Chapter 4

The Anterior Dentition of the Late Jurassic Multituberculate *Ctenacodon*

GEORGE F. ENGELMANN

ABSTRACT

Specimens from the Brushy Basin Member, Morrison Formation (Upper Jurassic), Dinosaur National Monument, Utah, provide new information on the anterior dentition of the early multituberculate *Ctenacodon*. An upper canine, previously thought to be lacking in *Ctenacodon*, is present as a simple, single-rooted tooth immediately mesial to the first premolar. The I3 has a strongly mesiodistally compressed principal cusp with a small, but distinct cusp placed low on the distobuccal corner of the tooth. The principal cusp bears vertical crests and ridges; wear results in a transverse apical wear facet that resembles that described in some paulchoffatiids. This pattern may have been produced by wear against the tip of the lower incisor at some phase of mastication.

Two small, isolated, teeth similar in morphology to the I3 may be deciduous incisors of *Ctenacodon*. Other possible deciduous teeth of that taxon are some small four-cusped premolars from the same locality.

INTRODUCTION

Collections of fossil mammals from the Upper Jurassic Morrison Formation of Dinosaur National Monument (DINO), Utah, have been made following discovery of a microvertebrate site (DNM 96) there in 1984 (Engelmann et al., 1989; Chure and Engelmann, 1989). Specimens of fossil mammals have been collected at the site by both hand-quarrying and screen-washing methods. Screen washing of sediment that had no apparent indication of contained fossils when initially quarried has produced a relatively diverse fauna that otherwise never would have come to light. But most of the numerous mammalian fossil specimens recovered by screen washing are isolated teeth. Complementing these specimens obtained by screen washing is a small number of specimens discovered and recovered by hand quarrying. Although few in number, these specimens are more completely preserved and provide much more information (both paleobiological and systematic) about the animals.

Engelmann and Callison (1998) described some of the specimens from the Morrison microfauna at DINO, selecting from the large number of isolated teeth those specimens that were readily identifiable as representing new or existing taxa. The greatest proportion of mammalian fossils consists of isolated teeth of multituberculates that range in quality from small fragments to complete teeth with relatively unworn crowns. Most of these teeth were referred (Engelmann and Callison, 1998) to the genus *Ctenacodon*, either *C. serratus* (for lower teeth) or *C. laticeps* (for uppers), based on their similarity in size and morphology to the sample of *Ctenacodon* from Como Bluff, Wyoming. Of the many specimens left undescribed, however, some remained unidentifiable despite relatively good preservation. A damaged, partial palate of the multituberculate *Ctenacodon* has helped identify some of these unknown specimens and extends our knowledge of this taxon.

MATERIAL

DINO 14989 (fig. 4.1) was discovered by hand quarrying, which resulted in damage that includes the loss of some teeth. Fortunately, impressions in matrix have preserved evidence of some of the lost teeth. The specimen is a crushed palate with parts of the left and right anterior dentition. Because of the crushing and breakage during collection, the palate is in two parts, the left and right sides, each side bearing some teeth and the alveoli and roots of broken teeth. Part of the lateral surface of each maxilla is preserved, including the infraorbital foramina and the anterior part of the zygomatic arch. Accompanying the specimen is a block of silicone molding compound that is a cast taken from the impression in matrix of part of the specimen. The cast preserves the lingual surface of the left, anterior dentition, from the canine to the fourth premolar. Comparisons with the type and referred specimens of *Ctenacodon laticeps* from Como Bluff reveal that the specimen falls within the range of size and known morphology of that species, and cannot be distinguished from it.

DESCRIPTION

PALATE

The left maxilla (fig. 4.1A) retains P3 and P5 in place, and is missing posterior to P5. Alveoli are present for the other premolars, P1, P2, and P4, which were broken off at the roots. The two roots of each tooth extend transversely across the base of the tooth. Immediately mesial to the mesial root of P1 is a single root with a circular cross section, that of the canine. The cast taken from the impression in matrix shows that all of the missing anterior teeth were present in the specimen until the specimen was exposed. The lingual surfaces of C1 through P4 are easily distinguishable on the cast. On the lateral surface of the maxilla, the larger of two infraorbital foramina opens anteriorly approximately above the position of P2. Just behind and below this is a smaller infraorbital foramen, approximately above the interdental area between P2 and P3. The anterior part of the zygomatic arch appears to have arisen above P3. Although broken, a slender anterior zygomatic arch is preserved.

