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EVIDENCE FOR NICHE PARTITIONING AMONG GROUND-HEIGHT BROWSING SAUROPODS FROM THE UPPER JURASSIC MORRISON FORMATION OF NORTH AMERICA

Julia B. McHugh



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An Ecosystem We Thought We Knew—
The Emerging Complexities of the Morrison Formation
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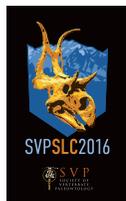
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Excavations of the Brushy Basin Member of the Morrison Formation (Upper Jurassic) at the Mygatt-Moore Quarry in western Colorado with a specimen of diplocid premaxilla fragment (MWC 8430) superimposed. Cover photograph by Julia B. McHugh (Museums of Western Colorado).



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Evidence for Niche Partitioning Among Ground-Height Browsing Sauropods from the Upper Jurassic Morrison Formation of North America

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ABSTRACT

Two tooth-bearing snout fragments from a diplodocid sauropod from the Brushy Basin Member of the Morrison Formation (Upper Jurassic) excavated from the Mygatt-Moore Quarry in Rabbit Valley, Colorado are described. The Mygatt-Moore Quarry has produced thousands of vertebrate fossils from the Brushy Basin Member, with the diplodocid *Apatosaurus* cf. *louisae* and the tetanuran *Allosaurus fragilis* dominating the assemblage. Additionally, remains of another diplodocid, *Diplodocus* sp., have been found near the quarry within Rabbit Valley. Both specimens in this study preserve eight teeth per alveolar position, as observed through broken surfaces at the gross anatomical level and also through computed tomography (CT) scans. This is inconsistent with the genus *Diplodocus* sp., which has been previously shown to have a maximum of six teeth per alveolus. The presence of eight replacement teeth per alveolus has previously only been reported in the Cretaceous rebbachisaurid *Nigersaurus taqueti*, which has been interpreted to have occupied a similar ground-height browsing feeding strategy to both *Diplodocus* and *Apatosaurus*. This is the first report of this type of high-count replacement teeth in a diplodocid sauropod from the Morrison Formation. The high number of replacement teeth in a close relative to the contemporaneous *Diplodocus* provides evidence for niche partitioning among the contemporary ground-height browsing diplodocid sauropods of the Late Jurassic Period in North America.

INTRODUCTION

Apatosaurus and *Diplodocus* are contemporary sauropod genera found within the Upper Jurassic Morrison Formation (Tschoop and others, 2015). These genera share a close phylogenetic history, as well as head and neck morphologies that allow for similar biomechanical adaptations to available vegetation zones (Stevens and Parrish, 1999, 2005; Upchurch, 2000; Wilson, 2005; Whitlock, 2010; Stevens, 2013; Woodruff, 2017). The presence of such similar, large-bodied herbivores

would have had a substantial impact on the available biomass in order to support populations of these two genera. Ecological niche partitioning in the Upper Jurassic Morrison Formation's landscape has traditionally been proposed to circumvent this problem (Turner and Peterson, 2004). However, empirical evidence supporting this partitioning among coeval genera, particularly between adult *Apatosaurus* and *Diplodocus*, has been limited (Fiorillo, 1998; Whitlock, 2011; D'Emic and others, 2013). Here, I describe new specimens that shed light on this ecological problem: two diplodocid

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snout fragments containing numerous teeth (Museums of Western Colorado specimens MWC 6002 and MWC 8430) from the Brushy Basin Member of the Morrison Formation excavated from Mygatt-Moore Quarry (MMQ) in Rabbit Valley, western Colorado (figure 1).

The MMQ is located within the McClinnis Canyons National Conservation Area and is co-managed by the Museums of Western Colorado (MWC) and the Bureau of Land Management (BLM). Excavations at the MMQ for over thirty years by crews from the MWC, as well as the Dinamation International Society, have facilitated the recovery of over 5000 vertebrate fossils, including holotype specimens of the bony fish "*Hulettia*" *hawesi* (Kirkland, 1998) and *Morrolepis schaefferi* (Kirkland, 1998), and the ankylosaur *Mymoorapelta mayisi* (Kirkland and Carpenter, 1994). However, fossil material from the tetanuran *Allosaurus fragilis* and the diplodocid *Apatosaurus* cf. *louisae* dominate the assemblage (Foster and others, 2007, 2018). Two diplodocid taxa are positively identified from the Rabbit Valley area: *Diplodocus* sp. and *Apatosaurus* cf. *louisae*. Of these two, only *Apatosaurus* cf. *louisae* has been recovered within the MMQ. Other sauropods recovered from the quarry include the macronarian, *Camarasaurus* sp., as well as several taxonomically ambiguous caudal vertebrae, which are identified as Diplodocinae indet. (Foster and others, 2018).

