

DESCRIPTION OF A NEARLY COMPLETE JUVENILE SKULL OF *DIPLODOCUS* (SAUROPODA: DIPLODOCOIDEA) FROM THE LATE JURASSIC OF NORTH AMERICA

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ABSTRACT—More than any other sauropod dinosaur group, the long-necked herbivores belonging to Diplodocoidea have been defined by their skulls. Their unique skull shape, which is extremely elongate antorbitally, with a transversely broad, square snout packed at its anterior extreme with narrow-crowned, pencil-like teeth, has served as a touchstone for describing the biology of these animals ever since the discovery of the first skull in the late 19th century. In particular, the unusual diplodocoid skull has been discussed frequently in the context of examining feeding behavior, spawning hypotheses ranging from branch stripping, propalinal shearing, and aquatic plant ‘grazing.’ Here, we describe a juvenile skull of *Diplodocus* (Carnegie Museum 11255) that does not share the unusually blunted snout and anteriorly sequestered teeth seen in adult specimens, suggesting that adults and juveniles may have differed greatly in their feeding behavior, an ontogenetic distinction that may be unique among sauropodomorphs.

INTRODUCTION

The skull of *Diplodocus* was first described by Marsh in 1884, and several additional, nearly complete skulls have been discovered and described since, making diplodocid cranial elements some of the best-known among Sauropoda (Marsh, 1884; Hatcher, 1901; Holland, 1906, 1924; Gilmore, 1932; Janensch, 1935–36; Haas, 1963; McIntosh and Berman, 1975; Berman and McIntosh, 1978; Connely, 1997). Since its discovery, the skull of *Diplodocus* has played a prominent role in distinguishing diplodocids from other sauropods. Cranial characters represent four of the seven features Marsh (1884) used in his initial diagnosis of the Family Diplodocidae, a trend that continues to this day. Wilson (2002) listed ten cranial characters as synapomorphies of Diplodocoidea (sauropods more closely related to *Diplodocus* than to *Saltasaurus*), as well as seven cranial synapomorphies for the subgroup Diplodocidae (sauropods more closely related to *Diplodocus* than to *Dicraeosaurus*) and six for Dicraeosauridae (sauropods more closely related to *Dicraeosaurus* than *Diplodocus*). Cranial characters made up 39.5% of the support for the node Diplodocoidea, nearly 10% more than for Macronaria (Wilson, 2002:table 14). Likewise, cranial specializations contributed much of the character support for Diplodocoidea and Diplodocidae in the analysis of Upchurch et al. (2004). Even at lower taxonomic levels, cranial characters are important qualifiers. Wilson (2002:appendix 4) lists 25 cranial characters as autapomorphies for the six included diplodocoid genera for which cranial material is preserved and that were included in his analysis. Both their unusual shape and their relative abundance—40% of diplodocoid genera are represented by some cranial material, compared to less than 33% of macronarians (Table 1)—have contributed to what has become an iconic impression of the diplodocoid skull.

The diplodocoid skull is typically described as elongate antorbitally, with the nares retracted to a position dorsomedial to the orbits and the jaws transversely expanded anteriorly, terminating in a blunt, square snout containing narrow-crowned teeth. The shape of the *Diplodocus* skull has been regarded as poorly suited to chewing or biting through stems (e.g., Hay, 1908; Holland, 1924), and, as a consequence, great interest has been taken in the potential uses of the skull for gathering food in other ways (Osborn, 1899; Hatcher, 1901; Holland, 1906, 1924; Hay, 1908; Tornier, 1911; Coombs, 1975; Bakker, 1986; Dodson, 1990; Fiorillo, 1991, 1995, 1998; Barrett and Upchurch, 1994; Calvo, 1994; Stevens and Parrish, 1999, 2005; Christiansen, 2000; Upchurch and Barrett, 2000). The unique skull shape of *Diplodocus* has led researchers to propose equally unique modes of feeding, including uprooting aquatic succulents (Hatcher, 1901), scraping algae from rocks (Holland, 1906), branch stripping (Coombs, 1975; Bakker, 1986; Barrett and Upchurch, 1994), and prehension of fish (Tornier, 1911) or bivalves (Sternfeld in Holland, 1924), as well as a feeding strategy employed by modern mega-herbivores: low-height cropping (Barrett and Upchurch, 1994; Stevens and Parrish, 1999; Upchurch and Barrett, 2000; Barrett and Willis, 2001; Sereno et al., 2007). Regardless of their specific functional interpretation, all studies agree that the feeding ecology of *Diplodocus* was clearly distinct from those employed by contemporaneous macronarian sauropods such as *Camarasaurus* and *Brachiosaurus*.

Here, we describe a juvenile skull attributable to *Diplodocus* that provides new insights into the life history and paleoecology of this giant herbivore. The reconstructed shape of the facial skeleton, particularly the anterior, tooth-bearing region, is transversely narrow and rounded anteriorly, in contrast to the square, blunt shape characteristic of adult diplodocids. This disparity in shapes between age classes implies a pattern of ontogenetic remodeling of the facial skeleton. We interpret this pattern as an indication of resource partitioning between rapidly growing juveniles and adults, which were primarily invested in maintaining body existing body mass. This pattern is then compared and

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TABLE 1. Described sauropod taxa known from cranial elements, not including taxa known solely from teeth

Category	Genus	Material	Key reference	
Non-Neosauropods	<i>Archaeodontosaurus</i>	Jaw fragment	Buffetaut, 2005	
	<i>Chebsaurus</i>	Skull fragments	Mahammed et al., 2005	
	<i>Chinshakiangosaurus</i>	Partial dentary	Upchurch et al., 2007	
	<i>Datousaurus</i>	Jaw fragments	Dong and Tang, 1984	
	<i>Gongxianosaurus</i>	Jaw fragment	He et al., 1998	
	<i>Lamplughsaura</i>	Partial skull	Kutty et al., 2007	
	Lufeng taxon	Partial maxilla	Barrett, 1999	
	<i>Mamenchisaurus</i>	Several partial skulls	Ouyang and Ye, 2002	
	<i>Omeisaurus</i>	Three partial skulls	He et al., 1988; Tang et al., 2001	
	<i>Patagosaurus</i>	Jaw fragments	Bonaparte, 1979; Rauhut, 2003	
	<i>Shunosaurus</i>	At least five partial skulls	Chatterjee and Zheng, 2002	
	<i>Tazoudasaurus</i>	Partial braincase, jaw fragments	Allain and Aquesbi, 2008	
	Diplodocoids	<i>Amargasaurus</i>	Braincase	Salgado and Bonaparte, 1991
		<i>Apatosaurus</i>	Multiple braincases, nearly complete skull	Berman and McIntosh, 1978
		<i>Dicraeosaurus</i>	Two braincases, jaw fragments	Janensch, 1935–36
<i>Diplodocus</i>		Multiple adult and sub-adult skulls	Holland, 1924	
<i>Limaysaurus</i>		Braincase	Calvo and Salgado, 1995	
<i>Nigersaurus</i>		Nearly complete skull	Sereno et al., 1999	
<i>Suuwassea</i>		Braincase, jaw fragments	Harris, 2006	
<i>Tornieria</i>		Braincase, possibly jaw fragments	Remes, 2006, 2009	
Macronarians		<i>Abrosaurus</i>	Skull	Ouyang, 1989
		<i>Ampelosaurus</i>	Partial braincase	Le Loeuff, 1995
	<i>Antarctosaurus</i>	Braincase, partial dentary	Huene, 1929	
	<i>Atlasaurus</i>	Braincase, jaw fragments	Monbaron et al., 1999	
	Auca Mahuevo taxon	Multiple embryonic skulls	Chiappe et al., 2001	
	<i>Bonatitan</i>	Braincase	Martinelli and Forasiepi, 2004	
	<i>Bonitasaura</i>	Partial skull	Apesteguía, 2004	
	<i>Brachiosaurus</i>	At least three partial skulls	Janensch, 1935–36	
	<i>Camarasaurus</i>	Multiple adult and sub-adult skulls	Madsen et al., 1995	
	<i>Euhelopus</i>	Nearly complete skull	Wiman, 1929	
	<i>Europasaurus</i>	At least 11 partial skulls	Sander et al., 2006	
	Glen Rose taxon	Partial braincase	Tidwell and Carpenter, 2003	
	<i>Isisaurus</i>	Partial braincase	Berman and Jain, 1982	
	<i>Jainosaurus</i>	Partial braincase	Huene and Matley, 1933	
	<i>Jobaria</i>	Partial adult skull and sub-adult braincase	Sereno et al., 1999	
	<i>Lirainosaurus</i>	Braincase fragment	Sanz et al., 1999	
	? <i>Magyarosaurus</i>	Braincase	Weishampel, 1991	
	<i>Malawisaurus</i>	Braincase, other dermal skull fragments	Gomani, 2005	
	<i>Nemegtosaurus</i>	Nearly complete skull	Nowinski, 1971; Wilson, 2005	
	<i>Neuquensaurus</i>	Skull fragments	Huene, 1929	
	Neuquén taxon	Partial braincase	Calvo and Kellner, 2006	
	<i>Paluxysaurus</i>	Skull fragments	Rose, 2007	
	<i>Phuwiangosaurus</i>	Jaw fragments	Martin et al., 1999	
	<i>Quaesitosaurus</i>	Partial skull	Kurzanov and Bannikov, 1983	
	<i>Rapetosaurus</i>	Partial adult and sub-adult skulls	Curry Rogers and Forster, 2004	
	Río Negro taxon	Partial braincase	García et al., 2008	
	<i>Saltasaurus</i>	Partial braincase	Bonaparte and Powell, 1980	

contrasted with the known record of cranial ontogeny in other dinosaurs.

