The Early Oligocene (Chadronian) Raben Ranch Local Fauna, Northwest Nebraska: Multituberculata; with Comments on the Extinction of the Allotheria

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THE EARLY OLIGOCENE (CHADRONIAN) RABEN RANCH LOCAL FAUNA, NORTHWEST NEBRASKA: MULTITUBERCULATA; WITH COMMENTS ON THE EXTINCTION OF THE ALLOTHERIA

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The Raben Ranch Local Fauna of northwestern Nebraska is the largest and most diverse Early Oligocene (Chadronian) microfauna recovered from the High Plains. Within the microfauna is the largest accumulation of teeth referable to the Multituberculata yet recovered from rocks of Early Oligocene age. The age of the fauna is Middle Chadronian and, along with fossils from Flagstaff Rim in Wyoming, may represent the youngest known occurrence of the Allotheria. Forty-seven specimens referred to the genus *Ectypodus* are described, and comparisons are made with previously described teeth from the Chadronian of Wyoming and Saskatchewan. The data presented by the Raben Ranch sample indicate the presence of only one species of *Ectypodus*. Eight problematical teeth are also described and questionably referred to the Multituberculata. In light of the geologic range extension of the Allotheria by the presence of teeth in Early Oligocene rocks, the theory of competitive inferiority is challenged as being the sole reason for the extinction of the group. It is hypothesized that a combination of factors caused the final extinction of the sub-class.

† † †

INTRODUCTION

This is one of several papers describing the eleven mammalian orders known in the Early Oligocene (Chadronian) Raben Ranch Local Fauna of Sioux County in northwestern Nebraska. New mammalian taxa in the fauna, locality data, and the geology of the Raben Ranch locality have been described (Ostrander, 1983:128). Additional information on Oligocene sediments of the area is given by Schultz and Stout (1955) and Schultz et al. (1955).

The first published report of the presence of multituberculates in the Early Oligocene of North America was that of Sutton and Black (1972:75). More recently, Ostrander et al. (1979) reported the recovery of a multituberculate tooth from the Chadron Formation of Nebraska, and Krishtalka et al. (1982) described seven additional multituberculate teeth from the Chadronian of Wyoming and Saskatchewan. The sample of multituberculate teeth in the Raben Ranch Local Fauna is significant because it totals at least 47 and perhaps 55, if eight questionably referred teeth are correctly identified. In contrast, no more than three teeth are known from any other Chadronian locality. In light of the fact that this is perhaps the geologically latest appearance of the Multituberculata, possible causes for their extinction are discussed.

All specimens recovered thus far, with the exception of one questionably referred incisor, are isolated cheek teeth. No post-cranial element has been recovered that can be referred to the Multituberculata with any degree of certainty. Four areas of the Raben Ranch locality were quarried and these have been designated V772-A, B, C, and D. All of the sub-localities are from the same stratigraphic level. All specimens are in the collection of the Museum of Geology, South Dakota School of Mines and Technology (SDSM), and specimen numbers are listed after the localities of referred materials.

Measurements were taken on complete teeth only. Anteroposterior length (L) was measured along the maximum anteroposterior axis of the tooth. Measurements were taken using a Leitz Ortholux microscope with a Leitz 251 Mechanical stage. All measurements are in millimeters (mm).

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
  Subclass Allotheria Marsh, 1880
    Order Multituberculata Cope, 1884
      Suborder Ptilodontoidea Sloan and Van Valen, 1965
        Family Neoplagiaulacidae Ameghino, 1890

Genus *Ectypodus* Matthew and Granger, 1921
Ectypodus sp.

Referred Material

V772-A: 10,503, P^4; 9,965, M_2; 9,966, M_1; 9,967, M^1; 9,968, M^2; 9,969, M^1; 9,970, M_2; 9,971, M_1; 9,972, M_2; 9,973, M^2; 9,974, M_1; 9,975, P_4; 9,992, M^1; 10,504, M^1; 10,505, M_1; 10,506, M_1; 10,507, M^2; 10,508, M^2; 10,509, M_2; 10,516, M^2; 10,525, M^1; 10,591, M^2, 11,008, P^4. *V772-B:* 9,976, M_1; 9,977, P_4; 9,978, M_2; 9,979, M^1; 9,980, M_2; 9,981, M^2; 9,983, P_4; 9,984, M_1; 9,985, M_1; 9,986, P_4; 10,510, M_2; 10,520, M^1; 10,521, M^1. *V772-C:* 9,987, M^2; 9,988, M^1; 9,989, P_4; 9,990, M^1; 9,991, M_1; 10,512, M_2; 10,513, M^2. *V772-D:* 10,588, M^1; 10,589, M_1.

