

A PREVIOUSLY UNREPORTED FORM OF DORSAL RIB PNEUMATICITY IN *APATOSAURUS* (DINOSAURIA: SAUROPODA) AND IMPLICATIONS FOR PNEUMATIC VARIATION AMONG DIPLODOCID DORSAL RIBS

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ABSTRACT—Postcranial pneumaticity is interpreted as a weight saving adaptation in sauropod dinosaurs, especially in the vertebral column. In some derived sauropods pneumatic features also occur on vertebral ribs. While pneumatic ribs are considered diagnostic of the clade Titanosauriformes, they are also infrequently found in diplodocid sauropods. Here, we describe a partial dorsal rib IV or V referable to *Apatosaurus* sp. that exhibits a series of superficial pneumatic fossae along its posterior surface. These fossae differ from the morphology found in other pneumatic dorsal ribs of diplodocids, including other apatosaurines and *Supersaurus*. Moreover, the pneumatic features of this rib are more distally located from the capitulum and tuberculum than in other diplodocids and titanosaurs. Based on our findings, we propose that rib pneumaticity among apatosaurine sauropods (and potentially all diplodocids) is individually variable, in addition to being a function of ontogeny. More broadly, we conclude that rib pneumaticity among diplodocids is morphologically variable when present and individually expressed rather than being ubiquitous throughout the clade. Our findings are consistent with the hypothesis that pneumatic ribs evolved independently between Diplodocidae and Titanosauriformes and make for poor clade-level characters among diplodocids.

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INTRODUCTION

Pneumatization of the postcranial skeleton by diverticula of the respiratory system is pervasive among sauropod dinosaurs (Janensch, 1947; O'Connor, 2006; Wedel, 2003b, 2005), and this has been hypothesized to be a crucial factor in the evolution of large body size and long necks in sauropods (Sander, 2013; Sander et al., 2011). Along the sauropod axial skeleton, pneumatic structures include external fossae and internal chambers in the cervical, dorsal, sacral, and caudal vertebrae. These fossae are indicative of where diverticula of the lungs or cervical and abdominal air sacs invaded the bones (Britt, 1993; Wedel, 2003b, 2005; Wedel & Taylor, 2013). Likewise, dorsal ribs of sauropods sometimes preserve fossae and foramina that are interpreted as being part of this pneumatic system. Rib pneumatic features are most often expressed as a cavity along the posterior surface of the rib head near the junction of capitulum and tuberculum, which may be a fossa or a similarly located foramen

leading to an internal cavity (Janensch, 1950; Wedel, 2005). The formation of these dorsal rib foramina is homologous to those found in the postcranial skeletal of extant birds where a pneumatic diverticulum advances opportunistically into surrounding bone (Britt, 1993; O'Connor, 2006).

Whereas pneumatic fossae and foramina are pervasive in the presacral vertebrae of eusauropods, and common in the sacral and caudal vertebrae of neosauropods (e.g., *Euhelopus*, *Brachiosaurus*; Wedel, 2003a, 2005; Wedel and Taylor, 2013; Wilson et al., 2011), pneumatic dorsal ribs are much less common among sauropods, and to date have only been found in the mamenchisaurid *Xinjiangtitan* (Zhang et al., 2022) and some members of Neosauropoda. Pneumatic dorsal ribs are apomorphic for the macronarian clade Titanosauriformes (Wedel, 2005; Wilson & Sereno, 1998; Woodward & Lehman, 2009) with pneumatic ribs present among brachiosaurids (Carpenter & Tidwell, 2005; Janensch, 1950; Riggs, 1904; Tidwell & Wilhite, 2005), early diverging sornphospondyls (Canudo et al., 2008; Carballido et al., 2011; Poropat et al., 2016; Rose, 2007; Taylor et al., 2011; Wilson & Sereno, 1998), and many other basally branching and derived titanosaurs (Cerdeña et al., 2012; D'Emic, 2013; Díez Díaz et al., 2013; Filippi et al., 2011; Gomani, 2005; González-Riga & David, 2014; Gorscak et al., 2014, 2017; Gorscak & O'Connor, 2019; Hocknull

