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Type:

Article

Running head:

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Keywords:

sauropoda, Dinosauria, Brachiosauridae, postcranial skeletal pneumaticity, costal pneumaticity

Variable pneumatic features in the ribs of *Brachiosaurus altithorax*

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Abstract

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Key words

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Introduction

In his three increasingly detailed descriptions of the giant sauropod dinosaur *Brachiosaurus altithorax*, Elmer S. Riggs (1901, 1903, 1904) had little to say about the ribs. Two of them preserve interestingly different pneumatic features, which we describe, illustrate and discuss.

Anatomical nomenclature

Some older authors, including Riggs and Marsh, refer to the head and tubercle of the rib. We use the now conventional terms capitulum and tuberculum respectively for these structures. Since the term “head” is also sometimes used informally to indicate the entire proximal portion of a rib, including both capitulum and tuberculum and the area in between them, we avoid this ambiguous term entirely and refer to the “proximal portion” when this is what we mean.

In life, the position and orientation of sauropod ribs was complex, and is not fully understood. Broadly speaking, in all tetrapods with bicapital (two-headed) ribs, they move during respiration as though rotating about a hinge along the line from diapophysis to parapophysis (i.e. from capitulum to tuberculum on the rib itself). But as the extent and shape of articular cartilage on

both the ribs and vertebrae of sauropods is unknown, it is not possible to make a precise assessment either of neutral position or range of motion.

Rather than attempt to discuss directions on ribs according to life position, then, we adopt the descriptive convention of a rib being oriented vertically. The proximal face of the rib that would in life have been oriented in some posteroventromedial direction is here considered to be posterior, so that the directions up and down the rib are proximal (towards the vertebra) and distal (towards the belly); and the directions across the shaft of the rib are medial and lateral (Figure 1).

Institutional abbreviations

- CM — Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.
- FMNH — Field Museum of Natural History, Chicago, Illinois, USA.
- Mal — Malawi Department of Antiquities Collection, Lilongwe and Nguludi, Malawi.
- MB — Humboldt Museum für Naturkunde Berlin, Berlin, Germany.
- OMNH — Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA.
- RRBP — Rukwa Rift Basin Project, Tanzanian Antiquities Unit, Dar es Salaam, Tanzania.
- SMM — Science Museum of Minnesota, Saint Paul, Minnesota, USA.
- PVL — Instituto Miguel Lillo, Collection of Vertebrate Paleontology, Tucumán, Argentina.

- USNM — United States National Museum of Natural History, Washington D.C., USA.
- YPM — Yale Peabody Museum, New Haven, Connecticut, USA.

Background

Brachiosaurus altithorax

The giant sauropod dinosaur *Brachiosaurus altithorax* was very briefly described, with no name, in a preliminary report by Riggs (1901). It was then formally named, and described in slightly more detail by Riggs (1903). Riggs did not mention a specimen number, but the holotype is FMNH PR 25107, and is held at the Field Museum of Natural History in Chicago.

The name that Riggs chose describes the animal's morphology: "*Brachiosaurus*" means arm-lizard, in reference to the proportionally long forelimbs, and "*altithorax*" means high-torso, in reference to the "great size ... of this specimen" (Riggs 1903:299) — presumably the length of the dorsal ribs in particular in light of "the immense size of the thorax" (Riggs 1903:300).

However, Riggs said little about the ribs in either of these publications. He followed these initial descriptions with a full descriptive monograph (Riggs 1904), but this too gives the ribs rather short shrift, describing them in a single paragraph (Riggs 1904:239) of only 17 lines, which does not even specify how many were recovered, or from which side of the animal.

His preliminary paper says only that "A complete rib, presumably from about the sixth presacral vertebra, measures more than nine feet in length. Some of the thoracic ribs have a secondary tubercle, and also a foramen leading to a cavity in the shaft." (Riggs 1901:549).

The formal description of the ribs is not much more informative (Riggs 1903:303–304):

The unusual length of the ribs bears evidence of the immense thorax of this animal. In the mid-thoracic region they measure fully nine feet (2.745 m) in length. The capitulum and tuberculum are almost equally developed and widely separated, to give the firm anchorage necessary to the great length of the ribs. In some instances the attachment is strengthened by a second tubercle on the posterior surface of the head similar to that figured by Marsh [1896:167] in the cervical ribs of *Apatosaurus*. The anterior surface of the shaft below the head is perforated by a large foramen which leads to an internal cavity in the shaft.

Finally, the monographic description provides a little more detail (Riggs 1904:239), along with some repetition. Here, we reproduce it in full:

The unusual length of the ribs, as well as the breadth of the head and tubercle and the strength of the shaft, bears evidence of the immense thorax of this animal. One of the more slender ribs from the mid-thoracic region measures fully nine feet (2.745 m) in length, Another has a shaft eight inches (.204 m) in breadth. The head and tubercle are almost equally developed and widely separated to give the firm attachments rendered necessary by the great length of the ribs. In some instances the attachment is strengthened by a second tubercle on the inferior surface of the head similar to that figured by Marsh on the cervical vertebrae of *Apatosaurus*, The anterior surface of the shaft below the head is perforated by a large foramen which leads to an internal cavity. On account of the elevation of the caputular facet on the vertebra, the head and tubercle are borne almost on a level. By reason of this the flattened surface of the proximal end passes insensibly into

the lateral surface of the shaft without that twist common to the ribs in animals of this group.

