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Last Evidence of Sauropod Dinosaurs (Saurischia: Sauropodomorpha) in the North American Mid-Cretaceous

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ABSTRACT

Teeth of sauropods, recovered from the Mussentuchit Member of the Cedar Mountain Formation of central Utah, represent the youngest evidence of sauropods from the North American mid-Cretaceous. The teeth bear a superficial resemblance to *Astrodon* cf *Pleurocoelus,* and *Brachiosaurus,* and most likely represent a brachiosaurid sauropod. All of the teeth of sauropods known from the Mussentuchit Member are extremely small. It is almost certain that the sample of teeth is truly representative of adult forms, rather than a reflection of some preservational or sampling bias that favors neonates and juveniles. The exclusively small teeth of adult individuals suggest that the Mussentuchit sauropod is a new, extremely small, possibly dwarf taxon of brachiosaurid.

INTRODUCTION

The sauropod dinosaurs (Saurischia: Sauropodomorpha) ranged in time from the earliest Jurassic to the end of the Cretaceous. Sauropods exhibited their greatest diversity and abundance during the Late Jurassic and comprised an important component of vertebrate faunas worldwide. They are not nearly so well known for the Early or Late Cretaceous (McIntosh, 1990). The absence of data for the Late Cretaceous is probably a true reflection of a reduced diversity and abundance of sauropods during the terminal Mesozoic. The perceived paucity of sauropods during the Early Cretaceous most likely reflects a notoriously incomplete rock and fossil record for the time period (Benton, 1989, 1998). Sauropods were relatively widespread throughout North America during the late Early Cretaceous, but they are virtually unknown from the continent throughout the Late Cretaceous. It has been suggested that sauropods suffered extinction in North America at the end of the Early Cretaceous (Lucas and Hunt, 1989) and that this continent-specific extinction was followed, approximately 25 million years later by the reintroduction of sauropods in the form of the titanosaurid *Alamosaurus.* Remains of *Alamosaurus* have been recovered from Maastrichtian sediments in Arizona, New Mexico and Texas (Lucas and Hunt, 1989).

Body fossils of North American Early Cretaceous sauropods are known from nonmarine formations of Aptian or Aptian-Albian age, but certainly no later than mid-late Albian. These include the Antlers Formation of Oklahoma (Wedel et al., 2000), the Arundel Formation of Maryland (Kranz, 1998), the lower Cedar Mountain Formation of Utah and Colorado (DeCourten, 1991; Tidwell et al., 1999) the Cloverly Formation of Montana and Wyoming (Ostrom, 1970), the DeQueen Formation of Arkansas (Pittman, 1986) and the Twin Mountains Formation of Texas (Langston, 1974; Winkler, Jacobs and Murray, 1997). The brachiosaurid *Sonorasaurus* has been described from the Lower Cretaceous Turney Ranch Formation of Arizona (Ratkevitch, 1998), but the age of the Formation is not well understood.

A slightly younger occurrence of sauropods was recorded only recently when an intensive investigation of the upper Cedar Mountain Formation (Albian-Cenomanian) of Utah revealed the presence of very small teeth, identified as those of a brachiosaurid (Cifelli et al., 1997, 1999; Kirkland et al., 1997, 1999). The teeth were detected by screenwashing of sediment from the Mussentuchit Member, which is the uppermost stratum of the Cedar Mountain Formation. The Mussentuchit Member is dated at approximately 98 mya and it is thought to span the boundary between the Albian and the Cenomanian and therefore

between the Early and the Late Cretaceous (Fig. 1). The teeth may be regarded as the last evidence of sauropods in the mid-Cretaceous of North America, before the apparent continent-wide extinction.

Abbreviation: OMNH, Oklahoma Museum of Natural History

MATERIAL

Approximately 20 teeth of sauropods were recovered from two sites in the Mussentuchit Member. Four teeth were selected for description here because all of them are well preserved and three of the four have complete crowns that exhibit excellent examples of wear facets and one overlap facet. The fourth tooth is broken at mid-crown level, providing a useful cross-section.