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et al., 2009; Lacovara et al., 2014; Malkani, 2003; Rogers, 2009; Woodward & Lehman, 2009). Other groups of neosauropods, such as rebbachisaurids and early diplodocids, have pneumatic dorsal ribs (Fernández-Baldor et al., 2011; Wedel, 2005). Pneumaticity in the dorsal ribs of derived diplodocids is limited to *Supersaurus* (Lovelace et al., 2003) and apatosaurines. The right dorsal rib II of CM 3018, the holotype of *Apatosaurus louisae*, bears a “large foramen that leads to an internal cavity” (i.e., invasive) on the anterior surface between the capitulum and tuberculum (Gilmore, 1936:212 and pl. 29). A dorsal rib referred to *Brontosaurus excelsus* by Marsh (1896) is illustrated with pneumatic openings on both the anterior and posterior surfaces of the tuberculum, similar to one of the dorsal ribs of *Giraffatitan* (Janensch 1950). The rib illustrated by Marsh (1896) was discovered by itself and may belong to a brachiosaur rather than a diplodocid (Carpenter and Tidwell, 2005). Wedel (2005) notes that pneumatic dorsal ribs evolved independently in both diplodocids and titanosauriforms but are more prominently found amongst titanosauriforms. The presence – or lack – of pneumatic features on diplodocid dorsal ribs and the variability in their pneumatic morphology is different from the ubiquity of pneumatic features in titanosauriforms. Again, as suggested by Wedel (2005), this variability in diplodocid pneumatic features makes for a poor diagnostic feature.

The Upper Jurassic Morrison Formation has provided thousands of bones referable to diplodocid genera over the past 150 years. Despite the intensity of collecting, few instances of rib pneumaticity have been reported in diplodocids from the Morrison Formation (Gilmore, 1936; Lovelace et al., 2007; Marsh, 1896). Herein we describe a series of superficial pneumatic fossae in MWC 9617, a dorsal rib of *Apatosaurus* sp., and also document for the first time pneumatic foramina in the dorsal ribs of YPM 1980, the holotype of *Brontosaurus excelsus*. The specimens in this study give new insights into the evolution of dorsal rib pneumaticity within Diplodocidae, individual pneumatic variation among sauropods, new anatomical data for *Apatosaurus*, and the morphology of pneumatic morphologies in the dorsal ribs of sauropods.

Institutional Abbreviations—MWC, Museums of Western Colorado, Grand Junction, CO, U.S.A.; WDC, Wyoming Dinosaur Center, Thermopolis, WY, U.S.A.; YPM, Yale Peabody Museum, New Haven, CT, U.S.A.

GEOLOGICAL SETTING

Specimen MWC 9617 was recovered from the Mygatt-Moore Quarry (MMQ; further described in McHugh et al. [2020]) west of Fruita, Colorado under BLM paleontological permit number COC76588. Located at the northern edge of the Uncompahgre uplift in western Colorado, MMQ lies within the Brushy Basin Member of the Upper Jurassic Morrison Formation. Geochronological analysis of ashfall zircons at the site returned a

TABLE 1. Length, width, and depth measurements taken from the total pneumatic area and individual fossae present along MWC 9617. Measurements were made with digital calipers with a 0.01-millimeter precision along the fossae’s longest and widest points and at the fossae’s deepest points. All measurements in millimeters. MPM (maximum pneumatic metrics), the total length of the sulcus that contains pneumatic fossae and the maximum width and depth of the fossae.

	Max. Length	Max. Width	Max. Depth
MPM	133.02	27.93	5.46
Proximal Fossa	34.90	27.93	5.46
Middle Fossa	29.21	21.11	3.53
Distal Fossa	46.68	15.68	1.99

maximum depositional U/Pb age of 152.18 ± 0.29 Ma (Trujillo et al., 2014). The quarry is above the local “clay change” that denotes the approximate middle of the Brushy Basin in the Colorado Plateau within a light gray, silty smectite mudstone (Turner & Peterson, 2004). The quarry mudstone is 1–2 m thick within the site and varies from laminated to medium-bedded, with increasing silt content stratigraphically higher in the quarry. Carbonized plant remains are abundant throughout the quarry. Small, 1 cm wide interference ripples and gastropod fossils are found stratigraphically high in the quarry above the bone bed, while larger dinosaurian fossil material is concentrated in the lower sections (Foster et al., 2018). The site is interpreted to represent an attritional overbank deposit with a high water table, potentially ephemeral ponds during wet periods (Foster, 2013; Foster et al., 2018). Vertebrate fossils from the site are generally well-preserved with many being pristine and with intact delicate structures and cortical tissue frequently being present (Kirkland & Carpenter, 1994). However, over 37% of the vertebrate fossils recovered from MMQ preserve taphonomic traces, indicating a large portion of the assemblage experienced prolonged surface exposure prior to burial (Drumheller et al., 2020; McHugh et al., 2020).

YPM 1980 is the holotype partial skeleton of *Brontosaurus excelsus* (Marsh, 1879), from Como Bluff. The history and geological setting of the specimen are ably covered elsewhere (e.g., Foster, 2020; Ostrom & McIntosh, 1966, and references therein) and we will not discuss them further.