Discovery of the Juvenile *Diplodocus* Skull

Several expeditions led by Earl Douglass in the early 20th century to the Carnegie Quarry in what is now Dinosaur National Monument yielded some of the most spectacular sauropod discoveries in North America, including several complete or nearly complete skulls (McIntosh, 1981). Most famous of these is probably the complete and largely undistorted adult *Diplodocus* skull (Carnegie Museum [CM] 11161) collected by Douglass in 1912. Three years later, a large sub-adult skull of this genus (CM 3452) was the first—and, to date, only described—diplodocid skull found articulated with postcranial elements. Following these successes, a third, much smaller *Diplodocus* skull was collected by Douglass and his team in 1921, near the discovery site of CM 11161 (Fig 1; McIntosh, 1981). This skull was mentioned and figured by Holland (1924:pl. 43), but until now has never been fully described.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, U.S.A.; **CM**, Carnegie Museum of

Natural History, Pittsburgh, U.S.A.; **CMC**, Cincinnati Museum Center, Cincinnati, U.S.A.; **MB**, Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany; **SMM**, Science Museum of Minnesota, St. Paul, U.S.A.; **USNM**, United States National Museum, Washington D.C., U.S.A.; **YPM**, Yale Peabody Museum, New Haven, U.S.A.; **Z. PAL**, Polish Academy of Science, Warsaw, Poland.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887
 SAUROPODOMORPHA Huene, 1932
 SAUROPODA Marsh, 1878
 DIPLODOCOIDEA Marsh, 1884
 FLAGELLICAUDATA Harris and Dodson, 2004
 DIPLODOCIDAE Marsh, 1884
DIPLODOCUS Marsh, 1878
 (Figs. 2–5)

CM 11255 is a diplodocid sauropod, sharing the following synapomorphies with other representatives of this clade: elongate prefrontal with a posterior projection approaching the parietal; squamosal-quadratojugal contact absent; paroccipital

process with rounded, tongue-like ventrolateral end; shallow quadrate fossa. CM 11255 displays a single autapomorphy of *Diplodocus*: sharply defined fossa surrounding preantorbital fenestra. CM 11255 is distinguishable from *Apatosaurus* by the following features: presence of a long quadratojugal process of the squamosal that nearly contacts the quadratojugal; basipterygoid recess present; basipterygoid process without marked anteroventral flaring; closely appressed, sheet-like basal tubera with posteriorly facing concavity; paroccipital processes strongly ventrally oriented. CM 11255 cannot be compared to the other Morrison Formation diplodocids, *Barosaurus*, and *Supersaurus*, due to their lack of recognized cranial material. CM 11255 is distinguishable from the East African diplodocid *Tornieria* by the presence of a basipterygoid recess and the comparatively larger contribution of the prefrontal to the margin of the orbit. It can also be tentatively distinguished by the location of the frontal-parietal suture, which is located near the anterior margin of the supratemporal fenestra in *Diplodocus* and probably CM 11255, but located more posteriorly in *Tornieria*. Lastly, CM 11255 is distinguishable from the indeterminate flagellicaudatan *Suuwassea* in the following characters: anteroposteriorly compressed basal tubera; basisphenoid concave ventrally, not visible in posterior view; basal tubera widely separated from occipital condyle, spike-like, dorsoventrally narrow parasphenoid rostrum.

Few characters have been shown to consistently distinguish the skulls of different diplodocid taxa, particularly *Apatosaurus* and *Diplodocus* (Berman and McIntosh, 1978). In the only description of a mostly complete skull referable to *Apatosaurus* (CM 11162), Berman and McIntosh (1978) noted several cranial distinctions between that genus and *Diplodocus*, although these are primarily proportional in nature. Due to the early ontogenetic stage of CM 11255, proportional characters are potentially unreliable. Nevertheless, the anteroventral flaring of the basipterygoid processes noted by those authors for *Apatosaurus* (CM 11162) is not present in CM 11255 or in any other specimen of *Diplodocus*, regardless of ontogenetic stage; the remainder of the characters listed by Berman and McIntosh (1978) cannot be evaluated on CM 11255 due to incomplete preservation.

Wilson (2002) distinguished between *Apatosaurus* and *Diplodocus* on the basis of the basipterygoid recess, which is absent in the former but present in the latter. The presence of a sharply defined fossa surrounding the preantorbital fenestra is listed as an autapomorphy of *Diplodocus* by Wilson (2002); this

fossa is present in CM 11255, but cannot be adequately evaluated in CM 11162; as such, its state is here considered unknown in *Apatosaurus*. The basal tubera, which are globose and laterally expanded in *Apatosaurus* (CM 11162, YPM 1860), are pendant and more anteroposteriorly compressed in CM 11255 and in other specimens of *Diplodocus* (CM 11161, CM 3452, USNM 2672).

Although there are no cranial remains known for two other Morrison diplodocids (*Supersaurus*, *Barosaurus*), the identification of two novel probable *Diplodocus* autapomorphies and the ease with which CM 11255 is distinguished from *Apatosaurus*, *Suuwassea*, and *Tornieria* support the current assignment of this specimen to *Diplodocus*. CM 11255 is not here assigned to a species within *Diplodocus*: no cranial characters yet known serve to differentiate between the various species of the genus, which currently remain distinguishable solely by postcranial features. As such, the lack of associated postcranial material for CM 11255 currently prevents a specific diagnosis.

DESCRIPTION

We use traditional anatomical terminology and orientational descriptors (e.g., 'anterior' rather than 'cranial') in the description below, following Wilson (2006).

Ontogenetic Stage

The early ontogenetic stage assigned to CM 11255 is based on the small size of the specimen and on the presence of a visible suture between the left and right parietal bones. The skull measures 29.2 cm from its anterior-most point to the posterior margin of the occipital condyle, which is approximately 58% the length of the adult *Diplodocus* CM 11161 and approximately 66% the length of the large sub-adult CM 3452. CM 11255 is therefore the ontogenetically youngest *Diplodocus* skull ever fully described.

Preservation

CM 11255 was recovered in isolation, with no associated postcrania or elements belonging to other individuals (Fig 1). It was recovered from, and to some extent is still obscured by, a poorly sorted sandstone matrix. The skull is crushed laterally, such that its left and right halves are disarticulated along the midline sutures, continuing posteriorly through the unfused parietals. Parts of the maxillae and premaxillae have been

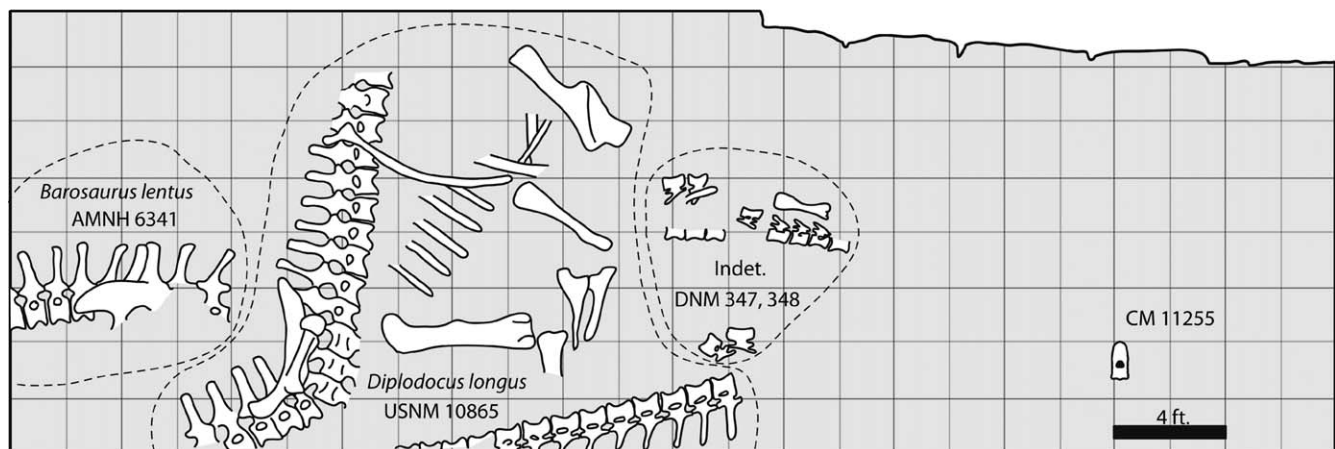


FIGURE 1. Quarry map showing the original location of the juvenile *Diplodocus* skull (CM 11255) relative to other dinosaurs excavated from Carnegie Quarry at Dinosaur National Monument. Redrawn from original quarry map at Carnegie Museum of Natural History. North at top of figure; grid lines are 2 feet (~0.61 m) apart.

damaged or destroyed, although the tooth row is well represented in these regions by in situ replacement teeth, preserved when sediment filled in around the highly resistant teeth after the thin bone surrounding them had been eroded away. This type of preservation is not uncommon (e.g., CM 21718 [McIntosh, 1981; pers. observ.], YPM 1922), although it is not typically found in direct association with other skull elements. The skull roof and occiput are represented primarily by elements from the right side, although median elements (supraoccipital, occipital condyle, basioccipital) are largely complete. The dermal skull roof (nasal, prefrontal, frontal, and parietal) is rotated away from the midline of the facial skeleton by approximately 7.5°.

The left and right elements of the lower jaw are disarticulated, and the left mandible is displaced slightly medially and posterodorsally. As seen in ventral view, the curvature of the jaws is similar in both elements. The lower jaw of the well-preserved skull of *Nemegtosaurus* (Z. PAL MgD-I/9) has a similar translation of one mandible relative to the other (Wilson, 2005). No deformation of the tooth-bearing elements was noted in that specimen, although the left and right mandibles were translated relative to each other; this suggests that the curvature seen in the preserved mandibular elements of CM 11255 is likely natural and undistorted.

Dermal Roof Complex

Premaxilla—The premaxillae are elongate tooth-bearing elements that contact each other medially and the maxillae laterally, terminating posteriorly at the external naris. Due to the lateral crushing, the anterior portion of the skull is deformed along the median suture between the premaxillae, creating an unusually steep angle between these bones and exaggerating their visibility in lateral view.

Four tooth positions are preserved in the right premaxilla and are presumed present in the left (Fig. 2). The anterior margins of the premaxillae are represented only by narrow, medial portions of the left and right premaxillae. Harris (2006) regarded the premaxillae of CM 11255 as similar in proportion and size to those of *Suuwassea*; however, the premaxillae in the present specimen appear to expand laterally without the distinct ‘step’ of *Suuwassea*, in which the transversely wide anterior portion is clearly demarcated by sharp lateral curvature in dorsal and ventral view. The narial fossae are not distinctly preserved.

The posterior extremes of the premaxillae are partially complete, preserving a portion of the anterior margin of the narial opening. There is no evidence for an elongate internarial bar, such as has been observed in some adult (USNM 2673) and subadult (CM 3452) *Diplodocus* skulls.

Maxilla—The maxillae are thin, sheet-like bones that are divided by the antorbital fenestra into an ascending process and a posteriorly directed process that contacts the jugal and quadratojugal (Fig. 2). As in adult *Diplodocus*, the preserved portion of the maxilla-jugal suture is coarsely sinuous in lateral view. The ascending process remains in contact with the premaxilla until they both reach the external naris. Posteriorly, the ascending process contacts the nasal and the lacrimal.

Similar to adult *Diplodocus* (AMNH 696, CM 11161, CM 3452, USNM 2672) and other diplodocoids (*Dicraeosaurus*, MB.R. 2336; *Apatosaurus*, CM 11162, CMC VP 7180), the external surfaces of the maxillae in this region are ornamented by several shallow, elongate depressions, roughly corresponding to the positions and orientations of tooth families within the bone. The lateral plate of the maxilla is partially preserved posteriorly. The poor anterior preservation contributes to the convex shape of the ventral margin as preserved.

Immediately posterior to the preserved dentigerous margin of the maxilla is a large, distinct fossa that dorsally overlaps the three posterior-most replacement teeth. The fossa is pierced

posteriorly by a large, subcircular preantorbital fenestra. The sharp outline of the fossa is best preserved on the left side (Fig. 2D). In other *Diplodocus* skulls (CM 11161, CM 3452, USNM 2672), the subnarial foramen and anterior maxillary foramen reside in a shallow groove situated slightly anterodorsal to the preantorbital fossa, along the contact with the premaxilla; neither these foramina nor the groove are distinctly preserved in CM 11255.