DESCRIPTION

All of the teeth are very small and slender with a slightly expanded, mildly spatulate crown. OMNH 28161 is the smallest tooth (Table 1) and the least worn of the three teeth that show wear facets. A small, mildly elliptical wear surface is seen on the apex of the crown, inclined at approximately 20 degrees to a vertical axis in the labio-lingual plane (Fig. 2A, B). The distal one-third of the crown shows a strong lingual curvature as it tapers towards its apex. OMNH 27902 shows the same strong lingual curvature (Fig. 3A). It differs from OMNH 28161, however in displaying a V-shaped wear facet, composed of mesial and distal surfaces, separated by a smooth ridge, on the lingual surface near the apex of the tooth (Fig. 3B). The ridge is deflected slightly toward the distal surface. Parallel, vertically orientated striations are particularly apparent on the mesial facet. An unworn ridge of lingual enamel arcs above the entire wear facet, except for where it is broken on the extreme tip of the tooth (Fig. 3B).

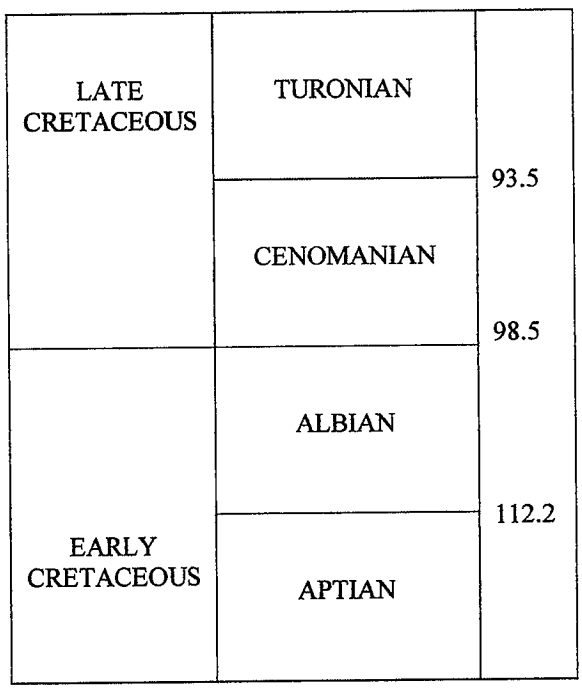

Figure 1. Estimated geological time (in million years) for stage boundaries for the last two stages of the Early Cretaceous and the first two stages of the Late Cretaceous. Data from Obradovich, 1993.

*Table 1. Length and anteroposterior width measurements for four teeth of sauropods, Cedar Mountain Formation, Utah. All measurements in millimeters. The symbol * denotes lack of preservation.*

Specimen	Length	Width (base of crown)	Width (mid-crown)
OMNH 28161	8.5	2.2	2.7
OMNH 27902	10.2	3.3	3.9
OMNH 28159	9.1	*	3.5
OMNH 28312	*	3.9	4.6

The crown of OMNH 28159 is rather narrow due to the presence of an extensive overlap facet on the mesial aspect of the tooth (Fig. 4A). The facet is concave and elongate, extending almost to mid-crown level. It terminates apically where it meets a wear facet that is present on the labial surface of the apex of the crown (Fig. 4B). The apically situated facet is sub-elliptical and inclined at approximately 45 degrees to a vertical labio-lingual axis. OMNH 28312 is the largest of the four teeth, although it is broken above mid-crown level (Fig 5). The exposed cross-section shows a strong labial ridge; a second ridge is present, situated approximately 105 degrees from the first ridge. The tooth is too incomplete to determine whether the other ridge is situated mesially or distally. Neither ridge is seen on any of the other teeth.