DESCRIPTION

Apatosaurus sp. MWC 9617

Specimen MWC 9617 consists of the head and partial midshaft sections of a dorsal rib that may be associated with each other, but lack of a precise fit, and the disarticulated nature of specimens in the MMQ make a definitive association difficult for these elements. For this reason, we focus solely on the proximal head of the rib (Fig. 1). The tuberculum is anteroposteriorly compressed and forms a thin, blade-like process that projects medially and deflects posteriorly. When viewed anteriorly, the capitulum is roughly rectangular in shape and is slightly damaged along its ventral margin, thus obscuring its articular surface. The tuberculum is a subrounded process that is both shorter and thicker than the capitulum. Dorsally, the tuberculum is oval in cross section with a rugose articular surface. The capitulum overhangs the tuberculum with a right angle being formed between the two processes. A thin, partially damaged capitulotubercular lamina connects the capitulum and tuberculum. The partial midshaft section of the rib is roughly T-shaped in cross section. The proximal end of the shaft does not fit with the broken edge of the distal end of the rib head. Unlike the proximal end of the rib, the shaft lacks unique characters. Neither the capitulum nor the tuberculum have enough information to narrow the taxonomic identity of MWC 9617 beyond *Apatosaurus*.

Within the sulcus of MWC 9617, the three fossae are separated by two bony elevations, of which the distal one is less prominent. There are three deep fossae on the posterior surface of the proximal portion of the rib within a sulcus that extends the preserved length of the rib (Fig. 1). All three fossae are distal to the capitulum and tuberculum. The first fossa, located proximally below the joining of the capitulum and tuberculum, is deep and roughly in the shape of an inverted triangle (Fig. 1; Table 1). Below the proximal fossa lies the middle fossa that is subrectangular in shape with a smaller diameter than the proximal fossa (Fig. 1; Table 1). The final, distal fossa is roughly ovalar in shape with the distal portion of the oval oriented towards the shaft of the rib (Fig. 1). The distal fossa is shallower than the proximal and middle fossae with it being shallowest at its