Nasal—The nasal is a roughly quadrangular element with anteriorly projecting rami that form the right and left posterolateral margins of the naris. The preserved portions of these rami contact the lacrimal and maxilla anteriorly; the main body of the nasal contacts the prefrontal laterally and would have contacted the frontal posteriorly, forming the anterior-most medial element of the braincase. The main body of the nasal rises dorsally above the orbit, elevating the posterior margin of the naris, as seen in some other individuals of *Diplodocus* (AMNH 696, CM 11161, CM 3452, USNM 2672; Figs. 2B, 3D). A small (~1 cm long) piece of the anterior ramus is preserved on the left side (Figs. 2D, 3C, 4C). This process forms the posterolateral margin of the naris. It is probable that the orientation of the rami and the main body of the nasal obscured the naris in lateral view and that the naris pointed strictly anterodorsally in life.

Jugal—The jugal is a V-shaped element that connects the maxilla and quadratojugal with the lacrimal and postorbital. Its contact with the maxilla is a broadly sinuous suture, whereas its contacts with the remaining three elements are more linear (Figs. 2C, D). A dorsally directed process along the lacrimal/jugal contact, as illustrated by Wilson and Sereno (1998:fig 6) in their reconstruction of *Diplodocus*, appears to be at least incipiently present, although less substantial in this specimen. Medially, the jugal has a small contact with the palate via a lateral process of the pterygoid.

As in adult *Diplodocus*, the jugal is broad, flat, and excluded from the ventral margin of the skull. It forms parts of the margins of three skull openings: the orbit, the antorbital fenestra, and the lateral temporal fenestra.

Lacrimal—The lacrimal is a bar-shaped element, oriented approximately dorsoventrally. It contacts the jugal ventrally, the nasal and prefrontal dorsally, and the maxilla along the dorsal portion of its anterior margin. The suture with the jugal is nearly linear, with a reduced version of the “stepped” contact in some adult skulls (CM 11161; Fig. 2). Ventral to its anterior contact with the maxilla, the lacrimal forms an anteroposteriorly elongate portion of the margin of the antorbital fenestra; the cross-sectional shape becomes more mediolaterally elongate dorsal to this fenestra. There, a strong ridge on the lateral surface of the lacrimal extends dorsally to join the laterally expanded prefrontal and form the anterior portion of the dorsal orbital margin.

The long axis of the lacrimal in CM 11255 is much more vertically oriented than is typical of more ontogenetically mature skulls, suggesting that the infraorbital and antorbital regions experienced a greater degree of anteroposterior and anteroventral lengthening during growth than did neighboring regions. A consequence of the orientation of the lacrimal is that the tear-drop shape typical of eusauropod orbits is not as strongly expressed; although there is still an anteroventral ‘corner’ on the orbit, the shape is generally subcircular.

Prefrontal—The prefrontal meets and slightly overlaps the lacrimal at a scarf joint. Along with the frontal, which it contacts posteriorly, the prefrontal forms most of the dorsal margin of the orbit. In lateral view, the prefrontal is anteroposteriorly broad, with only a gentle ventral concavity. In dorsal view, it is arcuate and contacts the frontal and nasal along a concave medial margin. This concavity lends the posterior half of the prefrontal a ‘hooked’ shape, which has been recognized as a diplodocid feature (Berman and McIntosh, 1978; Wilson, 2002). The prefrontal forms much of the lateral margin of the skull roof in dorsal view.

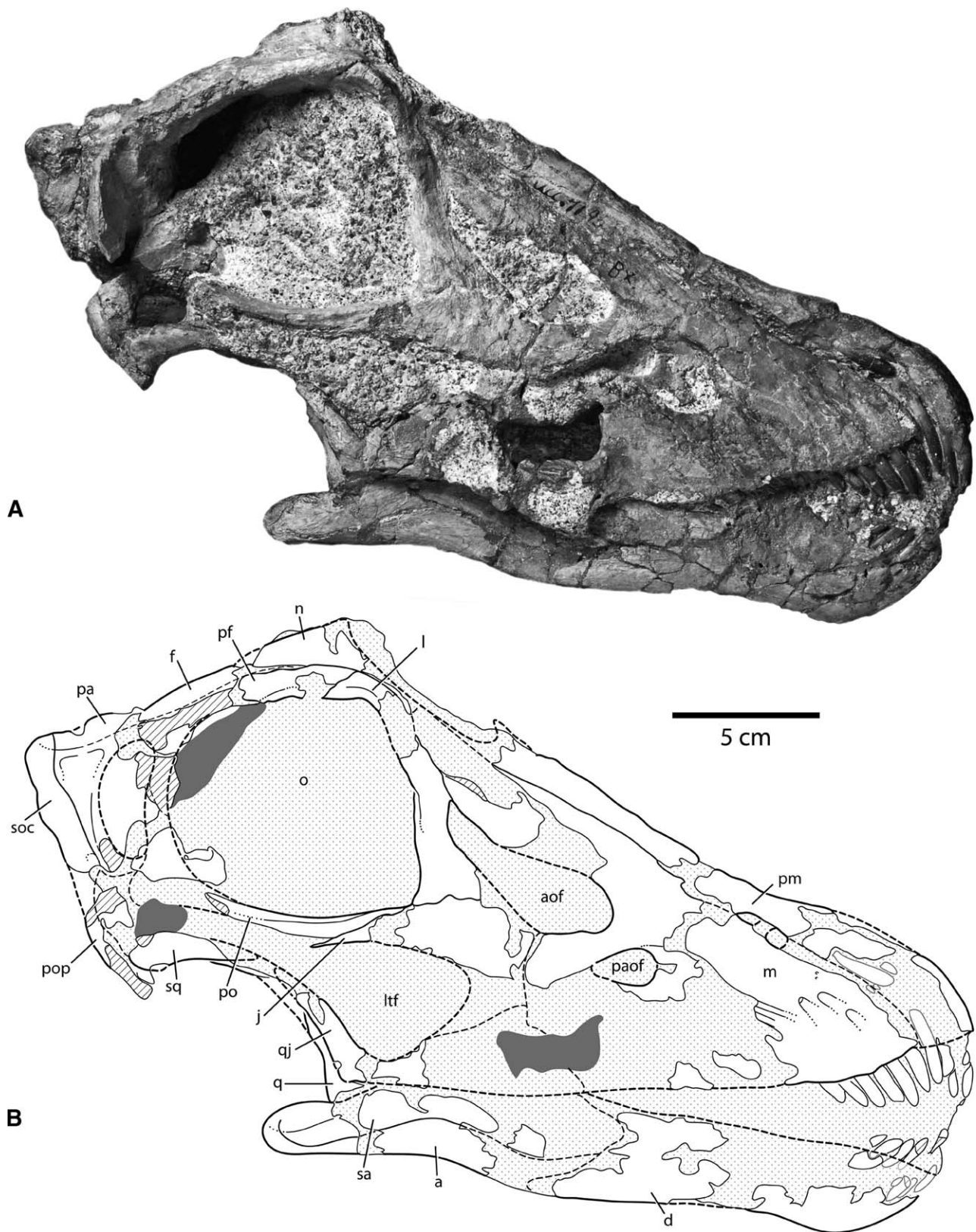
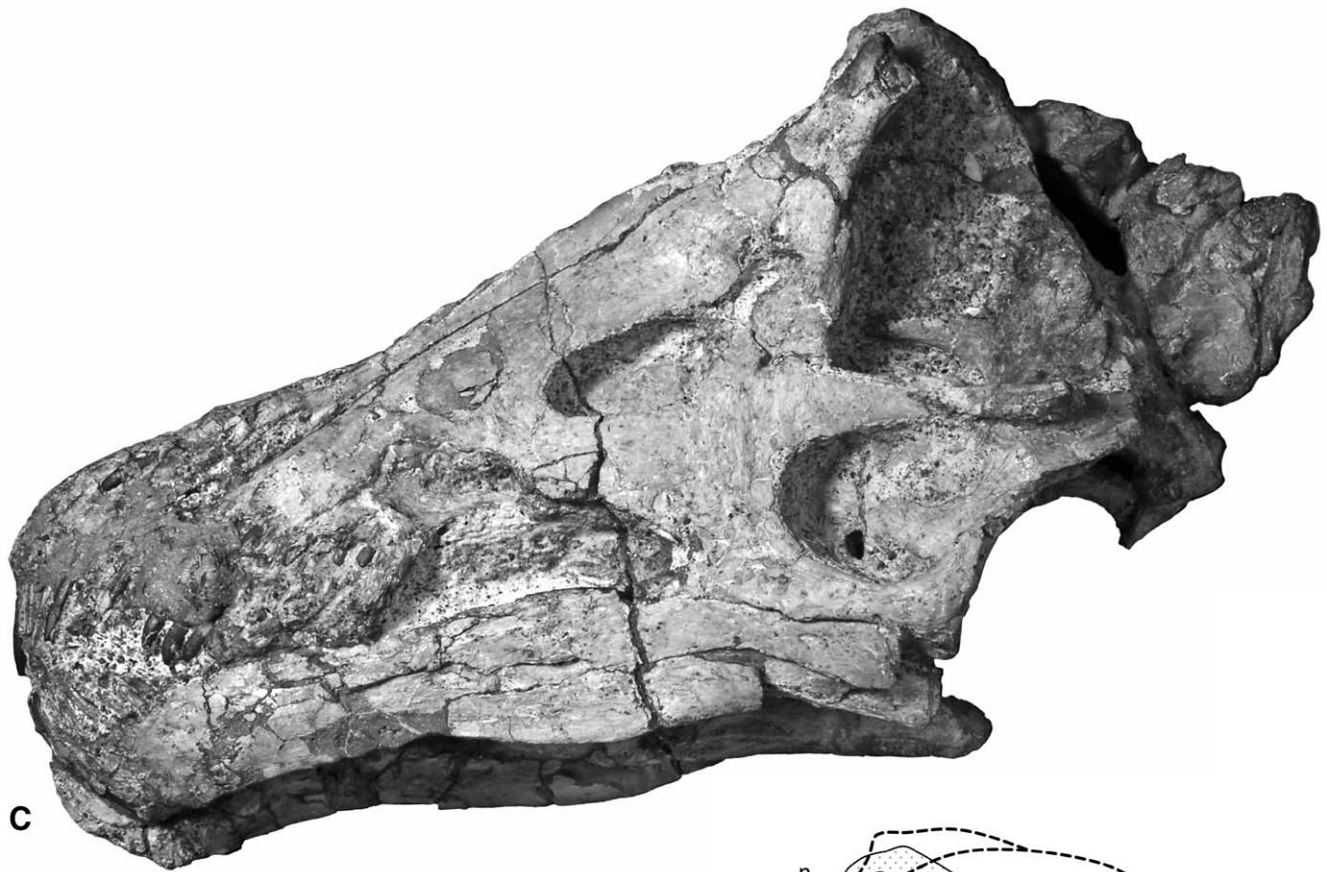


FIGURE 2. Photographs and interpretive line drawings of the juvenile skull of *Diplodocus* (CM 11255). **A, B**, right lateral view; **C, D**, left lateral view. Stippled areas indicate matrix; hatching indicates broken bone. Scale bar equals 5 cm. **Abbreviations:** **a**, angular; **aof**, antorbital fenestra; **bo**, basioccipital; **d**, dentary; **eo**, exoccipital-opisthotic; **f**, frontal; **j**, jugal; **ltf**, lateral temporal fenestra; **l**, lacrimal; **m**, maxilla; **mc**, Meckelian canal; **n**, nasal; **o**, orbit; **os/ls**, orbitosphenoid/laterosphenoid; **pa**, parietal; **paof**, preantorbital fenestra; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pop**, paroccipital process; **ps**, parasphenoid; **psaf**, posterior surangular foramen; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **soc**, supraoccipital; **spl**, splenial; **sq**, squamosal.