DISCUSSION

Teeth of sauropods exhibit considerable variation in their crown morphology and in the configuration of their wear facets. Traditionally, sauropod teeth were divided into two broad categories, based on the shape of their crowns; 1) robust teeth with expanded, spatulate- or spoon-shaped crowns, such as those seen in *Camarasaurus*; and 2) slender, peg-like teeth with unexpanded cylindrical crowns, typical of *Diplodocus* (Romer, 1956; McIntosh, 1990). It was also noted that the teeth of *Shunosaurus*,

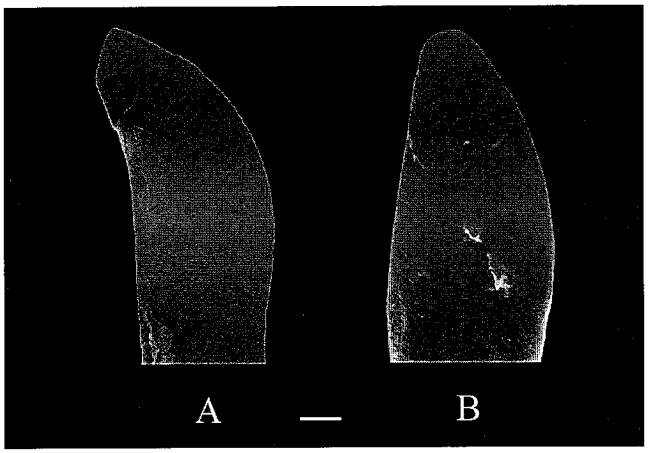

Figure 2. Scanning electron micrographs of sauropod tooth from the Cedar Mountain Formation OMNH 28161 in posterior (A) and lingual (B) views. Scale bar = 1 mm.

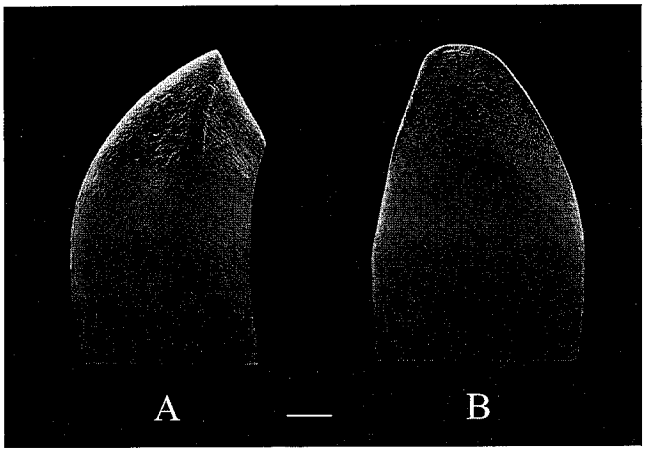

Figure 3. Scanning electron micrographs of sauropod tooth from the Cedar Mountain Formation OMNH 27902 in anterior (A) and posterior (B) views. Scale bar = 1 mm.

Pleurocoelus and *Brachiosaurus*, among others, seem to be intermediate to these two generalized morphologies (McIntosh, 1990; Salgado and Calvo, 1997). This bipartite scheme has been described as an oversimplification, as one that is not truly representative of the distribution of crown shapes throughout the members of Sauropoda (for example, Calvo, 1994; Salgado and Calvo, 1997; Wilson and Sereno, 1998). Detailed examinations of the distribution of crown forms and patterns of wear (Salgado and Calvo, 1997; Wilson and Sereno, 1998) suggest that the teeth of sauropods are not particularly diagnostic in many cases to even a gross taxonomic level. Accordingly caution should be exercised when attempting to identify teeth to generic or family level.

