Vertebrate Anatomy Morphology Palaeontology 10:91–100
ISSN 2292-1389

The biomechanical significance of bifurcated cervical ribs in apatosaurine sauropods

Mathew J. Wedel[1] and Michael P. Taylor[2,*]
[1]College of Osteopathic Medicine of the Pacific and College of Podiatric Medicine, Western University of Health Sciences, Pomona, California, USA; mathew.wedel@gmail.com
[2]Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK; dino@miketaylor.org.uk

Abstract: Bifurcated cervical ribs have evolved infrequently in dinosaurs. Previously documented examples include those in abelisaurid theropods, leptoceratopsid ceratopsians, and turiasaurian sauropods. In apatosaurine sauropods a spectrum of cervical rib morphologies exists, from cervical ribs with small dorsal processes extending from the shafts to completely bifurcated cervical ribs. Similar dorsal processes are also present in the dicraeosaurid sauropod *Dicraeosaurus*. The presence of dorsal processes and bifurcated cervical ribs suggests that the hypaxial neck muscles that inserted on the cervical ribs were oriented in divergent directions. In all the dinosaurian examples we have found, the cervical ribs are maximally bifurcated in the middle of the cervical series. We hypothesize that bifurcated cervical ribs are traces of diverging neck muscles that provided improved control in the middle of the neck, at some distance from both the head and the trunk.

INTRODUCTION

It is well known that sauropod dinosaurs had the longest necks of any terrestrial animals. But it is not widely recognised that the lengths of their necks exceeded those of their rivals by a factor of five: 15 m for *Supersaurus* compared with perhaps 3 m for the largest known azhdarchid pterosaurs, 2.4 m for the world-record giraffe, and a little over 2 m for various non-sauropod dinosaurs (see review in Taylor and Wedel 2013).

These long necks were key among the evolutionary innovations that enabled sauropods to grow so large (Sander et al. 2010; Sander 2013). Extreme neck elongation was made possible by a suite of anatomical properties including large absolute size, stable quadrupedal stance, reduced head size, increased number of cervical (neck) vertebrae, anteroposterior elongation of individual cervical vertebrae, an avian-style respiratory system, extensive vertebral pneumaticity, and various modifications to muscle attachment sites in the neck (Taylor and Wedel 2013), including the ribs of the cervical vertebrae.

In this contribution, we survey the occurrence of bifurcated cervical ribs in sauropods, describe several examples in apatosaurines, and speculate on their implications for muscle attachments.

Institutional Abbreviations

CM, Carnegie Museum, Pittsburgh, Pennsylvania, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; LACM, Los Angeles County Museum of Natural History, Los Angeles, California, USA; MACN, Museo Argentino de Ciencias Naturales “B. Rivadavia”, Buenos Aires, Argentina; MCSNB, Museo Civico di Scienze Naturali "E. Caffi" Bergamo, Bergamo, Italy; MB.R., Humboldt Museum für Naturkunde Berlin, Berlin, Germany; MWC, Museum of Western Colorado – Dinosaur Journey, Fruita, Colorado, USA; NSMT, National Science Museum, Tokyo, Japan; UA, Université d’Antananarivo, Antananarivo, Madagascar; UWGM, University of Wyoming Geological Museum, Laramie, Wyoming, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

BACKGROUND

Nomenclature – Herein we follow Tschopp et al. (2015) for diplodocoid phylogeny and Royo-Torres et al. (2017) for turiasaurian phylogeny. We also follow Tschopp et al. (2015) in referring to the bony protuberances on the dorsal or dorsolateral aspect of cervical rib shafts as “dorsal processes”, regardless of the angles formed between the pos-

Published November 26, 2023
*corresponding author, © 2023 by the authors; submitted August 16, 2023; revisions received October 23, 2023; accepted November 1, 2023. Handling editor: Robert Holmes. DOI 10.18435/vamp29394

Vertebrate Anatomy Morphology Palaeontology is an open access journal http://ejournals.library.ualberta.ca/index.php/VAMP Article copyright by the author(s). This open access work is distributed under a Creative Commons Attribution 4.0 International (CC By 4.0) License, meaning you must give appropriate credit, provide a link to the license, and indicate if changes were made. You may do so in any reasonable manner, but not in any way that suggests the licensor endorses you or your use. No additional restrictions — You may not apply legal terms or technological measures that legally restrict others from doing anything the license permits.

terior margins and the rib shafts of these processes (obtuse, right, or acute).

Cervical ribs of tetrapods –With few exceptions, the cervical vertebrae of most tetrapods have bicipital (two-headed) costal elements, which are serially homologous with both the freely-moving dorsal or thoracic ribs and the fused caudal ribs that provide the transverse processes of caudal vertebrae. Typically, each of these costal elements articulates ventrally with the vertebral centrum at the parapophysis, and dorsally with the neural arch at the diapophysis. (In dorsal vertebrae, the parapophysis may be shifted upwards onto the neural arch.) These two articulations form a bony tunnel or canal, the transverse foramen, through which the vertebral artery passes on either side of the vertebra.

Both the morphology and the nomenclature of the costal elements of the cervical region vary widely among tetrapod clades (Fig. 1). In non-avian reptiles, the costal elements of the cervical vertebrae are called "cervical ribs" (Romer 1956), whether they fuse to their respective vertebrae (as in sauropodomorphs) or retain synovial articulations with the vertebrae (as in non-avian theropods). The cervical ribs usually bear a posteriorly-projecting shaft of bone, which in extreme cases may overlap several vertebral centra and greatly exceed the lengths of the longest dorsal ribs (Russell and Zheng 1993:2089–2090; Wedel et al. 2000:358–359).