The reference to “a second tubercle on the posterior surface of the head” (1903) or “inferior surface” (1904) is puzzling. We have not been able to identify any structure on any of the preserved ribs that persuasively matches the designation “second tubercle”, but we highlight in Figures 2 and 3 candidate structures which Riggs could conceivably have been referring to.

But Marsh’s own (1896:167) illustration (reproduced here as Figure 4) is puzzling in its own right. It consists of his figures 7 and 8, captioned as “Cervical rib of *Apatosaurus ajax* Marsh” with “outer” (i.e. lateral or anterior) view on the left and “inner” (i.e. medial or posterior) view on the right. But the three prongs shown are labeled “anterior extremity”, “head” (i.e. capitulum) and “tubercle” (i.e. tuberculum), with no rib shaft shown. The structure is extremely difficult to interpret as a cervical rib, A “posterior process” is shown in lateral view, which could possibly be construed as a “second tubercle”, but if it was on the lateral aspect of the rib it could not have served as an additional articulation. Furthermore a third articulation for a rib would serve to restrict the rib’s movement: possible in a cervical rib, but surely not in a dorsal rib, the purpose of which is to move in order to ventilate the respiratory system.

In summary, Riggs’s “second tubercle” is difficult to find on the *Brachiosaurus* ribs, and probably not homologous with whatever structure Marsh illustrated, which in any case is difficult to interpret.

Janensch (1914) named a second *Brachiosaurus* species, *B. brancai*, based on material recovered from the Tendaguru Formation of Tanzania (then Deutsch-Ostafrika). This species is much better represented than *B. altithorax*, and a mounted skeleton based primarily on the referred specimen

MB.R.2181 forms the spectacular centerpiece of the atrium of the Museum für Naturkunde Berlin (Janensch 1950b). As a result the popular conception of *Brachiosaurus* has rested on this referred species. However, Paul (1988) showed that some significant differences exist between the species and proposed that *B. brancai* be placed in a subgenus *Brachiosaurus* (*Giraffatitan*). This suggestion was not followed, but Taylor (2009) demonstrated that the two species are distinguished by at least 26 characters of the dorsal and caudal vertebrae, coracoids, humeri, ilia, and femora, and placed the African species in its own full genus as *Giraffatitan brancai*. This name is now in general use for Janensch's species, and the name *Brachiosaurus* refers only to the type specimen.

As discussed by Taylor (2009:788–789), several further North American specimens have been referred to the species *Brachiosaurus altithorax*, but none of these referrals can be made confidently due to a lack of overlapping material with the type specimen. D'Emic and Carrano (2019) tentatively referred the skull USNM 5730 and the Potter Creek postcranial material BYU 9754(4744)/USNM 21903 to *Brachiosaurus altithorax*, but did so only “based on lack of evidence for more than one brachiosaurid from the Upper Jurassic of North America” (D'Emic and Carrano 2019:736). There is definitely evidence for multiple individuals of brachiosaurids in the Late Jurassic of North America (e.g. Maltese et al. 2018), but they are not necessarily referable to the species *Brachiosaurus altithorax* or even the genus *Brachiosaurus*. As a result, FMNH PR 25107 remains the only definitive specimen of *Brachiosaurus* at the time of writing.

Pneumaticity in sauropod ribs

Among extant animals, crocodilians, birds, and mammals have pneumatic spaces in their skulls, but these are found in the postcranial skeletons of only one group: birds (e.g. Duncker 1971).

Among extinct animals, postcranial skeletal pneumaticity (PSP) is more widely distributed, occurring in pterosaurs, theropod dinosaurs (including birds) and sauropodomorphs — but not ornithischian dinosaurs (e.g. Benson et al. 2011).

In sauropods, PSP is found most often in the vertebrae, where it is all but ubiquitous, but is also found less frequently in other sites including the scapulae, coracoids and ilia (e.g. Cerda et al. 2012). Among the sites of pneumatic features are the dorsal ribs. A variety of different features are found on different parts of ribs: principally the capitulum and tuberculum and the area between them; most often on the posterior face of the rib but not infrequently on the anterior. Features include fossae (wide, shallow excavations), foramina (narrow, deep excavations leading to an internal air-space) and other possible traces of pneumatic diverticula pressed up against the ribs (Figure 5).

As with pneumatic features in other bones, it is likely that the excavation of ribs by diverticula of the pulmonary system followed paths laid down by blood vessels, so that vascular foramina grew to become pneumatic fossae and foramina (Taylor and Wedel 2021).