Nomenclatorial confusion

The Cedar Mountain sauropod teeth were first noted by Cifelli et al., (1997) and Kirkland et al., (1997), then again two years later by the same senior authors (Cifelli et al., 1999; Kirkland et al., 1999). The authors made no attempt to describe them, with the teeth simply likened to those described for *Astrodon* cf. *Pleurocoelus* and therefore identified tentatively as those of a brachiosaurid. There is evident confusion and uncertainty over the use of the generic names *Astrodon* and *Pleurocoelus*. Each genus is based on material recovered from the Arundel Formation of Maryland. *Astrodon* (Leidy, 1865) was named 23 years before *Pleurocoelus* (Marsh, 1888). However, *Astrodon* (known only from *A. johnstoni*) is based on an isolated tooth, whereas the type material for *Pleurocoelus* (known by two probably synonymous species) although poor, consists of disarticulated skeletal elements that together are more diagnostic than a solitary tooth. Accordingly, most authors favor *Pleurocoelus* (for example, McIntosh, 1990; Salgado et al., 1997; Wilson and Sereno, 1998), despite *Astrodon* having chronological priority. Lipka (1998) recently used *Astrodon* in specific preference to *Pleurocoelus*, whereas Kirkland et al. (1998: Appendix) use *Astrodon* and *Pleurocoelus* for different occurrences, despite synonymising the two in the accompanying text. *Pleurocoelus* also sees use as a receptacle for much sauropod vertebral material that is not particularly diagnostic (e.g., Hatcher, 1903; Langston, 1974; DeCourten, 1991). Clearly this is a taxonomic problem seeking resolution and further work is required to elucidate the affinities and possible synonymy of *Astrodon* and *Pleurocoelus*. Also apparent is the fact that the referral of isolated teeth to *Astrodon* or *Pleurocoelus* would not, in any case, be very illuminating.

Affinities of the teeth from the Cedar Mountain Formation

The teeth described here exhibit a morphology that is superficially similar to the intermediate condition described by McIntosh (1990) and Salgado and Calvo (1997), in which the slender basal portion of the crown becomes mildly spatulate distally. Calvo (1994) has described this as a compressed cone, chisel-like condition, typical of *Brachiosaurus* and *Astrodon*. A fine example of this chisel-like form is seen in OMNH 34192 (Fig. 6A–C) from the Antlers Formation of Oklahoma. The degree of expansion of the distal crown, responsible for the development of the spatulate form, is rather slight in the Cedar Mountain specimens, with the result that the mid-crown is not much broader than the root of the tooth or the proximal crown. In addition, the Cedar Mountain teeth exhibit what appears to be an exaggerated lingual curvature, with

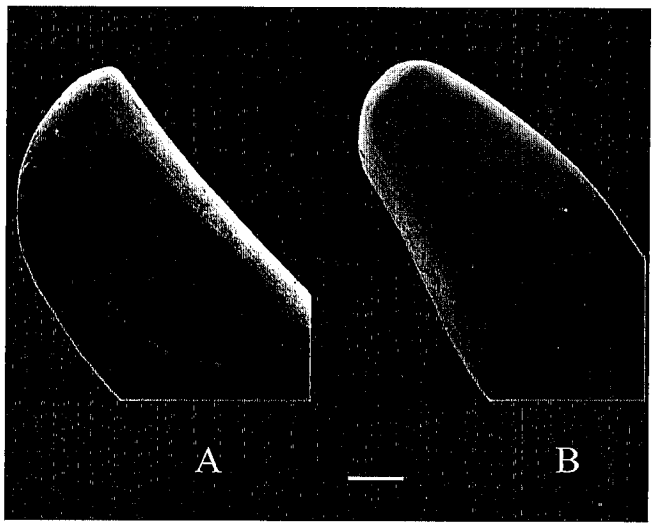

Figure 4. Scanning electron micrographs of sauropod tooth from the Cedar Mountain Formation OMNH 28159 in anterior (A) and anteriolingual (B) views. Scale bar = 1 mm.

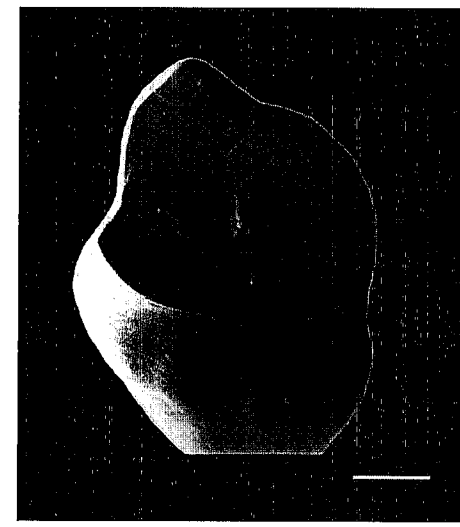

Figure 5. Scanning electron micrograph of sauropod tooth from the Cedar Mountain Formation OMNH 28312 showing a mid-crown cross-section. See text for details. Scale bar = 1 mm.