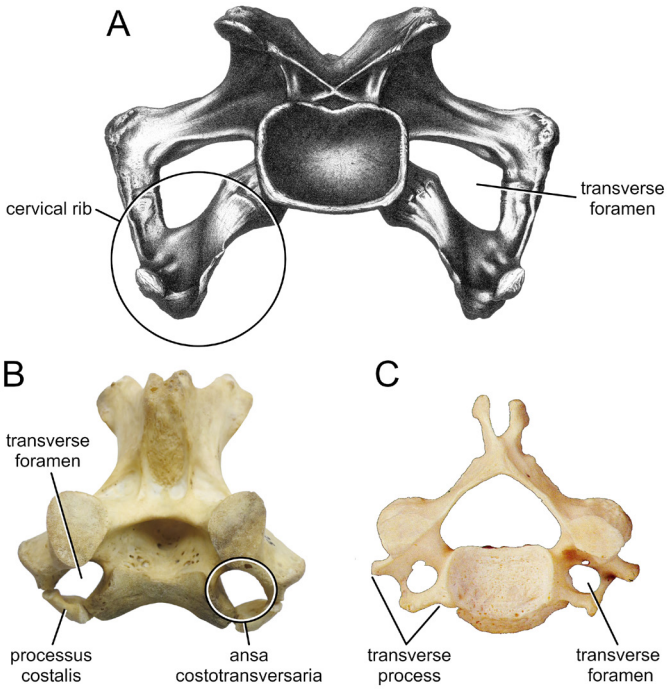

Figure 1. Varying terminology for cervical ribs among tetrapods obscures their underlying homology. In all three cases, a bicipital costal element articulates with the centrum and neural arch to form a bony loop around the transverse foramen. A, *Apatosaurus ajax* referred specimen YPM 1861, cervical ?13 in posterior view (modified from Ostrom and McIntosh 1966, plate 15). B, *Struthio camelus* LACM Ornithology 116205, a posterior cervical vertebra of an ostrich in anterodorsal view. C, *Homo sapiens* middle cervical vertebra, uncatalogued specimen from the anthropology teaching collection at the University of California, Santa Cruz, in anterior view. Photographs by the authors.

In birds, the costal elements of the cervical region fuse to the vertebrae and are known as costal processes (*processus costalis*, Zweers et al. 1987; Baumel and Witmer 1993). The bony loop formed by the fusion of each costal element to its respective vertebra is called the ansa costotransversaria.

In mammals, including humans, the cervical costal elements fuse to their respective vertebrae and are referred to as transverse processes (Schaefer et al. 2009; White et al. 2011). In human anatomy and medicine, the term cervical rib refers to a developmental segmentation anomaly in which one or more of the cervical vertebrae bears a large, mobile (unfused) rib like those of the thoracic vertebrae (Beck 1905; Todd 1912). These unfused cervical ribs may be present unilaterally or bilaterally, and they often pathologically compress the large blood vessels and nerves at the thoracic outlet and deep to the clavicles (Sanders and Hammond 2002; Henry et al. 2018).

The human anatomical and clinical terminology is unfortunate because it almost completely obscures the homology of the costal elements and their attachments with those of other tetrapods. In humans, the fused costal elements are referred to as transverse processes, but in other tetrapods the transverse process is the portion of the neural arch that the costal element articulates with, not the costal element itself. In most other tetrapods, the cervical costal elements are known as cervical ribs, but in humans the term "cervical rib" is instead used for rare cases of developmentally displaced thoracic ribs. The "cervical transverse processes" of humans and the "cervical ribs" of sauropods are both bicipital costal elements, which start out as separate ossifications but fuse to their respective vertebrae over the course of ontogeny, forming a complete bony loop that bounds the transverse foramen, and both serve as anchors for hypaxial neck muscles.

Sauropod cervical rib morphology – Although different sauropod lineages evolved cervical ribs of various shapes, sizes, and lengths, the basic structure of a sauropod cervical rib is highly conserved (Fig. 2). Each rib consists of: 1) the capitulum and tuberculum, which in skeletally mature individuals fuse to the vertebral parapophysis and diapophysis, respectively; 2) a blunt or tapering anterior process, which is usually small and short, but which can project slightly farther forward than the anterior ball of the centrum in a few taxa (e.g., *Trigonosaurus*, Campos et al. 2005), and which is reduced or lost in some apatosaurines (e.g., *Apatosaurus louisae*, Gilmore 1936); and 3) the pos-

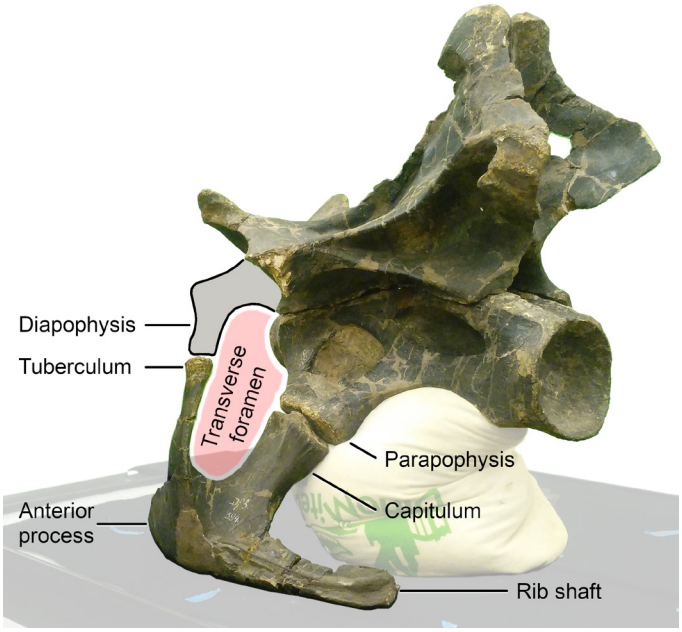

Figure 2. Cervical rib in position relative to its centrum. *Brontosaurus parvus* CM 555, C6 and associated left cervical rib in left posterodorsal view. The parts of the rib are labelled (capitulum, tuberculum, anterior process, shaft), as are the parts of the vertebra that articulate with it (parapophysis, diapophysis). The transverse foramen, bound by the diapophysis, centrum wall, parapophysis and cervical rib, is highlighted in pink. Photograph by the authors.

teriorly-directed shaft of the cervical rib, which is typically rather longer than the anterior process.

The lengths of sauropod cervical rib shafts vary among clades. Long cervical ribs that extend posteriorly under one or more subsequent centra are primitive for sauropods (Klein et al. 2012). Particularly elongated cervical ribs evolved independently in mamenchisaurids (Young and Zhao 1972; Russell and Zheng 1993; Zhang et al. 2018) and in basal titanosauriforms such as *Giraffatitan* (Janensch 1950) and *Sauroposeidon* (Wedel et al. 2000). Cervical ribs in these taxa overlapped, forming vertically-stacked bundles. In contrast, diplodocoids evolved apomorphically short cervical ribs, which typically do not extend past the posterior ends of their respective centra (Tschopp et al. 2015:231). This tendency reaches its greatest extreme in apatosaurine diplodocids, in which the ribs are extraordinarily robust and displaced far ventrally from their centra on long, robust parapophyseal rami. Cervical ribs projecting well below the centra are recognized as an apatosaurine apomorphy by Tschopp et al. (2015:248). For an extreme example, see C6 of the *Brontosaurus excelsus* holotype YPM 1980, illustrated by Marsh (1896:plate XX:figs. 3, 4).