Description of *Brachiosaurus* ribs

The preserved material of the *Brachiosaurus altithorax* holotype FMNH PR 25107 does not include any cervical ribs, or indeed any cervical material. Of the two caudal vertebrae, one is complete and includes the short and featureless caudal ribs that are fused to the centrum and neural arch, appearing as transverse processes of the vertebra. The dorsal ribs are the material of interest. Riggs did not give a count of these ribs, but as we shall see below, there are five of them.

Two of the ribs are preserved in much more detail than the others — in particular, they are the only ribs that preserve the capitulum and tuberculum. Their serial positions cannot be determined, beyond that they were not positioned very anteriorly or posteriorly within the trunk, so we arbitrarily designate these as Rib A and Rib B.

Rib A

Rib A (Figure 2) was illustrated by Riggs (1903:fig 6) and slightly more informatively by Riggs (1904:plate LXXV:figure 5). It consists of a complete proximal end and some but not all of the more distal portion, and is broken into two pieces. We interpret it as a right rib with the posterior aspect facing upwards in the jacket, based on the concavity of the available face and the curvature of the shaft. The rib is well preserved except for signs of reconstruction in the too-neat lamination of the tuberculum. It measures 53 cm across the capitulum and tuberculum.

The rib's most interesting feature is a small, oval pneumatic opening located about 60 cm down the shaft. It has been carefully prepared, and has finished bone inside: it is not a result of damage or an artifact of preparation. The opening measures 49 mm proximodistally and 25 mm mediolaterally. Its depth is 22 mm at both the medial edge and proximal end, and 18 mm at both the proximal edge and distal end. It is difficult to see the inner margins of the cavity. However, feeling around inside the opening, it seems likely that it extended further distally into the rib, although the possible extension has understandably not been prepared out. This is in agreement with Riggs's (1903:304-305) description "The anterior surface of the shaft below the head is perforated by a large foramen which leads to an internal cavity in the shaft".

(Riggs 1903:304 and Riggs 1904:239 both say that this opening is on the anterior face, and Taylor 2009:792 followed his assessment, but this is incorrect.)

Rib B

Rib B was not described or illustrated by Riggs, but it may be the rib measuring “fully nine feet (2.745m) in length” that he refers to (Riggs 1903:304, 1904:239). Like Rib A, it consists of a complete proximal end, and some but not all of the more distal portion, well preserved. It is possible that some more distal part of Rib A or B has been lost, making up the full length of 9 feet that Riggs repeatedly cites. We interpret Rib B as a left rib with the posterior aspect upwards. It measures 56 cm across the capitulum and tuberculum.

The pneumatic opening in this rib is not described by Riggs (1903, 1904), though it was mentioned briefly by Taylor (2009:792). It more closely resembles that documented by Marsh (1896:figure 7–8) in *Brontosaurus excelsus* (Figure 5A) and those found in other sauropods, in that it invades the tuberculum rather than the shaft. Specifically, the lateral portion of the tuberculum is anteroposteriorly deeper than the medial part, projecting posteriorly from the surface of the rib, and the opening is in the medial face of this projection, extending laterally into the bone. The opening has been fully prepared out and is lined with finished bone. It is shaped like a teardrop flattened on one side, extending parallel to the rib shaft. It measures 120 mm proximodistally and has a maximum width of about 33 mm, near its distal end: an exact measurement is impossible to determine as the medial margin of the opening merges smoothly onto the posterior face of the rib rather than ending in a lip, as the lateral margin does. The depth of the opening is about 50 mm towards its proximal end and 33 mm at its distal end. It is possible that the opening extended further proximally into the tuberculum.

Other ribs of the *Brachiosaurus altithorax* holotype

Riggs's descriptions mention Rib A and possibly Rib B, as discussed above. The collections contain three further ribs, for a total of five. Of these, one has only part of the proximal end, one only a section of the shaft, and one a partial proximal end and a broken-off more distal portion.

None of these ribs have visible pneumatic features. All of the ribs are large, heavy, and presumably fragile, and we have not attempted to move them from their supporting jackets. It is possible the hidden faces of these ribs have pneumatic features, but there is no particular reason to expect that they do.

Pneumaticity in ribs of referred *Brachiosaurus* specimens

Jensen (1985, 1987) referred several specimens to the brachiosauridae, and tentatively to the species *Brachiosaurus altithorax*. These include at least one rib, probably three, although ambiguities in his papers make it uncertain what he intended:

1. Jensen (1987:figure 1F) illustrates the proximal portion of a rib, but the caption does not specify what specimen or taxon it was considered to belong to. It is implied but not stated to be part of the Potter Creek brachiosaur, and appears to have a featureless surface.
2. Jensen (1987:figure 6B) (also appearing as Jensen 1985:figure 4B) shows a fiberglass resit cast of a “Jensen/Jensen quarry brachiosaur rib”, but the image contains almost no detail beyond the fact that is not the same rib as the one in his figure 1F.
3. Jensen (1987:figure 8B) shows the proximal portion of another rib, visible different from both the others, but the caption says “*Supersaurus vivianae*, right lateral view of mid-

cervical vertebra”, which is obviously incorrect. The identity and assignment of this rib is therefore unknown.