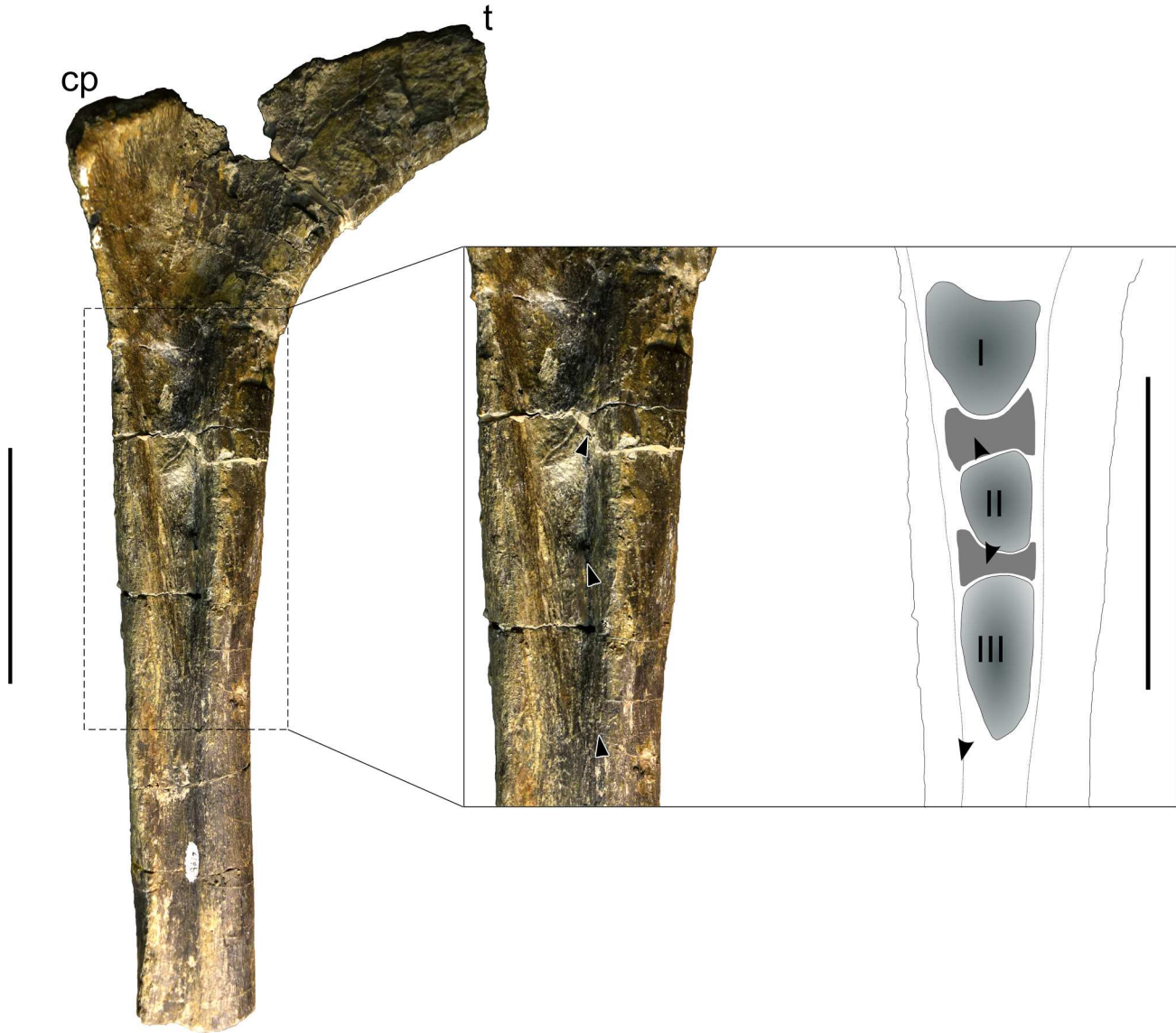


FIGURE 1. Proximal rib head that comprises MWC 9617 in posterior view. The inset image depicts a line drawing of the section of the rib that preserves pneumatic fossae within the rib canal sulcus. **Abbreviations:** cp, capitulum; I, proximal pneumatic fossa; II, middle pneumatic fossa; III, distal pneumatic fossa; t, tuberculum. Scale bar equals 5 cm.

distalmost point. The fossae become shallower distally (Table 1). There are no rough or worn edges present along the lateral margins of the fossae to suggest that they were encased in bone prior to death and then later exposed due to pre- or post-burial taphonomic processes. These fossae described here do not extend to the partial midshaft.

Brontosaurus excelsus YPM 1980

We also had the opportunity to study YPM 1980, the holotype of *Brontosaurus excelsus* (as defined by Tschopp et al., 2015), while it was unmounted for additional preparation and re-mounting by Research Casting International. Left rib I and right rib II are both pneumatic (Fig. 2). In left rib I, the posterior surface of the tuberculum bears an oval pneumatic fossa. The fossa is approximately 7 cm tall dorsoventrally and 4 cm wide mediolaterally, and it contains a foramen that penetrates laterally into the bony corpus of the tuberculum. A

second fossa, which lacks a foramen, is present more distally on the posterior surface of the rib, where the rib head blends into the shaft.

A similar proximal fossa and foramen are present on the posterior surface of the tuberculum of right rib II. The pneumatic fossa is 9.5 cm tall dorsoventrally, but its original mediolateral width is impossible to determine because of poor preservation and heavy reconstruction of that portion of the rib during its initial preparation. Owing to poor preservation, it is impossible to determine if a distal fossa like that of left rib I was present in right rib II. In each rib the proximal pneumatic foramen is a narrow slit, much taller than wide, and this does not appear to be the result of taphonomic distortion.

DISCUSSION

We interpret MWC 9617 as most likely belonging to the genus *Apatosaurus* for a few reasons. First, *Apatosaurus* is the most