Sauropod dinosaurs include the largest terrestrial herbivores that the Earth has ever known. Understanding their biology and interactions with plant biomass and other sauropods within Mesozoic ecosystems has been the subject of much research (Barrett and Upchurch, 1995; Stevens and Parrish, 1999, 2005; Upchurch, 2000; Upchurch and Barrett, 2000; Hummel and others, 2008; Yates and others, 2010; Gee, 2011; Tütken, 2011). Sauropods have been broadly divided into "high browsing" and "ground height" browsing ecological types based upon snout shape and neck position (Whitlock, 2011), but estimations of neck biomechanics indicate considerable overlap in the range of feeding between disparate types of sauropods (Stevens and Parrish, 1999, 2005). Additionally, co-occurring genera within these broad categories, such as *Apatosaurus* and *Diplodocus*, are known from the Morrison Formation (Tschopp and others, 2015).

The refining of these broad ecological groups was attempted using snout shape morphometrics (Whitlock, 2011). Snout shapes were quantified for six diplodocoid genera (*Apatosaurus* sp., *Dicraeosaurus* sp., *Diplodocus* sp., *Nigersaurus taqueti*, *Suuwassea emilieae*, and *Tornieria africana*) using the ratio of the depth to and breadth in the upper jaw, the premaxillary-maxillary index, and the divergence angle of the premaxillae (Whitlock, 2011). Whereas some taxa were found to be mathematically distinct from each other; unfortunately, these metrics were unable to separate the broad snouted *Apatosaurus* and *Diplodocus* into disparate ecological groups (Whitlock, 2011).

Tooth microwear has also been used to distinguish among ecological resource use in sauropod dinosaurs (Fiorillo, 1998; Whitlock, 2011). However, while tooth wear and microwear have been useful in differentiating feeding strategies between co-occurring taxa like *Camarasaurus* sp. and *Diplodocus* sp. (Fiorillo, 1998; Whitlock, 2011), suitable teeth from *Apatosaurus* sp. for this type of analysis have been lacking (Whitlock, 2011). Although shed teeth are relatively common for predators like *Allosaurus fragilis*, especially at the MMQ, shed teeth from species of *Apatosaurus* are less common and are often difficult to differentiate from those of *Diplodocus*. Additional dental material is required to assess the microwear in the genus *Apatosaurus*, and for this type of analysis to be useful in partitioning the ecological niches of *Apatosaurus* and *Diplodocus*.

Observations of modern herbivores show that ecological niche partitioning is common among similar taxa within an environmental landscape (i.e., Bovidae), and that their dental and jaw morphologies are also correlated to this partitioning (Spencer, 1995). However, with considerable morphological and biomechanical overlap in sauropod dinosaurs between established ecological types, estimation of niche partitioning at lower taxonomic levels has proven difficult (Fiorillo, 1998; Whitlock, 2011). Tooth replacement may be an illuminating piece of evidence in fully assessing the niche partitioning among sauropods. Since variable hardness within food sources can tend to create inconsistent wear on herbivore teeth, a higher level of tooth replacement is often associated with tougher vegetation.

