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Source: American Museum Novitates, 2018(3911) : 1-16

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/3911.1

AMERICAN MUSEUM NOVITATES

Number 3911, 16 pp. October 25, 2018

Complex Overlapping Joints between Facial Bones Allowing Limited Anterior Sliding Movements of the Snout in Diplodocid Sauropods

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ABSTRACT

Diplodocid sauropods had a unique skull morphology, with posteriorly retracted nares, an elongated snout, and anteriorly restricted, peglike teeth. Because of the lack of extant analogs in skull structure and tooth morphology, understanding their feeding strategy and diet has been difficult. Furthermore, the general rarity of sauropod skulls and the fragility of their facial elements resulted in a restricted knowledge of cranial anatomy, in particular regarding the internal surface of the facial skull. Here, we describe in detail a well-preserved diplodocid skull visible in medial view. Diagnostic features recognized in other skulls observable in lateral view, such as the extended contribution of the jugal to the antorbital fenestra, are obliterated in medial view due to extensive overlapping joints between the maxilla, jugal, quadratojugal, and the lacrimal. These overlapping joints permitted limited anterior sliding movement of the snout, which likely served as a kind of "shock-absorbing" mechanism during feeding. Diplodocid skulls therefore seem to have evolved to alleviate stresses inflicted on the snout during backward movements of the head, as would be expected during branch-stripping or raking.

INTRODUCTION

Finds of sauropod dinosaur skulls are very rare, particularly the facial elements (Chure et al., 2010; Poropat and Kear, 2013). Their rarity might in part be due to their fragile construc-

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ISSN 0003-0082

tion, with paper-thin bones composing most of the facial region of the skull. This fragility is extreme in the elongate and slender skulls of diplodocoids like *Apatosaurus* (Holland, 1915; Berman and McIntosh, 1978), *Diplodocus* (Marsh, 1896; Holland, 1924; McIntosh and Berman, 1975; Whitlock et al., 2010), *Nigersaurus* (Sereno et al., 2007), *Kaatedocus* (Tschopp and Mateus, 2013), and *Galeamopus* (Tschopp and Mateus, 2017). Even though diplodocoid skulls, and in particular diplodocid skulls, are relatively common compared to other sauropods (Chure et al., 2010; Whitlock et al., 2010; Poropat and Kear, 2013), their fragile construction hampers complete preparation of both the lateral and medial sides of the skull, because doing so would potentially compromise the structural integrity of the fossil. In fact, most articulated specimens of nearly complete diplodocid skulls have their medial side at least partly obscured by matrix that was kept in place to stabilize the fossil (e.g., AMNH FARB 681; CM 3452, 11161, 11162, 11255; USNM V 2672, V 2673; fig. 1A). In other cases, mounted skull elements are stabilized medially by a specifically fabricated structure (e.g., SMA 0004 [see fig. 1B], 0011; Tschopp and Mateus, 2017). Recently, CT-scans of some of these skulls have revealed some of the internal structures (Holliday and Witmer, 2008; Witmer et al., 2008; Whitlock et al., 2010; Young et al., 2012), but the resolution was often insufficient to recognize minute features or virtually prepare single elements for detailed osteological study. Therefore, our knowledge of diplodocid cranial osteology is mostly confined to the lateral skull surface and the braincase. Only a few detailed descriptions of the palatal complex and medial side of the facial elements of diplodocids exist (e.g., McIntosh and Berman, 1975; Whitlock et al., 2010). Here, we describe some peculiar features from the medial surface of the facial skull of a newly excavated specimen from Wyoming (AMNH FARB 33054; fig. 2).

Material

The skull AMNH FARB 33054 was collected in 2016 at Cosm Quarry, a new Late Jurassic (Tithonian) locality from the upper Morrison Formation in the northern Bighorn Basin, northern Wyoming (Saleiro and Mateus, 2017). Exact locality data are not provided here as it is an active quarry, but are available for qualified researchers upon request.

The skull was found semiarticulated, exposing the internal surface of the nearly complete right side. The palatal complex was not preserved. The left maxilla was detached, flipped such that the medial surface now faces externally, and rotated such that the anterior tip points ventrally. Because of the peculiar disarticulation and rotation of the left maxilla, all the facial bones of the skull and the snout have their internal surfaces exposed (fig. 2). The length of the entire skull (measured from the tip of the snout to the occipital condyle) is approximately 510 mm.

Excavation and preparation was done mechanically, and the skull was extracted in a single block. During preparation the entire skull was kept in the position in which it was found. Preparation was done manually under a microscope, using needles. Pedestals of sediment were left in place to provide support for the thinnest and most exposed structures (e.g., the postorbital, basipterygoid processes, and the parasphenoid rostrum).

