C. calgariensis* greatly reduced the size of M^2 relative to M_1 , corroborating an observation also made by Middleton (1982: p. 1206). Although limited material prevents an assessment of size variability within *Catopsalis waddleae*, the relative sizes of UM 90215 (M^2) and UM 90042 (M_1) are conformable to the observed areal ratios of other taeniolabidid species.

Based on comparisons with the outgroups used by Simmons & Miao (1986), character states of *Catopsalis waddleae* can be compared with those of closely related sister taxa (other species of *Catopsalis* as well as species of *Taeniolabis*.) The low cusp formula of *C. waddleae* is primitive relative to *C. fissidens* and *Taeniolabis* and derived relative to *C. joyneri*, *C. alexanderi*, and *C. foliatus*. The absence of a posterobuccal cingulum on M_1 is shared with all members of the genus except *C. calgariensis*; the presence of a cingulum is uncertain in *C. fissidens* and is variable in *Taeniolabis*. The large size of M_1 within the observed range of *C. calgariensis*, is slightly larger than *C. fissidens*, and much larger than the remaining members of the genus. The large size of M^2 is larger than that of all other species of *Catopsalis*, falling within the size range of *Taeniolabis*. The fact that the Puercan *C. waddleae* has a lower cusp formula than and is larger than *C. fissidens* from the Torrejonian indicates that temporal range and size are not directly correlated, and therefore that the genus probably does not represent a simple direct lineage as proposed by Sloan (1987).

Johnston & Fox (1984) described several fragmentary specimens of a large taeniolabidid from the Puercan NALMA RAV W-1 horizon of the MHBT Quarry of Saskatchewan. They referred this material to *Taeniolabis* sp., although morphology was noted as suggestive of *Catopsalis*. The referral to *Taeniolabis* was based primarily on the large size of the specimens and the lack of evidence of any species of *Catopsalis* approaching *Taeniolabis* in size until the late Torrejonian or early Tiffanian. Johnston & Fox (1984: p. 187) state that if their form 'does represent a species of *Catopsalis*, it is prematurely large'.

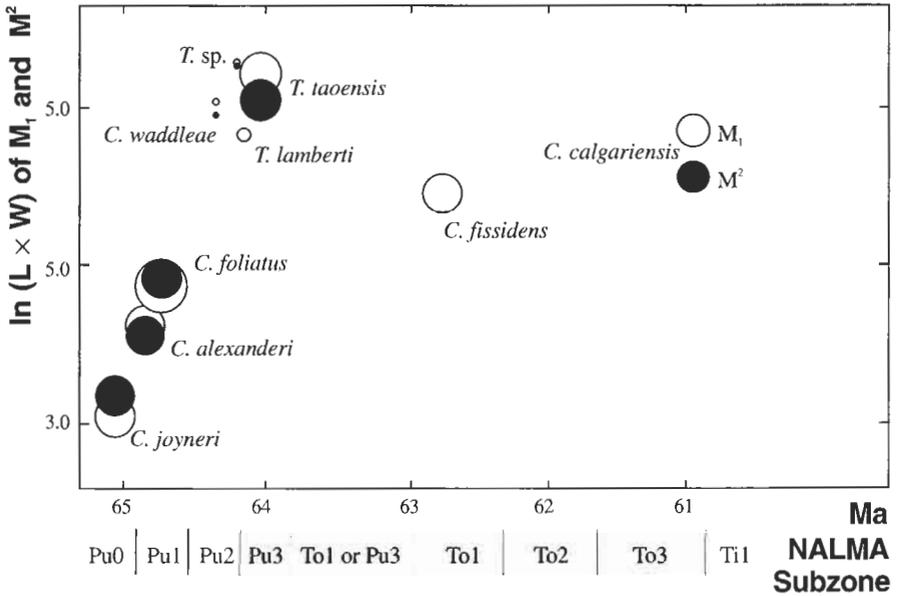


Fig. 4. Size ranges of M_1 and M_2 of North American Taeniolabididae and their approximate temporal ranges. Circle diameter reflects known size variability and potential temporal extent. Correlation of time scale and NALMA subzones from Archibald *et al.* (1987) and Berggren *et al.* (in press).

After examining the Saskatchewan material, I suggest that *Taeniolabis* sp. of Johnston & Fox (1984) may be conspecific with *Catopsalis waddleae*, based on their similarities in relative size, cusp proportions, and degree of molar complexity. The implication of the taxa being conspecific is more than taxonomical. The referral of the Saskatchewan material to *Taeniolabis* represented the first potential occurrence of the genus in the Pu2 interval-zone of the Puercan NALMA, precluding its use as an index fossil for the Pu3 interval-zone. This prompted Archibald *et al.* (1987) to include the specific name in the designation of Pu3, making it the *Taeniolabis taoensis* Interval-Zone. If the RAV W-1 taxon is conspecific with *Catopsalis waddleae*, however, then *Taeniolabis* may remain restricted to Pu3 faunas.

In their cladistic analysis of the Taeniolabididae, Simmons & Miao (1986) indicated an unresolved polytomy between several species of *Catopsalis* and the genus *Taeniolabis*, which first appears in the middle or late Puercan of North America. An M_1 , from a dentary that has P_4-M_2 (CCM 70–110), of *T. lamberti* Simmons 1987 from the Ludlow Formation of eastern Montana (Simmons 1987) closely resembles the M_1 of *C. waddleae* in several features, including size (length M_1 = 16.0 mm) and degree of complexity of M_1 (enamel infolding restricted to distal cusps, no development of a distobuccal cingulum or accessory cusps). *T. lamberti* does, however, have the higher cusp formula diagnostic of the genus *Taeniolabis* (M_1 , 8: 6).

The revised generic diagnosis of *Taeniolabis* (Simmons 1987) precludes assignment of the Simpson Quarry material to that genus. The molar cusp formulas of *Taeniolabis* are consistently higher than in *Catopsalis* and are the most diagnostic characters separating the two genera. Although low molar cusp formulas are plesiomorphic characters and do not validly unite known species of *Catopsalis* into a monophyletic group, high cusp formulas do ably serve as synapomorphies distinguishing all species of *Taeniolabis* as such (Simmons & Miao 1986; Simmons 1987).

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Streszczenie

W oparciu o trzy zęby trzonowe z wczesnopaleoceńskiej (Puercan NALMA, PU2/3) formacji Bear z basenu Crazy Mountains płd. części centralnej Montany opisano nowy gatunek *Catopsalis waddleae* sp. n. wieloguzkowca z rodziny Taeniolabididae Granger & Simpson 1929.

Catopsalis jest rodzajem definiowanym przez cechy plezjomorficzne, wskutek czego jego monofiletizm jest niepewny i często poddawany w wątpliwość. Jako gatunek *C. waddleae* sp. n. odróżnia się od innych zaliczanych do rodzaju *Catopsalis* swoistą kombinacją cech plezjomorficznych zębów z ich dużymi rozmiarami, które to rozmiary uznano za nową cechę gatunku. Zęby *C. waddleae* sp. n. osiągają w już puerkanie wielkość charakterystyczną dla młodszego stratygraficznie paleoceńskiego (późny Torrejonian po wczesny Tiffanian) gatunku *C. calgariensis*, świadcząc o większym niż sądzono wcześniej zróżnicowaniu wewnątrz rodzaju *Catopsalis*.