Tooth replacement rates among Diplodocoidea

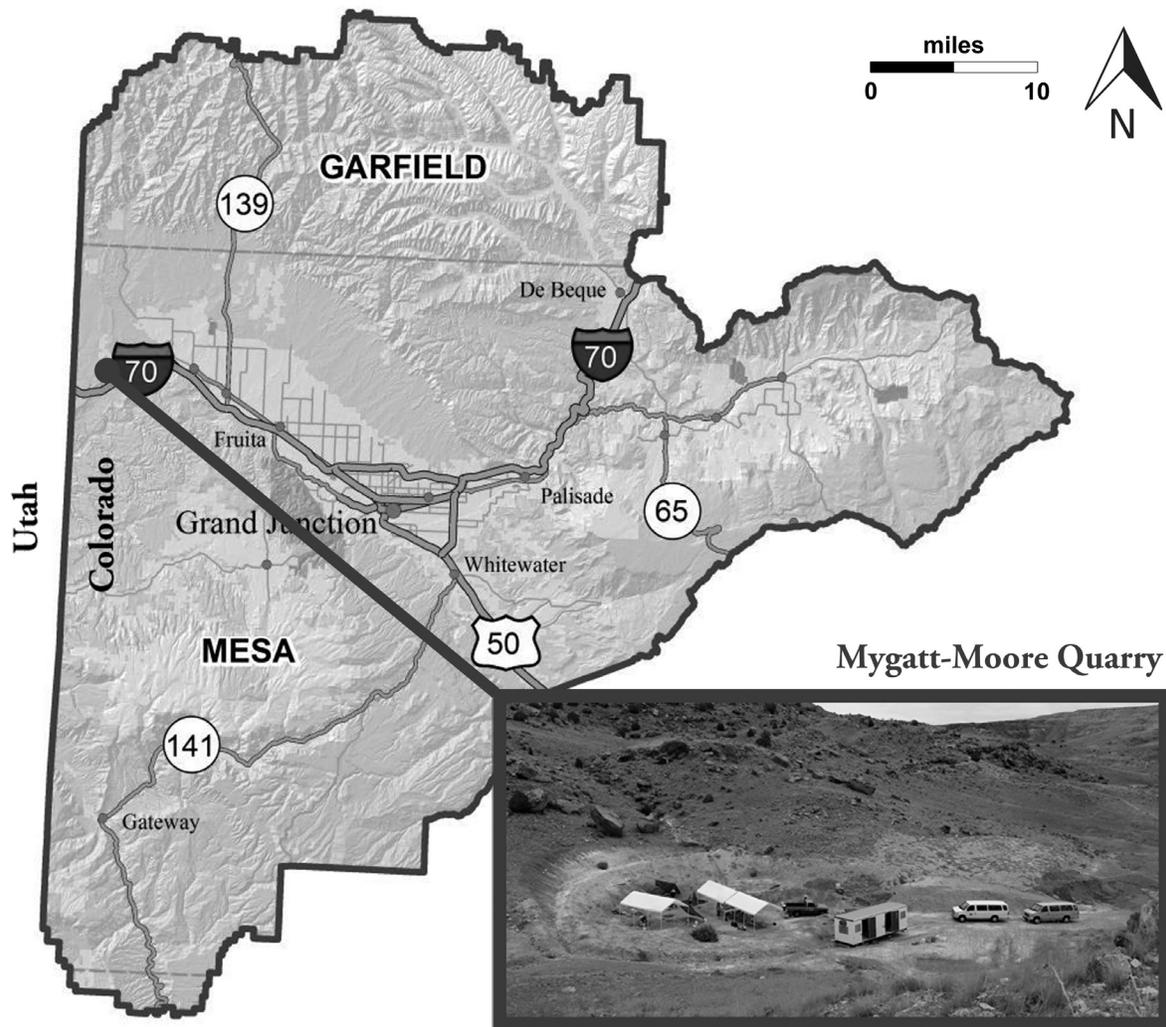


Figure 1. Map of Mesa County in western Colorado showing the location of the Mygatt-Moore Quarry. Insert shows excavations at the quarry during 2014.

have previously been described in *Camarasaurus* sp., *Diplodocus* sp., *Dicraeosaurus hansemanni*, and *Nigersaurus taqueti* (Sereno and others, 2005; D’Emic and others, 2013; Schwarz and others, 2015). The number of teeth per alveolus within the premaxillae (including both replacement and erupted tooth positions) vary among taxa, with four reported in *Camarasaurus* sp., six in *Diplodocus* sp., five to six in *Dicraeosaurus hansemanni*, and eight in *Nigersaurus taqueti* (Sereno and others, 2005; D’Emic and others, 2013; Schwarz and others, 2015). D’Emic and others (2013) suggest the lower number of teeth in *Camarasaurus* sp. is correlated to the relative increase in tooth volume, and thus a

physiological investment in individual teeth rather than a biological investment in a lot of teeth. I present here the first description of tooth replacement in a non-*Diplodocus* diplodocid from the Morrison Formation that provides empirical evidence for an ecological partition between this taxon and *Diplodocus* sp.