There are no discernible pneumatic features on any of these ribs in Jensen’s illustrations, and Colin Boisvert (pers. comm., 2023) inspected these elements in collections and found no pneumatic features. These elements, together with all the brachiosaur material from Dry Mesa and Jensen/Jensen quarries are currently under restudy.

Pneumaticity in ribs of other brachiosaurids

We are now in a position to survey occurrences of pneumaticity in the dorsal ribs of all known brachiosaurids:

- *Brachiosaurus* — two different pneumatic features in two ribs in the holotype specimen, no other features recognised in type or referred specimens.
- *Giraffatitan* — foramina in both anterior and posterior faces of the tuberculum in a single rib on MB.R.2181, but not apparently in any other rib.
- *Cedarosaurus* — no pneumatic features observed: two ribs “retain portions of the rib heads and clearly show that no pneumatic foramina was present” (Tidwell et al. 1999:25).
- *Venenosaurus* — 40 mm wide pneumatic foramen on the posterior surface of a right-sided rib leading proximally into a cavity in the capitulum (Tidwell et al. 2001:153).
- *Lusotitan* — although some dorsal rib fragments were excavated (Lapparent and Zbyszewski 1957), they were only briefly described and could not be located for the redescription of Mannion et al. (2013).
- *Vouivria* — “No rib heads are complete enough to determine whether the posterior surface was excavated” (Mannion et al. 2017:37).

- *Abydosaurus* — no dorsal rib material was included in the specimens reported by Chure et al. (2010).

In summary, pneumatic features are known from the ribs only of *Brachiosaurus* itself (two ribs), *Giraffatitan* (one rib) and *Venenosaurus* (one rib) — although see below on asymmetry of inference.

Discussion

Pneumatic sites in sauropod ribs

The most common location of pneumatic features in the ribs of sauropods is in the tuberculum, as seen in, among others, *Brontosaurus excelsus* (Figure 5A) and *Giraffatitan brancai* (Figure 5B). The pneumatic opening of Rib B conforms to that pattern, although the shape and orientation of the opening is different from previously observed features. In particular, the invasion of bone in Rib B extends in a lateral direction and excavates a laterally positioned ridge on the posterior face of the rib, whereas other observed openings penetrate the bone anteriorly (from the posterior face) or posteriorly (from the anterior face).

The next most common pneumatic location is the space between the tuberculum and capitulum, as seen in *Apatosaurus louisae* (Figure 5C) and *Malawisaurus dixeyi* (Figure 5D), and in a different form in *Brontomerus mcintoshii* (Figure 5E; Taylor et al. 2011:84–85).

Pneumatization of the capitulum is for some reason much rarer, and to date has only been recorded in *Venenosaurus dicrocei* (Tidwell et al. 2001:figure 11.9).

Other pneumatic configurations also exist: for example the complex of fossae and foramina in *Rapetosaurus kraussei* (Figure 5F) and the “pneumatic webbing” between the capitulum and tuberculum of *Rukwatitan* (Figure 5G–H; Gorscak et al. 2014:1142). This “webbing” is also found in a less developed form in *Mnyamawamtuka moyowamkia* (Gorscak and O’Connor 2019:figure 18).

The location of the foramen on Rib A of the *Brachiosaurus altithorax* holotype FMNH PR 25107 represents a unique location, appearing as it does some way down the shaft of a rib whose proximal portion appears devoid of pneumatic features. The closest approximation to this condition in another sauropod is perhaps in a right dorsal rib of the mamenchisaurid *Xinjiantitan shanshanensis* SSV 12001 (Zhang et al. 2022:figure 14A), but the foramen in that case is located much more proximally than in Rib A.

All of these pneumatic fossae and foramina correspond to the seven-location schema of Wedel and Taylor (in review, a), which predicts that pneumatic features in costal elements would follow vascular foramina from the segmental and intercostal arteries.

The segmental arteries pass behind the ribs on their circuit of the centrum, providing channels for pneumatization of the posterior aspect of the proximal portion of the ribs — the tubercula and capitula and region between them. (Note that “posterior” here is really posteromedial, as the parapophysis is usually anteroventral to the diapophysis rather than directly ventral, so that the rib is “folded back” against the torso.) The segmental arteries also less frequently vascularize and subsequently lead to pneumatization of the anterior aspect of the next vertebra’s ribs. Meanwhile, the intercostal arteries extend along and beyond the length of the rib shaft, providing opportunities for vascularization and subsequent pneumatization.

However, while the pneumatization of the proximal portion of ribs — likely by diverticula following the segmental arteries — are relatively common in sauropods, pneumatization of the shaft — likely by diverticula following the intercostal arteries — is rare. *Brachiosaurus* Rib A provides the only documented occurrence.