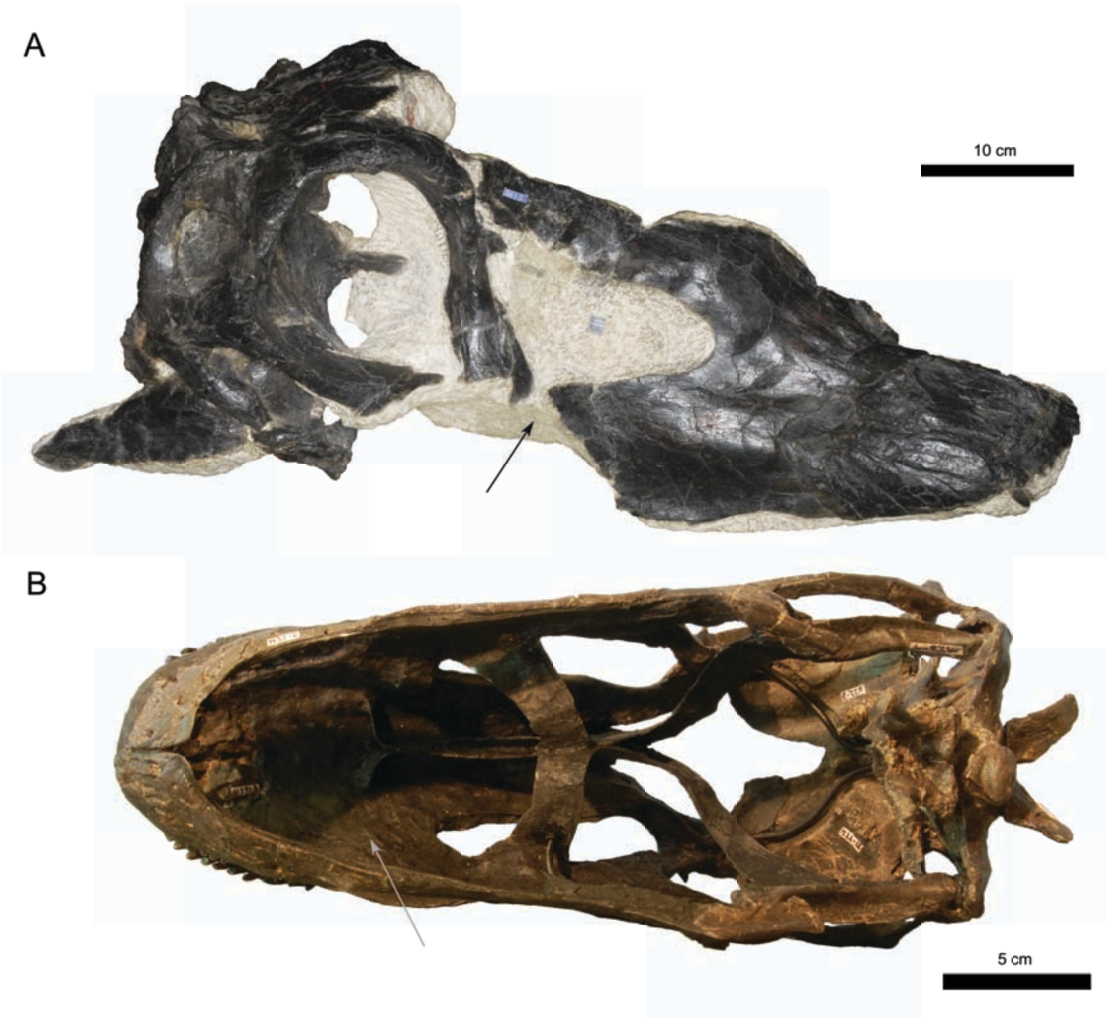
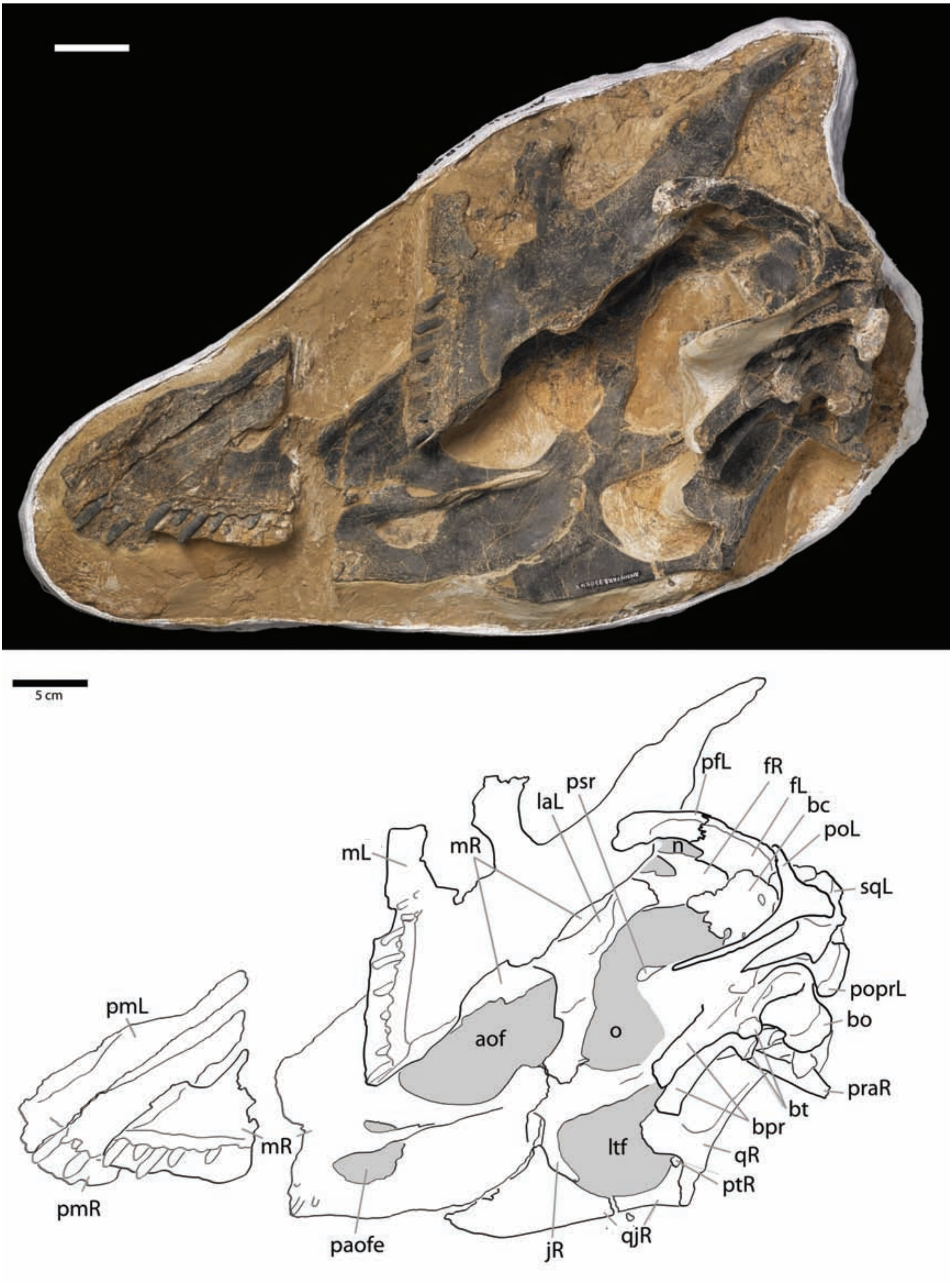