GEOLOGICAL SETTING

The fossil-bearing horizon at the MMQ is a 1- to 2-m-thick unit exposed within laminated to medium-bedded gray silty mudstone of the Brushy Basin

Member of the Morrison Formation (Kirkland and Carpenter, 1994; Foster, 2003; Foster and others, 2007, 2018; Foster and Hunt-Foster, 2011). Radiometric analysis of ash-fall zircons from the quarry have returned an age of 152.18 ± 0.29 Ma, which places the quarry on Kimmeridgian–Tithonian boundary during the Late Jurassic Period (Trujillo and others, 2014).

The MMQ is interpreted to preserve an ecosystem with abundant vegetation and a high water table, but with standing water at the surface occurring only seasonally (Foster, 2003; Trujillo and others, 2014; Foster and others, 2018). The site preserves a dinosaur-dominated assemblage with abundant plant material, with crocodylomorph, turtle, and invertebrate remains being rare (Foster 2007; Foster and others, 2018). Previous taphonomic work has shown the site represents an autochthonous assemblage within an attritional deposit in an overbank setting with few articulated specimens and no preferred orientation of skeletal elements (Foster and others, 2018). Despite the lack of transport evident in the assemblage, fossils often preserve bone surface modifications (e.g., breakage, abrasion, and feeding traces) that suggest a reworked death assemblage by subsequent living individuals, possibly through feeding and trampling (Foster and others, 2018).

DESCRIPTION

Both specimens in this study were excavated from the gray mudstone of the Brushy Basin Member of the Morrison Formation at the MMQ using hand-quarrying techniques. Both specimens were collected as isolated elements with no additional associated cranial or postcranial material. These specimens were mechanically prepared at the MWC fossil preparation lab, repaired, and stabilized using polyvinyl acetate dissolved in acetone, as well as cyanoacrylate (PaleoBOND™ 750) adhesives, and then imaged using two-dimensional (2-D) photography and a 64-slice computed tomography (CT) scanner at Colorado Canyons Hospital in Fruita, Colorado.

MWC 6002—Diplodocid Maxilla

Specimen MWC 6002 is a partial maxilla that preserves eight sets of teeth, with each set representing a

single alveolus. The mesial suture between the premaxilla and maxilla is poorly preserved and the ventrodistal margin is incomplete. Therefore, it is doubtful that all maxillary alveoli are present in the specimen, and alveolar positions are instead referred to as mx1-mx8 and not to their exact maxillary placement (figure 2).

The number of replacement teeth per alveolus decreases from medial to distal. The mesial-most four alveolar positions (mx1-mx4) each preserve seven to eight replacement teeth, similar to the numbers preserved in specimen MWC 8430. The next two alveoli (mx5-mx6) preserve six and five replacement teeth, respectively, whereas the distal-most positions preserve only four and three replacement teeth (mx7, mx8). This reduction in the number of replacement teeth reflects the decreasing volume in maxillary space distally. Tooth replacement positions *vi-viii* are labial-lingually compressed. Erupted crown morphology and the lingual inflection at the separation of root and crown are both distinguishable by position *v* and become more pronounced towards the erupted tooth position (*i*) (figures 3 and 4).

MWC 8430—Diplodocid Premaxilla Fragment

Specimen MWC 8430 is a well-preserved, isolated premaxilla fragment that preserves four sets of replacement teeth, each representing a single alveolus in the upper jaw. However, lack of preservation on the exterior surface has not preserved the alveoli themselves. The lingual face of the premaxilla is preserved as a thin, trapezoidal fragment with a smooth surface morphology. The fragmental nature of specimen MWC 8430 allows for determination of lingual/labial and superior/inferior orientations, but not mesial/distal and it prohibits assignment to precise tooth row placement. The alveolar positions are therefore referred to as px1-px4 (figure 5).