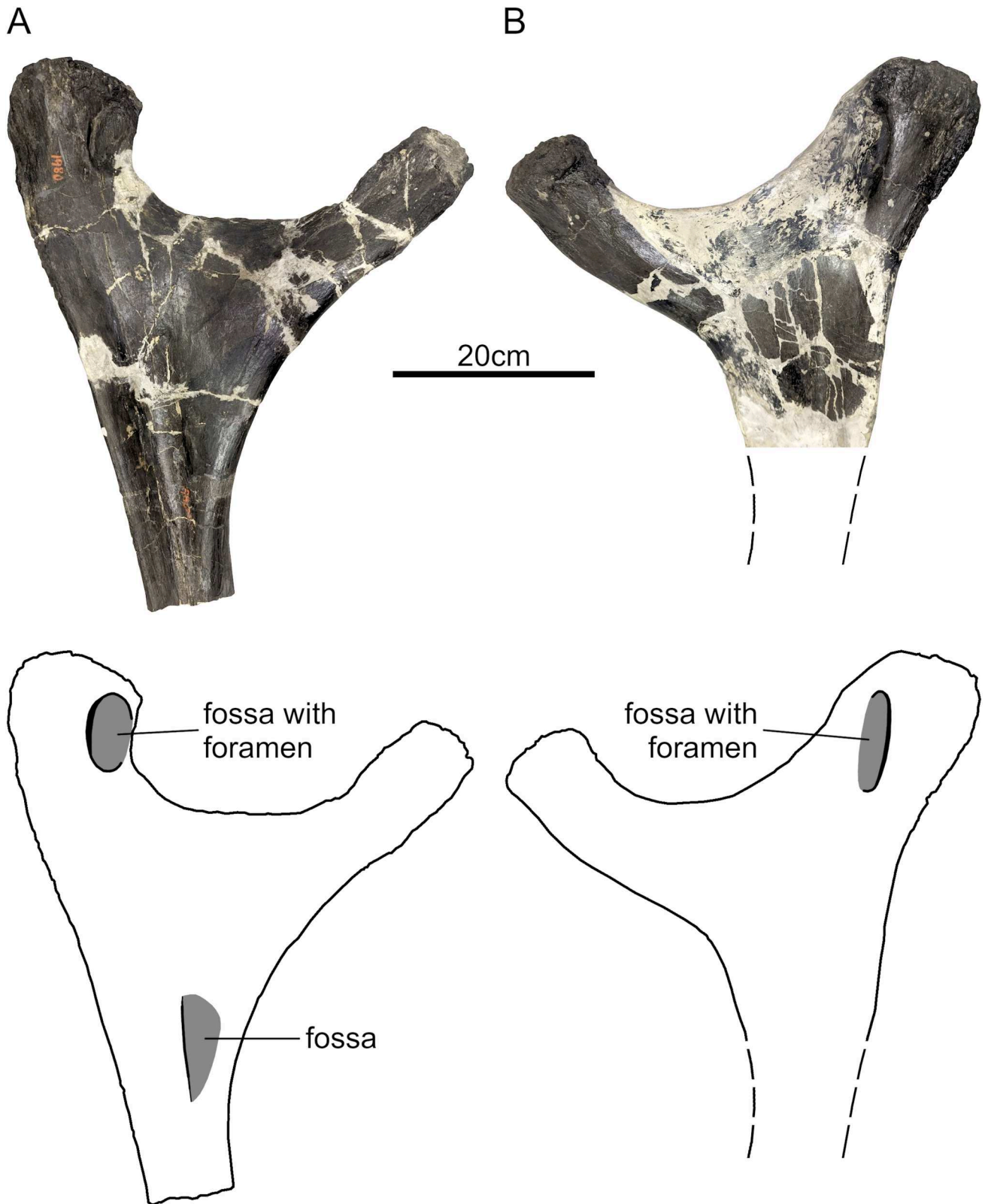


FIGURE 2. **A**, left rib I, and **B**, right rib II of YPM 1980, the holotype of *Brontosaurus excelsus*, in posterior view.

common sauropod genus recovered from MMQ (Foster et al., 2018); other sauropods from the quarry include *Camarasaurus* and an indeterminate diplodocine. Although the capitulum and tuberculum of both *Apatosaurus* and *Camarasaurus* are

dichocephalous and roughly sub-rectangular in shape, there are some differences between the dorsal rib anatomy of *Camarasaurus* and MWC 9617. Waskow and Sander (2014) demonstrate that the *Camarasaurus* capitulum is proportionally more gracile