5 cm

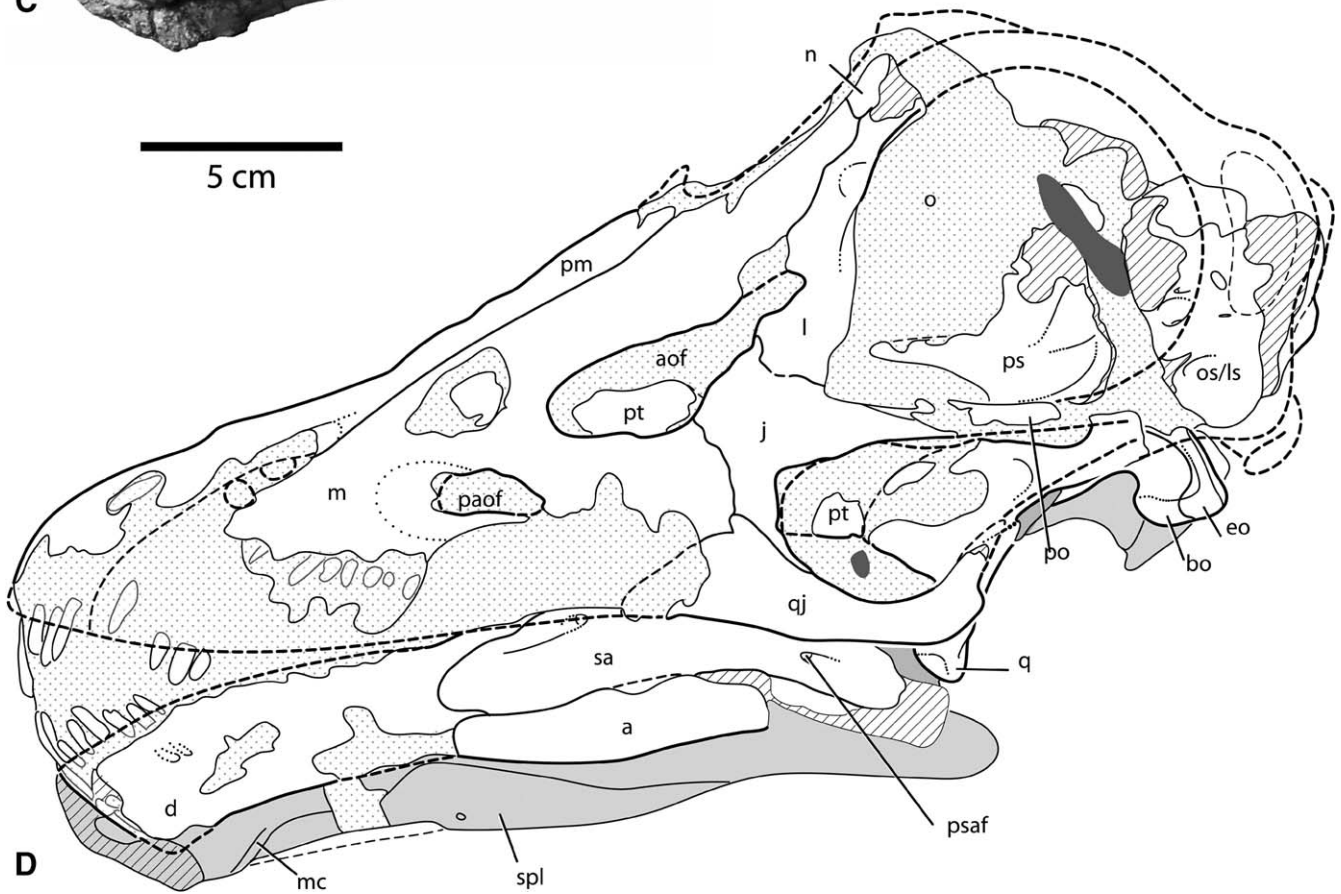


FIGURE 2. (Continued)

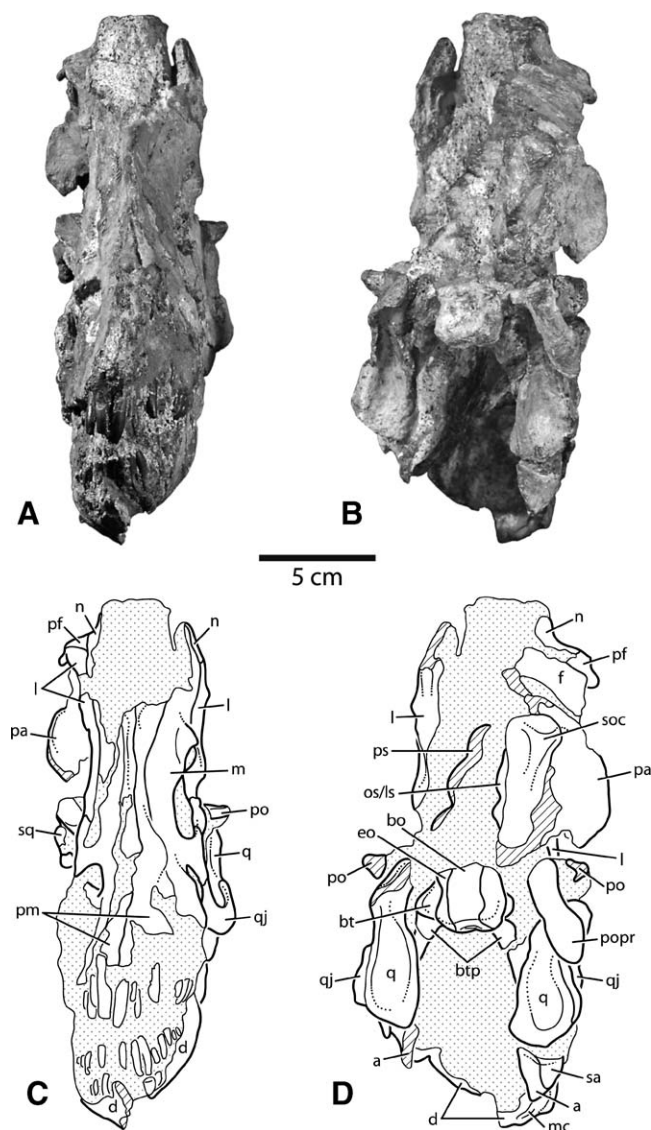


FIGURE 3. Photographs and interpretive line drawings of the skull of *Diplodocus* (CM 11255). **A, C**, anterior view; **B, D**, posterior view. Stippled areas indicate matrix, hatching indicates broken bone. Scale bar equals 5 cm. **Abbreviations:** a, angular; bo, basioccipital; bt, basal tubera; btp, basipterygoid processes; d, dentary; eo, exoccipital-opisthotic; f, frontal; l, lacrima; m, maxilla; mc, Meckelian canal; n, nasal; os/ls, orbitosphenoid/laterosphenoid; pa, parietal; pf, prefrontal; po, postorbital; popr, paroccipital process; pm, premaxilla; ps, parasphenoid; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; soc, supraoccipital.

Frontal—In lateral view, the frontal is a narrow, arcuate element that contacts the prefrontal anteriorly and the postorbital laterally. In dorsal view, the frontals can be seen to contact the parietals posteriorly and the nasal anteriorly. The frontal-parietal suture is obscured and so cannot be compared to the relatively linear suture of *Suuwassea* (Harris, 2006) or the sinuous sutures known in *Apatosaurus* (CM 11162) and *Diplodocus* (CM 11161). The frontal forms much of the dorsal skull roof, and contacts the orbitosphenoid ventrally.

The lateral margin of the right frontal has been eroded away, exposing the trabecular internal structure of the bone, bordered by a thin veneer of cortical bone on the dorsal and ventral faces. In other specimens of *Diplodocus* (CM 11161, CM 3452, USNM

2672, USNM 2673), the lateral portion of the frontal that forms the orbital margin is greatly expanded laterally, creating a broad shelf dorsal to the orbit. A notch is commonly associated with the anterior margin of this expanded margin. In *Apatosaurus* (CM 11162), this expansion is well developed, and increases the width of the skull in this region well beyond the lateral extent of the parietals. Based on the mediolateral position of the posterior-most preserved portion of the postorbital, CM 11255 did not have such a prominent lateral expansion.

Postorbital—The postorbital is a triradiate element, with elongate processes contacting the frontal dorsally and the jugal anteriorly. The third process is comparatively short and inserts into a groove in the squamosal. CM 11255 preserves the jugal process, which forms most of the ventral margin of the orbit. The contact with the jugal occurs along a shallowly angled, planar suture. Although the postorbital and lacrimal are closely situated in adult specimens, this relationship in CM 11255 appears unusually close. There is a longitudinal ridge along the lateral surface of the jugal process, expanding the element into a flat shelf dorsally and rendering it triangular in cross-section. This creates a narrow fossa surrounding the lateral temporal fenestra.

Squamosal—The squamosal is an arcuate element when viewed laterally, contacting the parietal, postorbital, and quadrate, and forming a portion of the margin of both temporal fenestrae. The right side of CM 11255 preserves a small portion of the anteriorly directed process that overlies the head of the quadrate in lateral view. In CM 11255, this process is partially obscured by matrix (Fig. 2A), but is revealed by computed tomography (CT) to extend anteriorly to nearly contact the posterodorsally directed squamosal process of the quadratojugal, which contrasts with the widely spaced position of these elements in adult *Diplodocus* (CM 11161). In posterior view, the preserved portion of the squamosal is almost entirely obscured by the paroccipital process, although a small portion of the lateral margin can be seen overlapping the quadrate (Fig. 3B, D).

Quadratojugal—The quadratojugal of CM 11255 is an antero-posteriorly elongate, dorsoventrally narrow element that contacts and laterally overlaps the quadrate; its elongate squamosal process extends 2.3 cm along the lateral margin of the quadrate toward the squamosal. This process tapers dorsally and terminates in a broken surface; it can be inferred to have extended to near the midpoint of the quadrate, within a centimeter of contact with the squamosal. The anteroventral corner of the lateral temporal fenestra is preserved on the left side only. Much of the anterior contact with the maxilla is not preserved.

The dorsal margin of the quadratojugal is broadly sinuous. It is dorsally convex anteriorly along the contacts with the maxilla and jugal, and it is concave posteriorly where it forms the anteroventral corner of the lateral temporal fenestra. In dorsal and ventral views, the quadratojugal bulges laterally as it overlaps the articular head of the quadrate (Fig. 4).

Parietal—The parietal of CM 11255 contacts the frontal anteriorly and delimits the dorsomedial margin of the supratemporal fenestra. The partially preserved median contact between the parietals is a highly interdigitated suture. In adult and large sub-adult *Diplodocus* (CM 11161, CM 3452, USNM 2672, USNM 2673), the parietals are fused. Coupled with the small size of the specimen, the presence of a patent interparietal suture in CM 11255 suggests that fusion of these elements only occurred as the animal approached maturity.