The maximum number of replacement teeth (eight) in an individual set are found within px1, with px2 and px3 each preserving seven teeth, and px4 with four teeth. Teeth in the replacement rows incrementally increase in length towards the erupted tooth position. Tooth replacement positions *vi-viii* are labial-lingually compressed. Erupted crown morphology is distin-

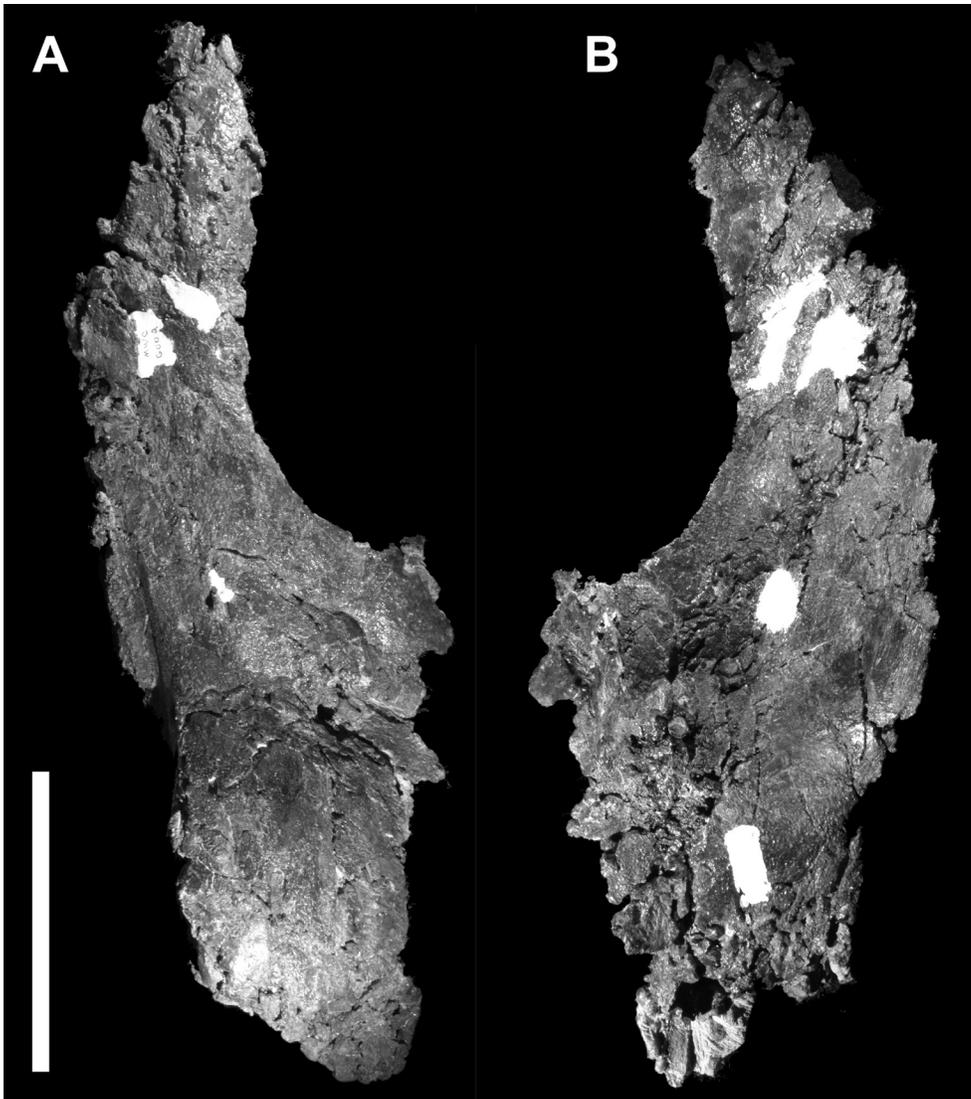


Figure 2. Diplodocid maxilla (specimen MWC 6002). (A) dorsal view. (B) ventral view. Scale bar equal 10 cm.

guishable by position v and becomes more pronounced towards the erupted tooth position (i). Also visible at position v is the lingual inflection at the separation of root and crown (figures 5 and 6).