FIGURE 1. Usual preservation of diplodocid skulls. **A.** *Galeamopus pabsti* USNM V 2673 (right lateral view) is preserved on a slab of matrix (black arrow). **B.** *Kaatedocus siberi* SMA 0004 (ventral view) is mounted on a metal structure mimicking the palatal complex, which is fixed onto the medial side of the facial bones (black elements in center of image, and gray arrow). Photographs by M. Eklund (A) and E. Tschopp (B).

The skull is clearly diplodocid due to the broad contact between the quadratojugal and the maxilla (Rauhut et al., 2005), the concave dorsal margin of the antorbital fenestra (Wilson, 2002), the hooked posterior process of the prefrontal (Berman and McIntosh, 1978), and the medially curving medial margin of the prefrontal that embraces the frontal anteromedially (Tschopp et al., 2015). Identification to a lower taxonomic level is currently not possible because most of the diagnostic cranial features of less-inclusive clades are located on the external surface of the skull. However, a systematic assessment of the skull AMNH FARB 33054 is not within the scope of this paper; this will be addressed elsewhere.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Institutional Abbreviations

AMNH FARB, American Museum of Natural History, Collection of Fossil Amphibians, Reptiles and Birds, New York; **CM,** Carnegie Museum, Pittsburgh; **SMA,** Sauriermuseum Aathal, Aathal, Switzerland; **USNM,** National Museum of Natural History, Washington D.C.; **YPM,** Yale Peabody Museum, New Haven, Connecticut.

DESCRIPTION

The unique preservation of AMNH FARB 33054 provides unobstructed views of the medial surface of the facial region. It shows peculiar features implying an intricate pattern of bone overlap between the facial elements. In particular, the maxilla, quadratojugal, jugal, and lacrimal form complex, overlapping joints such that the internal articulation among the skull bones differs from the arrangement visible in lateral view. These overlapping joints are described in detail. A complete description of the cranial osteology is outside the scope of this paper. This is because it is likely that additional, associated material will be recovered from Cosm Quarry.

Terminology

We use anterior and posterior as synonyms of rostral and caudal as directional terms, following general usage in sauropod osteology (e.g., Wilson et al., 2016; Moore et al., 2018). However, these terms do not necessarily reflect the orientation of the skulls in life, as the snout of diplodocoids is generally thought to point anteroventrally, based on the orientation of the occipital condyle and the semicircular canals (Sereno et al., 2007; Witmer et al., 2008). Here, we use directional terms in relation to a horizontally oriented tooth-bearing margin of the maxilla, which would therefore represent the ventral margin. The term *facet* is used to describe an articular surface that is clearly confined by a ridge, a steplike transition, or a sulcus, and that exhibits a different surface texture than the rest of the bone. Measurements of the estimated area of the facets were taken in Adobe Photoshop CC 2018, using the lasso tool.

Maxilla

The maxilla bears an eye-shaped facet along the posteriormost part of the ventral margin (fig. 3). The facet is well defined dorsally by a narrow bony crest. It is approximately 50 mm in antero-

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FIGURE 2. Photograph and interpretative line drawing of diplodocid skull AMNH FARB 33054 in medial view. Note the anterior dislocation of the right maxilla, revealing the underlying sediment. Photograph by M. Ellison. Abbreviations: **aof,** antorbital fenestra; **bc,** braincase; **bo,** basioccipital; **bpr,** basipterygoid process; **bt,** basal tubera; **f,** frontal; **j,** jugal; **L,** left; **la,** lacrimal; **ltf,** laterotemporal fenestra; **m,** maxilla; **n,** external nares; **o,** orbit; **paofe,** preantorbital fenestra; **pf,** prefrontal; **pm,** premaxilla; **po,** postorbital; **popr,** paroccipital process; **pra,** proatlas; **psr,** parasphenoid rostrum; **pt,** pterygoid; **q,** quadrate; **qj,** quadratojugal; **R,** right**; sq,** squamosal.