In all extant vertebrates with cervical ribs, these ribs either lack posterior processes entirely, or have short, simple posterior processes. The cervical ribs of crocodylians are more robust than those of birds, but not nearly to the extent found in apatosaurines. The cervical ribs of crocodylians and birds serve as the insertions of lateral and ventral (hypaxial) neck muscles (Tsuihiji 2007). The same function is hypothesized for sauropod cervical ribs, based both on homology (Wedel and Sanders 2002; Taylor and Wedel 2013) and on bone histology, which shows that the rib shafts are ossified tendons (Klein et al. 2012).

Bifurcation in sauropod cervical ribs – In some sauropods, the posterior ends of the cervical ribs are bifurcated into two prongs pointing in different directions — e.g., *Moabosaurus* (Britt et al. 2017). In this paper, we document occurrences of bifurcated and incipiently bifurcated cervical ribs in various sauropod clades and consider what they tell us about soft-tissue anatomy in the necks of these animals.

A cervical rib is described as bifurcated when the posteriorly-directed shaft splits into two sub-parallel shafts separated by a distinct notch. To date, bifurcated cervical ribs have been reported in just a handful of sauropod genera. Royo-Torres et al. (2006) described and illustrated bifurcated cervical ribs in *Turiasaurus*, and Britt et al. (2017) described and illustrated bifurcated cervical ribs in *Moabosaurus* (Fig. 3A). *Turiasaurus* and *Moabosaurus* are both members of the clade Turiasauria, but bifurcated ribs are absent in *Mierasaurus*, which Royo-Torres et al. (2017) recovered as the sister taxon of *Moabosaurus* within Turiasauria. This implies either a single origin of bifurcated cervical ribs in Turiasauria, with a reversal in *Mierasaurus*, or parallel origins of bifurcated cervical ribs in *Turiasaurus* and *Moabosaurus*. In both *Turiasaurus* and *Moabosaurus*, the bifurcation of the cervical rib shaft manifests in the presence of a dorsal process whose trajectory diverges only slightly from that of the longer principal shaft.

Outside of Turiasauria, Tschopp et al. (2015: character 217, p. 99–100, fig. 49) recognized a "posteriorly projecting spur on dorsolateral edge of posterior shaft" of the cervical rib in the diplodocid *Dicraeosaurus* and some apatosaurines, but to date these processes have not been described or illustrated in detail. Herein we describe dorsal processes and fully bifurcated cervical ribs in several apatosaurine specimens, and compare them to similar cervical ribs in turiasaurs and *Dicraeosaurus*.

Sereno et al. (1999) reported that cervical ribs 3–6 of *Jobaria* have an "accessory anterior process" as opposed to a bifurcated posterior shaft. This might mean that some of the anterior processes of the cervical ribs are bifurcated in *Jobaria*, but the character state is not illustrated and we have not been able to observe the relevant fossils firsthand. Because our investigation is concerned with the bifurcation of the posterior shafts of sauropod cervical ribs, we regard the accessory anterior processes in *Jobaria* as inherently interesting but outside our scope.

Bifurcated cervical ribs in other tetrapods – Bifurcated or incipiently bifurcated cervical ribs are occasionally found in animals other than sauropods.

Among theropod dinosaurs, some abelisaurs display this morphology. The holotype of *Carnotaurus sastrei* MACN-CH 894 has dorsal processes on some of its cervical ribs, most prominently on that of C5 (Bonaparte et al. 1990:fig. 24b; Fig. 4). *Majungasaurus crenatissimus* specimen UA 8678 has bifurcated ribs from positions 4–7 (O'Connor 2007:fig. 20b–e; see also Sampson et al. 1998:fig. 2d).

Among ornithischian dinosaurs, Xu et al. (2010) described bifurcated ribs in the leptoceratopsid ceratopsian *Zhuchengceratops inexpectus*, including in their diagnosis "middle cervical ribs bifurcated due to presence of prominent accessory dorsal process (condition poorly known in other ceratopsians)". They illustrate this condition, which is especially clear in the 6th cervical rib (Xu et al. 2010:fig. 7k–l), and imply that this feature may also be present in other ceratopsians including *Triceratops*.

Elsewhere, the tanystropheid species *Sclerostropheus* (= "*Tanystropheus*") *fossai* is known only from a holotype, MCSNB 4035, that differs from all other *Tanystopheus* specimens in apparently having bifurcated cervical ribs. These are however very different in form to those described here in sauropods and ceratopsians, and were considered by Spiekman and Scheyer (2019:25) to be probably pathological in origin. Their illustration of these cervical ribs (Spiekman and Scheyer 2019:fig. 8b) is too small to be informative.