The lateral wing of the parietal arches strongly dorsolaterally, obscuring the supratemporal fenestra in posterior view—a condition described as characterizing *Diplodocus* by Berman and McIntosh (1978). The dorsolateral margin of the parietal in *Apatosaurus* is nearly linear, unlike the state preserved in CM 11255.

In dorsal view, a nuchal fossa can be seen between the lateral wing of the parietal and the parietal-supraoccipital suture. Although the depth of this fossa is somewhat exaggerated by an

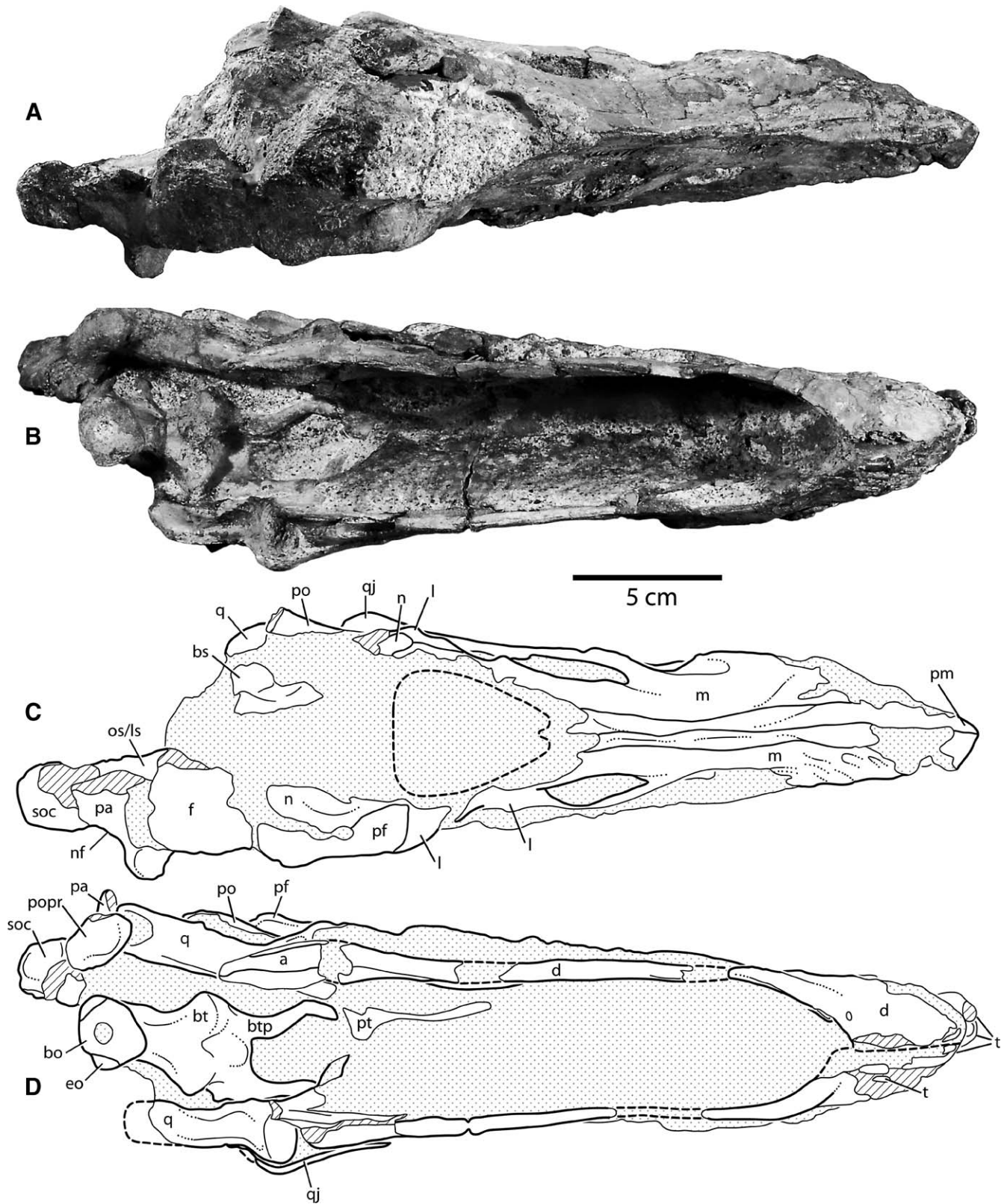


FIGURE 4. Photographs and interpretive line drawings of the juvenile skull of *Diplodocus* (CM 11255). **A, C**, dorsal view; **B, D**, ventral view. Stippled areas indicate matrix, hatching indicates broken bone. Scale bar equals 5 cm. **Abbreviations:** a, angular; bo, basioccipital; bs, basisphenoid; bt, basal tubera; btp, basiptyergoid processes; d, dentary; eo, exoccipital-opisthotic; f, frontal; l, lacrimal; m, maxilla; n, nasal; nf, nuchal fossa; os/ls, orbitosphenoid/laterosphenoid; pa, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; popr, paroccipital process; pt, pterygoid; q, quadrate; qj, quadratojugal; soc, supraoccipital; t, teeth.

area of broken bone in the center of the concavity, the nuchal fossa appears to invade quite deeply, reaching nearly to the depth of the parietal-frontal suture, and is therefore more strongly concave than that seen in *Suuwassea* (Harris, 2006) and some specimens of *Diplodocus* (CM 11161). It is quite similar to the fossae in some other *Diplodocus* specimens, however, including other presumed sub-adult skulls (CM 3452), as well as in *Apatosaurus* (CM 11162).

The supratemporal region is narrow in dorsal view. The preserved mediolateral width of the right parietal at the greatest extent of the lateral wing is 4.1 cm, resulting in a minimum total transverse width estimate of 8.2 cm, roughly 24% of the total skull length (compared to ~29% in adult *Diplodocus* and ~46% in *Apatosaurus*). The proportional width of CM 11255 is more congruent with smaller *Diplodocus* skulls (SMM P84.15.3; Erickson and Hanks, 2001).

Palatal Complex

The palatal complex of CM 11255 is represented by the quadrates, pterygoids, ectopterygoids, palatines, and vomers (Fig. 5). The latter four structures are visible entirely or in large part only through CT scanning.

Quadrate—The quadrate connects the palate with the dermal skull roof through its insertion into a recess of the squamosal posterodorsally and with the facial skeleton by contact with the quadratojugal laterally. The quadrate also contacts the

paroccipital process posteriorly (Fig. 3B, D). The wing-like pterygoid flange of the quadrate extends anteromedially, and is visible in lateral view through the lateral temporal fenestra. This flange is broad and flat, terminating in a broad, arcuate contact with pterygoid.

In lateral view, the quadrate is distinctly concave posteriorly, unlike the relatively straight or only slightly bent condition seen in adult exemplars of *Apatosaurus* (CM 11162), *Diplodocus* (CM 11161), and *Suuwassea* (Harris, 2006). This curvature is slightly exaggerated by breakage at mid-shaft, but even allowing for some distortion the quadrate was much more strongly curved than those of larger *Diplodocus* skulls. The quadrate fossa is shallow, as in other diplodocoids, and does not continue onto other elements laterally.

The articular surface of the quadrate condyle is visible in lateral view, with the medial aspect projecting well beyond the ventral margin of the quadratojugal. The articular face is roughly triangular with a peak facing posteriorly. The surface is beveled such that it faces slightly ventrolaterally.

Pterygoid—The pterygoid forms much of the posterior portion of the palate, contacting the pterygoid wing of the quadrate posteriorly, the palatine and ectopterygoid laterally, and the vomer anteriorly. Anteriorly, the pterygoid bifurcates into anterodorsally and anteroventrally directed processes. The anterodorsal process is broad and sheet-like and has a slightly concave, elongate dorsal margin that extends anteriorly to contact the palatine and vomer (Fig. 5). Much of the ventral portion of this process is indistinguishable from matrix in the CT images, suggesting that portion of the element was quite thin. The pterygoid anteroventral process contacts the ectopterygoid to form the transverse pterygoid hook. In contrast to the autapomorphic condition described for adult *Diplodocus* by Wilson (2002), the pterygoid is situated posterolateral to the ectopterygoid when the two elements are articulated (Fig. 5).

Like the other dermal skull elements of the left side, the left pterygoid is displaced dorsally, posteriorly, and slightly medially. The pterygoids are vaulted inward at an angle of approximately 37.3° from vertical and arch dorsally as they approach their mid-line contact (Fig. 5C). The right pterygoid is more strongly inclined dorsomedially (35° from the vertical) than the left (2.3°). In adult *Diplodocus* (CM 11161), the pterygoids are inclined at approximately 30° from the vertical (McIntosh and Berman, 1975).

Palatine—The palatine is thin and arcuate in CM 11255, contacting the pterygoid posteriorly along a concave, anterodorsally inclined suture. The dorsal portion of the palatine and the contact with the vomer is not well preserved (see Vomer, below). The anteroventral portion of the palatine forms a dorsoventrally flattened process that contacts the maxilla along its lateral and anterior margins. The anterior-most portion of this process is overlapped by a posterior process of the maxilla that projects from the floor of the preantorbital fenestra. The ectopterygoid contacts the palatine along the palatine's ventral margin, near the posterior margin of the maxillary contact.

Vomer—The vomer is trapezoidal in lateral view, contacting the maxilla anteriorly and the pterygoid posteriorly. It is overlapped to some degree along its posteroventral margin by the palatine, although that contact is poorly preserved. The vomers are strongly vaulted, although this is probably exaggerated by the minor lateral compression of the skull.

Ectopterygoid—The ectopterygoid is an arched, strap-like element that articulates laterally with the maxilla and posteromedially with the pterygoid in a ventrally directed, anteroposteriorly elongate 'hook' that extends to near the level of the ventral margin of the maxilla. As discussed above, the articulation of the ectopterygoid with the pterygoid appears to position the former anteromedial to the latter, unlike the condition described for adult *Diplodocus* by Wilson (2002). In both cases, the articulation is primarily along the posterior margin of the ectopterygoid,

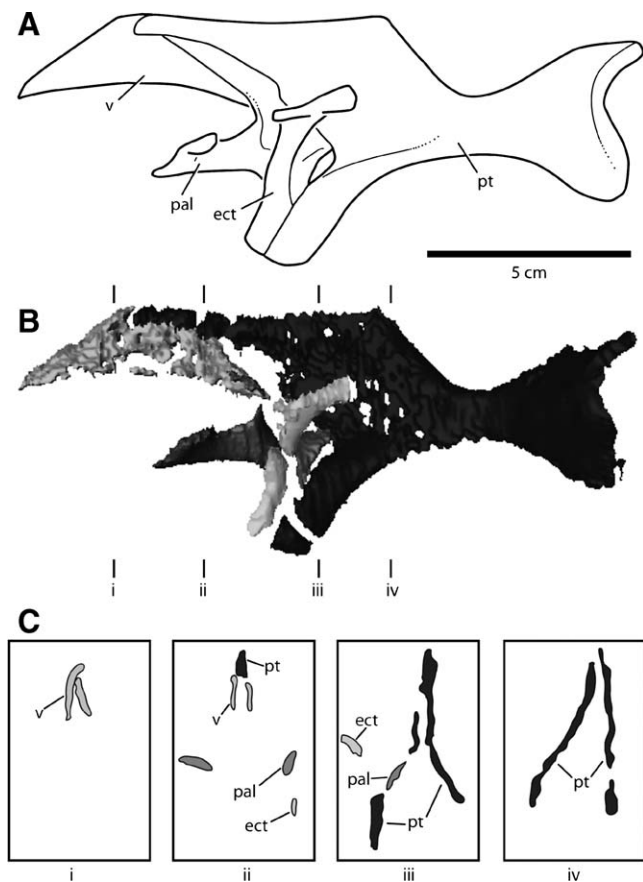


FIGURE 5. Palatal complex of juvenile *Diplodocus* (CM 11255), based on data obtained using computed tomography (CT) scanning. **A**, Reconstruction of the palate in left lateral view; **B**, palatal complex in lateral view; **C**, Cross-sections taken through **B** at transects i–iv. Cross-sections in anterior view. Scale bar equals 5 cm. **Abbreviations:** ect, ectopterygoid; pal, palatine; pt, pterygoid; v, vomer.

and the ectopterygoid process of the pterygoid curves laterally to meet the ectopterygoid, so the variation seen here is perhaps not significant.