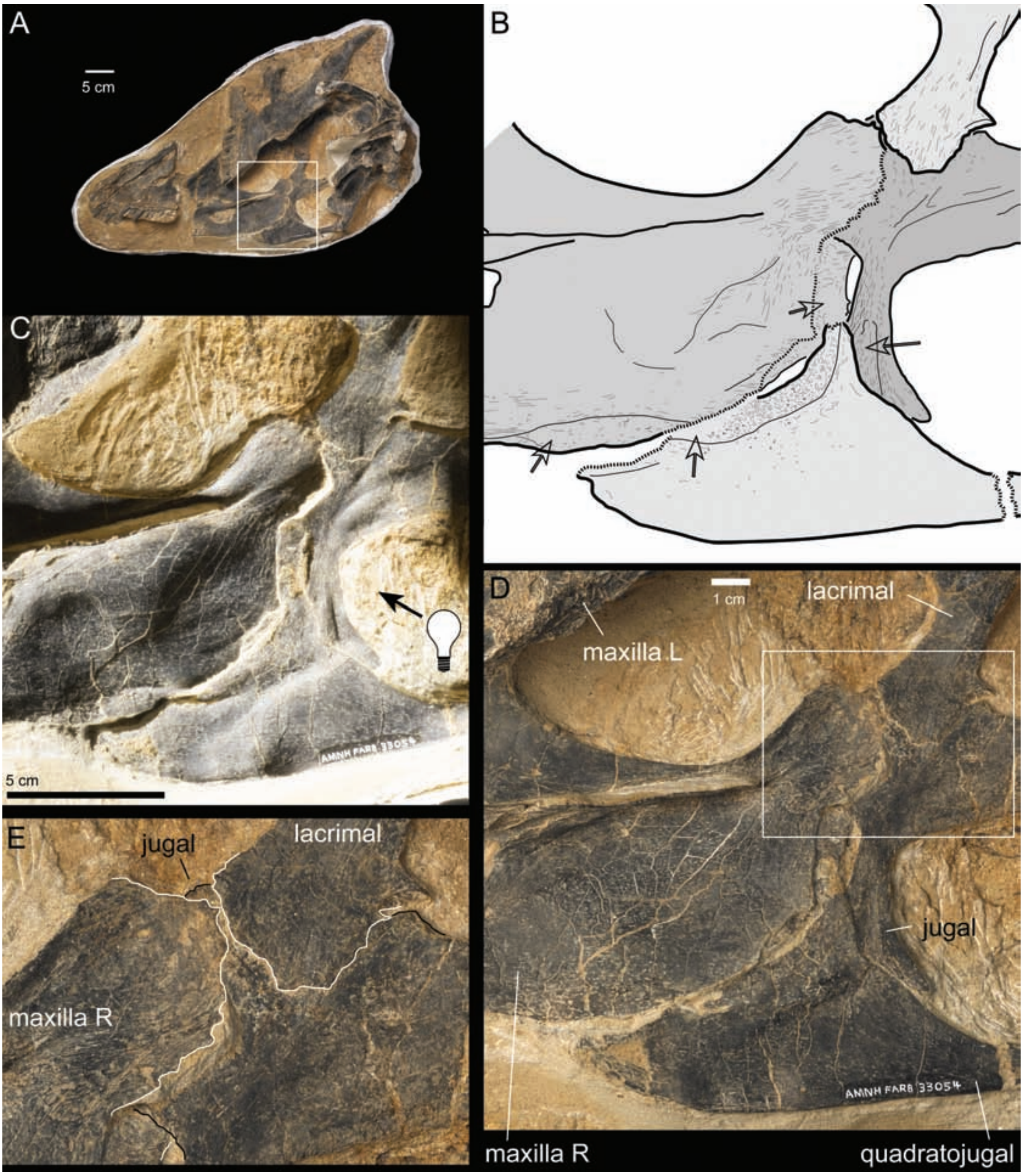

FIGURE 3. Overlapping joints in the diplodocid skull AMNH FARB 33054. **A.** Overview of the entire skull. **B.** Drawing of the overlapping joints between the maxilla, quadratojugal, jugal, and lacrimal in medial view, traced from photograph in D. Articular facets indicated with arrows. **C.** Photograph under oblique lighting (light source located at the bottom right, see icon) to highlight subtle ridges delimiting the facets on the maxilla, quadratojugal, and jugal. **D.** Photograph under usual lighting, indicating the visible bones; white rectangular indicates area enlarged in E. **E.** Detail of overlapping joints between maxilla, jugal, and lacrimal, showing the contribution of the jugal in the margin of the antorbital fenestra on the lateral surface of the skull. White (maxilla and lacrimal) and black (jugal) lines highlight the margins of the bones as preserved. Photographs by M. Ellison (A, D, E) and M. Eklund (C).

posterior length and has an estimated area of 270 mm^2. Its surface is slightly irregular and marked by numerous small foramina, some of which have a circular cross section; and others are anteroposteriorly elongate. Additional foramina are located alongside the facet, dorsal to the crest, but their number decreases considerably with distance from the facet. Articulation with the quadratojugal indicates that this portion of the maxilla covered the anterodorsal portion of the anterior process of the quadratojugal laterally. Just posterior to this area, the margin of the posterior ramus of the maxilla curves dorsally, and slightly bifurcates. The medial surface expands medially at the bifurcated posterior end of the posterior ramus of the maxilla, but the extremities are broken, so it remains unclear how deep the bifurcation is. Further dorsally, just above the dorsalmost extension of the articulation with the quadratojugal, the bifurcation grades into a steplike transition, and becomes bifurcated again towards the dorsalmost point of the posterior ramus of the maxilla. Here, the maxilla overlies the jugal both laterally and medially. The medial overlap extends posterodorsally to a point where it contacts the lacrimal, essentially excluding the jugal from participation in the margin of the antorbital fenestra on the medial side. A large contribution of the jugal to the antorbital fenestra has been proposed as a synapomorphy for Diplodocidae (Upchurch, 1998) and recovered as a synapomorphy of Diplodocoidea by Tschopp et al. (2015), but these observations are based on the numerous specimens where this portion of the skull is visible only in lateral view. Indeed, Madsen et al. (1995) correctly recognized that a medial contact of the maxilla and lacrimal might be present in diplodocids, which is confirmed in the specimen AMNH FARB 33054. However, due to the slightly broken margin of the medial portion of the maxilla that overlaps the jugal and contacts the lacrimal, a portion of the jugal participating in the antorbital fenestra on the lateral side of the skull can be observed in AMNH FARB 33054 (fig. 3E). Even though we cannot assess the extension of this contribution on the lateral side of AMNH FARB 33054 without a CT-scan, it is very likely that it possesses the diplodocoid synapomorphy as identified by Upchurch (1998) and Tschopp et al. (2015). This extensive medial and lateral overlap of osseous elements in diplodocid facial skulls could therefore potentially lead to erroneously generalized interpretations of bone contacts, if only one view is available.