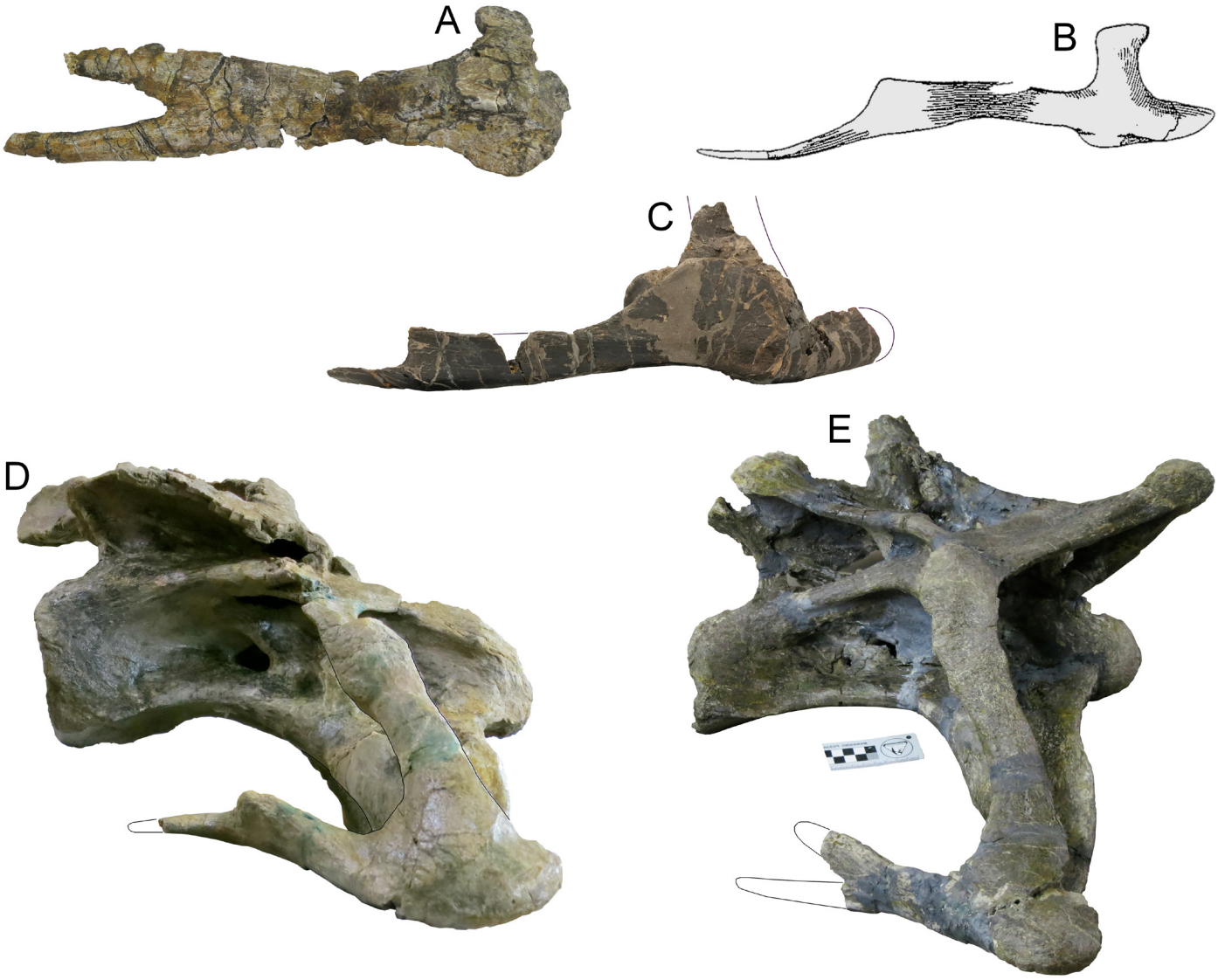

Figure 3. Bifurcated and incipiently bifurcated cervical ribs of sauropods. A, *Moabosaurus utahensis* holotype individual, left cervical rib BYU 14063 (not right as stated by Britt et al. 2017), probably associated with C5, in medial view. B, *Dicraeosaurus hansemanni* holotype MB.R.2379, right cervical rib 8 in lateral view. Modified from Janensch (1929, fig. 21). C, *Brontosaurus parvus* CM 555, right cervical rib 7 in lateral view. D, *Apatosaurus louisae* MWC 1946, cervical vertebra in right lateral view. E, *Apatasaurus louisae* MWC 5659, cervical vertebra in left lateral view (reversed). All photographs by the authors.

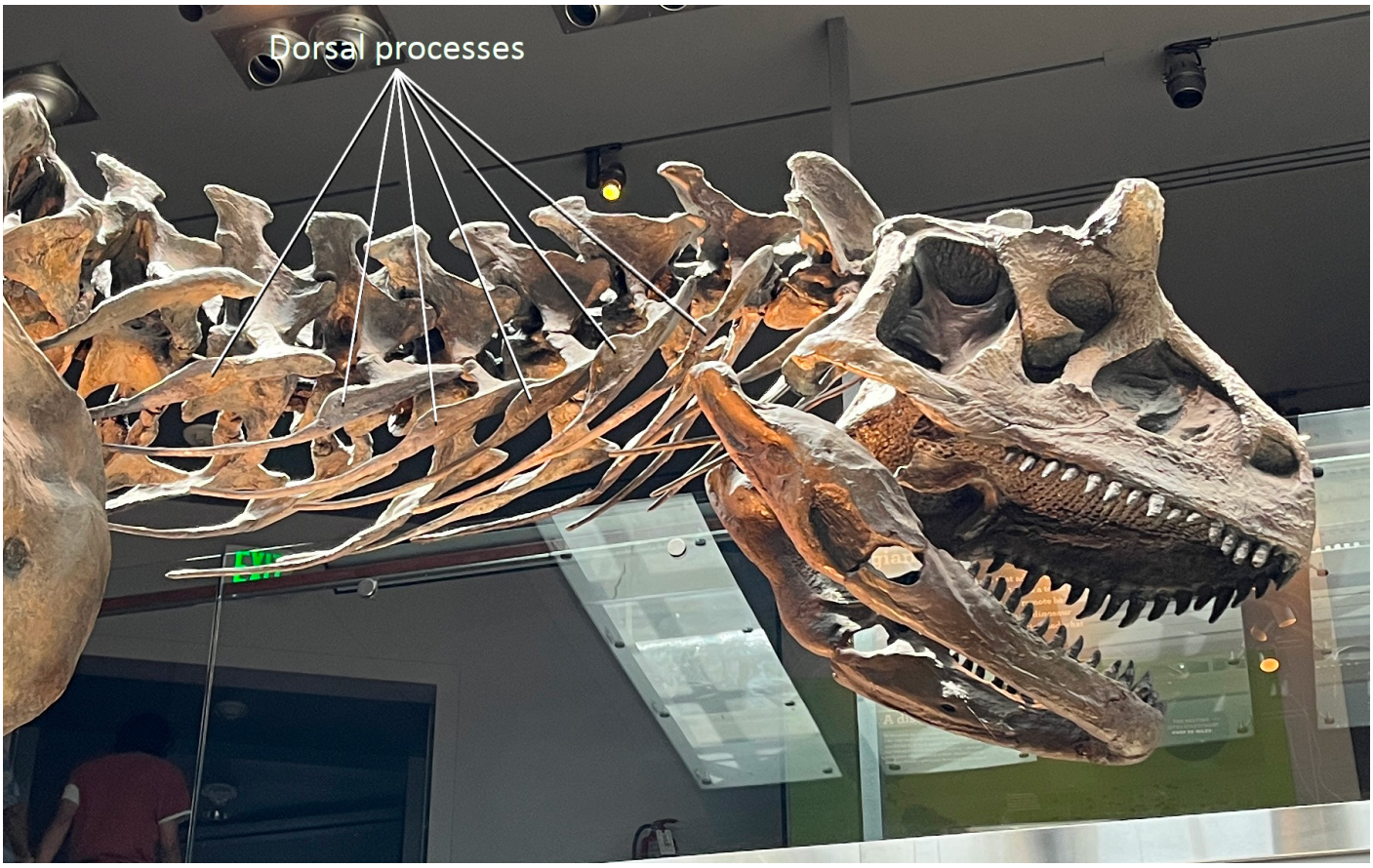

Figure 4. Head and neck of mounted *Carnotaurus sastrei* cast LACM 127704 in right ventrolateral view, showing incipiently bifurcated cervical ribs. Photograph by the authors.