Braincase

The braincase is largely missing, particularly those elements surrounding the foramen magnum. As with the circumorbital and skull roof elements, the right side preserves more of these bones than does the left. The braincase is oriented at the same slight angle to the facial skeleton as is the skull roof.

Basioccipital—The basioccipital makes up the main body of the occipital condyle, and in CM 11255 it is mostly complete. Little of the foramen magnum remains dorsal to it, including the portion of the margin that was presumably formed by this element. The condyle is D-shaped in occipital view, with a nearly flat posterodorsal margin. Including allowances for ventral rotation of the structure, the occipital condyle is oriented strongly ventrally. The suture between the basioccipital and the exoccipital-opisthotic that forms the dorsolateral ‘shoulder’ of the condyle is plainly visible on both sides (Fig. 3B, D).

Supraoccipital—The supraoccipital is a midline element that contacts the parietals and the exoccipital-opisthotics. In CM 11255, the supraoccipital is represented primarily by a large, triangular eminence formed by the confluence of two crests: a transverse crest that extends laterally towards the nuchal fossa, the insertion of which is obscured by a broken surface; and a prominent, sagittal crest that extends down the midline of the element, flaring slightly at its dorsal terminus (Fig. 3B, D). In *Apatosaurus*, *Suuwassea*, and other crania of *Diplodocus*, a narrow isthmus of the supraoccipital extends ventrally to form a small portion of the dorsal margin of the foramen magnum, although this cannot be determined in CM 11255 due to a lack of preservation.

Exoccipital-Opisthotic—The exoccipital-opisthotic forms part of the posterior braincase, contacting the supraoccipital and basioccipital medially, the parietal dorsally, and the squamosal laterally. Together, the right and left exoccipital opisthotics form much of the lateral margin of the foramen magnum. In CM 11255, these elements are primarily represented by the left and right paroccipital processes. The blade-like paroccipital processes are strongly angled ventrally, as in other *Diplodocus* specimens (CM 11161, CM 3452). This is in contrast to the more laterally directed processes seen in *Suuwassea* (Harris, 2006) and *Apatosaurus* (CM 11162). As in other diplodocid sauropods, the paroccipital process expands ventrolaterally, predominantly on its dorsal margin. The exoccipital-opisthotic makes a small contribution to the ‘shoulders’ of the occipital condyle (Figs. 3, 4).

Basisphenoid—In diplodocids, the basisphenoid serves as the only bony connection between the braincase and palate, contacting the pterygoids via elongate basiptyergoid processes. Posteriorly, it meets the basioccipital at the base of the neck of the occipital condyle. Dorsally, the basisphenoid projects anteriorly as the parasphenoid rostrum, visible though the left orbit. This process is rod-like and elongate, reaching anteriorly to near the anterior margin of the orbit. It is generally similar in shape and proportion to its homologues in adult *Diplodocus*, and is unlike the much larger, dorsoventrally expanded parasphenoid rostrum of *Suuwassea* (Harris, 2006). A prominent ridge just dorsal to the parasphenoid rostrum is identified as the ventral extreme of the antotic crest.

Near its contact with the basioccipital, the basisphenoid is expanded into paired basal tubera that are separated from each other by a narrow sulcus. A narrow pit (the ‘basiptyergoid recess’; Wilson, 2002) is present just posterior to this sulcus, as in other specimens of *Diplodocus*. The basal tubera of CM 11255 are diagnostic for this genus in two ways. First, unlike the more massive, globose basal tubera seen in *Apatosaurus*, those of CM 11255 are flat and semi-concave posteriorly, as in other *Diplodocus*

skulls (CM 11161, CM 3452). Second, as in other specimens of *Diplodocus*, the basal tubera of CM 11255 are pendulous, primarily visible ventral to the occipital condyle in occipital view. In *Apatosaurus* (CM 11162, CMC VP 7180, YPM 1860), the basal tubera do not descend as far ventrally and are more laterally oriented, such that they are primarily visible lateral to the condyle.

Anteroventral to the basal tubera, a deep concavity separates the paired basiptyergoid processes. In CM 11255, the basiptyergoid processes are thin and elongate, similar in shape to those of other *Diplodocus* crania. Anteroventrally, there is a condyle for articulation with the pterygoid. Unlike their counterparts in *Apatosaurus*, the basiptyergoid processes of CM 11255 do not flare anteroventrally. The angle between the basiptyergoid processes cannot be determined due to deformation of the left process and breakage of the right process.

Orbitosphenoid and Laterosphenoid—Posterodorsal to the parasphenoid, the right orbitosphenoid and laterosphenoid are visible in medial view (Fig. 2C, D). Much of the internal surface of the orbitosphenoid has been destroyed, including the foramina for cranial nerves I and IV, respectively. A small foramen for the passage of cranial nerve III is preserved near the ventral margin of the orbitosphenoid. An ovate, anteroposteriorly oriented foramen situated slightly posterodorsal to the foramen for cranial nerve III may have accommodated the endolymphatic sac. Ventrally, the orbitosphenoid meets the parietal in a sinuous, patent suture. Posteriorly, the orbitosphenoid abuts the supraoccipital in a straight, dorsoventrally oriented patent suture. The internal surface of the laterosphenoid is marked by a large, approximately anteroposteriorly oriented tuberosity, the dorsal margin of which forms the ventral margin of the foramen for cranial nerve V. The anteroventral corner of this tuberosity, where the openings for cranial nerves IX–XI are expected, has been destroyed.

Cranial Openings

Six cranial openings can be identified in CM 11255: the preantorbital fenestra, the antorbital fenestra, the orbit, the external naris, the supratemporal fenestra, and the lateral temporal fenestra. The subnasal foramen, anterior maxillary foramen, and posttemporal fenestra are not preserved.

Preantorbital Fenestra—The preantorbital fenestra is a small, elliptical opening that pierces the maxilla in the posterodorsal corner of a sharply defined fossa that extends anteriorly and ventrally. As in other neosauropods, the preantorbital fenestra is internally connected with the antorbital fenestra by a narrow bridge of bone composed of a posteromedial projection of the maxilla and an anterior projection of the palatine, inserting on the ventral margin of the preantorbital fenestra. The preantorbital fenestra may therefore represent a pneumatic continuation of the antorbital fenestra, similar to the invasions of the maxilla by the antorbital sinus in some theropods (Witmer, 1997).

Antorbital Fenestra—Located posterodorsal to the preantorbital fenestra, the antorbital fenestra opens laterally and is without a distinct fossa surrounding it. It is bound largely by processes of the maxilla; the ascending process surrounds the fenestra on its dorsal margin, and the posterior process contributes most of the anteroventral margin. The remainder of the antorbital fenestra is enclosed by the jugal and the lacrimal; the nasal is excluded from its margin.

As in adult *Diplodocus*, the outline of the antorbital fenestra of CM 11255 is roughly teardrop-shaped, with the acute posterodorsal corner formed by the confluence of the maxilla and lacrimal. The dorsal margin is not as concave as in adult *Diplodocus* (CM 11161, USNM 2672, USNM 2673), more closely resembling the condition seen in other sub-adult *Diplodocus* (CM 3452).

Orbit—Five bones bound the orbit: the lacrimal, prefrontal, frontal, postorbital, and jugal. It is a subcircular opening in CM 11255, with the sharply notched ventral margin typical of eu-sauropods weakly expressed (Wilson and Sereno, 1998). The primary cause of this shape disparity is the vertical orientation of the lacrimal, creating a wider angle between that element and the postorbital process of the jugal. The expansion of this angle gives the orbit its rounded appearance. The orbit is more strongly arched dorsally, where it is bounded by the prefrontal and frontal, than it is ventrally, where it is proscribed by the postorbital. The anteroposterior length of the orbit is difficult to determine due to the loss of the frontal process of the postorbital.

External Naris—The external naris is bounded posteriorly and posterolaterally by the nasal, anterolaterally by the maxillae, and anteriorly by the premaxillae. From the position of preserved elements surrounding it, the naris faced entirely dorsally. The transverse breadth of the naris expands posteriorly, giving the opening a triangular shape in dorsal view. There is no evidence for a large internarial bar dividing the naris anteriorly, although such bars have been observed in other *Diplodocus* crania (CM 3452, USNM 2762).

Supratemporal Fenestra—In adult skulls of *Diplodocus*, the supratemporal fenestrae are bounded by the frontals and postorbitals anteriorly, the parietals posteriorly, and the squamosal ventrally. However, due to the incomplete preservation of these elements in CM 11255, little is known about the condition of the supratemporal fenestra in this specimen. It was likely a mediolaterally elongate, oval opening, largely obstructed in posterior view by the large lateral wing of the parietal. The partially preserved right supratemporal fenestra is fully visible in lateral view.

Lateral Temporal Fenestra—The lateral temporal fenestra is poorly preserved, although an estimate of its shape can be inferred from the bones forming its margin. As in other diplodocids, it is roughly divisible into two sections: a rounded, anterior portion and a dorsoventrally compressed, anteroposteriorly elongate posterior portion. In CM 11255, its anterior margin is approximately even with the anterior margin of the orbit in lateral view. This is unlike the condition in larger *Diplodocus* skulls (e.g., CM 11161), in which the lateral temporal fenestra extends well anterior to the orbit.

Lower Jaw

The lower jaw is similar to that described for larger specimens of *Diplodocus*, save only for its rounded anterior end, which distinguishes it from the iconic squared shape of adults.

Dentary—As in other *Diplodocus* (CM 11161, USNM 2672), the dentary of CM 11255 comprises approximately one-half the length of the mandible. The internal surfaces of both dentaries are preserved medially, and the ventral margin is visible in both elements as well. As a consequence of the lateral crushing of the skull, the dentaries are disarticulated from each other at the symphysis, and the left is displaced posteriorly, dorsally, and medially. In ventral view, the dentaries are similar, although the better-preserved right element is slightly more strongly curved. The orientation of the symphysis suggests that the two dentaries would have met at a sharp angle, unlike the symphysis in adult *Diplodocus*, which was oriented essentially perpendicular to the anterior rami of the dentaries. The Meckelian groove is visible on the medial surface of the right dentary, arching dorsally to the broken edge of the bone.