Quadratojugal

The quadratojugal bears an eye-shaped facet, similar to that seen on the maxilla, along its anterodorsal margin (fig. 3). The facet extends posterodorsally onto a dorsal projection on the anterior process of the quadratojugal. The estimated area of the facet is 510 mm^2, and the distance from the anteriormost point to the dorsalmost point (corresponding to the maximum elongation of the facet) is 54 mm. The facet is ventrally bordered by a narrow, subhorizontal, bony crest, which is in line with the narrow crest delimiting the facet on the maxilla dorsally. Although the crest fades posteriorly, the facet is distinct from the rest of the medial surface of the quadratojugal because of its more irregular surface, which, like the facet on the maxilla, is pitted by foramina. As preserved, the facet on the quadratojugal is posteriorly adjacent to the bifurcated posterior margin of the maxilla, so that the incomplete medial portion of the bifurcated maxilla overlaps the facet medially and probably also laterally, at least in part. As preserved, the anterior process is pointed, with a concave dorsal margin, but this portion is broken and was likely slightly convex, following the shape of the narrow crest delimiting the maxillary facet. The dorsal projection on the anterior ramus extends between the jugal and the maxilla. It has a thick posterior border, which forms the posterior limit of the facet for the reception of the maxilla on the medial surface of the quadratojugal. This projection cannot be seen in diplodocid skulls exposed only in lateral view (Marsh, 1884; Holland, 1906, 1924; Berman and McIntosh, 1978; Wilson and Sereno, 1998), and has indeed never been described or reconstructed (see drawings in Wilson, 2002; Whitlock et al., 2010; Mateus and Tschopp, 2017), even though it was visible in the disarticulated quadratojugal of *Galeamopus pabsti* SMA 0011 (Tschopp and Mateus, 2017: fig. 4). This indicates that the clasping articulation with the maxilla anteriorly and the lap joint with the jugal posteriorly completely cover the lateral surface of the dorsal projection of the anterior process of the quadratojugal, so that it is invisible in lateral view in articulated skulls.

Jugal

The jugal bears a distinct facet on the medial surface of the ventral process delimiting the laterotemporal fenestra anteriorly (fig. 3). The facet is posteriorly delimited by a distinct, steplike margin, and receives the dorsal projection of the anterior ramus of the quadratojugal. It has a dorsoventral expansion of 27 mm, and an estimated area of 300 mm^2. This dorsal quadratojugal projection is, therefore, laterally covered by both the jugal and the maxilla, and has thus never been recognized (see the reconstructions in Wilson, 2002; Whitlock et al., 2010; Mateus and Tschopp, 2017). The ventral process of the jugal of AMNH FARB 33054 is anteroposteriorly narrow, especially when compared with the jugal of *Galeamopus pabsti* SMA 0011 (Tschopp and Mateus, 2017: fig. 4), but the anterior margin is broken. Further dorsally, the preserved portion of the jugal extends anteriorly between the two lamellae of the bifurcate posterior margin of the maxilla. Dorsally, the jugal is covered medially by both the posterodorsal corner of the posterior ramus of the maxilla, and by the ventral extension of the lacrimal, but a short portion of its anterior margin can be observed to participate in the antorbital fenestra (fig. 3E).

Lacrimal

The lacrimal bears no facet on its medial surface, indicating that no bone overlapped the lacrimal medially (fig. 3). Instead, the ventral end of the lacrimal overlaps the jugal medially. Dorsally, an elongate anterior process overlaps the posterior ascending process of the maxilla, as was described in *Galeamopus pabsti* SMA 0011 (Tschopp and Mateus, 2017).

DISCUSSION

Comparative Anatomy

Overlapping joints are common in dinosaur skulls. In diplodocids in particular, overlapping, nonsutured joints have been recognized between: the posterior ascending process of the maxilla and (1) the lacrimal and (2) prefrontal; the quadrate and (3) the quadratojugal, (4) the squamosal, and (5) the pterygoid; and the postorbital and the (6) jugal and (7) squamosal (Whitlock et al., 2010; Tschopp and Mateus, 2013, 2017). However, such an extensive overlap of the maxilla, quadratojugal, jugal, and lacrimal has not yet been described in diplodocids. The facets of the overlapping joints between the maxilla and the lacrimal and prefrontal, between the quadrate and the pterygoid, and between the jugal and the postorbital are relatively smooth; thus, they are similar to the ones described above, although generally larger. In contrast, the articular facet on the quadrate for the quadratojugal displays relatively strong striations (AMNH FARB 30070; USNM V 2673; YPM VP.001860; Tschopp, personal obs.), whereas the articulations between the squamosal and the postorbital and the squamosal and the quadrate are strongly confined by ridges that enclose the entire facet on the squamosal (AMNH FARB 33054; USNM V 2673; Tschopp, personal obs.).