DESCRIPTION

Dorsal Processes and Bifurcated Cervical Ribs in Apatosaurines

***Brontosaurus parvus*, CM 555** – CM 555 is a partial skeleton of an immature apatosaurine collected in 1900 from the Carnegie Museum Quarry D at Sheep Creek, Albany County, Wyoming — the same quarry that yielded the Carnegie *Diplodocus* CM 84, casts of which are found in more than a dozen museums around the world. CM 555 has a somewhat complicated taxonomic history, for which see McIntosh (1981:25). CM 566, the holotype of *Brontosaurus parvus* (formerly *Elosaurus parvus* Peterson and Gilmore, 1902), is from the nearby Quarry E at Sheep Creek (Upchurch et al. 2004; Tschopp et al. 2015). All the apatosaurine specimens from the Carnegie Museum quarries at Sheep Creek are considered to belong to a single species (McIntosh 1981), so pending a more complete description and analysis we tentatively consider CM 555 to be an immature individual of *Brontosaurus parvus*.

Very few of the cervical ribs of CM 555 are complete, and most were heavily restored at some point, presumably early in the 20th century. A right cervical rib probably pertaining to C7 has a dorsal process in the form of a mediolaterally thin (< 5 mm) bony ridge. This ridge extends dorsally from the lateral border of the otherwise flattened cervical rib shaft for approximately 80% of its preserved length (Fig. 3C). The distal end of the dorsal process is squared off, forming a right angle with the remainder of the rib shaft, and it consists of rugose, finished bone, with no sign of breakage. Because the end of the dorsal process forms a right angle rather than an acute angle with the shaft, the rib cannot be described as truly bifurcated, but we consider it to be a point on a morphological spectrum from low dorsal processes to fully bifurcated cervical ribs (see Discussion below). No other cervical ribs of CM 555 show such a well-developed or well-preserved dorsal process.

***Apatosaurus louisae*, CM 3018** – CM 3018 is the holotype specimen of *Apatosaurus louisae*, from the Carnegie Quarry at what is now Dinosaur National Monument (Gilmore 1936; Carpenter 2013). Dorsal ridges or processes similar to that described above for CM 555 are visible on the cervical ribs of C4 through C11, but reach their greatest development in C6 (Fig. 5 and Gilmore 1936:plate 24). As in CM 555, the dorsal ridges are mediolaterally thin (~1 cm) plates of bone. In C6, the distal

end of each dorsal ridge forms an acute but broad angle with the remainder of the cervical rib shaft, creating a very shallow notch or incipient bifurcation.

***Apatosaurus louisae*, MWC 1946** – MWC 1946 is a cervical vertebra of an apatosaurine from the Mygatt-Moore Quarry in western Colorado. The neural spine and prezygapophyses are missing, but the massive and extremely broad cervical ribs show that the vertebra pertains to an apatosaurine. The specimen was illustrated by Foster et al. (2018:fig. 18a, b; note that the specimen is erroneously labelled as MWC 1916 in the figure caption). Foster et al. referred the apatosaurine material from the Mygatt-Moore Quarry to *Apatosaurus louisae* — correctly, in our opinion.

Both cervical ribs are preserved in MWC 1946 and both show evidence of dorsal processes, but the left cervical rib is less well-preserved and what remains is too worn down to be informative. The right cervical rib is better preserved and complete except for the distal tip of the rib shaft (Fig. 3D). In contrast to the mediolaterally thin dorsal processes described above for CM 555 and CM 3018, the dorsal process of this rib takes the form of a rounded bony spike. The posterior margin of this dorsal process forms a right angle with the shaft, but the primary axis of the spike is oriented posterodorsally, at an acute but broad angle to the shaft. Whether this rib can be described as bifurcated therefore depends on whether we follow the angle of the entire dorsal process (acute angle, therefore bifurcated), or merely its distal margin (right angle, therefore not bifurcated). Nevertheless, it seems clear that powerful forces were exerted on this rib from two divergent directions — a point that we discuss below.

***Apatosaurus louisae*, MWC 5659** – MWC 5659 is another isolated apatosaurine cervical vertebra from the Mygatt-Moore Quarry. (Because this quarry contains several apatosaurine individuals, there is no evidence that this vertebra and MWC 1946 are from the same animal —

Figure 5. Partial neck skeleton of *Apatosaurus louisae* holotype CM 3018, mounted at the Carnegie Museum in Pittsburgh. C4 (posterior half), 5–7, and 8 (anterior half), in left anteroventrolateral view. White circles highlight the cervical ribs of C6, showing the dorsolaterally directed processes. Photograph by the authors.

and no evidence that they are not.) It was illustrated but not identified by specimen number in Foster et al. (2018, fig:18e, f). The right cervical rib is not preserved. The left cervical rib is clearly bifurcated (Fig. 3E). Unfortunately, both the shaft and the dorsal process are broken, but enough remains of the dorsal process to show that it was a round bony spike projecting posterodorsally and forming an acute angle with the shaft of the rib.

Apatosaurinae incertae sedis, BYU 18531 – BYU 18531 is a partial skeleton of an apatosaurine from the Morrison Formation of eastern Utah. The specimen includes a nearly complete presacral vertebral series, lacking only the atlas and one of the dorsals. The left cervical rib of C7 (Fig. 6) is completely bifurcated, with a deep, acute notch between two prominent bony prongs, but with the bifurcation primarily mediolateral rather than dorsoventral. Both prongs are missing their distal ends, but the lateral prong is smaller, and in lateral view its margin is very slightly elevated compared to the medial prong. We interpret the lateral prong as the dorsal process, even though it is directed more laterally than dorsally, and the medial prong as the principal shaft of the rib. The right cervical rib of the same vertebra is too incomplete to determine if it was bifurcated, and we did not note any other bifurcated cervical ribs in this specimen.

Other apatosaurines – We have examined the mounted apatosaurine skeletons in the American Museum of Natural History in New York (AMNH 460), Field Museum of Natural History in Chicago (FMNH P25112), and Yale Peabody Museum in New Haven (YPM 1980). We have not noted any bifurcated cervical ribs in these specimens, but the dorsal processes can be subtle and difficult to spot from floor level. Our opportunity to study CM 3018 up close, using a mechanical lift, was therefore especially valuable. We have not visited in person the mounted skeletons in the University of Wyoming Geological Museum in Laramie (UWGM 15556, formerly CM 563) or the National Science Museum in Tokyo (NSMT-PV 20375), but no dorsal processes are apparent in the published illustrations of those specimens (Gilmore 1936 and Upchurch et al. 2004, respectively). Still, a more thorough survey of apatosaurines may well turn up further examples beyond those noted here.