Variability of pneumatic features

There is no reason to suppose that the vascularization of the vertebra that carried Rib A was any different from that of Rib B. (Or, if they are the left and right ribs of the same vertebrae, that this vertebra was vascularized differently on one side from the other.) Yet in following the segmental and intercostal arteries, the pneumatic diverticula in the region of these ribs did very different things. In Rib A, the proximal part of the rib — which is the only part pneumatized in most sauropod specimens — is entirely devoid of pneumatic features, yet a small, lipped foramen penetrates the shaft about 60 cm down. In Rib B, a broader, less well-defined pneumatic fossa is in the lateral ridge on the posterior face of the tuberculum, and there are no discernable pneumatic features on the shaft.

Variability of pneumatic features in sauropod bones has been documented in the literature — differences between different species or specimens (e.g. McIntosh 1990), among successive vertebrae of a single individual (e.g. *Diplodocus carnegii* CM 82, Hatcher 1901), including bilateral asymmetry that may be consistent along the column (e.g. *Saltasaurus loricatus* PVL 4017, Zurriaguz and Alvarez 2014) or seemingly random (e.g. *Giraffatitan brancai* MB.R.2181, Wedel and Taylor 2013), and even asymmetry within a single vertebra (e.g. *Xenoposeidon proneneukos* NHMUK PV R2095, Taylor and Naish 2007). All of this is in accord with Witmer's

(1997:64) conception of pneumatic diverticula as “opportunistic pneumatizing machines”, and similar variability in pneumaticity of ribs further corroborates this interpretation.

It is particularly odd that even in well-preserved specimens with complete or nearly-complete sets of ribs, pneumatic cavities are typically only present in one or two ribs in a given individual; examples include CM 3018, the holotype of *Apatosaurus louisae* (Gilmore 1936:plate 29), and *Giraffatitan brancai* MB.R.2181 (Janensch 1950:figures 89–108). The quest to understand the evolution of postcranial pneumaticity in dinosaurs is already complicated by an asymmetry of inference: pneumatization of a single bone, such as a middle caudal vertebra of *Giraffatitan*, is sufficient to demonstrate that diverticula of the respiratory system at least occasionally pneumatized that element in that taxon, but no number of apneumatic examples can prove the inverse (see discussion in Wedel and Taylor 2013). This problem becomes extreme in the case of dorsal ribs: if CM 3018 had a nearly complete set of dorsal ribs, missing only the right second rib, we would have no reason to suspect that dorsal rib pneumaticity was present in that specimen or in the species *Apatosaurus louisae* more generally; in fact, given a nearly full set of 19 apneumatic ribs, we might confidently but erroneously infer that dorsal rib pneumaticity was absent. We know of no antidote to this problem other than to keep documenting every available instance of dorsal rib pneumaticity.

New anatomy in old specimens

FMNH PR 25107 is a well-known and even iconic specimen: not only was it described in some detail in the three papers by Riggs (1901, 1903, 1904) and revisited by Taylor (2009), it has provided scorings in multiple phylogenetic analyses, including those of Mannion et al. (2013) regarding the Portuguese brachiosaurid *Lusotitan*, and many subsequent analyses that use this

matrix as a starting point. Furthermore, casts of the preserved material (the last seven dorsal vertebrae, sacrum, first two caudals, dorsal ribs, left coracoid, right humerus, ilium and femur) provided the core of a skeletal mount that was erected at the Field Museum in 1993 by Prehistoric Animal Structures, Inc. (Pridmore 1933, Carlozo 1993, Taylor 2014). It was the centerpiece of the museum until its removal in 1999 to make way for the *Tyrannosaurus rex* “Sue”. At this point it was transferred to Terminal 1 at O’Hare Airport on indefinite loan to United Airlines (Keown and staff, 2000), where it remains to this day and is seen by sixty thousand people every day. It is striking that even such a well known specimen, a hundred and twenty years after its description, can continue to provide unique anatomical features leading to novel insights.

Acknowledgements

We thank Bill Simpson (Field Museum of Natural History) for arranging a collections visit for MPT at very short notice. Eric Gorscak (Midwestern University) kindly supplied photographs of the ribs of *Malawisaurus*; he and Patrick O’Connor (Ohio University) supplied the photograph of the rib of *Rukwatitan*. Kristina Curry Rogers (Macalester College) supplied the photograph of the rib of *Rapetosaurus*. We thank Colin Boisvert for permissions to cite a personal communication.