DISCUSSION

Despite the lack of association with more diagnostic material, some taxonomic assessments for specimens MWC 6002 and MWC 8430 are possible. These specimens both bear the characteristic peg-like teeth of Diplodocoidea. However, they are not consistent with the known pattern of tooth replacement in *Diplodocus* sp. or the African taxon *Dicraeosaurus hansemanni* which have been shown to support no more than five to six

tooth positions per alveolus in the premaxilla, including the erupted tooth (D’Emic and others, 2013; Schwarz, 2015). The newly described specimens MWC 6002 and MWC 8430, although incomplete, preserve a maximum of eight teeth (both replacement teeth and erupted tooth) per alveolus. The premaxilla exhibits the maximum number of replacement teeth, as supported by the mesial increase in the number of tooth replacement position seen in the maxilla, specimen MWC 6002. However, this mesial increase in tooth replacement positions may not be characteristic of all sauropods, for example in the titanosaur *Euhelopus zdanskyi*, the maximum number of tooth replacement positions is located within the maxilla and not the premaxilla (Poropat and

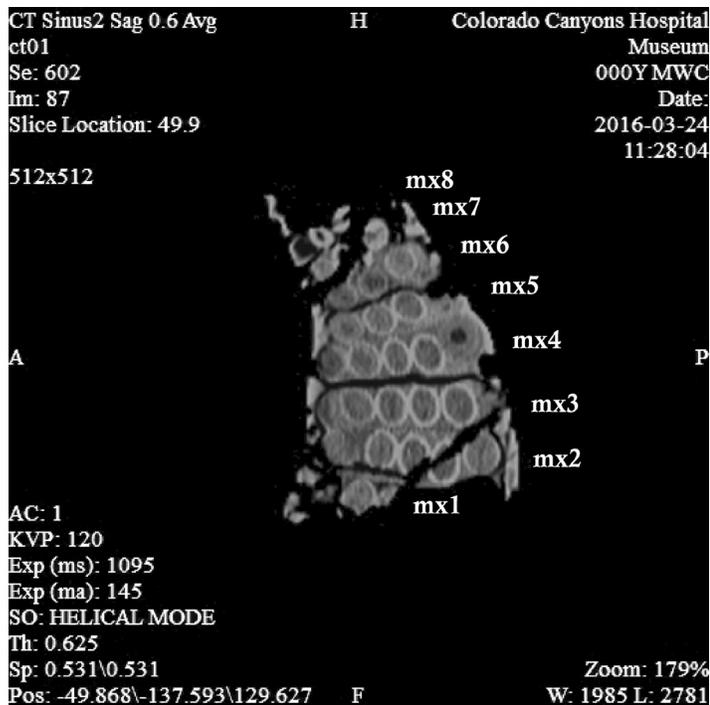


Figure 3. CT scan of specimen MWC 6002 in and superior view. Alveolar positions are indicated with mx1-mx8 labels.

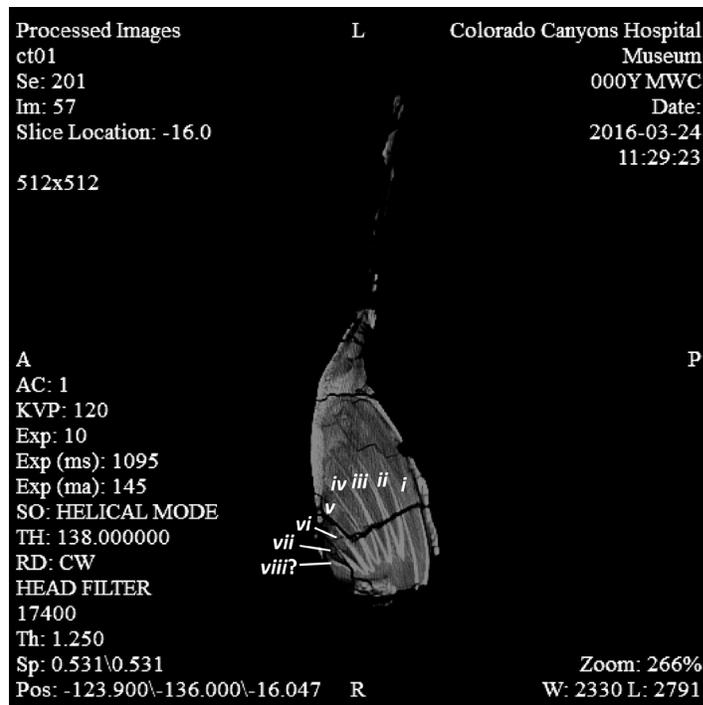


Figure 4. CT scan of specimen MWC 6002 in and mesial view. Roman numerals indicate tooth positions for the mx2 alveolus.