Outside Diplodocidae, similar overlapping joints between the maxilla and its posteriorly adjacent bones were reported in the sauropods *Giraffatitan* (Janensch, 1935), *Camarasaurus* (White, 1958; Madsen et al., 1995), *Mamenchisaurus* (Ouyang and Ye, 2002), *Nemegtosaurus* (Wilson, 2005), *Turiasaurus* (Royo-Torres and Upchurch, 2012), *Euhelopus* (Poropat and Kear, 2013), *Europasaurus* (Marpmann et al., 2015), *Sarmientosaurus* (Martínez et al., 2016), *Tapuiasaurus* (Wilson et al., 2016), cf. *Brachiosaurus* and *Bellusaurus* (Moore et al., 2018). However, as in diplodocids, most of these skulls are only partly visible in medial view, so most of the descriptions are restricted to overlapping bones on the lateral surface. Here, we compile the available information on the various joints.

MAXILLA-JUGAL CONTACT: In sauropods, when this portion of the skull is known, the maxillae cover the jugals laterally (*Giraffatitan*, *Mamenchisaurus, Nemegtosaurus*, *Turiasaurus*, *Europasaurus*, *Bellusaurus*; Janensch, 1935; Ouyang and Ye, 2002; Wilson, 2005; Royo-Torres and Upchurch, 2012; Marpmann et al., 2015; Moore et al., 2018). The facets on the anterior processes of the jugals and the medial surfaces of the posterior processes of the maxillae of *Giraffatitan* and *Europasaurus* are distinct (Janensch, 1935; Marpmann et al., 2015). The facet on the jugal of *Nemegtosaurus* cannot be seen because all the known, well-preserved elements are articulated with the maxilla (Wilson, 2005). Royo-Torres and Upchurch (2012) describe a longitudinal groove on the main body of the jugal of *Turiasaurus* as the articular facet for the maxilla. Generally, articulation between the maxilla and the jugal is interpreted as a lap joint, although Moore et al. (2018) do not exclude a slightly more complex structure. Indeed, in *Turiasaurus*, the groove, combined with an autapomorphic boss, seems to weakly clasp the maxilla (Moore et al., 2018). *Bellusaurus* has facets on both the medial and lateral surfaces of the maxilla, but because all the elements are disarticulated, it remains unclear if both of them articulated with a clasping jugal or the jugal and the quadratojugal (Moore et al., 2018). In a disarticulated maxilla of *Camarasaurus* (AMNH FARB 5761), the posterior process is slightly broken but preserves a vertical groove on the dorsal portion of its posterior surface, with thin flanges of bone that would have projected further posteriorly (if completely preserved), clasping the adjacent bone—contrary to the state in *Bellusaurus* (Moore et al., 2018). Given that the maxilla of AMNH FARB 5761 was disarticulated, it remains unclear if the groove was for the articulation with the lacrimal, the jugal, or both (Tschopp, personal obs. 2018).

The morphology in AMNH FARB 33054 is more complex than a simple lap or clasping joint. The articulation between the maxilla and the jugal changes from a clasping joint ventrally to a short section of a steplike lap joint, and back to a clasping joint towards the dorsalmost extension of the contact with the jugal. Although it is unclear how extensive the lateral overlap would be in AMNH FARB 33054 (the maxilla appears to be incomplete here, see above), the fact that the jugal likely participates in the rim of the antorbital fenestra on the lateral surface (see description above) implies that the overlap on the medial side, where the maxilla contacts the lacrimal, must be more extensive than that on the lateral side. The condition in AMNH FARB 33054 therefore appears to be most similar to that found in *Camarasaurus*.

Maxilla-quadratojugal contact: A broad contact between these two bones was recovered as a synapomorphy of Diplodocidae by Rauhut et al. (2005) and Tschopp et al. (2015). Similarly, broad contacts evolved convergently in nemegtosaurids (Upchurch, 1998; Wilson, 2005) and *Turiasaurus* (Royo-Torres and Upchurch, 2012), and reduced contacts occur in *Camarasaurus* as well as some non-neosauropod eusauropods (Royo-Torres and Upchurch, 2012; Tschopp et al., 2015). In more basal sauropods and titanosauriforms, the two bones do not contact each other (Upchurch, 1998; Royo-Torres and Upchurch, 2012). The morphology of the more extensive maxilla-quadratojugal joint in *Nemegtosaurus* and *Turiasaurus* (Wilson, 2005; Royo-Torres and Upchurch, 2012) remains unknown because of the way in which they are preserved, and no facets similar to the complex joint in AMNH FARB 33054 have yet been described in any other taxon.

Jugal-quadratojugal contact: In AMNH FARB 33054, *Turiasaurus*, *Giraffatitan*, and *Nemegtosaurus*, the jugal overlaps the quadratojugal laterally. There are distinct facets on the medial surface of the jugal in *Giraffatitan* (Janensch, 1935) and *Turiasaurus* (Royo-Torres and Upchurch, 2012), and on the lateral surface of the quadratojugal in both *Giraffatitan* and *Nemegtosaurus* (Janensch, 1935; Wilson, 2005). It is possible that an equivalent facet is also present on the medial surface of the jugal in *Nemegtosaurus*, but that area is covered by matrix (Wilson, 2005). The facets on the jugals of *Giraffatitan* and *Turiasaurus* are dorsally bordered by a distinct crest, and have a roughened surface (*Giraffatitan*; Janensch, 1935), or form a distinct groove (*Turiasaurus*; Royo-Torres and Upchurch, 2012), whereas the one in AMNH FARB 33054 bears a vertical crest posterior to the facet and is relatively smooth. In contrast to the taxa mentioned above, quadratojugals of *Camarasaurus* expand anteriorly and cover the jugals laterally (Madsen et al., 1995).