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Figure Captions

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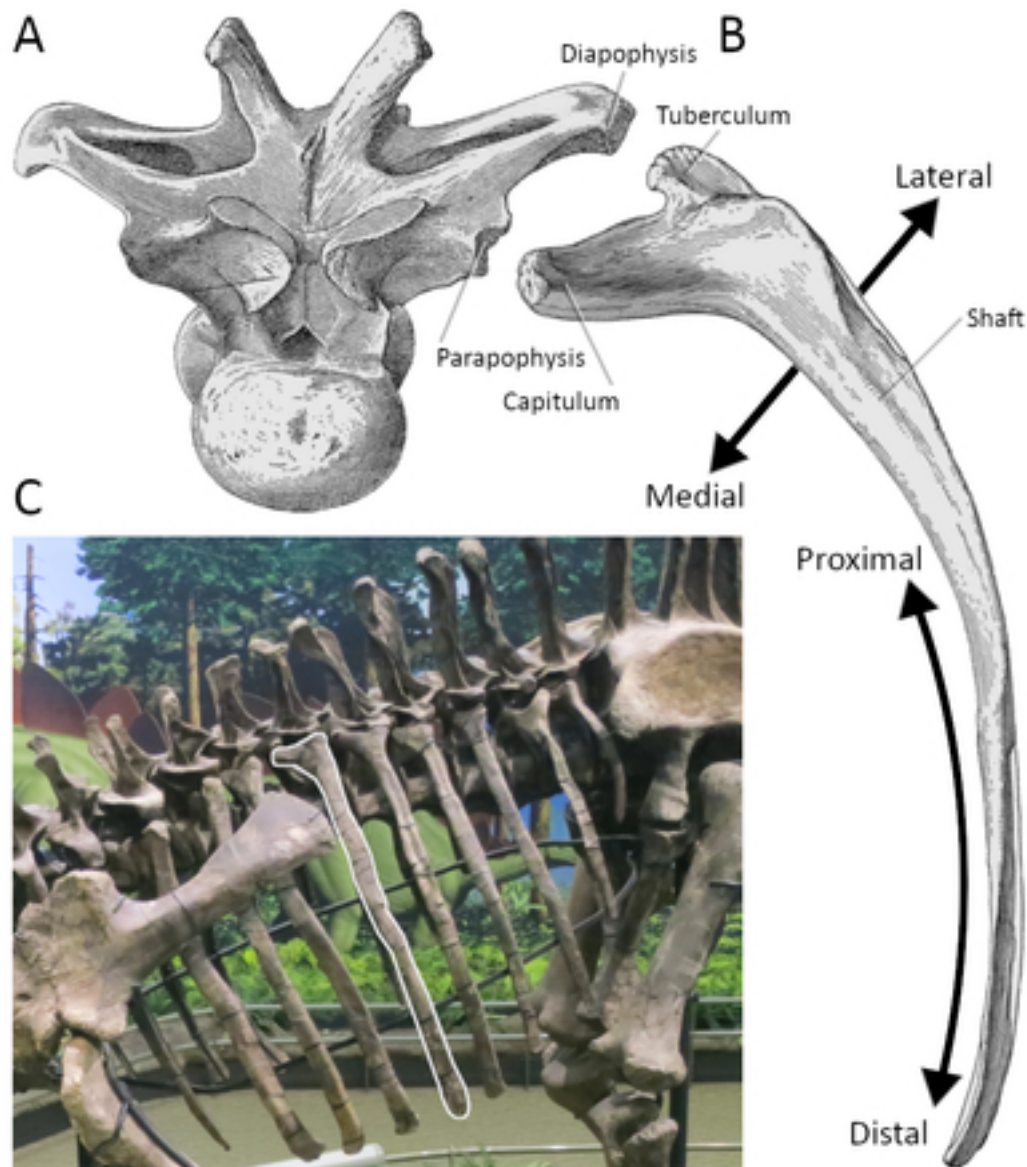


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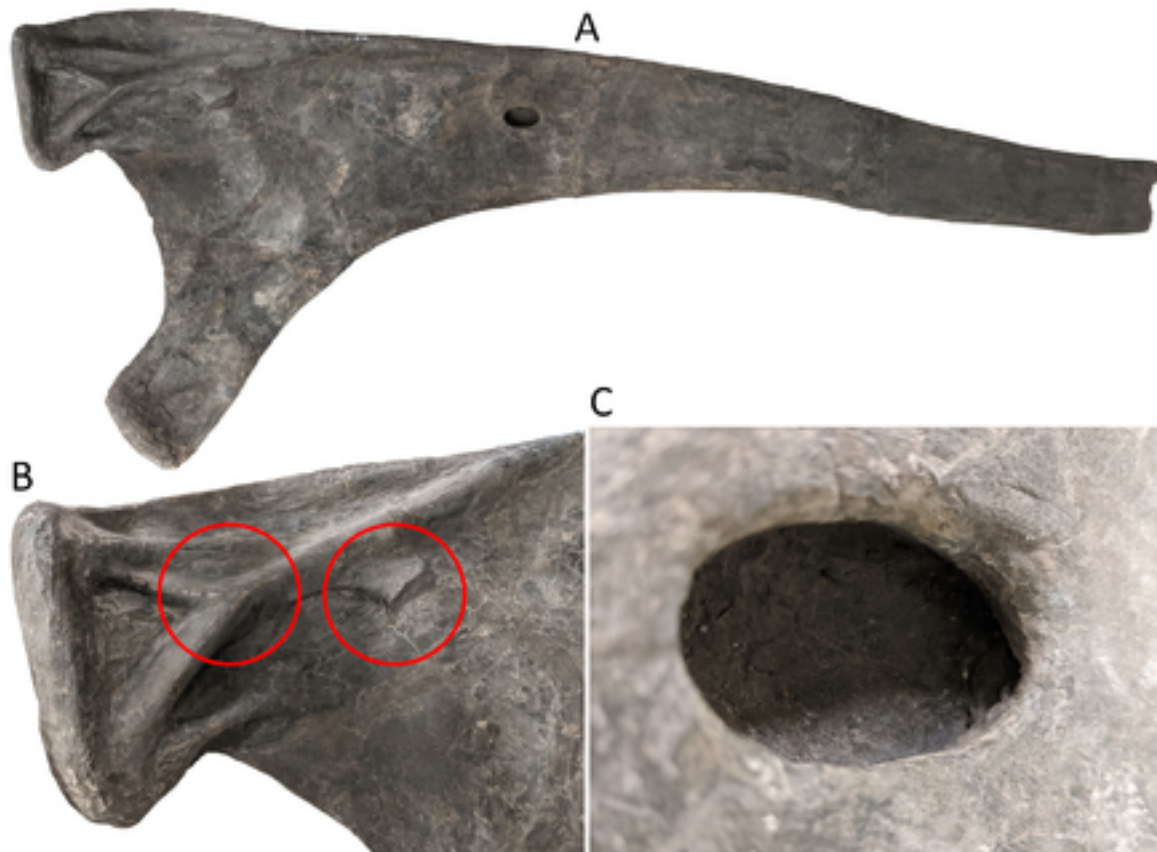