DISCUSSION

Single-shafted and fully bifurcated cervical ribs are not opposed binary states, but the endpoints on a morphological spectrum with many intermediate conditions. The development of a dorsal process or degree of bifurcation can vary greatly among the cervical vertebrae of a single individual. The holotype of *Apatosaurus louisae* (CM 3018) helpfully illustrates this point; the cervical ribs of C6 are truly but shallowly bifurcated, with a distinct notch between the dorsal process and the posterior shaft, but in most of the other cervical ribs the dorsal process is a low ridge or bump as in some cervical vertebrae of *Dicraeosaurus* (Fig. 3B).

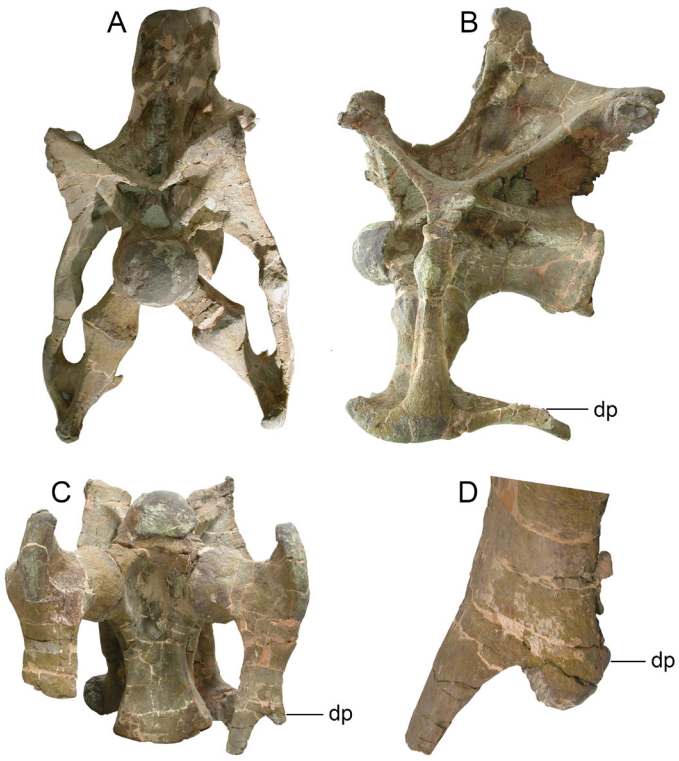

Figure 6. Cervical vertebra 7 of the apatosaurine BYU 18531. A, anterior view. B, left lateral view. C, ventral view. D, close-up of bifurcated cervical rib in left ventrolateral view, with anterior to the top. Abbreviation: dp, dorsal process. The process is very apparent in ventral and ventrolatereral views, but more difficult to pick out in lateral view because it projects more medially than dorsally. Photographs by the authors.

A roughly similar spectrum of cervical rib bifurcation is present in the holotype specimen of *Zhuchengceratops* (Xu et al. 2010). Even more deeply bifurcated cervical ribs are present in the specimen referred to *Apatosaurus louisae* (MWC 5659) and in BYU 18531.

The best examples we have found of bifurcated cervical ribs in apatosaurines are in the holotype of *Apatosaurus louisae* (CM 3018) and referred specimens (MWC 1946, 5659), and in BYU 18531, for which a full description is in progress (Colin Boisvert, pers. comm., 2023). The prominent dorsal process in a cervical rib of *Brontosaurus parvus* CM 555 shows that at least the potential for bifurcation was present in both *Apatosaurus* and *Brontosaurus*.

Wedel et al. (2000) proposed that the cervical rib shafts of sauropods were ossified tendons. That hypothesis has been confirmed by numerous histological studies (Cerda 2009; Klein et al. 2012; Lacovara et al. 2014; Brum et al.

2021). In birds, the cervical ribs (= costal processes) serve as the insertions of the flexor colli lateralis and longus colli ventralis muscles (Zweers et al. 1987), and presumably the cervical ribs of sauropods served the same function (Wedel and Sanders 2002; Taylor and Wedel 2013). The most straightforward inference is that bifurcated cervical ribs were produced when two of the muscles that inserted on the ribs pulled in divergent directions.

Possibly the very large cervical ribs of apatosaurines, which were typically displaced much farther ventrolaterally from the centra than in other sauropods, caused the hypaxial neck muscles to approach from more divergent directions than in most other sauropods (Fig. 7). Although that hypothesis is intuitively appealing, it fails to account for the presence of dorsal processes or fully bifurcated cervical ribs in turiasaurs and dicraeosaurids, neither of which have cervicals ribs that are large or located far from the cervical centra. Despite the differences in the gross size of the cervical ribs, it is perhaps telling that turiasaurs, dicraeosaurids, and apatosaurines all have comparatively short cervical ribs that do not extend beyond the posterior end of the centrum, in contrast to most other sauropods. Similarly short cervical ribs are present in most diplodocoids, and it is possible that dorsal processes or bifurcated cervical ribs await discovery in rebbachisaurids, diplodocines, or other diplodocoids.

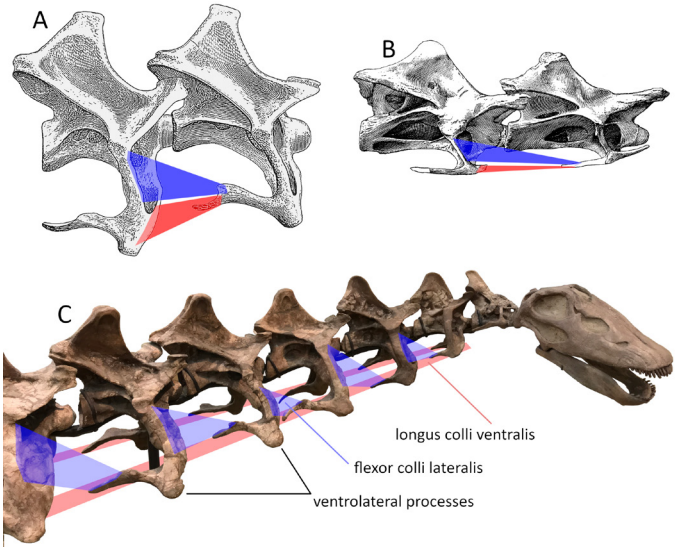

Figure 7. Schematic reconstructions of ventral neck musculature in two diplodocid sauropods. A, *Apatosaurus louisae* holotype CM 3018, cervicals 6 and 7 in left lateral view (reversed), modified from Gilmore (1936, plate 24). B, *Diplodocus carnegie* holotype CM 84, cervicals 6 and 7 in right lateral view, modified from Hatcher (1901, plate 3). C, mounted skeleton of *Apatosaurus louisae* in the Carnegie Museum of Natural History, skull and first seven and a half cervical vertebrae in right posterolateral view. Red lines represent the longus colli ventralis muscles, originating on the anterior aspect of one cervical rib and inserting on the shaft of a more anterior vertebra. Blue lines represent the flexor colli lateralis muscles, originating on the anterior aspect of the tuberculum of one vertebra and inserting on the dorsal part of the shaft of a more anterior vertebra. In *Apatosaurus* the attachment areas are all much larger: in particular, the insertion of the flexor colli lateralis is increased in size by the incipient bifurcation.