The right side of the palate (fig. 4.1B) includes parts of the maxilla and the premaxilla. The two elements have separated and pulled apart slightly across the premaxillary-maxillary suture. The premaxilla is broken across the alveolus for I2, which contains a large root with an oval cross section. A single-rooted I3 is present in the premaxilla. The right maxilla contains P1 and P3, which are well preserved and relatively unworn. Molding compound applied to the specimen before it was prepared from the matrix preserves, as casts in the positions of the original teeth, a small part of the buccal surface of P2 and parts of the crowns of P4 and P5. Crushing had displaced the latter two from their position in the tooth row. Immediately mesial to P1 and distal to the premaxillary-maxillary suture is the small, circular, empty alveolus of the canine. Part of the opening of a relatively large infraorbital foramen is preserved above the position of P2, but the lateral surface of the maxilla is broken away posterior to this point, exposing the roots of P3.

DENTITION

All premolar tooth positions are represented by at least one tooth, or by a cast of at least part of the crown. Insofar as the morphology of the premolars is preserved, it is similar to that seen in specimens of *Ctenacodon laticeps* from Como Bluff (Simpson, 1929) and DINO (Engelmann and Callison, 1998). P1 through P3 are all three-cusped teeth, each with a rounded subtriangular crown in occlusal view. Two lingual cusps are aligned and connected by a weak, mesiodistal crest, and the buccal cusp is weakly connected to the distolingual cusp. P4 and P5 are more elongate, with four cusps connected by a weak crest and aligned along the long axis of the tooth, as well as with the lingual cusps of more anterior teeth. The left P5 has two small but distinct buccal cusps mesially and two weakly developed cusps low on the lingual surface of the tooth. It is likely that these cusps would be completely obliterated in more heavily worn teeth.

Although no actual canine tooth is remaining in the specimen, there is no doubt that the dentition included an upper canine. As noted above, the premaxillary-maxillary suture is clear on the right side of the palate, and the alveolus for a relatively small, single-