Jugal-lacrimal contact: A distinct facet on the medial side of the anterior process of the jugal of *Giraffatitan* and *Europasaurus* (Janensch, 1935; Marpmann et al., 2015: fig. 5B, D) shows that the jugal overlaps the ventral end of the lacrimal laterally, similar to *Camarasaurus* (White, 1958; Madsen et al., 1995) and AMNH FARB 33054. In *Giraffatitan*, an additional small but distinct facet for the articulation with the lacrimal lies on the lateral surface of the anterior process of the jugal, above the articular facet for the maxilla. Both of these facets in *Giraffatitan* have a rough surface (Janensch, 1935). The lacrimal of *Giraffatitan* therefore has two ventral processes that extend anterolaterally and posteromedially from the main shaft of the lacrimal, overlapping the jugal laterally and medially, respectively (Janensch, 1935: abb. 21).

A similar condition appears to occur in *Galeamopus pabsti* (Tschopp and Mateus, 2017: fig. 4), and could be the case in the closely related AMNH FARB 33054, but this cannot be determined without further preparation or high-resolution CT-scanning. *Turiasaurus* bears a dorsoventrally oriented facet on the lateral surface of the dorsal process of the jugal, implying that the lacrimal overlapped the jugal laterally (Royo-Torres and Upchurch, 2012), but no facet for the lacrimal was recognized on the medial surface.

Implications for Definition of Diagnostic Features and Reconstructions

The external surfaces of sauropod skulls are generally better preserved and preferentially prepared relative to the internal ones; consequently, they are often the only surfaces readily accessible for morphological study. Therefore, diagnostic features recognized in the skull are mostly from the external surface, although this is rarely specified. The participation of the jugal in the margin of the antorbital fenestra is a good example here. Recovered as a synapomorphic feature for Diplodocidae (Upchurch, 1998) or Diplodocoidea (Tschopp et al., 2015), this contribution is only visible in lateral view, because thin sheets of the maxilla and lacrimal cover the jugal medially to an extent that they contact each other along the antorbital fenestra (see above). Also, features like the dorsal projection on the anterior process of the quadratojugal, recognized in the diplodocids AMNH FARB 33054 and *Galeamopus pabsti* SMA 0011, might represent diagnostic characters but are not recognized as such because they are not exposed laterally. In fact, no such dorsal projection occurs in disarticulated quadratojugals of *Turiasaurus*, *Camarasaurus*, *Europasaurus*, and *Euhelopus* (Madsen et al., 1995; Royo-Torres and Upchurch, 2012; Poropat and Kear, 2013; Marpmann et al., 2015), indicating that the projection might be a unique feature in diplodocoids or a less inclusive clade. Thus, there seems to be a large amount of previously overlooked variation and morphological information that might be useful for phylogenetic analyses (table 1), and that should be considered in functional analyses (see below). Also, it is crucial to highlight in diagnoses and phylogenetic characters, in which view a certain feature can be recognized so that incomplete finds, visible in one view only, are not identified incorrectly.

Sauropod skull reconstructions are routinely drawn in lateral view (Janensch, 1935; McIntosh, 1990; Calvo, 1994; Wilson and Sereno, 1998; Christiansen, 2000; Mateus and Tschopp, 2017; Moore et al., 2018). Although this makes intuitive sense, the extensive bone overlaps and complex joints among the facial elements described herein and elsewhere, make accurate representations of the extent of any single bone in a reconstruction of an articulated skull difficult. Moreover, the thin sheets of bone that form the lap and/or clasp joints between bones are easily broken. It is therefore possible that mounted skulls based on disarticulated elements (even if associated), such as *Galeamopus pabsti* SMA 0011 (Tschopp and Mateus, 2017), show parts of the lateral surface of bones that would normally be hidden if the overlapping element were complete. This impacts the accuracy of reconstructions and further demonstrates why characters should not be coded from anything but photographs, scans or personal inspection.

TABLE 1. Distribution of suture types and other features in facial skull elements among selected sauropod taxa.

		Sutures				Features	
		maxilla -jugal	maxilla-quadratojugal	jugal-quadratojugal	jugal-lacrimal	facet on jugal	dorsal projection on quadratojugal
Nonneosauropod Eusauropoda	*Turiasaurus*	jugal clasps maxilla	broad contact	jugal covers quadratojugal laterally	lacrimal covers jugal laterally	delimited by horizontal crest dorsally, forms groove	absent
	Mamenchisaurus	maxilla covers jugal laterally	contact zone of intermediate size	?		?	?
Macronaria	*Bellusaurus*	jugal likely clasps maxilla	?	?		?	?
	Camarasaurus	maxilla clasps jugal	short contact	quadratojugal covers jugal laterally	lacrimal covers jugal medially or clasps it	?	absent
	Europasaurus	maxilla covers jugal laterally	no contact	?	lacrimal covers jugal medially or clasps it	?	absent
	Giraffatitan	maxilla covers jugal laterally	no contact	jugal covers quadratojugal laterally	lacrimal clasps jugal	delimited by horizontal crest dorsally, roughened surface	?
	Nemegtosaurus	maxilla covers jugal laterally	broad contact	jugal covers quadratojugal laterally		?	?
Diplodocoidea	AMNH FARB 33054	maxilla clasps jugal	broad, complex contact with both elements overlapping each other in different points	jugal overlaps quadratojugal laterally	lacrimal covers jugal medially or clasps it	delimited by vertical crest posteriorly, roughened surface	present
	Galeamopus	?	?	jugal overlaps quadratojugal laterally	lacrimal clasps jugal	?	present