Our focus herein has been on bifurcated cervical ribs in apatosaurines and other sauropods, but given the homology of ventral neck muscles across diapsids (Tsuihiji 2007), our hypothesis that bifurcated cervical ribs represent divergent muscle attachments probably generalizes to other dinosaurs with bifurcated cervical ribs. We also note that in the apatosaurine specimens we've examined for which the serial position is known, the bifurcation of the cervical ribs is best developed in C6 or C7, about midway through the neck. The same is true of the dorsal processes or bifurcated cervical ribs in *Dicraeosaurus*, *Carnotaurus*, *Majungasaurus*, and *Zhuchengceratops*. Possibly the divergent muscle insertion angles implied by bifurcated cervical ribs were related to improved muscular control in the middle of the neck, at some distance from both the head and the trunk. Detailed, phylogenetically-informed descriptive and comparative work like that of Snively and Russell (2007a, b) is our best hope for learning more about the functions of these unusual osteological features.

ACKNOWLEDGEMENTS

We thank M. Lamanna and A. Henrici of the Carnegie Museum for access to specimens, D. Pickering for assistance in inspecting the large mounted skeleton of *Apatosaurus louisae* in the public gallery, and J. McHugh of the Museum of Western Colorado – Dinosaur Journey who generously provided curatorial assistance and access to specimens in her care. Andrew Farke (Raymond M. Alf Museum of Paleontology) first made us aware of the existence of bifurcated cervical ribs in non-sauropods, and T. van der Linden (Oertijdmuseum, Boxtel, The Netherlands) pointed us to numerous examples in other animals. C. Boisvert allowed us to cite a personal communication. We obtained the translation of Janensch (1929) by S. Klutzny, and the translation of Young and Zhao (1972) by W. Downs, from the Polyglot Paleontologist website (https://naturalhistory.si.edu/research/paleobiology/research/carrano-lab/polyglot-paleontologist).

We are grateful to R. B. Holmes (University of Alberta) for his efficient handling of this manuscript and to Y.-Y. Wang (University of Alberta) and J. D. Harris (Utah Tech University) for their generous and helpful reviews.

LITERATURE CITED

Baumel, J.J., and L.M. Witmer. 1993. Osteologia; pp. 45–132 in J.J. Baumel (ed.). Handbook of Avian Anatomy: Nomina

Anatomica Avium, 2nd edition. Publications of the Nuttall Ornithological Club No. 23, Cambridge.

Beck, C., 1905. The surgical importance of the cervical rib. Journal of the American Medical Association, 44:1913–1915.

Bonaparte, J.F., F.E. Novas, and R.A. Coria. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. Contributions in Science, Natural History Museum of Los Angeles County 416:1–41.

Britt, B.B., R.D. Scheetz, M.F. Whiting, and D.R Wilhite. 2017. *Moabosaurus utahensis*, n. gen., n. sp., a new sauropod from the Early Cretaceous (Aptian) of North America. Contributions from the Museum of Paleontology, University of Michigan 32:189–243.

Brum, A.S., K.L. Bandeira, B. Holgado, L.G. Souza, R.V. Pêgas, J.M. Sayão, D.A. Campos, and A.W.A. Kellner. 2021. Palaeohistology and palaeopathology of an Aeolosaurini (Sauropoda: Titanosauria) from Morro do Cambambe (Upper Cretaceous, Brazil). Spanish Journal of Palaeontology 36:1–17.

Campos, D.D.A., W.A. Alexander, R. Kellner, J. Bertini, M. Rodrigo., and R.M. Santucci. 2005. On a titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru Group, Late Cretaceous of Brazil. Arquivos do Museu Nacional, Rio de Janeiro 63:565–593.

Carpenter, K. 2013. History, sedimentology, and taphonomy of the Carnegie Quarry, Dinosaur National Monument, Utah. Annals of the Carnegie Museum 81:153–232.

Cerda, I.A. 2009. Consideraciones sobre la histogenesis de las costillas cervicales en los dinosaurios sauropodos. Ameghiniana 46:193–198.

Foster, J.R., R.K. Hunt-Foster, M.A. Gorman, K.C. Trujillo, C. Suarez, J.B. McHugh, J.E. Peterson, J.P. Warnock, and H.E. Schoenstein. 2018. Paleontology, taphonomy, and sedimentology of the Mygatt-Moore Quarry, a large dinosaur bonebed in the Morrison Formation, western Colorado — Implications for Upper Jurassic dinosaur preservation modes. Geology of the Intermountain West 5:23–93. doi:10.31711/GIW.V5I0.19

Gilmore, C.W. 1936. Osteology of *Apatosaurus* with special reference to specimens in the Carnegie Museum. Memoirs of the Carnegie Museum 11:175–300 and plates XXI–XXXIV.

Hatcher, J.B. 1901. *Diplodocus* (Marsh): its osteology, taxonomy and probable habits, with a restoration of the skeleton. Memoirs of the Carnegie Museum 1:1–63 and plates I-XIII.

Henry, B.M., J. Vikse, B. Sanna, D. Taterra, M. Gomulska, P.A. Pękala, R.S. Tubbs, and K.A. Tomaszewski. 2018. Cervical rib prevalence and its association with thoracic outlet syndrome: a meta-analysis of 141 studies with surgical considerations. World Neurosurgery 110:e965-e978.

Janensch, W. 1929. Die Wirbelsäule der Gattung *Dicraeosaurus*. Palaeontographica, Supplement 7, 2:39–133 and plates I–VII.

Janensch, W. 1950. Die Wirbelsaule von *Brachiosaurus brancai*. Palaeontographica, Supplement 7, 3:27–93 and plates I–V.

Klein, N., A. Christian, and P.M. Sander. 2012. Histology shows that elongated neck ribs in sauropod dinosaurs are ossified tendons. Biology Letters 8:1032–1035. doi:10.1098/rsbl.2012.0778

Lacovara, K. J., L.M. Ibiricu, M.C. Lamanna, J.C. Poole, E.R. Schroeter, P.V. Ullmann, K.K. Voegele, Z.M. Boles, V.M. Egerton, J.D. Harris, R.D. Martínez, and F.E. Novas. 2014. A gigantic, exceptionally complete titanosaurian sauropod dinosaur from southern Patagonia, Argentina. Scientific Reports. doi:10.1038/srep06196.