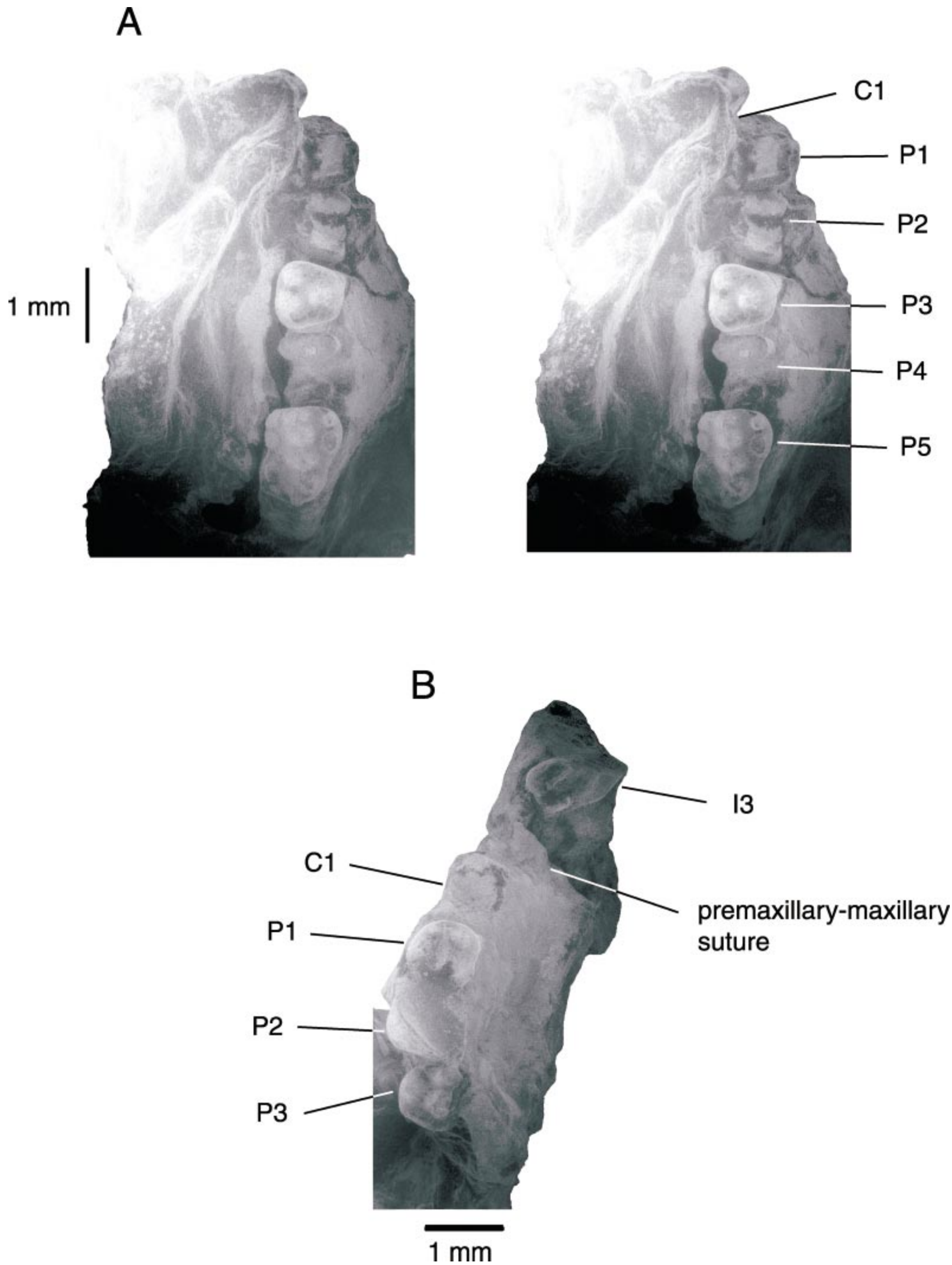

Fig. 4.1. Scanning electron micrographs of *Ctenacodon laticeps,* DINO 14989. **A,** stereomicrographs of the left palate. P3 and P5 are in place and the roots of C1 through P2 and of P4 are present in their alveoli, although the preserved part of the root of C1 is not visible from this perspective, but the lingual margin of the canine alveolus is apparent. **B,** right palate of *Ctenacodon laticeps,* DINO 14989. Part of the premaxilla is preserved with I3 and the root of I2 (not visible) in place. The premaxilla and maxilla

rooted canine is located between this suture and P1. On the left maxilla, the broken root of the canine remains in the specimen, and the lingual surface of the canine is apparent in the cast taken from the matrix impression. This cast of the canine includes part of the root and the base of the crown. The single root is small and cylindrical. The base of the crown appears as a pronounced swelling that seems to be part of a simple tooth with a circular cross section. Above the swelling, the crown tapers, as if toward a single cusp, although the cast does not show the apex. The canine was close to the P1, which was immediately behind it.

The I3 is preserved in the right premaxilla. Larger than the canine, it is comparable in size to the anterior premolars and has a very distinctive morphology. The principal cusp is bladelike and is oriented transversely to slightly obliquely to the axis of the tooth row. It is not a simple cusp, but has vertical crests or low ridges that descend from near the base of the crown toward the apex of the cusp, and the enamel surface has gentle crenulations with the same orientation. Two fine crests define a flat buccal margin of this bladelike cusp, converging as the mesiodistal thickness of the cusp diminishes toward the apex. Low ridges descend the mesial and distal faces of the cusp approximately at the middle. A very small cusp is located at the base of the crown, at the distobuccal edge of the tooth. This cusp is relatively sharp and well defined, with good separation from the principal cusp. The tooth is truncated by a flat apical wear facet that is normal to the axis of the large cusp. Because of the mesial and distal ridges, the wear surface is not a simple oval, but has slight irregularities. The small cusp shows no significant wear. The only information concerning I2 is that it had a large root with an oval cross section.

Isolated Teeth

Among the teeth collected by screen washing were some small, bladelike teeth, each with a very small accessory cusp. When these teeth were first collected, we were not certain that they should even be referred to Mammalia. It is clear from the *Ctenacodon* specimen described above that these represent I3s of the same species. Three teeth, DINO specimens 12831, 12832, and 12835, are morphologically indistinguishable from the I3 of DINO 14989. DINO 12835 (fig. 4.2A and B) is a left I3 very like that of DINO 14989, even representing a similar stage of wear, but with the lingual edge broken away. DINO 12831 (fig. 4.2C), also a left I3 and broken lingually, differs from other specimens in being virtually unworn. The principal cusp tapers to a sharp transverse crest with a sharp point at the apex. The crenulations noted above become more pronounced toward the apex. Finally, DINO 12832 (fig. 4.2D), a right I3, is similar to that of DINO 14989 except that it is much more heavily worn, with wear extending down to the base of the crown. The apical wear is, as in the other worn I3s, developed as a planar surface normal to the axis of the cusp. But in this specimen, wear has reduced the larger cusp to the level of the small distal cusp, and the small cusp also has an apical wear facet that appears to fall in the same plane as that of the larger cusp. On the other specimens, this small posterior cusp is virtually unworn, and it appears that it remains so until the principal cusp has been reduced to that level.