Description and Comparison

P_4. Five examples of P_4 are present in the Raben Ranch sample and all are incomplete. All of the specimens are posterior fragments, thus making it impossible to count the serrations accurately. However, all five teeth are similar in morphology.

Krishtalka and Black (1975:289) stated, "the angle formed at the posterodorsal corner of P_4, between the slope and the vertical posterior border of the blade, may be indicative of the generic affinities among certain ectypodontids" (neoplagiaulacids). They also stated that the angle was approximately 140° for *Parectypodus* and 110° to 125° for *Ectypodus* and *Mesodma*. The angles on all but one of the Raben Ranch teeth measure between these two extremes (Table I). Little else can be determined from these five fragmentary teeth; therefore, they are of little use in determining the species to which they should be referred. The only other Chadronian multituberculate P_4 yet recovered is a broken specimen from Flagstaff Rim in Wyoming, which Krishtalka et al. (1982) referred to *E. lovei*.

M_1. Four of the nine specimens are complete, and three of these have a cusp count of 7:4. The other, SDSM 9,966, has a count of 8:4. On all of the teeth the cusps of the external row are crescentic. The internal cusps are quadrate at the base becoming elongated anteroposteriorly at the top of the cusp (Fig. 1E). The tooth is slightly wider at the posterior end than at the anterior end. The anterior end is rounded

TABLE I. Measurements and cusp counts of *Ectypodus* sp.

Tooth	Angle of posterodorsal corner		
P_4			
9,975	130°		
9,977	135°		
9,982	135°		
9,983	120°		
9,986	130°		
	Length	*Width*	*Cusp count*
M_1			
9,966	1.67	1.11	8:4
9,974	1.85	0.95	7:4
9,984	1.78	0.98	7:4
9,985	1.86	1.06	7:4
M_2			
9,965	1.02	1.09	4:2
9,970	0.85	0.92	3:2
9,972	1.01	1.10	4:2
9,980	1.09	1.17	4:2
10,509	1.09	1.14	4:2
10,510	1.04	1.09	4:2
10,512	1.06	1.08	4:2
M^1			
9,969	2.50	1.30	7:9:5
9,990	2.22	1.12	8:8:6
10,504	2.36	1.17	8:8:6
10,521	2.34	1.20	8:9:7
10,525	2.33	1.17	8:9:7
10,526	2.39	1.30	8:10:6
10,588	2.31	1.17	8:9:7
M^2			
9,968	1.13	1.25	1:3:4
9,973	0.99	1.10	1:3:3
9,978	1.17	1.18	1:3:3
9,981	0.99	1.10	1:3:3
10,507	0.99	1.04	1:3:3
10,513	1.10	1.15	1:3:3
10,591	1.10	1.18	1:3:4

and the posterior border is oblique. The external margin of the tooth is more nearly straight than convex.