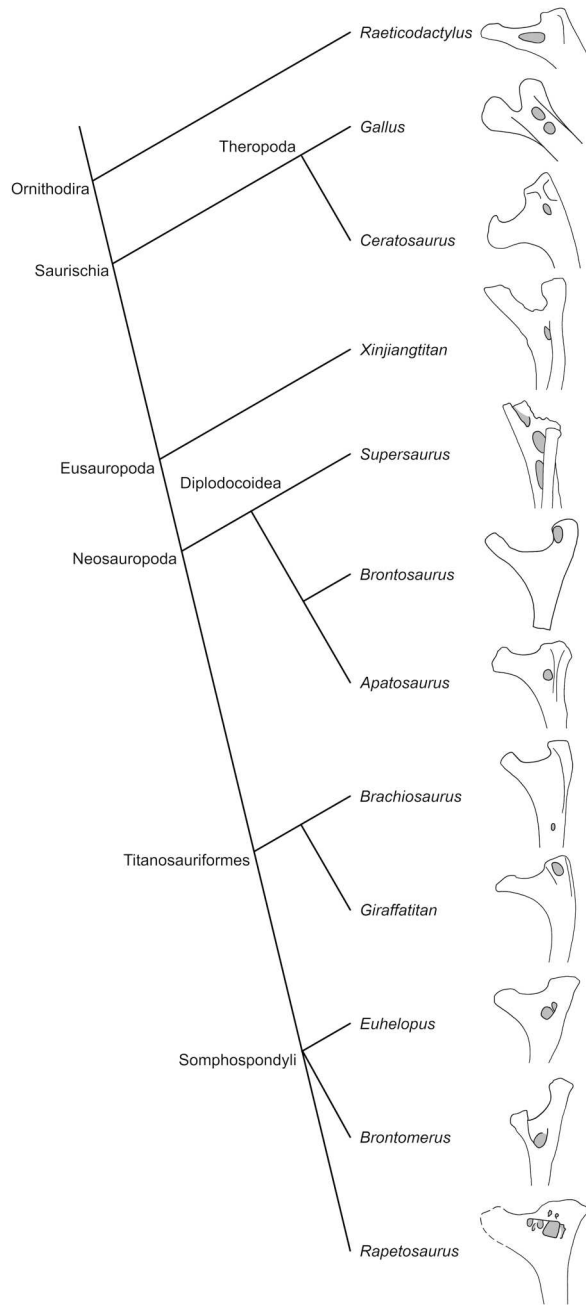


FIGURE 3. Pneumatic dorsal ribs in a selection of ornithodiran taxa. Clades that lack pneumatic ribs have been omitted, including non-dinosaurian dinosauriforms, ornithischians, all early diverging sauropodomorphs, and numerous sauropods. The only included clade for which dorsal rib pneumaticity might be synapomorphic is Titanosauriformes. Phylogenetic relationships of the sauropods are based on Mannion et al. (2013) for titanosauriforms (note that the position of *Brontomerus* is uncertain), Tschopp et al. (2015) for diplodocoids, and Zhang et al. (2022) for *Xinjiangtitan*. Ribs are not shown to scale. Ribs traced from Butler et al. (2009:fig. 1b, *Raeticodactylus*), Campana (1875:fig. 8, *Gallus*), Madsen Jr. and Welles (2000:plate 19, *Ceratosaurus*), Zhang et al. (2022:fig. 14, reversed, *Xinjiangtitan*), a photo of WDC-DMJ-021-134 provided by David Lovelace (*Supersaurus*; see Lovelace et al., 2007), Gilmore (1936:plate 29, reversed, *Apatosaurus*), Riggs (1904:plate 75, *Brachiosaurus*), Janensch (1950:fig. 108, reversed, *Giraffatitan*), Wilson and Upchurch (2009:fig. 21, reversed, *Euhelopus*), Taylor et al. (2011:fig. 7, *Brontomerus*), and Curry-Rogers (2009:fig. 30, *Rapetosaurus*).

than the tuberculum and has a prominent ridge that originates near the tuberculum and extends distally. MWC 9617 has a capitulum that is more comparable to the tuberculum in size.

Moreover, the ridge along the anterior surface of MWC 9617 is sinuous and deflects towards the capitulum as it extends along the rib head, unlike the straight ridge figured for *Camarasaurus* by Waskow and Sander (2014). Also, the tuberculum of *Apatosaurus ajax* is noted to be morphologically different from that of *Camarasaurus lewisi* in a couple of notable ways. *A. ajax* has a tuberculum that is described as having a posterolateral edge that strongly projects posteriorly in its anterior dorsal ribs (Upchurch et al., 2004). *Camarasaurus* species – such as *C. supremus* (Osborn & Mook, 1921) and *C. lewisi* (McIntosh et al., 1996) – are not described nor imaged as having any form of deflection along their tubercula. Furthermore, the location of the tuberculum in relation to the capitulum gives further information about the location of MWC 9617 in the dorsal rib series. Upchurch et al. (2004) notes that the posterior deflection of the tuberculum is present along the anterior ribs of *A. ajax*. The anterior series of ribs of *A. ajax* (ribs I–V) are characterized by having the capitulum and tuberculum at approximately the same level when viewed anteriorly or posteriorly until rib III onward where the tuberculum dips below the plane of the capitulum (Upchurch et al., 2004:fig. 2). The point where the tuberculum dips below the plane of the capitulum differs in *C. supremus* and *C. lewisi*. In *C. supremus*, the tuberculum does not noticeably dip below the plane of the capitulum until dorsal rib VI (Osborn & Mook, 1921:plate LXXVIII–LXXXI). The tuberculum's location relative to the capitulum of *C. lewisi* is closer to that of *A. ajax* where the tuberculum is lower than the capitulum in dorsal rib V depending on how the ribs are viewed, but the tuberculum does not reliably sink below the plane of the capitulum until dorsal rib VI (McIntosh et al., 1996:figs. 6–8). While we cannot make a species-level diagnosis based on the capitular and tubercular anatomy, we consider MWC 9617 to belong to an indeterminate species of *Apatosaurus* based on the presence of a posteriorly deflected tuberculum on an anterior dorsal rib. Secondly, the only Morrison Formation sauropods for which pneumatic dorsal ribs have been reported are the apatosaurines *Apatosaurus* and *Brontosaurus* (Gilmore, 1936; Marsh, 1896), *Brachiosaurus* (Riggs, 1904), and *Supersaurus* (Lovelace et al., 2007). Given that the invasive pneumatic structures of *Brachiosaurus* and *Supersaurus* are inconsistent with those found in MWC 9617 (see below) and neither taxon is known from MMQ, and that dorsal rib pneumaticity is not known in *Camarasaurus* or any of the Morrison diplodocines, the presence of a probable pneumatic fossa on MWC 9617 is most consistent with an apatosaurine identification. Using the classification of *Apatosaurus* ribs proposed by Upchurch et al. (2004:35–38), we interpret MWC 9617 as the left anterior dorsal rib IV or V based on the prominence of the capitulum when compared with the tuberculum.