Kear, 2013).

Minimally, specimens MWC 6002 and MWC 8430 can be assigned as a non-*Diplodocus* diplodocid. The only other known diplodocid taxa from the Rabbit Valley consists of the very abundant *Apatosaurus* cf. *louisae* and the ambiguous vertebrae not positively identified beyond Diplodocinae indet. The MMQ in Rabbit Valley has been explored in scientific earnest for more than three decades, producing thousands of fossils, none of which were positively assigned to any diplodocid taxon other than *Apatosaurus* cf. *louisae*. And although the possibility of future diplodocid discoveries at the site cannot be discounted, given the present data available, it is most parsimonious for specimens MWC 6002 and MWC 8430 to be tentatively referred to *Apatosaurus* sp., pending the recovery of more diagnosable cranial material.

Despite a closer phylogenetic, geographic, and stratigraphic relationship with *Diplodocus* sp., the specimens in this study that are referred to *Apatosaurus* sp. are more similar to the tooth replacement counts seen in the Cretaceous African form *Nigersaurus taqueti*.

A higher number of replacement teeth than the coeval *Diplodocus* sp. indicates that these large-bodied, “ground height” browsing herbivores were orally processing different types of vegetation, with *Apatosaurus* sp. potentially adapted for tougher, more abrasive vegetation than *Diplodocus* sp. The Morrison Formation is interpreted as representing a predominantly riparian landscape with limited botanical biomass (Foster, 2003; Engelmann and others, 2004; Rees and others, 2004; Turner and Peterson, 2004; Hummel and others, 2008; Gee, 2011). This partitioning of resources between large herbivores would have been critical for survival in this limiting environment, and may have been the key to the success and diversity of the sauropods in the Late Jurassic Period.

CONCLUSIONS

Populations of co-occurring herbivores in modern landscapes often partition plant biomass resources to facilitate survival in competitive environments. Using modern analogs, paleontologists have long hypothe-