Marsh, O.C. 1896. The dinosaurs of North America. Extract from the 16th annual report of the U. S. Geological Survey, 1894-95, part I, pp. 133–244 and plates II–LXXXV. doi:10.5962/bhl.title.60562

McIntosh, J.S. 1981. Annotated catalogue of the dinosaurs (Reptilia, Archosauria) in the collections of Carnegie Museum of Natural History. Bulletin of the Carnegie Museum 18:1–67.

O'Connor, P.M. 2007. The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 27(S2):127–163.

Peterson, O.A., and C.W. Gilmore. 1902. *Elosaurus parvus*: a new genus and species of the Sauropoda. Annals of Carnegie Museum 1:490–499.

Royo-Torres, R., A. Cobos, and L. Alcalá. 2006. A giant European dinosaur and a new sauropod clade. Science 314:1925–1927.

Royo-Torres, R., P. Upchurch, J.I. Kirkland, D.D. DeBlieux, J.R. Foster, A. Cobos, and L. Alcalá. 2017. Descendants of the Jurassic turiasaurs from Iberia found refuge in the Early Cretaceous of western USA. Scientific Reports 7:14311. doi:10.1038/s41598-017-14677-2

Russell, D.A., and Z. Zheng. 1993. A large mamenchisaurid from the Junggar Basin, Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences 30:2082–2095. doi:10.1139/e93-180

Sampson, S.D., L.M. Witmer, C.A. Forster, D.W. Krause, P.M. O'Connor, P. Dodson and F. Ravoavy. 1998. Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. Science 280(5366):1048–1051.

Sander, P.M. 2013. An evolutionary cascade model for sauropod dinosaur gigantism – overview, update and tests. PLOS ONE 8(10):e78573. doi:10.1371/journal.pone.0078573

Sander, P.M., A. Christian, M. Clauss, R. Fechner, C.T. Gee, E.-M. Griebeler, H.-C. Gunga, J. Hummel, H. Mallison, S. F. Perry, H. Preuschoft, O.W.M. Rauhut, K. Remes, T. Tütken, O. Wings, and U. Witzel. 2010. Biology of the sauropod dinosaurs: the evolution of gigantism. Biological Reviews 86:117–155. doi:10.1111/j.1469-185X.2010.00137.x

Sanders, R.J., and S.L. Hammond. 2002. Management of cervical ribs and anomalous first ribs causing neurogenic thoracic outlet syndrome. Journal of Vascular Surgery 36:51–56.

Schaefer, M., S.M. Black, and L. Scheuer. 2009. Juvenile Osteology: A Laboratory and Field Manual. Academic Press, Cambridge, MA, 384 pp.

Sereno, P.C., A.L. Beck, D.B. Dutheil, H.C.E. Larsson, G.H. Lyon, B. Moussa, R.W. Sadleir, C.A. Sidor, D.J. Varricchio, G. P. Wilson, and J.A. Wilson. 1999. Cretaceous sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. Science 282:1342–1347.

Snively, E., and A.P. Russell. 2007a. Functional variation of neck muscles and their relation to feeding style in Tyrannosauridae and other large theropod dinosaurs. The Anatomical Record 290:934–957.

Snively, E., and A.P. Russell. 2007b. Functional morphology of neck musculature in the Tyrannosauridae (Dinosauria, Theropoda) as determined via a hierarchical inferential approach. Zoological Journal of the Linnean Society 151:759–808.

Spiekman, S.N.F., and T.M. Scheyer. 2019. A taxonomic revision of the genus *Tanystropheus* (Archosauromorpha, Tanystropheidae). Palaeontologia Electronica 22.3.80:1–46.

Taylor, M.P., and M.J. Wedel. 2013. Why sauropods had long necks; and why giraffes have short necks. PeerJ 1:e36. doi:10.7717/peerj.36

Todd, T.W. 1912. "Cervical rib": Factors controlling its presence and its size. Its bearing on the morphology and development of the shoulder. Journal of Anatomy and Physiology 46:244–288.

Tschopp, E., O. Mateus, and R.B.J. Benson. 2015. A specimen-level phylogenetic analysis and taxonomic revision of Diplodocidae (Dinosauria, Sauropoda). PeerJ 2:e857. doi:10.7717/peerj.857

Tsuihiji, T. 2007. Homologies of the longissimus, iliocostalis, and hypaxial muscles in the anterior presacral region of extant Diapsida. Journal of Morphology 268:986–1020. doi:10.1002/jmor.10565

Upchurch, P., T. Yukimitsu, and P.M. Barrett. 2004. A new specimen of *Apatosaurus ajax* (Sauropoda: Diplodocidae) from the Morrison Formation (Upper Jurassic) of Wyoming, USA. National Science Museum Monographs 26:1–108.

Wedel, M.J., and R.K. Sanders. 2002. Osteological correlates of cervical musculature in Aves and Sauropoda (Dinosauria: Saurischia), with comments on the cervical ribs of *Apatosaurus*. PaleoBios 22:1–12.

Wedel, M.J., R.L. Cifelli, and R.K. Sanders. 2000. Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*. Acta Palaeontologica Polonica 45:343–388.

White, T.D., M.T. Black, and P.A. Folkens. 2011. Human Osteology, 3rd edition. Academic Press, Cambridge, MA, 688 pp.

Xu, X., K. Wang, X. Zhao, C. Sullivan, and S. Chen. 2010. A new leptoceratopsid (Ornithischia: Ceratopsia) from the Upper Cretaceous of Shandong, China and its implications for neoceratopsian evolution. PLOS ONE 5(11):e13835. doi:10.1371/journal.pone.0013835

Young, C.-C., and X. Zhao. 1972. *Mamenchisaurus hochuanensis s*p. nov. Institute of Vertebrate Paleontology and Paleoanthropology Monograph Series I, 8:1–30. [In Chinese]

Zhang, X.-Q., L.-D. Qing, X. Yan, and H.-L. You. 2018. Redescription of the cervical vertebrae of the mamenchisaurid mauropod *Xinjiangtitan shanshanesis* Wu et al. 2013. Historical Biology 32(6):803–822. doi:10.1080/08912963.2018.1539970

Zweers, G.A., J.C. Vanden Berge, and R. Koppendraier. 1987. Avian cranio-cervical systems. Part I: Anatomy of the cervical column in the chicken (Gallus gallus L.). Acta Morphologica Neerlando-Scandinavica 25:131–155.