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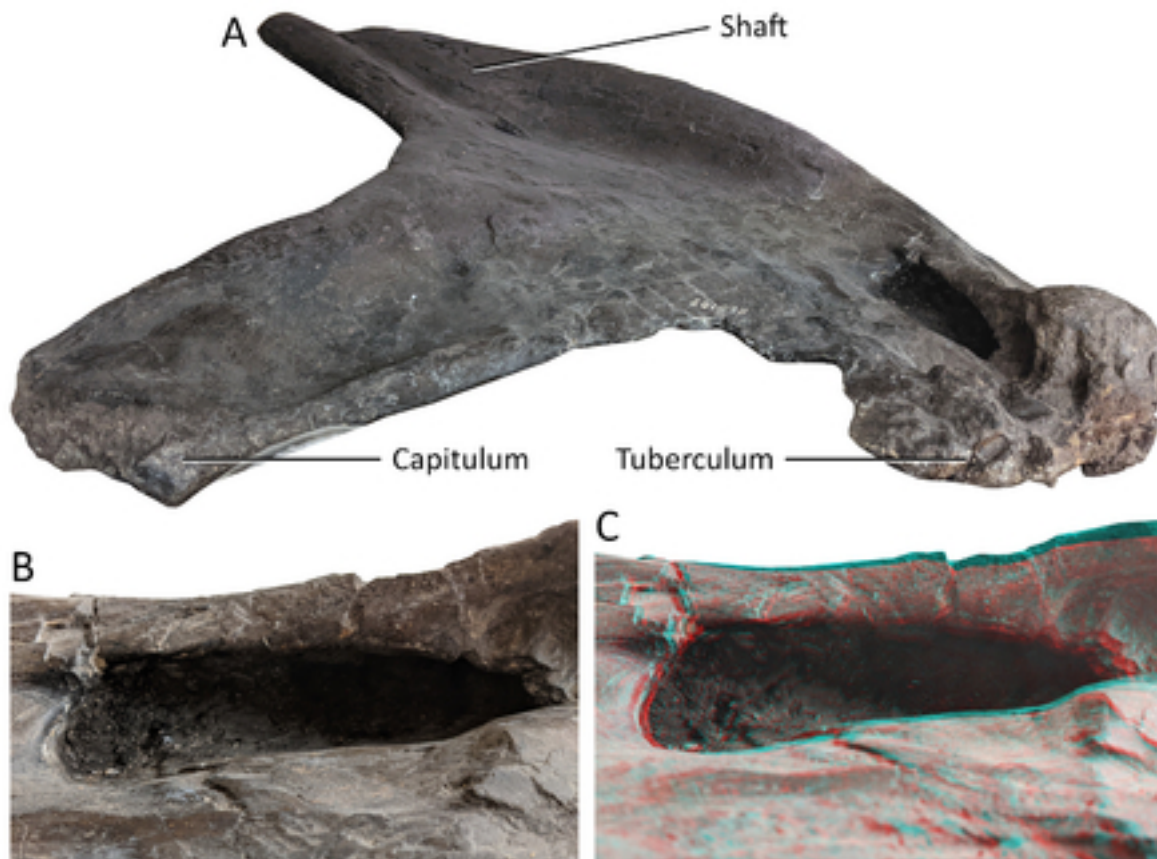