Krishtalka and Black (1975) referred Badwater specimens with cusp counts of 6:4 to *E. lovei* and those with cusp counts of 7:4 or 8:4 to *E.* sp. All of the complete Raben Ranch M_1 specimens have cusp counts of 7:4 or 8:4. The Raben Ranch teeth do not have a convex external margin or a bulge at the level of the fifth or sixth external cusp as does the M_1 of *E.* sp. from Badwater. In fact the Raben Ranch specimens are more nearly straight along the external margin, as is the case
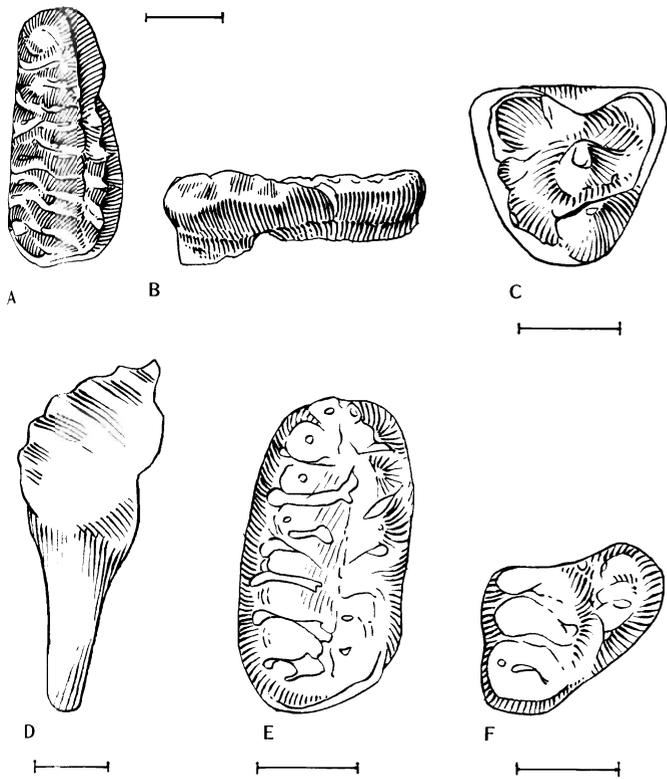
P_4. Two specimens have been recovered, but only the anterior half of each tooth is preserved. On both teeth the anterior root is square and relatively short. The crown overhangs the root and the anterior profile is straight. Four cusps of the internal row are preserved on both specimens, with the first cusp located on the anterolingual corner of the crown (Fig. 2F). The cusps are widely separated and become progressively taller posteriorly. There are four external cusps with the first opposite the second cusp of the internal row (Fig. 2D) on SDSM 10,503. The second external cusp is smaller
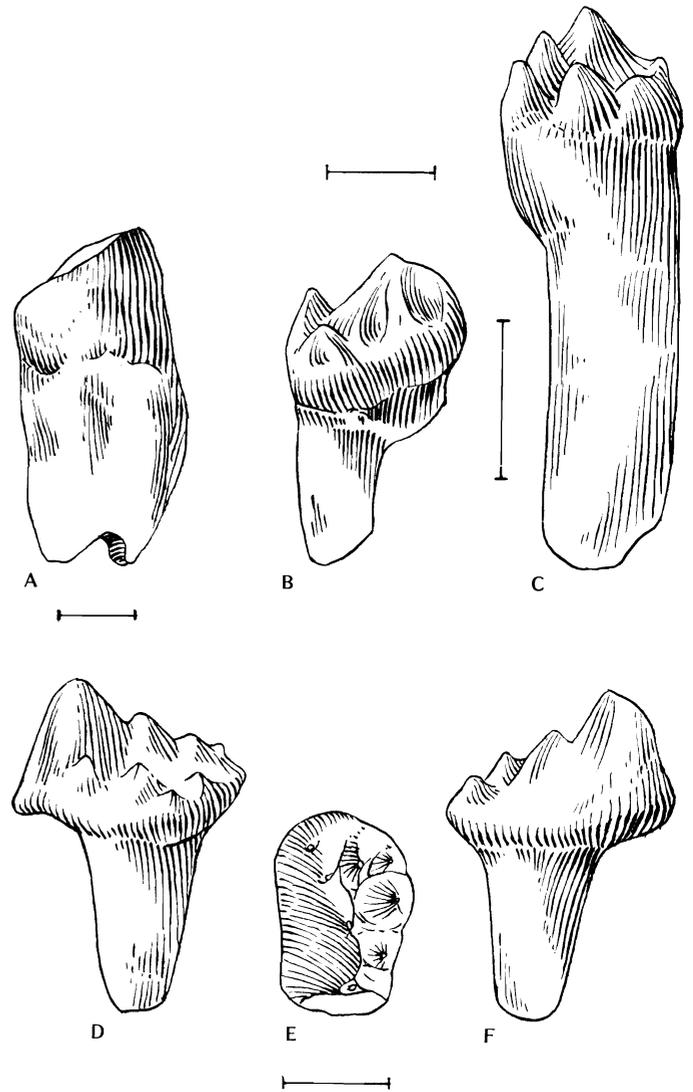
FIGURE 1. Drawings of teeth from *Ectypodus* sp. **A.** Occlusal view of right M^1, SDSM 9,992. **B.** Lingual view of right M^1, SDSM 9,992. **C.** Occlusal view of left M^2, SDSM 9,968. **D.** Buccal view of right P_4, SDSM 9,983. **E.** Occlusal view of left M_1, SDSM 9,966. **F.** Occlusal view of left M_2, SDSM 9,972. Scale equals 1 mm.

on M_1 of *E. lovei.* The length-to-width ratio of M_1 from Raben Ranch is more variable than that of either *E. lovei* or *E.* sp. from Badwater, ranging from 1.60 to 1.95 compared to 1.60 to 1.80 for *E.* sp. and 1.66 to 1.75 for *E. lovei.* The size of the Raben Ranch specimens is generally larger than that of *E. lovei,* but this is greatly variable. The only other known Chadronian M_1 is from Flagstaff Rim in Wyoming (Krishtalka et al., 1982), and it is broken, rendering it of little use for comparison.

$M_2.$ The cusps of M_2 are crescentic, the anterior edge of the tooth is S-shaped to varying degrees, and the posterior edge is straight. Seven of the nine specimens are complete, and the cusp count on six of these is 4:2. The other, SDSM 9,970, has a cusp count of 3:2 and is noticeably smaller (Table I) than the other specimens. An M_2 from Flagstaff Rim, with a cusp count of 3:2, was referred to *E. lovei* by Krishtalka et al. (1982), and they referred a specimen from Pilgrim Creek, with a cusp count of 4:2, to *E.* sp.