Two other isolated teeth, DINO 10789 and DINO 13530, display morphology similar to that described above, but in a tooth that is substantially smaller, only about 60% as large. These teeth also are bladelike, with a small, sharp cusp low on one side of the blade, presumably distobuccally placed. On

←

have been separated at the suture and offset by crushing. The maxilla contains P1 and P3 in place, and the alveoli for C1 and P2. A mass of molding compound between P1 and P3 was applied to the specimen before preparation to preserve a cast of the buccal surface of P2. Similar masses of molding compound not visible from this perspective preserve some of the crown morphology of P4 and P5. Scale bars equal 1 mm.

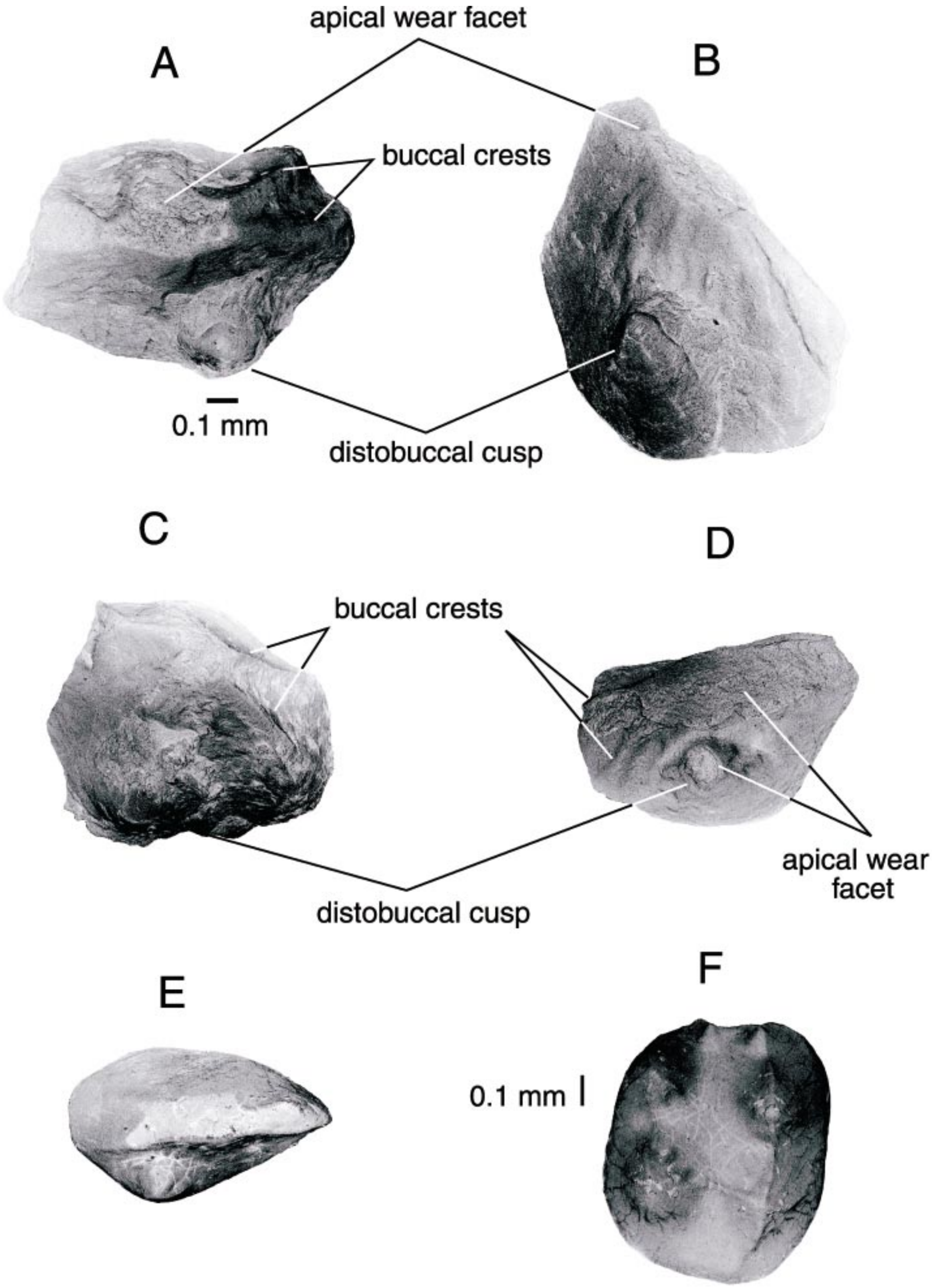

Fig. 4.2. Scanning electron micrographs of isolated teeth collected at DINO. **A,** left I3 of *Ctenacodon*, DINO 12835. Apical/occlusal view of the tooth. The lingual edge of the tooth (left side of the image) is broken. **B,** distobuccal view of DINO 12835. **C,** left I3 of *Ctenacodon*, DINO 12831. View is from slightly distal of direct occlusal view. Lingual side of tooth (left side of image) is a broken edge. **D,** heavily worn right I3 of *Ctenacodon*, DINO 12832. Slightly distobuccal view. **E,** possible deciduous tooth of *Ctenacodon*.? right dI DINO 10789. Near occlusal view showing distal cusp, buccal crests, distal ridge, and wear facet. **F,** occlusal view of right? deciduous upper premolar, DINO 10748, with four principal cusps and two mesial (top of image) cuspules. Scale bars equal 0.1 mm.

DINO 10789 (fig. 4.2E), the better preserved of the two, there even appear to be two faintly developed vertical crests on the buccal edge of the tooth. The enamel of these teeth is relatively smooth and free of crenulations, possibly a consequence of their smaller size. These may represent the deciduous incisors of *Ctenacodon*.

DISCUSSION

All previous accounts have given a dental formula for *Ctenacodon* indicating the absence of an upper canine. The condition is significant in that apparent absence of the canine has been taken as one of only a few characters in which Allodontidae is not wholly plesiomorphic among multituberculates (e.g., Hahn and Hahn, 1992; Kielan-Jaworowska and Hurum, 2001). This