The three fossae are not pathological as they lack prominent or irregular enlargement of the bone surrounding the fossae (Tan et al., 2022), pathological remodeling (Xing et al., 2018), or overgrowth of the bone surrounding the fossae or bony partitions (Tschopp et al., 2014). While the fossae are similar to some pathological pitting that has been observed on other sauropod and sauropodomorph bones (see figures in Tan et al. [2022] and Xing et al. [2018]), the borders of the fossae are smooth rather than abrupt or raised, have a surface texture that reflects more light when compared with the bone outside of the fossae, and are not indicative of ailments such as osteochondritis (Tschopp et al., 2014). Rather, the three fossae and the bony ridges form a regular motif commonly observed in pneumatic-related structures of sauropods. Similar examples in other taxa include regularly spaced pneumatic foramina in a cervical vertebra of *Paluxysaurus* (Rose 2007:fig. 10, Wedel, 2003b:fig. 10b) and pneumatic ‘webbing’ in the dorsal ribs of some titanosaurs (see below) that look aesthetically similar to those found along MWC 9617. Wilson (1999) coined the term ‘subfossae’ for these ‘fossae within fossae.’ In summary, the row of fossae on

MWC 9617 are consistent with accepted pneumatic features in both location and morphology.

These pneumatic features differ, however, from those on typical diplodocid and titanosaur dorsal ribs (Fig. 3). In sauropod ribs, pneumatization is most frequently expressed as a single foramen on the posterior surface, which is located ventrally between the capitulum and tuberculum (e.g., González-Riga & David, 2014). Morphologically, the pneumatic excavations of MWC 9617 manifest as three separate fossae rather than a single opening on the surface of the rib (Fig. 1). The linearly repeating fossae present in MWC 9617 are similar to the “capitulum-tubercular webbing” in the dorsal ribs of some titanosaurs (Gorscak et al., 2014; Gorscak & O’Connor, 2019), albeit at a larger spatial scale. Interestingly, Gorscak et al. (2014) identify superficial pneumatic fossae along a dorsal rib of *Rukwatitan* that are morphologically similar (albeit it on the anterior surface) to those along MWC 9617, but also identifies an invasive pneumatic foramen at the base of the capitulum and tuberculum on the posterior surface (Gorscak et al., 2014:fig. 8C, D). This supports a degree of variability of pneumatic features in titanosauriforms as we propose for diplodocids. A similar pair of fossae separated by a bony ridge are present in a dorsal rib of *Astrophocaudia* (D’Emic, 2013), although the repeating fossae in MWC 9617 are located more distally along the rib. All of these examples are consistent with the description of subfossae, or fossae-within-fossae, as defined by Wilson (1999).

The separate subfossae in MWC 9617 could represent different waves of pneumatization by a single ramifying diverticulum, or the impression of multiple lobes of a single complex diverticulum, like the large vertebral diverticula in extant ostriches. None of the three fossae present along MWC 9617 are enclosed by bone, suggesting that they would have been open directly to the chest cavity rather than covered (Fig. 1), which could represent pneumatization of the rib by diverticula of the respiratory system (Müller, 1907). Moreover, the fossae formed by diverticula impressions along MWC 9617 are located distally from the rib head along the neck of the rib (Figs. 1, 3) rather than just below the junction of the capitulum and tuberculum. The location of the diverticula is more reminiscent of those found in *Giraffatitan* (Janensch, 1950) rather than other diplodocids (e.g., Lovelace et al., 2003), somphospondyls (e.g., Wilson & Upchurch, 2009), or titanosaurs (e.g., Rogers, 2009), though distinct in morphology. Based on this, we conclude that pneumatic morphologies found in dorsal ribs are potentially highly variable within apatosaurines and are not bound to proximal or distal locations of the rib head.