the apex tapering to a fine point. It is not unusual for unworn teeth of sauropods to exhibit finely pointed distal crowns, such as those seen in, for example *Nemegtosaurus* (Nowinski, 1971; Plate XIII) or *Diplodocus* (Berman and McIntosh, 1978; Figs. 2, 9). A less pronounced lingual curvature of the distal crown is seen in many forms, such as, for example *Camarasaurus* (Wilson and Sereno, 1998; Fig. 7) and *Astrodon* (Lull, 1911; Plate XIX, Fig. 5), however an exaggerated lingual curvature of the distal crown appears to be rare among other sauropods. It is possible that the perceived greater degree of curvature is related to the small size of the teeth, because a similar condition is demonstrated in OMNH 60891, a very small tooth from the Antlers Formation (Fig. 7).

The intermediate crown morphology and the wear surface patterns of the Cedar Mountain teeth suggest that they probably represent a very small brachiosaurid sauropod. The teeth bear some resemblance to that illustrated for *Astrodon* (Lull, 1911: Plate XIX, Fig. 5), and less of a resemblance to those illustrated for *Pleurocoelus* (Brachiosauridae) (Lull, 1911: Plate XIX, Fig. 4), bearing in mind the likely synonymy of the two genera. The Cedar Mountain teeth are also somewhat similar to those of *Brachiosaurus,* in that they approach the compressed cone, mildly spatulate condition in crown morphology, although they lack the moderate breadth of a typical tooth of *Brachiosaurus* (Janensch, 1935–36). As discussed above, caution should be exercised when attempting to attribute isolated teeth of sauropods to genera or families, but there is little doubt that the Cedar Mountain teeth are unlike the broad spatulate teeth typical of camarasaurids, or the elongate, cylindrical teeth typical of most titanosaurids and diplodocids (Fig. 8).

One of the teeth described here (OMNH 27902) possesses a v-shaped wear facet (Fig. 3B), typical of *Brachiosaurus, Nemegtosaurus, Omeisaurus* and *Shunosaurus* (Wilson and Sereno, 1998), but there is an obvious elliptical wear facet on OMNH 28161 (Fig. 2A, B). The presence of two different wear facets on teeth of what is presumed to be one species (see below) might seem contradictory, but it is not unprecedented to have both wear patterns in one species, or even in one individual, as demonstrated for the titanosauriform *Nemegtosaurus* (Nowinski, 1971; Salgado et al., 1997; Wilson and Sereno, 1998).

OMNH 28159 exhibits an overlap facet (Fig. 4A). Calvo (1994) states that in *Brachiosaurus* one tooth can meet one or two teeth in the opposing tooth row, but Wilson and Sereno (1998) state that the crowns do not contact one another. The general condition for Brachiosauridae is unclear, so it is difficult to attribute any significance to the single overlap facet observed in the sample.

All of the teeth recovered from the Mussentuchit Member of the Cedar Mountain Formation are very small (Table 1). The known teeth were recovered by intensive sampling of the Mussentuchit Member, using both micro- and macrovertebrate techniques (Cifelli et al., 1999). Neither skeletal elements (which are readily identified, even from small fragments) nor teeth of a moderate- to large-size sauropod have been found in the fauna. Caution must be used in interpreting negative evidence. Nonethe-

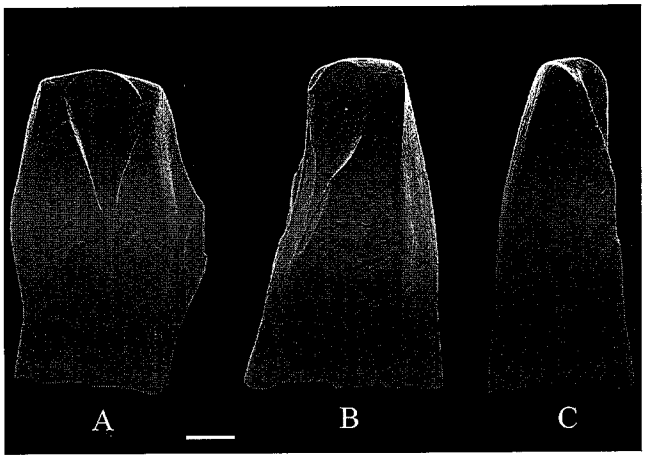

Figure 6. Scanning electron micrograph of OMNH 34192, an unidentified sauropod tooth from the Antlers Formation of Oklahoma, in lingual (A), posterior (B), and anterior (C) views. Scale bar = 1 mm.