determination has been based on Simpson's (1929) interpretation of the type specimen of *Ctenacodon laticeps* (Yale Peabody Museum specimen YPM 11761), a left palate with all the premolars and molars in place. Immediately mesial to the P1, there is an empty, circular alveolus. Simpson argued that since this alveolus is close to the premaxillary-maxillary suture and anteriorly inclined, it likely represents the root of I3, which extended posteriorly across the suture into the maxilla, and that there was no canine tooth. The fact that the specimen is incomplete, with a broken alveolar margin, precludes the possibility of testing this interpretation in the type specimen. However, the canine is unambiguously present in DINO 14989. And morphological evidence strongly supports referral of this specimen to *Ctenacodon laticeps*. Hence, the dental formula for *Ctenacodon* should be revised to indicate the presence of an upper canine, and this genus should be regarded as plesiomorphic among multituberculates in one more character.

Information about the morphology of the incisors of *Ctenacodon* has been limited to what can be reasonably inferred from the related taxa *Psalodon* (Simpson, 1929) and *Glirodon* (Engelmann and Callison, 1999). It seems likely, though unproven, that there were three upper incisors. Although DINO 14989 indicates that I2 is a large tooth, as expected, its crown morphology remains unknown. But good examples of the morphology of I3 and its pattern of wear have added to the available information. The specimens from DINO show that I3 of *Ctenacodon* is more complex than those of *Psalodon* or *Glirodon*. The I3 of *Glirodon* is a simple, almost peglike tooth (Engelmann and Callison, 1999). It is slightly compressed mesiodistally, so that it is slightly more like a transverse blade than a conical tooth. The I3 of *Psalodon* has a more pronounced transverse crest than that of *Glirodon*, and bears a small distal accessory cusp (Simpson, 1929). The I3 of the *Ctenacodon* from DINO differs from these taxa in that it is more compressed and bladelike than in the other two, and there are clearly developed crests that are consistent among all of the specimens, the two crests on the buccal edge of the tooth, the mesial ridge, and a much subtler distal ridge.