Together with CM 3018, the holotype of *Apatosaurus louisae*, YPM 1980 shows that dorsal rib pneumaticity was present in at least some members of both the *Apatosaurus* and *Brontosaurus* lineages. The seemingly random occurrences of diverticula within the dorsal ribs of apatosaurines cannot be explained as a sampling bias because rib anatomy from multiple individuals of many diplodocids has been published multiple times in great detail (e.g., Gilmore, 1936; Marsh, 1877; Lovelace et al., 2003; Tschoop et al., 2015; Upchurch et al., 2004) with pneumatic ribs repeatedly being a rarity. Schwarz et al. (2007) suggest that the lack of pneumatic foramina on a juvenile diplodocid specimen (SMA 09) could be due to its ontogenetically immature stage, where pneumatic structures become better developed in ontogenetically older individuals. The specimen studied here, MWC 9617, is from a large, assumedly subadult to mature diplodocid based on its size. The variable presence of such well-developed pneumatic fossae in this specimen of *Apatosaurus* sp., as well as in the large *Apatosaurus* specimen described by Gilmore (1936), may indicate other, non-ontogenetic sources of variation. Although the Gilmore (1936) specimen and MWC 9617 may be from similarly aged individuals, the morphology of the pneumatic structures is quite variable between the two

specimens, and largely absent among the published dorsal ribs of other apatosaurines. Therefore, we suggest that the pneumatization of apatosaurine dorsal ribs is heavily influenced by individual variation in addition to ontogeny. Pneumatic variation among apatosaurine individuals is further supported by CM 3018 (Gilmore, 1936) in which a foramen leading to an internal cavity is both a different morphology (foramen vs. subfossae) and is present on the anterior surface of a dorsal rib, whereas the pneumatic traces in MWC 9617 and YPM 1980 are present on the posterior surfaces of the ribs. However, we cannot rule out the possibility that dorsal rib pneumaticity is rare amongst apatosaurine sauropods but remains a diagnosable character for *B. excelsus*. This possibility remains uncertain until *B. excelsus* dorsal ribs are more closely investigated. In contrast, pneumatic foramina morphologies and locations are more standardized in titanosaur ribs – i.e., a single foramen or pneumatic webbing between the capitulum and tuberculum (Gonzalez-Riga & David, 2014; Gorscak et al. 2014). Individual variation would also account for why dorsal rib pneumaticity is rare outside of Titanosauriformes, and variable in morphology when it is present. Assuming that we are correct in referring MWC 9617 to *Apatosaurus*, our findings are consistent with the suggestion that dorsal rib pneumaticity evolved independently in Diplodocidae and Titanosauriformes (Wedel, 2005). Due to the low frequency of expression and high variability in location and morphology of pneumatic traces within the dorsal ribs of apatosaurine sauropods, pneumatization of dorsal ribs should not be considered a clade-level character as proposed by Lovelace et al. (2007).

CONCLUSION

Here, we describe a series of three superficial pneumatic fossae from a proximal left dorsal rib IV or V fragment from *Apatosaurus* sp. Our diagnosis of *Apatosaurus* sp. is based on the presence of a posteriorly deflected tuberculum and the tuberculum being lower than the capitulum in posterior and anterior views; no species identification can be made based on the preserved anatomy. The three fossae are variable in shape and depth (Table 1) but are diagnosed as being pneumatic features instead of pathological since no extraneous bone growth is found surrounding the fossae and the bone shows no sign of a healed injury. Unlike other diplodocids, including other apatosaurine sauropods, that preserve pneumatic fossae, MWC 9617 exhibits superficial fossae rather than invasive fossae. While diplodocids do display ontogenetic variability between juveniles and adults, MWC 9617 is estimated to be more mature based on its size and exhibits pneumatic fossae that are morphologically distinct from other large apatosaurine individuals. Due to this, we suggest that while ontogeny does play a role in the pneumatic features of diplodocids, individual variation is also responsible for the expression of pneumatic features along dorsal ribs of at least *Apatosaurus*. Considering the pneumatic features of diplodocids are not ubiquitous throughout the clade as they are in titanosauriforms, our findings support previous work that suggests pneumaticity in diplodocids is a poor diagnostic character for the clade (Wedel, 2005).

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


DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

AUTHOR CONTRIBUTIONS

L. K., J. M., and M. W. devised the project. L. K. described the material and wrote the first draft of the manuscript. J. M. provided access to the specimen. M. W. provided background information and specialist information about pneumaticity. All authors provided input and writing to the final draft.

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