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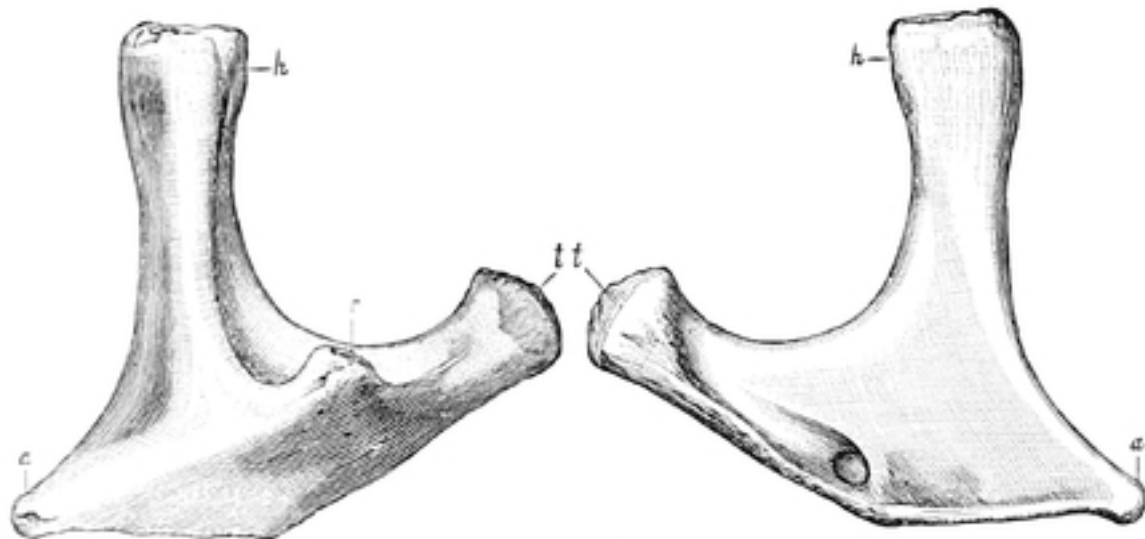


FIG. 7.—Cervical rib of *Apatosaurus ajax* Marsh; outer view.

FIG. 8.—The same rib; inner view.

Both figures are one-eighth natural size. *a*, anterior extremity; *h*, head; *r*, posterior process; *t*, tubercle.

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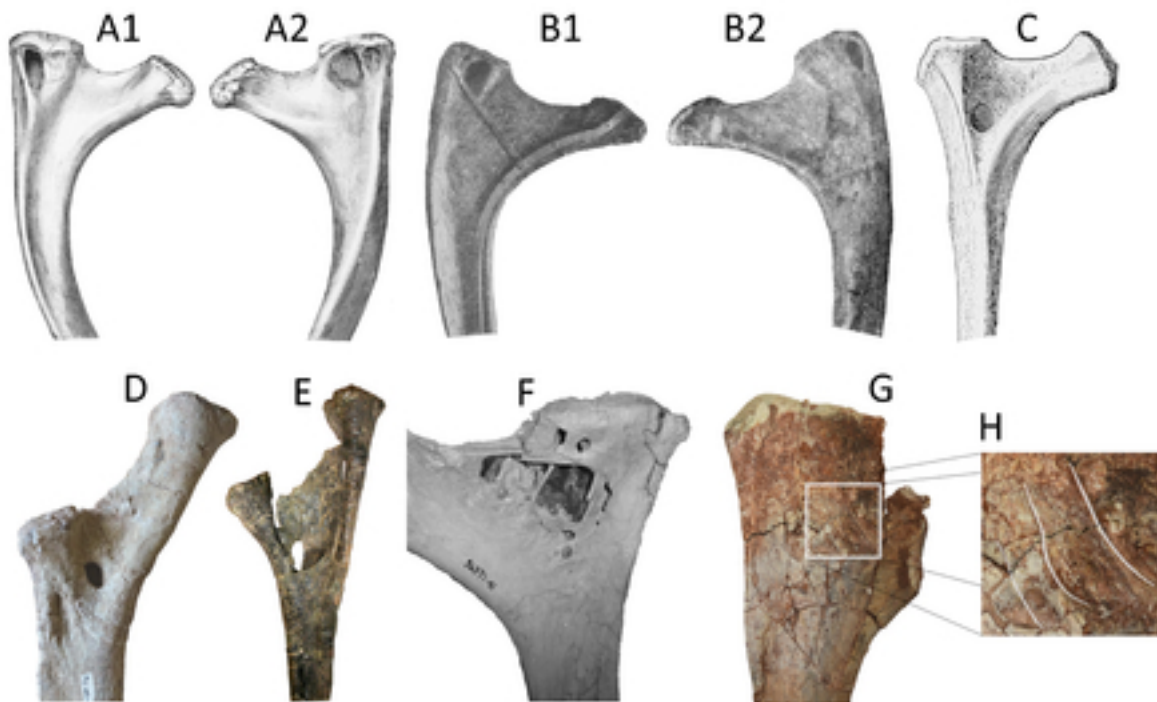


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Figures

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