FIGURE 2. A–C. Drawings of teeth from ?Multituberculata, family indet., gen. et sp. indet. **A.** Lateral view of upper incisor, SDSM 10,511. **B.** Buccal view of right premolar?, SDSM 10,434. **C.** Lingual view of premolar?, SDSM 9,964. D–F. Drawings of teeth from *Ectypodus* sp. **D.** Lingual view of left P^4, SDSM 10,503. **E.** Occlusal view of left P^4, SDSM 10,503. **F.** Buccal view of left P^4, SDSM 10,503. Scale equals 1 mm.

than the first and third external cusps and is located on the anterobuccal corner of the crown, buccal to the other cusps of the external row. This cusp is opposite the gap between the second and third cusp of the internal row. The third external cusp is the largest of the external cusps and is opposite the third internal cusp. The fourth external cusp is small and is located on the anterobuccal corner of the base of the fourth internal cusp. All of the cusps are conical. SDSM 11,008 has only one external cusp, located opposite the second cusp of the internal cusp row. In all other respects SDSM 11,008 resembles SDSM 10,503.

The two teeth from Raben Ranch are the only examples of P^4 yet recovered from Chadronian deposits and thus must be compared to the two Late Eocene specimens from Badwater. Krishtalka and Black (1975:290) referred these two teeth to *Ectypodus lovei*. The Raben Ranch teeth are similar to the specimens from Badwater in that they have straight anterior profiles. The P^4 of *E. lovei* has two external cusps as opposed to four external cusps on SDSM 10,503 and one on SDSM 11,008. Krause (1980 and 1982) demonstrated the variability in cusp counts of P^4 of neoplagiaulacid multituberculates referable to both *Ectypodus* and *Parectypodus*, and this may explain the difference in cusp counts in specimens from Badwater and Raben Ranch. Still, cusp formulae alone are of questionable value in determining species within these genera. The alignment of the cusps in both cusp rows of SDSM 10,503 is different from that of the P^4 of either *Parectypodus* or *Ectypodus*, but the cusp shape, anterior crown overhang, occlusal outline, and size indicate that SDSM 10,503 and 11,008 are properly referred to *Ectypodus*. The Raben Ranch teeth, based on comparison of known specimens, are not referable to *E. lovei*, however.

M^1. Seven of twelve upper first molars are complete, and the cusps on all of the specimens are crescentic and decrease in size anteriorly. On unworn specimens the cusps hook anteriorly, especially those of the middle row (Fig. 1A). The anterior end of the tooth is rectangular and the posterior end is rounded. The cusp count and point of origin of the external cusp row are highly variable in specimens from Raben Ranch. SDSM 9,969 has a cusp count of 7:9:5, and the external row originates at the level of the fourth medial cusp from the anterior end of the tooth. Two specimens (SDSM 9,990 and 10,504) have a cusp count of 8:8:6 with the external row beginning opposite the second medial cusp. Three specimens (SDSM 10,521, 10,525, and 10,588) have cusp counts of 8:9:7 with the external row originating opposite the space between the second and third medial cusps. One tooth (SDSM 10,525) has a cusp count of 8:10:6 with the external row originating opposite the space between the third and fourth medial cusps.

This member of the tooth series is the most variable in the Raben Ranch sample. Krishtalka and Black (1975:190)

pointed out that this was the case for the M^1 sample from Badwater. The Badwater specimens referred to *E. lovei* have a cusp count of 7:9-10:5 or 6 and are anteroposteriorly shorter than those referred to *E.* sp. from Badwater, which have cusp counts of 9:9:6. The only Raben Ranch specimen (SDSM 9,969) possessing a cusp count of 7:9:5 is also the largest (Table I) in the sample. No Raben Ranch specimen has a cusp count of 9:9:6 as does the M^1 of *E.* sp. from Badwater. The M^1 specimens from Raben Ranch thus show little similarity to the M^1 of either *E. lovei* or *E.* sp. from Badwater. An M^1 from the Chadronian of Saskatchewan has a cusp count of 7 or 8:9:5, and Krishtalka et al. (1982) referred this tooth to *E.* sp. In most respects this tooth is similar to SDSM 9,969.

M^2. Nine specimens were recovered, and five have cusp counts of 1:3:3, two have cusp counts of 1:3:4, and two teeth are broken so that a cusp count cannot be determined. The M^2 is triangular in occlusal outline, and the cusps are crescentic like those of M^1. On the two specimens with cusp counts of 1:3:4 (SDSM 9,968 and 10,591), the internal cusp row is positioned slightly ahead of the middle row, whereas on the other specimens the two rows are transversely aligned. The extra cusp on the internal row is located on the anterolingual corner of the crown, and the external cusp is more prominent than on the other specimens.