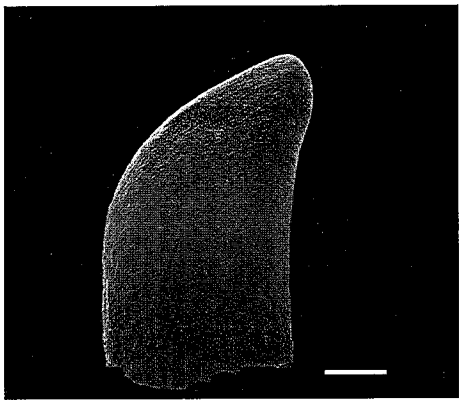

Figure 7. Scanning electron micrograph of OMNH 60891, an unidentified sauropod tooth from the Antlers Formation of Oklahoma, in anterior view. Scale bar = 1 mm.

less, the presence of only very small teeth is more suggestive of an extremely small sauropod taxon, rather than a preservational or sampling bias that favored the preservation or the recovery of teeth of neonates or juveniles (Cifelli et al., 1999). All of the teeth exhibit a similar mode of preservation and the same crown morphology, and it seems reasonable to assume that they represent one species. Dwarfed sauropods are not unprecedented, with the titanosaur, *Magyarosaurus dacus* described recently as a heterochronic dwarf (Jianu and Weishampel, 1999).

CONCLUSIONS

The teeth described here from the Mussentuchit Member of the Cedar Mountain Formation likely represent a new, very small, possibly dwarf taxon of sauropod, most probably a brachiosaurid. They are dissimilar to the peg-like and chisel-like teeth of diplodocids and titanosaurids, and bear little resemblance to the broadly spatulate teeth of camarasaurids. Although they bear a superficial resemblance to the teeth of *Astrodon* cf. *Pleurocoelus* and *Brachiosaurus,* there are fundamental differences between the teeth of each of these taxa. No attempt is made to erect a new taxon, based on teeth alone, because of the peril associated with any attempt to identify isolated teeth of sauropods to even familial level.

The teeth appear to be unique to the Mussentuchit Member, differing from several teeth of sauropods recovered from the slightly older Cloverly Formation of south-central Montana and the Antlers Formation of Oklahoma, and from published accounts of teeth from other late Early Cretaceous faunas throughout North America.

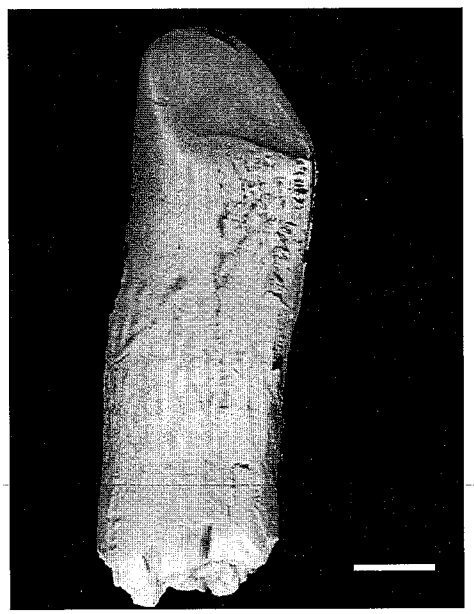

Figure 8. Scanning electron micrograph of OMNH 34023, an unidentified sauropod tooth from the Cloverly Formation of Montana, in lingual view. The long, subcylindrical crown is characteristic of many diplodocid and titanosaurid sauropods. Scale bar = 5 mm. f

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