Surangular—The surangular forms the dorsal portion of the posterior half of the mandible. In lateral view, it contacts the dentary anteroventrally and the angular ventrally. Medially, it contacts the dentary anteriorly and the splenial and prearticular ventrally. The surangular contacts the articular posteriorly in other exemplars of *Diplodocus*, but this cannot be confirmed in CM 11255. The surangular is broad and sheet-like, and there is no ev-

idence for a well-developed coronoid eminence. There is also no evidence of the anterior surangular foramen that occurs in other *Diplodocus* (CM 11161, CM 3452).

The surangular and angular (along with the articular) form the retroarticular process, which protrudes farther posterior to the quadrate in CM 11255 than is seen in adult *Diplodocus*. In this way, it is more similar to the condition of the large sub-adult CM 3452. As in that specimen, however, the mandibular cotyle does not extend greatly posterior to the articular head of the quadrate, being instead quite rounded dorsally. This indicates that the lower jaw of CM 11255 was not capable of being significantly displaced anteriorly during the bite stroke, in contrast to what has been previously proposed for adult *Diplodocus* (Barrett and Upchurch, 1994; Calvo, 1994; Upchurch and Barrett, 2000; Barrett and Upchurch, 2005).

Angular—The angular forms the ventral margin of the mandible and contributes to the unusually well developed retroarticular process. In lateral view, it contacts the surangular dorsally and the dentary anteriorly. Medially, it contacts the splenial anterodorsally and the prearticular dorsally.

Splenial—The splenial is a triradiate bone with two closely appressed anterior processes that contact the dentary and a posterior process that separates the prearticular from the angular. The anteroventral process is elongate and triangular in shape. The anterodorsal process is also triangular in shape, but much broader at the base and does not extend far anteriorly. Whether the anterodorsal process is further subdivided (as in CM 11161; McIntosh and Berman, 1975) cannot be determined.

Prearticular—The prearticular is a subquadrangular element that contacts the surangular dorsally and the angular and splenial ventrally. It arches slightly dorsally at mid-length, where it forms a portion of the ventral margin of the adductor fossa, and is very similar to the prearticular described for the adult *Diplodocus* CM 11161 (McIntosh and Berman, 1975).

Dentition

The teeth of CM 11255 are of the narrow-crowned type typical of diplodocoids (Calvo, 1994). As in other *Diplodocus*, they lack marginal denticles. Seven functional maxillary tooth positions are preserved on the right side, and 10–11 are estimated on the left. This is the standard *Diplodocus* condition (AMNH 696, CM 11161, CM 3452, USNM 2672). In the lower jaw, there are eight preserved functional teeth in the left dentary and six in the right. Based on other *Diplodocus* skulls, CM 11255 would have had between 10 and 11 dentary teeth. The upper teeth are larger than their lower counterparts, and are generally in a better state of preservation. None show definite traces of wear.

Similar to adult teeth, those of CM 11255 are subcircular in cross-section near the apicobasal midpoint of the crown, and become labiolingually compressed more apically. The upper teeth are unusual for a diplodocoid, however, in having mesiodistal asymmetry. Unlike the teeth preserved in specimens of adult *Diplodocus* (AMNH 696, CM 11161, USNM 2672, USNM 2673), the apices of each tooth of CM 11255 are slightly distally inclined. The teeth are sharply pointed, a condition Holland (1924) considered unusual. However, in situ teeth in other *Diplodocus* skulls (CM 3452, USNM 2672, and USNM 2673) are also pointed, suggesting that this shape is in fact typical for unworn crowns. As in those skulls (but not CM 11161), the teeth of CM 11255 are also closely appressed, occasionally contacting their mesial and/or distal neighbors.

In adult diplodocoids, the dentition is restricted to the anterior extremity of the snout. Although much of the ventral margins of the maxillae of CM 11255 are missing, a large proportion of the dentition is represented by both functional (Fig. 2A, B) and replacement (Fig. 2C, D) teeth. The preservation of the

replacement teeth allows the reconstruction of the position of the distal-most maxillary tooth, which is located farther posteriorly than is typical for adult *Diplodocus* (Fig. 2). That is, the tooth row in adults ends well anterior to the preantorbital fenestra, and often anterior to the subnarial foramen. Conversely, in CM 11255, the tooth row appears to end posterior to at least the subnarial foramen, and perhaps quite close to the anterior margin of the preantorbital fenestra.

The replacement teeth in each maxillary tooth family are first formed well within the bone, with the most distally located replacement tooth forming nearly within the preantorbital fossa (2D). The most mesially positioned upper teeth (i.e., those in the premaxilla and the mesial-most positions of the maxilla) appear to travel in an arcuate path through the jaw bones as a result of the 'stepped' shape of the snout visible in lateral view; more distal teeth seem to form in more linear families. The erupted teeth are oriented at a slight angle to the ventral margin of the jaw and tilted slightly mesially (Fig. 2A, C), as in other sub-adult *Diplodocus* (CM 3452). Visual estimates of the size and position of the replacement teeth of CM 11255 suggest that, even as juveniles, *Diplodocus* individuals carried in excess of four or five replacement teeth per alveolus in the maxilla. In the dentary of CM 11255, replacement teeth are present within 7 mm of the preserved ventral margin of the jaw, possibly explaining the ventrally projecting 'chin' of diplodocids as a reservoir for replacement teeth (Wilson and Sereno, 1998). The presence of so many teeth in such a small jaw may be evidence of rapid replacement rates, such as that observed in the rebbachisaurid diplodocoid *Niger-saurus* (Sereno et al., 2007).

DISCUSSION

Reconstructing the Snout of CM 11255

Adult individuals of *Diplodocus* and most other diplodocoids are well known for having snouts that are broad and square in dorsoventral view, with anteriorly sequestered teeth. The youngest known juvenile *Diplodocus* (CM 11255), however, has a highly rounded snout and a tooth row that extends farther posteriorly than in adults (Figs. 6, 7). Although taphonomic processes have slightly distorted the snout, there are three main lines of evidence that suggest that we have correctly reconstructed its shape: the preserved position of the teeth, the orientation and size of the palatal elements, and the shape of the dentary.

Evidence from Teeth—In adult *Diplodocus*, the posterior-most tooth in the maxillary tooth row (tooth 10 or 11) is located very far anteriorly in the jaw, well anterior to the preantorbital fenestra. The lateral compression experienced by CM 11255 is unlikely to have displaced its tooth row posteriorly; displacement of that type would result in visible damage or deformation to the pre-preantorbital region of the skull, which is not evident in the specimen. In contrast, the most likely consequence of lateral crushing is exaggeration of the length of the skull due to folding at the premaxillary symphysis, causing the anterior ends of the premaxillae to protrude farther anteriorly than they did in life. This can be refuted as a major impactor here due to the close association of the anterior end of the preserved upper tooth row with the anterior end of the right dentary.

Evidence from the Palate—The pterygoids are elements with multiple local angles when viewed in cross-section (Fig. 5C). In *Diplodocus* and *Apatosaurus*, the angle between the pterygoids at mid-height is approximately 60° (Berman and McIntosh, 1978). The right pterygoid of CM 11255—the better preserved of the two—has an angle with the vertical of 35°. If the right pterygoid is mirrored, the resultant median angle is 70°, greater than that seen in adult *Diplodocus*. This suggests that the right pterygoid is largely undistorted, and when mirrored provides a conservative estimate of palatal width. Using the right pterygoid to reconstruct the width of the palate indicates that the width to be added is only

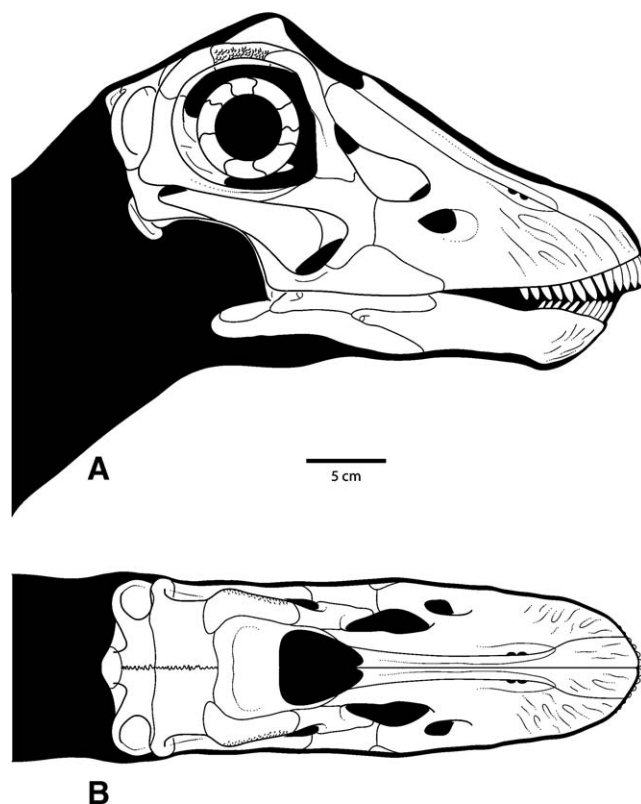


FIGURE 6. Reconstruction of CM 11255. **A**, lateral view; **B**, dorsal view. Scale bar equals 5 cm.

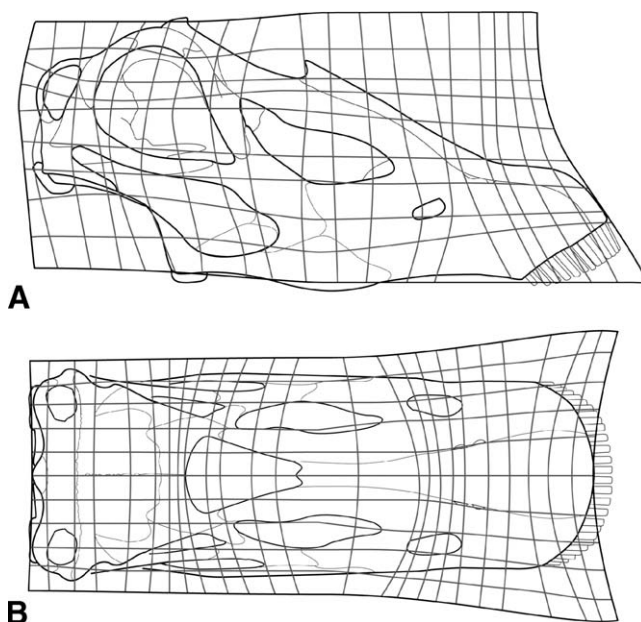


FIGURE 7. Transformation grids based on sutures and other landmarks showing the regions of the *Diplodocus* skull that underwent the greatest amount of shape change through ontogeny. Grids based on Figure 6 and a reconstruction of the adult skull of *Diplodocus* (Wilson and Sereno, 1998:fig. 6). **A**, lateral view; **B**, dorsal view.

11 mm, for a maximum skull width of 88 mm at the quadrates. If the entire right side of the skull, to the midline suggested by the right pterygoid, is mirrored, the maximum skull width is only 102 mm. Even using this higher estimate, the reconstructed snout is still quite round in comparison to adults (see Comparisons with Adult *Diplodocus*, below).