Functional Significance

The shape of the bone overlap between the maxilla and its adjacent bones (quadratojugal, jugal, lacrimal) indicates that minimal amounts of forward sliding movement was possible at the junction of these elements, which were likely held together by ligaments (Upchurch and Barrett, 2000). The horizontal crests delimiting the facets on the maxilla dorsally and on the quadratojugal ventrally likely inhibited dorsoventral shearing and rotation. The vertical steplike transition delimiting the facet on the jugal posteriorly, as well as the anterior portion of the bifurcated posterior margin of the maxilla, would have helped to resist compression and restrict backward movement. However, it is possible that the maxilla could be slightly dislocated anteriorly in respect to its adjacent bones. Such a dislocation has happened postmortem (fig. 2), amounting to a horizontal distance of approximately 11 mm, or approximately 2% of the entire skull length. Given the otherwise excellent preservation of the material, we hypothesize that this represents the maximum stretching distance of the ligaments or slightly more than what was possible during life. Although it is unlikely that this stretching movement could have been actively controlled (implying some kind of cranial kinesis), because of the reduced attachment sites of protractor muscles that would be needed for an active movement on the pterygoid in diplodocids (Holliday and Witmer, 2008; Young et al., 2012), it seems plausible that the overlapping joints of the maxilla and its posteriorly adjacent bones in diplodocids functioned to passively dissipate stress during feeding, as occurs in ratites (Gussekloo and Bout, 2005; Holliday and Witmer, 2008). Such movement would have been facilitated by the lack of an internarial bar, which is a synapomorphy of Flagellicaudata (Janensch, 1935; Upchurch et al., 2004; Harris, 2006; Tschopp et al., 2015). The articulation between the posterior ascending process of the maxilla and the skull roof in diplodocids is an overlapping suture, where the maxilla primarily overlaps the lacrimal laterally (Tschopp and Mateus, 2017). Internally, the snout is connected with the palatal complex through relatively tight sutures (McIntosh and Berman, 1975; Whitlock et al., 2010), meaning that the palate likely moved in tandem with the snout. The likely synovial basipterygoid-pterygoid joints (Holliday and Witmer, 2008) and the overlapping pterygoid-quadrate joint (McIntosh and Berman, 1975; Whitlock et al., 2010; Tschopp and Mateus, 2017) probably allowed for limited movement.

Similar "shock absorbing" overlapping joints that allowed sliding movements have been reported in other dinosaurs, like the theropod *Allosaurus* (Rayfield, 2005) and nonsauropod sauropodomorphs (Barrett and Upchurch, 2007). In diplodocids, slight forward movements of the snout would have alleviated the degree of stress placed on the teeth—and the lateral plate that covered them labially—when feeding was performed through backward movement of the skull. This would support interpretations of branch-stripping or raking through low-level vegetation as the main feeding strategies of diplodocid sauropods (Barrett and Upchurch, 1994; Whitlock, 2011; Young et al., 2012). However, it is important to note that branch-stripping has recently been questioned in diplodocids, because propalinal movements of the lower jaw (proposed to be necessary for this feeding strategy by Barrett and Upchurch, 1994) appear to be incompatible with the morphology of the jaw joint (Whitlock, 2017). Additional information and potentially more detailed models will be needed to solve the question of diplodocid feeding entirely.

CONCLUSIONS

An exquisitely preserved new skull of a diplodocid sauropod from the Upper Jurassic Morrison Formation provides unique insights into the morphology of the medial surface of the facial elements. Articulations between the maxilla and posteriorly adjacent bones form complex patterns of overlapping joints. These extensive overlaps result in considerably different contact zones between the bones compared to those visible on the lateral and medial surfaces. Potentially diagnostic features can be hidden either laterally or medially, so that the definition of diagnostic and phylogenetic characters should always include the view in which they can be observed. The articular facets on the maxilla, quadratojugal, jugal, and lacrimal restrict movements dorsoventrally and posteriorly but appear to allow anterior dislocation of the maxilla as a shock-absorbing mechanism during branch-stripping.

ACKNOWLEDGMENTS

We thank Amanda Millhouse and Matthew Carrano (USNM) for the loan of USNM V 2673. Specimen access to other diplodocid skulls was facilitated by Hans-Jakob Siber (SMA), Matthew Lamanna, Amy Henrici, and Dan Pickering (CM), and Dan Brinkman and Jacques Gauthier (YPM). Enrica Sarotto (New York) provided invaluable support during the collection visit to CM. Many thanks to Mike Eklund (University of Texas at Austin) and Mick Ellison (AMNH) for the photographs we used in our figures. We also thank the Wyoming Field Office of the BLM in Worland for their support and the entire team of the excavations in Wyoming in 2016, which produced the new diplodocid skull. A special thanks goes to Amy Davidson (AMNH) for the beautiful preparation of the skull, without which these features would not have been visible. The excavations were done under the BLM permit PA16-WY-256. Stephen Poropat and José Carballido provided very helpful reviews.

E. Tschopp currently holds a Theodore Roosevelt Memorial Fund and Division of Paleontology Postdoctoral Fellowship by the Richard Gilder Graduate School at American Museum of Natural History.

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