All of the Badwater teeth referred to *E. lovei* and *E.* sp. by Krishtalka and Black (1975) have cusp counts of 1:3:3. The major distinctions between the two Badwater species are that the posterior margin of the tooth of *E. lovei* is rounded, as opposed to angular on *E.* sp., and the external cusp is weak on *E. lovei*, as opposed to being better developed on *E.* sp. The specimens from Raben Ranch, with two exceptions, have cusp counts of 1:3:3 and rounded posterior margins as on the M^2 of *E. lovei*. The specimens differing in cusp count (SDSM 9,968 and 10,591) have cusp counts of 1:3:4. The posterior margins of these two teeth are not as rounded as that of the M^2 of *E. lovei*, but neither are they as angular as that of *E.* sp. The two teeth do not differ greatly in size (Table I) from the rest of the second upper molars from Raben Ranch, and the internal cusp row positioned anterior to the middle row is a feature distinct from both *E. lovei* and *E.* sp. No other Chadronian second upper molar has been recovered.

Discussion

Much variation exists among other species of *Ectypodus* as demonstrated by McKenna (1960:35) for *E. hunteri*. Krause (1977:19) also documented this variability and placed *E. hunteri* in the genus *Neoplagiaulax*. As stated earlier, cusp counts are greatly variable (Krause, 1980 and 1982) among neoplagaulacids such as *E. powelli* and *E. tardus*. Thus, much variability in dental morphology seems to be common within species of *Ectypodus*.

Krishtalka and Black (1975) interpreted the Late Eocene Badwater Creek multituberculate sample as representing two species of *Ectypodus*. Krishtalka et al. (1982) followed this interpretation in their discussion of the Early Oligocene multituberculates from Wyoming and Saskatchewan. The Raben Ranch multituberculates compare closely to the teeth from Badwater and the Chadronian of Wyoming and Saskatchewan in size, cusp count, and cusp shape, at least closely enough to warrant assignment to *Ectypodus*. Specific determination in the sample, however, is more complex.

Krishtalka and Black (1975:294) stated that the most clearly diagnostic criteria for Tertiary neoplagiaulacid taxa are based on the morphology of P_4^4. Because this was of admittedly little use in samples made up of mostly isolated molars, they used characters such as size, shape of the external margin on M , length-to-width ratio of M_1, shape of the posterior margin of M^2, and cusp count. All of these characters are applicable to the Raben Ranch sample and have been utilized in determining to which species the specimens should be assigned. There is no consistent suite of characters, such as size/cusp count, that supports splitting the Raben Ranch sample into two species. Single character states also indicate only one species of *Ectypodus* at Raben Ranch. For example, the range given for the length-to-width ratio of M_1 of *E. lovei* from Badwater falls within that of *E.* sp. from Badwater, and both fall within the range of specimens from Raben Ranch. Because of these considerations and the fact that all specimens came from one stratigraphic level, it is concluded that only one species of *Ectypodus* is present at Raben Ranch. Whether this species is *E. lovei* or the undetermined species from Badwater cannot be ascertained from the material at hand. Summary statistics given in Table II support this conclusion.

TABLE II. Summary statistics of *Ectypodus* sp.

Parameter Tooth	M_1	M_2	M^1	M^2
n	4	7	7	7
x̄ length	1.77	1.02	2.36	1.06
Observed range (length)	1.67–1.86	0.85–1.09	2.22–2.50	0.99–1.17
S.D. length	0.09	0.09	0.09	0.08
x̄ width	1.01	1.09	1.21	1.14
Observed range (width)	0.95–1.11	0.92–1.17	1.12–1.30	1.04–1.25
S.D. width	0.09	0.09	0.07	0.07

Order ?Multituberculata
Family indeterminate

Genus and Species indeterminate

Referred Material

V772-A: 10,397, premolar?; 10,514, premolar?; 10,590, premolar?; 10,515, premolar?; 9,964, premolar?. *V772-B:* 10,433, premolar?. *V772-C:* 10,511, upper incisor; 10,434, premolar?.

Description and Discussion

Upper incisor. The tooth is bicuspid and is slightly curved (Fig. 2A). The enamel is uniform in thickness nearly all the way around the tooth and is lightly rugose on the dorsolingual side. There is a shallow groove on the buccal side, and the root is not preserved.

This tooth is similar to those belonging to several genera of multituberculates but also resembles the upper incisors of some eutherians. For example, Russell et al. (1979:214–215) described and figured a tooth that they referred to *Apatemys mutiniacus* from the Lower Eocene of Europe. They questionably assigned the tooth as I^1. The tooth resembles SDSM 10,511, and the apatemyid *Sinclairella dakotensis* is present in the Raben Ranch fauna. However, Jepsen (1934:291) described and figured the I^1 of *S. dakotensis*, and it is not bifid. This rules out the reference of SDSM 10,511 to *S. dakotensis*, but bifid incisors are relatively common among several insectivore and primate taxa from the Early Tertiary.