A comparison of the I3 of *Ctenacodon* with the I3 of paulchoffatiids as described and illustrated by Hahn (1977) is of interest in that the latter have been regarded as a clade (Hahn, 1993; Kielan-Jaworowska and Hurum, 2001) or paraphyletic branches (Simmons, 1993) basal within the multituberculates. As has been pointed out by Hahn (1977), and others since then (Clemens and Kielan-Jaworowska, 1979; Kielan-Jaworowska and Hurum, 2001), the I3 of paulchoffatiids is relatively large and bears accessory cusps both mesial and distal to the large, principal cusp. The large central cusp is crossed by a crest that is oblique to the line of the tooth row and is reduced by apical wear. Although the I3 of *Ctenacodon* is smaller relative to other teeth in the dentition and is a simpler tooth, lacking a mesial cusp, there are similarities. It is this last characteristic in which the I3s of paulchoffatiids most resemble those of *Ctenacodon*. The oblique crest of the principal cusp is similarly oriented in both taxa, and similar apical wear facets develop on this cusp. The shape of this wear facet on I3 of the holotype of *Henkelodon naias* illustrated by Hahn (1977: fig. 10) closely resembles that seen on I3s of *Ctenacodon*. In both, the facet has the form of a narrow ellipsoid with sharp terminations and with slight mesial and distal bulges where the mesial and distal ridges intersect the facet.

The similarities among North American Jurassic multituberculates and the paulchoffatiids of Europe raise questions about the ability to distinguish them as monophyletic groups. The common dental formula appears to be clearly a plesiomorphic character within the multituberculates. The significance of the common characteristics in the morphology of the I3 is less clear. Does it indicate the presence in North America of paulchoffatiids, or does it simply identify another feature in which paulchoffatiids must be considered plesiomorphic within the group?

The nature of incisor wear (and therefore use) in the specimens described above is evident in the facets. The tip of the tallest cusp suffers the heaviest wear; the small, distal cusp remains virtually unworn until a fairly advanced stage. The wear facet that is produced is in the form of a simple plane; this same plane includes the wear facet that eventually develops on the smaller cusp at a very advanced stage of wear. This implies that it was only the highest parts of the crown that came in contact with another object during mastication, and that it was a simple stroke that caused the wear. The tip of the lower incisor seems to be the only possible opposing feature that could produce such a pattern.

Several of the isolated teeth from DINO (fig. 4.2F) are undoubtedly anterior, upper premolars. However, they are unlike the permanent, three-cusped premolars of *Ctenacodon* in that they have four more or less equally developed cusps, and sometimes, additional mesial, distal, or buccal cuspules as well. Engelmann and Callison (1998: fig. 12) mentioned these teeth and figured some examples. At that time we pointed out that this morphology was similar to anterior premolars of paulchoffatiids, but suggested that they might be deciduous premolars of *Ctenacodon*. These teeth are comparable in size to the anterior premolars of *Ctenacodon*, only slightly smaller.

Szalay (1965) described a specimen of *Cimolodon* in which both a deciduous P2 and its permanent successor are preserved. The permanent tooth in this case is a three-cusped tooth, and its deciduous precursor has five cusps, two each aligned on the lingual and buccal sides of the tooth and a distal, median cusp. This pattern of deciduous premolars that are more complex or more molariform than their successors appears to be the plesiomorphic condition within mammals as seen in the dentitions of triconodonts (Simpson, 1928), dryolestids, marsupials and placentals (Martin, 1997), and other basal tribosphenic mammals (Kobayashi et al., 2002). If a similar relationship between the morphology of adult premolars and the morphology of their deciduous precursors were to hold true for plagiaulacoid multituberculates, teeth such as the small, four-cusped premolars noted above are exactly what we would expect for the deciduous premolars of *Ctenacodon*.

ACKNOWLEDGMENTS

I thank the National Park Service and the staff at Dinosaur National Monument for the opportunity to conduct field projects there and to study specimens from the collections. I especially thank Park Paleontologist Daniel J. Chure, who has done the most to make this work possible and who has been a helpful colleague and collaborator. Special thanks also to Scott Madsen, who discovered the multituberculate palate described here and used his considerable skills to maximize the amount of information preserved and prepared for study. I greatly appreciate the support of fieldwork at Dinosaur National Monument by the Center for Field Research and especially the Earthwatch volunteers who helped collect many specimens including some of those described here. Thanks also to Richard L. Cifelli for his generous offer to make use of the SEM at the Sam Noble Museum for illustration of the specimens, and to Cindy Gordon who spent hours operating the SEM.