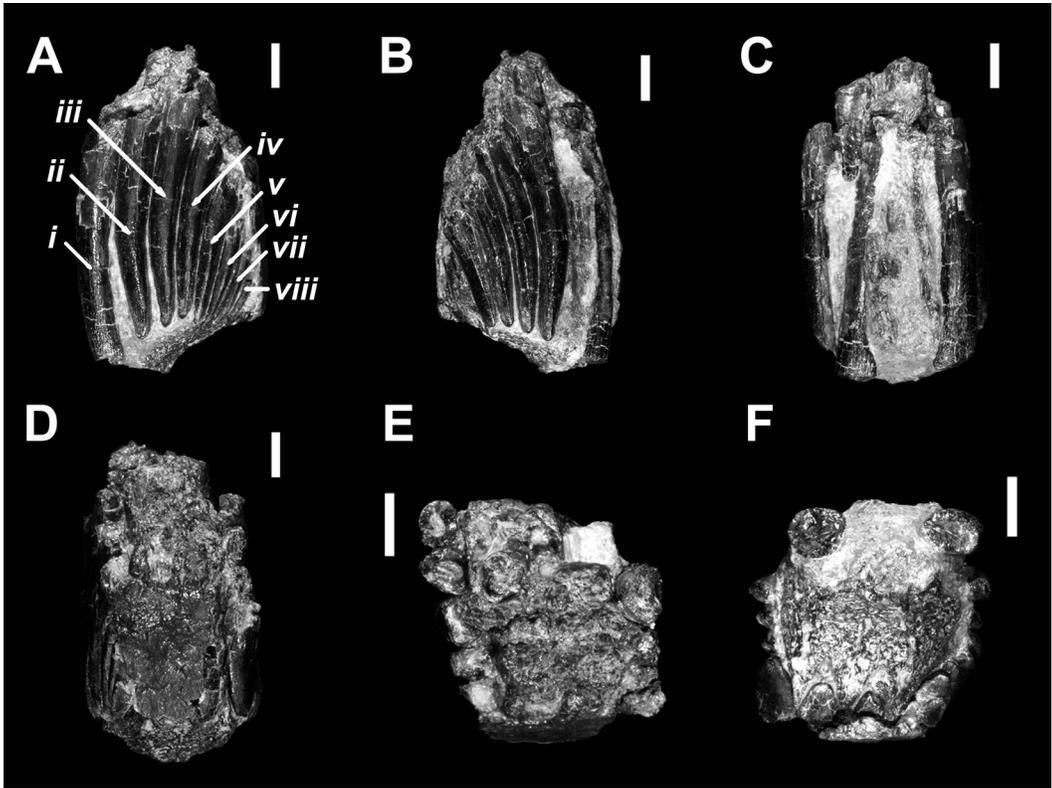


Figure 5. Specimen MWC 8430 in (A) ?mesial, (B) ?distal, (C) labial, (D) lingual, (E) superior, and (F) inferior views. Roman numerals indicate tooth positions for an individual alveolus. All scale bars equal 1 cm.

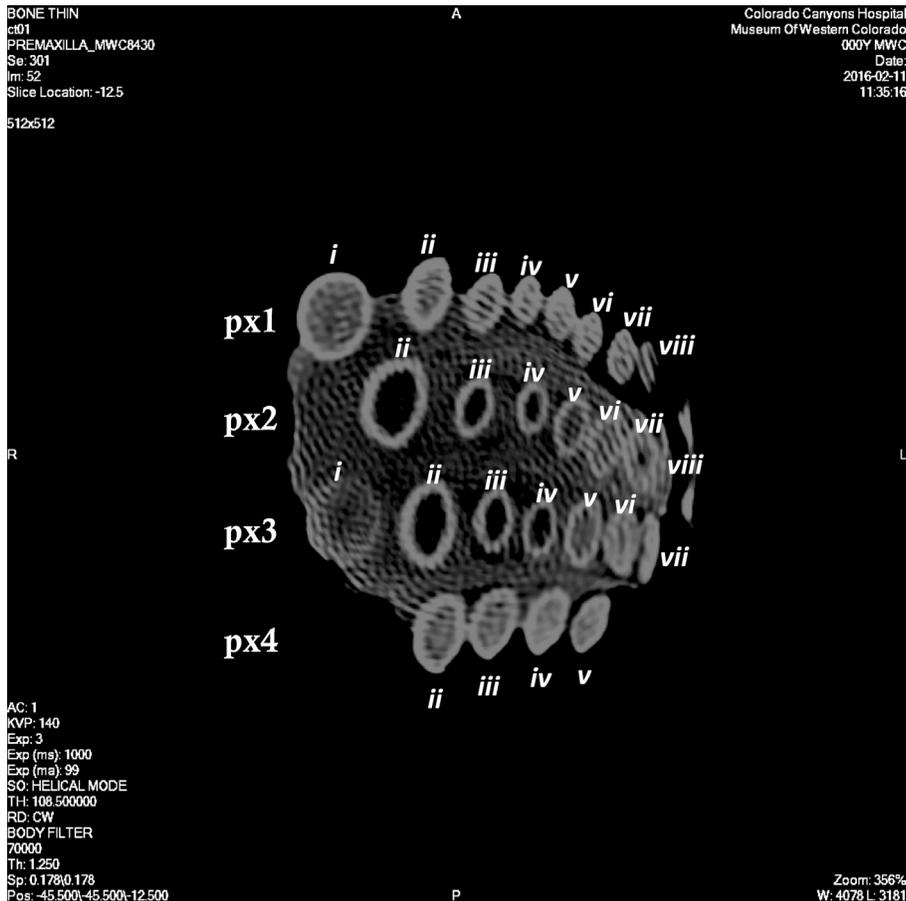


Figure 6. CT scan of specimen MWC 8430 in and inferior view. Roman numerals indicate tooth positions for individual alveoli. Alveolar positions are indicated with px1-px4 labels.

sized similar niche partitioning among large sauropod dinosaurs in the Mesozoic. New specimens from the MMQ in Rabbit Valley, Colorado, reveal higher counts of tooth replacement in *Apatosaurus* sp. than in *Diplodocus* sp. This indicates that species of *Apatosaurus* may have been selectively feeding on tougher vegetation (e.g., cycads and conifers) than species of *Diplodocus* and provides the strong empirical evidence for niche partitioning among these coeval and morphologically similar taxa.

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