Among the multituberculate taxa having bifid incisors are *Henkelodon naias*, *Kuehneodon dryas*, and *K. simpsoni* from the Lower Kimmeridgian of Portugal (Hahn, 1977). Sahni (1972:90) figured a bifid upper incisor of *Meniscoessus robustus* from the Late Cretaceous Lance Formation of Wyoming. All of these teeth differ from SDSM 10,511 in that the anterior cuspid is longer than the posterior cuspid, whereas on SDSM 10,511 the two cuspids are equal in length. Most of the taxa mentioned above also have considerably larger incisors than the Raben Ranch specimen.

Krause (1977: Plate 8) figured the I^2 of *Microcosmodon conus* and (1980:1,174) the I^2 of *Microcosmodon rosei*. These teeth are similar to SDSM 10,511 in that they all have blunt bicuspid tips and a shallow buccal groove. The enamel of I^2 of *M. conus* is much thicker on the buccal side than on the lingual (Krause, 1977:27) as opposed to SDSM 10,511 which has the enamel distributed evenly except on the posteroventral edge where it is thinner than for the remainder of the tooth. The I^2 of *M. conus* also has a more pronounced curvature than does SDSM 10,511.

Krause (1980:1,170) questionably assigned several specimens to *Ectypodus powelli* that he considered to be either deciduous or permanent upper incisors. If Krause is correct in this assignment, SDSM 10,511 would not seem to be referable to *Ectypodus* because all specimens of *E. powelli* are unicuspid.

Premolar? SDSM 9,964 is fragmentary and consists of a single, round root and the attached portion of the crown (Fig. 2C). The crown has five cusps that are conical and arranged in two parallel rows. Three cusps are preserved in one row and two cusps in the other (anteroposterior and buccolingual orientation of this tooth cannot be determined with certainty). The cusps of the two-cusp row are equal in size and height, with the third cusp being slightly taller. The crown does not overhang the root.

This tooth may represent the posterior fragment of a neoplagiaulacid P^4, but there are some differences between it and described upper fourth premolars of neoplagiaulacids. Krause (1980:1,170) stated that some specimens of *Ectypodus powelli* have twinned posterobasal cusps. The two cusps in one row on SDSM 9,964 could be a twinned posterobasal cusp. However, the crown of SDSM 9,964 does not overhang the root, and this is a consistent feature of neoplagiaulacid upper fourth premolars. The root of SDSM 9,964 is also much longer than that of SDSM 10,503 and is round rather than square as that of SDSM 10,503. The roots of P^4 on most of the described neoplagiaulacid genera are either square or compressed transversely. In light of these differences, the tooth could be a more anterior premolar as these teeth are unknown for most neoplagiaulacid taxa. Another possibility is that the tooth is a deciduous P^4, assuming that P^4 is replaced in neoplagiaulacids, as this tooth is unknown for any of the taxa of the family.

The remaining specimens tentatively assigned as premolars have two roots and a single bladelike cusp (Fig. 2B). At the anterior end of the tooth is a smaller cusp, which is anteroposteriorly aligned with the principal cusp. On the buccal side of the anterior cusp is a smaller cusp. The posterior edge of the principal cusp slopes directly to the posterior margin of the tooth on all of the specimens except SDSM 10,433. On this tooth the posterior edge is concave midway between the apex and the posterior margin of the tooth. In lateral view this gives the appearance of there being a third posteriorly located cusp. There is a tiny cuspule on the anterior face of the anterior cusp on SDSM 10,397 and 10,433. This is a character that does not occur on the other specimens but is presumably absent due to wear. All of the complete teeth are similar in size (Table III).

Several multituberculate teeth, all presumably deciduous, have been described that approximate the morphology of Raben Ranch teeth. Some of these include the dP_1-dP_4 of

TABLE III. Measurements of ?Multituberculata Family indet., gen. et sp. indet.

Premolar?	Length	Width	Cusp count
10,433	1.18	0.74	1:3
10,434	1.11	0.67	1:2
10,514	0.98	0.61	1:2
10,515	1.04	0.65	1:2

Kuehneodon dietrichi described by Hahn (1978:27), Lance multituberculate type J described by Clemens (1963:98), and non-ptilodontid multituberculate type C described by Krause (1977:30). If the Raben Ranch specimens are referable to the Multituberculata, they are most likely deciduous premolars.