Evidence from the Dentary—As noted above, lateral crushing of the skull has displaced the left mandible, disarticulating it from the right at the dentary symphysis. This disarticulation and subsequent displacement appears to have been the main impact of compression on the mandibles because their longitudinal rami appear to be relatively straight and the anterior curvature of each dentary is similar (Fig. 4B, D). These elements are gently rounded in ventral view, not squared as seen in larger *Diplodocus* skulls.

Lateral crushing of this extent is not typically seen in larger *Diplodocus* skulls, although slight crushing is apparent in two other specimens, one adult (USNM 2672), and a larger subadult (CM 3452). In both of these latter specimens, the dentaries are symmetrical and appear to retain their original morphology (squared in USNM 2672, more gently rounded in CM 3452) and are, again, disarticulated along the symphysis, with one mandible displaced. Even in a clearly distorted skull (USNM 2673), the deformation occurs along the lateral ramus of the mandible, not at its anterolateral corner. The only observed case of deformation altering the anterior shape of the dentary is the dicraeosaurid diplodocoid *Dicraeosaurus* (MB.R. 2372), in which the squareness of the dentary is exaggerated, although the ventral margin is itself undeformed. It is unlikely, then, that taphonomic deformation has greatly altered the shape of the dentaries of CM 11255, and consequently these elements constitute a reasonable proxy for snout shape in this specimen.

Comparisons with Adult *Diplodocus*

Varricchio (1997) listed ten ways in which the crania of dinosaurs have been shown to vary ontogenetically, two of which (increase in tooth count, shortening and deepening of the skull) are potentially related to changes in feeding behavior. Others (relative decrease in size of the orbit, relative increase in antorbital length) are common in many amniote groups and are not directly related to feeding behavior.

As expected, the relative contributions of the orbit and braincase to overall skull size are dramatically larger in CM 11255 relative to large adult skulls (Fig. 7). Accordingly, there is a smaller contribution of the antorbital region to skull length in CM 11255, which has the effect of shortening the face. This shorter proportional length is accompanied by a snout that is narrower and rounder in dorsal view. The upper tooth row occupies a much larger proportion of the jaw margin and extends much farther posteriorly than in adults. This suggests a large-scale ontogenetic remodeling of the facial skeleton involving rearrangement of the food-gathering apparatus, which has not been previously reported for any sauropodomorph dinosaur.

Implications for Facial Remodeling in *Diplodocus*—In mammals, snout shape has been shown to serve as a proxy for feeding behavior (Boué, 1970; Solounias et al., 1988; Dompierre and Churcher, 1996). Broad, anteriorly flat snouts belong to mammals that crop low-lying grasses near the ground, and narrow, pointed snouts belong to mammals that selectively browse for particular plants or plant parts. Using a modification of a metric used by Solounias et al. (1988), the snout shape of sauropods can be quantified. The premaxillary-maxillary index (PMI) is calculated by superimposing a triangle over a dorsal view of the snout with the hypotenuse drawn at 26°. The area of this triangle that is covered by snout is divided by the total area of the triangle to determine the PMI; higher numbers indicate squarer snouts. The most conservative reconstruction of CM 11255 has a PMI of

56%; this is well below that of adult *Diplodocus* (PMI = 84%; Whitlock, 2007). This pointed snout is also seen in other juvenile specimens of *Diplodocus* (CMC VP 8300; Whitlock, 2006). The ontogenetic disparity in snout shapes in this genus may be evidence of resource partitioning between adults and juveniles that might have had vastly different energetic needs. Fiorillo (1998) presented patterns of enamel microwear as evidence for resource partitioning between adults and juveniles of a different Morrison sauropod, *Camarasaurus*. Ongoing research has shown a difference in wear patterns between relatively round snouted (*Dicraeosaurus*) and relatively square snouted (*Apatosaurus*, adult *Diplodocus*) diplodocoids that is consistent with selective browsing versus non-specific browsing similar to the 'grazing' behavior of ruminants (Whitlock, 2007). Unfortunately, microwear has not yet been recovered from a definitive juvenile *Diplodocus* tooth for comparison with adult patterns.

Curry (1999) and Lehman and Woodward (2008) presented sigmoidal growth curves for the diplodocid *Apatosaurus*. Assuming that these curves accurately represent the pattern of growth rates through diplodocid ontogeny, juvenile *Diplodocus* in the exponential growth phase may have required more energy-rich foodstuffs than adults that had reached their growth plateau. Barrett (2000) suggested a similar scenario for basal sauropodomorphs involving opportunistic carnivory in juveniles. Jarman (1974) noted that small ungulates, which have comparably higher metabolic rates than large ungulates, have narrow snouts for selective browsing of plant parts with high digestibility and high caloric content. It is possible that a similar scenario could have occurred in an organism whose growth curve involves many orders of magnitude increase in mass. Earlier ontogenetic stages likely required easily digestible, high-calorie foods to maintain a higher metabolism, and used a narrow, pointed snout to selectively obtain them. Once full size had been reached, energetic goals may have been attained by higher-volume, less nutritious, non-specific browsing by blunt-snouted adult *Diplodocus* individuals. Resource partitioning may also have occurred out of necessity, easing intraspecific competition between adults and their offspring, or, as noted by Jarman (1974), because a larger skull (such as that of adult *Diplodocus*) is less suited for selective herbivory.

Comparisons with Other Dinosaurs

Of the numerous dinosaurian taxa that have been examined for ontogenetic cranial variation, six are of particular interest. Three related taxa, the sauropodomorphs *Camarasaurus*, *Rapetosaurus*, and *Massospondylus*, are examined, as well as the theropods *Albertosaurus* and *Tyrannosaurus*. To elucidate the condition in an ornithischian, the basal ceratopsian *Psittacosaurus* is also discussed.

Camarasaurus—*Camarasaurus* is known from multiple skulls, including a juvenile preserving most of the facial skeleton (CM 11338). Ikejiri (2004) and Ikejiri et al. (2005) suggested that there was little remodeling of the craniofacial skeleton throughout the ontogeny of this genus. McIntosh et al. (1996) posited that a reduction in alveolar count did occur with advancing ontogenetic stage, contrary to the typical dinosaurian condition (Varricchio, 1997; but see Carr, 1999). Fiorillo (1998) used enamel microwear patterns to suggest resource partitioning between adults and juveniles in browse height, but not necessarily browse type. For sauropods like *Camarasaurus*, whose relatively high forelimb-to-hind limb and low neck-to-torso ratios suggest a higher browse height than is posited for diplodocoids, browse height was most likely a function of body size and therefore maturity. In other words, given their smaller size, younger individuals necessarily browsed at lower heights than older individuals. In contrast, *Diplodocus* has been interpreted as a mid- to low-height feeder throughout its ontogeny (Barrett and Upchurch, 1994; Stevens

and Parrish, 1999, 2005; Upchurch and Barrett, 2000). The variation in resource acquisition may have been as much a function of behavior as it is of physiology.

Rapetosaurus—The derived titanosaurian sauropod *Rapetosaurus* is known from cranial elements belonging to an adult and a juvenile, including facial bones from each (Curry Rogers and Forster, 2004). However, the reconstructed skull of this taxon is based almost entirely on the adult, because very little of the facial skeleton is preserved in the juvenile (Curry Rogers and Forster, 2004:Fig. 1). Although the reconstructed snout is somewhat rounded in dorsal view, the preserved dentary (Curry Rogers and Forster, 2004:fig. 28) approaches a square shape, more so than in the juvenile *Diplodocus* but less than in adults. In the absence of more complete juvenile skulls, little can be said about the ontogenetic development of the blunt snout in *Rapetosaurus*.

Massospondylus—Sues et al. (2004) described four skulls attributable to *Massospondylus carinatus*, representing several stages of growth. *M. carinatus* appears to have added maxillary tooth positions with age, and there are more denticles per crown in juvenile specimens than in adults, but the general shape of the snout does not appear to have varied greatly (Sues et al., 2004). Gow (1990) noted a few ontogenetic changes in the braincase of *M. carinatus*, primarily the late ossification of a posterior extension of the laterosphenoid separating the vena cerebialis media and cranial nerve V, and increased muscle scarring on the supraoccipital. Reconstructions of three skulls of *M. carinatus* (Gow et al., 1990:fig. 7) suggest that the orbit became proportionally smaller and the antorbital region proportionally longer with increasing size, as is typical of many other dinosaurian taxa (Varricchio, 1997).

Albertosaurus and Tyrannosaurus—The premaxillae and maxillae of *Albertosaurus* were subject to ontogenetic variation, particularly in the later sub-adult stages, when the snout broadened transversely (Carr, 1999). Additionally, the skull as a whole became more robust with age, a pattern also seen in *Tyrannosaurus*. Carr (1999) hypothesized that this variation may be the result of variation in foraging behaviors, such that older individuals were more capable of grasping and holding live prey or tearing apart large carrion; an alternate explanation proposed was that the increased robustness and broadness was a physiological response to increased skull size and bite force. Additionally, the teeth became more robust throughout ontogeny, with a corresponding reduction in the number of alveoli. The implication is that, as in *Diplodocus*, tyrannosaurid theropods were capable of variation in response to differing feeding behaviors or requirements at different ontogenetic stages.

Psittacosaurus—The basal ceratopsian *Psittacosaurus* is known from many individuals of varying sizes and stages of ontogeny. In *P. mongoliensis*, alveolar count more than doubles throughout ontogeny, eventually reaching 12 maxillary and dentary teeth from approximately five in the youngest individuals (Serenó, 1990). In *P. mongoliensis* and *P. xinjiangensis*, the large sagittal crest is not present in young individuals and developed as the animal matured (Serenó and Chao, 1988). Additionally, Makovicky et al. (2006) demonstrated that the presence of a well-developed flange on the dentary is age related, only appearing in older sub-adults. Those authors also found that overall skull shape, however, did not significantly vary with age. Unlike in *Diplodocus*, it appears that the ontogenetic variation in *Psittacosaurus* was not related to a substantial change in feeding behavior, but was instead a response to increased body size and muscle development with age.

CONCLUSION

CM 11255 is the smallest recognized skull of *Diplodocus*. It shares several synapomorphies with adult skulls, but the presence of unfused parietal bones and the small size of the specimen

(60% of the anteroposterior length of the adult skull CM 11161) indicate that it pertains to a juvenile individual. Unique to this individual are the extreme posterior position of the distal-most tooth in the maxillary tooth row and the rounded dental arcade, in contrast to the squared snout and anteriorly sequestered tooth row in adults. The larger sub-adult *Diplodocus* CM 3452 strongly resembles CM 11255 in both conditions, and it is hypothesized that juvenile and sub-adult individuals of *Diplodocus* share a facial morphology that is distinct from that of adults, particularly with regard to the tooth bearing elements and the dental arcade. Similar morphologies (rounded versus blunt snouts) have been shown to be related to food gathering in mammals. The condition in *Diplodocus* indicates ontogenetic niche partitioning, as has been suggested for *Camarasaurus* and tyrannosaurid theropods. Juvenile and sub-adult *Diplodocus* appear to have been selective browsers, whereas square-snouted adults were likely low-height non-selective browsers, similar to what has been proposed for the diplodocoids *Brachyrachelopon* (Rauhut et al., 2005), *Dicraeosaurus* (Upchurch and Barrett, 2000; Barrett and Upchurch, 2005), and *Nigersaurus* (Serenó et al., 2007).

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