I especially appreciate the opportunity to contribute to a volume in honor of Malcolm C. McKenna, the compleat paleontologist. Throughout his career, Malcolm has been a leader in all areas of paleontological research. He has been a master of both biological and geological aspects of the fossil record and has maintained a perspective of the big picture that unites them, what might be called natural history. He has always been willing to go beyond the fossils and eager to gather and understand information from any

source that might help fill out the picture. Malcolm has instilled this attitude in students, official or unofficial, by example and by provocation. His mentoring and influence have certainly broadened and otherwise affected my interests.

Malcolm has also fostered in others his own love of fieldwork and commitment to adding new specimens to the documented record, and not just any specimens. Malcolm seems to keep a mental catalogue of interesting problems in paleontology that he is always mindful of: problems in systematics, biostratigraphy, and biogeography; problems that are missing key pieces of information that could be found. He has always admired persistent efforts to get such evidence and has collected quite a bit of it himself.

The work presented here describes new material that may provide some additional insight into the early history of the multituberculates, an early group of mammals. I hope it reflects some of the spirit of Malcolm's work. It is also appropriate that some of the specimens described were collected by screen washing, a technique Malcolm pioneered in its application to the early record of the mammals.

REFERENCES

Chure, D.J., and G.F. Engelmann. 1989. The fauna of the Morrison Formation in Dinosaur National Monument. *In* J.J. Flynn (editor), Mesozoic/Cenozoic vertebrate paleontology: classic localities, contemporary approaches (28th International Geological Congress Field Trip Guidebook T322): 8–14. Washington, DC: American Geophysical Union.

Clemens, W.A., and Z. Kielan-Jaworowska. 1979. Multituberculata. *In* J.A. Lillegraven, Z. Kielan-Jaworowska, and W.A. Clemens (editors), Mesozoic mammals: the first two-thirds of mammalian history: 99–149. Berkeley: University of California Press.

Engelmann, G.F., and G. Callison. 1998. Mammalian faunas of the Morrison Formation. *In* K. Carpenter, D.J. Chure, and J. Kirkland (editors), The Upper Jurassic Morrison Formation: an interdisciplinary study: Part 2. Modern Geology 23: 343–379.

Engelmann, G.F., and G. Callison. 1999. *Glirodon grandis* a new multituberculate mammal from the Jurassic Morrison Formation. *In* D.D. Gillette (editor), Vertebrate paleontology in Utah: 160–177. Salt Lake City: Utah Geological Survey Miscellaneous Publication 99–1.

Engelmann, G.F., D.J. Chure, and S.K. Madsen. 1989. A mammalian fauna from the Jurassic Morrison Formation of Dinosaur National Monument. Journal of Vertebrate Paleontology 9(3 suppl.): 19A.

Hahn, G. 1977. Neue Schadel-Reste von Multituberculaten (Mamm.) aus dem Malm Portugals. Geologica et Palaeontologica 11: 161–186.

Hahn, G., and R. Hahn. 1992. Neue Multituberculaten-Zahne aus der Unter-Kreide (Barremium) von Spanien (Galve und Una). Geologica et Palaeontologica 10: 143–162.

Kielan-Jaworowska, Z., and J.H. Hurum. 2001. Phylogeny and systematics of multituberculate mammals. Palaeontology 44(3): 389–429.

Kobayashi, Y., D.A. Winkler, and L.L. Jacobs. 2002 Origin of the tooth replacement pattern in therian mammals: evidence from a 110 Myr old fossil. Proceedings of the Royal Society of London, Biological Sciences, 269(1489): 369–373.

Martin, T. 1997. Tooth replacement in Late Jurassic Dryolestidae (Eupantotheria, Mammalia). Journal of Mammalian Evolution 4: 1–18.

Simmons, N.B. 1993. Phylogeny of Multituberculata. *In* F.S. Szalay, M.J. Novacek, and M.C. McKenna (editors) Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early therians and marsupials: 146–164. New York: Springer-Verlag.

Simpson, G.G. 1928. A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. London: British Museum (Natural History).

Simpson, G.G. 1929. American Mesozoic Mammalia. Memoirs of the Yale Peabody Museum 3(1): 235.

Szalay, F.S. 1965. First evidence of tooth replacement in the subclass Allotheria (Mammalia). American Museum Novitates 2226: 1–12.