AGE OF THE
RABEN RANCH MULTITUBERCULATES

The multituberculates from the Raben Ranch fauna may prove to be one of the two youngest known occurrences of the Allotheria. Krishtalka et al. (1982) considered the fauna from the level at Flagstaff Rim from which the multituberculates were recovered to be between the Early Chadronian Yoder Local Fauna and the Middle Chadronian Pipestone Springs Local Fauna in age. They concluded that Pilgrim Creek is the earliest known Chadronian multituberculate site and that Calf Creek is Late Early Chadronian. Preliminary comparisons (complete faunas from these localities have not been published) indicate that the Raben Ranch Local Fauna is close to level B at Flagstaff Rim in age (Ostrander, 1980). If the present assignments are correct for these localities, the multituberculates from Flagstaff Rim and Raben Ranch represent the youngest known occurrences of the Allotheria.

EXTINCTION OF THE ALLOTHERIA

Matthew (1897:261) was the first to suggest that the initial appearance of rodents had something to do with the extinction of multituberculates. However, Jepsen (1949:489) was the first to discuss extensively the theory that multituberculates declined and became extinct due to increased competition from rodents. He based this theory on the similarity of the lower incisors, similar size, and overall similar morphology of the two groups and the fact that rodents, but not multituberculates, are present at Bear Creek, Montana, a Late Paleocene locality. Several others (Wilson, 1951; Simpson, 1953; McKenna, 1961; and Wood, 1962) subsequently

commented on this theory. They all pointed to the strati-graphic record and to the fact that multituberculates are common in Paleocene rocks and are rare to nonexistent in Eocene rocks where rodents are common. Van Valen and Sloan (1966) expanded this theory by proposing that progressively, competition from condylarths, primates, and rodents caused the extinction of the multituberculates. Hopson (1967) joined the previous workers in acceptance of this theory and argued that competitive inferiority of the multituberculates was due to the fact that they were not as biologically advanced as eutherians.

Landry (1965) was the only worker to publish a conflicting opinion. He argued that the competitive inferiority theory was based on the morphological similarities between some multituberculates and rodents for a gnawing adaptation. He pointed out that among multituberculates only the eucosmodontoids were truly gnawing forms and that the ptilodontoid *Ectypodus* had been found in Late Eocene sediments as reported by Robinson et al. (1964). Landry agreed that at least some groups of multituberculates were forced into extinction through competitive inferiority, mainly the eucosmodontoids. But, he also argued that the coexistence of multituberculates and rodents in the Eocene ruled out competitive inferiority as the cause of final extinction of the Allotheria.

Since the publication of these papers in the mid-1960s, knowledge of numbers, diversity, and geologic range of the multituberculates has changed considerably. For example, Krause (1980) reported on multituberculates from the Clarkforkian and stated that they were more diverse than previously thought. He also showed that, contrary to what Van Valen and Sloan (1966: Fig. 3) had concluded, multituberculate diversity declined most dramatically from Tiffanian to Clarkforkian time as opposed to Clarkforkian to Wasatchian time. Krause also demonstrated that there was a sharp decline in number of multituberculates in the Tiffanian as opposed to the gradual decline from Late Cretaceous to Eocene as depicted by Van Valen and Sloan (1966: Fig. 2). Krause (1982) and Stuckey and Krishtalka (1982) reported the recovery of multituberculates from Late Wasatchian sediments, a level from which they had not previously been recovered. Multituberculates are now known from Uintan–Duchesnean and Chadronian sediments.

Another recent study contradicts information supplied by Van Valen and Sloan (1966) and has a bearing on the competitive inferiority theory. Van Valen and Sloan (1966:276) suggested that multituberculates were inferior to therians based on several morphological features. Although they did not specify which taxa they were using as examples, it was stated that due to the acetabulum being open dorsally, and the resulting femoral articulation, there would be a small possibility of arboreal activity. Jenkins and Krause (1983) studied

newly recovered post-cranial skeletal material and concluded that *Ptilodus* and most ptilodontoids (including *Ectypodus*) were arboreal or at least had arboreal capabilities.

It is significant that from the time of the first appearance of rodents to the last appearance of multituberculates at least 15 million years elapsed. Throughout this period rodents and multituberculates were associated at virtually all known localities (the one exception is Bear Creek, Montana), although in all of these cases rodents far outnumbered multituberculates. This indicates that they coexisted in generally similar paleoecological situations and that the neoplagiaulacids were able to withstand resource competition from rodents. As Van Valen and Sloan (1966:262) pointed out, there are five possibilities when two taxa enter into competition for resource space. The first, that one taxon may retire from competition either by specialization or by expansion or shift of adaptive zone, seems unlikely in the case of *Ectypodus*. Jepsen (1949: 488) and Krause (1982:292) stated that morphologic change in neoplagaulacids, and *Ectypodus* specifically, was extremely limited from Late Cretaceous to Early Oligocene time. This means that *Ectypodus* did not "retire from competition" by means of specialization through morphological change. The fossil record also shows, as stated earlier, that *Ectypodus* and rodents are found together, indicating that at least they did not occupy vastly different niches. The second possibility, "elimination," did not take place until the multituberculates and rodents had coexisted for at least 15 million years. Any of the other three possibilities, "a form of alternate resource," "alternating dominance," or "resource space partitioning," could have occurred, or a combination of these three may have taken place. Determination from the fossil record is presently impossible.

If competitive inferiority did not "eliminate" the multituberculates, what did? I am convinced that a combination of factors caused the final extinction of the Allotheria. First, competitive inferiority, although not responsible for the final and complete extinction of the multituberculates, probably aided in the extensive drop in numbers and diversity of the group. The final demise of multituberculates was more likely caused by a combination of changes in climate, vegetation, and predatory pressure.

The evidence for these changes has been documented by many workers. Dorf (1959), Clark et al. (1967), Webb (1977), Schultz and Stout (1980), and Retallack (1983a,b), among others, discussed and presented evidence that during the Late Eocene the High Plains were forested and had a humid, subtropical climate. This type of vegetational and climatic regime continued through the Early Oligocene, although faunal, paleobotanical, and sedimentological evidence indicate it was becoming cooler, drier, and more savannalike throughout the Chadronian. The Middle Oligocene was predominantly a

temperate, semiarid-to-arid savanna ecosystem with forested areas restricted to river banks and near ponds.

If *Ectypodus* were primarily aboreal, then the change from predominantly a forested ecosystem to that of predominantly a savanna ecosystem would place a large constraint on resource space. This change in climate and vegetation was also detrimental to several other mammalian genera during the Chadronian. Lillegraven (1972) graphically depicted the large-scale changes in ordinal and familial diversity in the Early Oligocene. He summarized these changes with the following statement: "The probability also seems likely that the two great periods of modernization of mammalian and angiospermous family assemblages (i.e., Late Eocene through Early Oligocene and Early through Medial Miocene) were considerably influenced by widespread important climatic changes and their resultant physiological stresses upon all organisms." This can be illustrated by rodent families that may or may not have been in direct competition with multituberculates for resource space. The Cylindrodontidae, Eomyidae, and Paramyidae occurred in the Late Eocene. The cylindrodontids did not survive into the Orellan, seven of ten eomyid genera did not survive past the Chadronian, and only one paramyid genus, *Manitsha,* was still present in the Orellan. On the other hand, some rodent families, including the Castoridae, Cricetidae, and Heteromyidae, became more abundant and diverse by the close of the Oligocene. Webb (1977:362-363) and Wilson (1972:220) both suggested this was due to the change in climate and vegetation during the Chadronian.

One other factor appears to have some bearing on the extinction of the Allotheria. The carnivorous and at least partially arboreal (Romer, 1966:232) Miacidae appeared during the Puercan (Savage and Russell, 1983:25) and diversified during the Torrejonian and Tiffanian. As discussed previously, the diversity of multituberculates was at its peak during the Torrejonian and Tiffanian and declined sharply thereafter. In addition, by the Early Oligocene such carnivores as *Dinictis, Hesperocyon, Hoplophoneus,* and *Palaeogale,* all possessing at least some tree-climbing ability (Romer, 1966: 233-234), were present. Morphological features described by Van Valen and Sloan (1966:276), such as the straight, short cochlea and the smooth brain of multituberculates, could have put them at a distinct disadvantage against predators that were evolving more highly refined hunting skills. Such a disadvantage would have been at least as great as that caused by these features in the competition with rodents for resource space. The multituberculates that survived into the Chadronian probably did so due in part to their omnivorous habits (Clemens and Kielan-Jaworoska, 1979:145), which allowed them to utilize a variety of food sources. However, the combination of competition with therians, better adapted to compete for resource space, the evolution of carnivorous forms that were better adapted to hunt, catch, and kill their prey, and finally the loss of available resource space, all combined over a 15- to 20-million-year period to force the extinction of the Allotheria.

SUMMARY

The multituberculate teeth from Raben Ranch, along with those from Flagstaff Rim in Wyoming, may represent the youngest known occurrence of the Allotheria. The Raben Ranch sample is the largest sample of Chadronian multituberculates from a single locality. The sample does not demonstrate the presence of two species of *Ectypodus,* but rather indicates one highly variable species.

The immigration and radiation of competitors, such as condylarths, primates, and rodents, probably caused the decline of the multituberculates. Superiorly adapted carnivores aided in this decline. Finally, in combination with these factors, the loss of the niche(s) open to multituberculates caused by climatic and vegetational changes during the Chadronian contributed to their extinction.

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