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Almost all known sauropod necks are incomplete and distorted

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Abstract

Sauropods are familiar dinosaurs, immediately recognisable by their great size and long necks. However, their necks are much less well known than is usually assumed. Very few complete necks have been described in the literature, and even important specimens such as the Carnegie *Diplodocus* and *Apatosaurus*, and the giant Berlin brachiosaur, in fact have imperfectly known necks. In older specimens, missing bone is often difficult to spot due to over-enthusiastic restoration. Worse still, even those vertebrae that are complete are often badly distorted – for example, in consecutive cervicals of the Carnegie *Diplodocus* CM 84, the aspect ratio of the posterior articular facet of the centrum varies so dramatically that C14 appears 35% broader proportionally than C13. Widespread incompleteness and distortion are both inevitable due to sauropod anatomy: large size made it almost impossible for whole individuals to be preserved because sediment cannot be deposited quickly enough to cover a giant carcass; and distortion of presacral vertebrae is common due their lightweight pneumatic construction. This ubiquitous incompleteness and unpredictable distortion compromise attempts to determine habitual neck posture and range of motion by modelling articulations between vertebrae.

Keywords: Sauropod, Dinosaur, Neck, Cervical vertebrae, Preservation

Introduction

In our recent paper on how the long necks of sauropods did not evolve primarily due to sexual selection (Taylor et al. 2011), one of the ideas we discussed is that sexual dimorphism between the necks of male and female sauropods, expressed as a ratio of neck lengths to shoulder height, might be an indicator of sexual selection. Rather despairingly, we wrote (Taylor et al. 2011:4): “Available samples of sauropod taxa are unfortunately not large enough to demonstrate bimodal distribution of morphological features within any sauropod species.”

Sauropod specimens are rarely found in a form complete enough to allow even relatively rudimentary measurements to be made – for example, neck length or shoulder height. In fact, the problem is more profound than is generally realised. It is not just that we do not have large populations of well-preserved sauropod individuals, capable of being subject to statistical analyses; even individual complete sauropods are extremely rare.

In this short paper I will first show that even the best-preserved and best-known sauropod specimens have necks that are incomplete, then show that distortion of what cervical vertebrae we do have is ubiquitous and unpredictable, and finally explore the implications of this on what we can know of how these necks behaved in life.

Institutional Abbreviations

BYU — Brigham Young University, Provo, Utah (USA)

CCG — Chengdu College of Geology, Chengdu (China)

CM — Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (USA)

GCP — Grupo Cultural Paleontológico de Elche, Museo Paleontológico de Elche (Spain)

IVPP — Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing (China)

MfN — Museum für Naturkunde Berlin, Berlin (Germany) (collection numbers for fossil reptiles: MB.R.nnnn)

MPM — Museo Padre Molina, Río Gallegos, Santa Cruz (Argentina)

OMNH — Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma (USA)

YPM — Yale Peabody Museum, New Haven, Connecticut (USA)

ZDM — Zigong Dinosaur Museum, Zigong, Sichuan (China)

Incompleteness

Unambiguously complete necks are known from published account of only six species of sauropod, two of which are species of the same genus. In chronological order:

- *Camarasaurus lentus* is known from a fine juvenile specimen, CM 11338, described by Gilmore (1925). Many other *Camarasaurus* specimens exist, but are less complete than Gilmore's. Unfortunately, as this specimen is not adult, it does not reflect the mature morphology.

- *Apatosaurus louisae*, as discussed below, is known from a complete sequence of vertebrae, but the last three are badly damaged (Gilmore 1936).
- *Mamenchisaurus hochuanensis* was described by Young and Zhao (1972). The holotype specimen, CCG V 20401, includes a complete, articulated sequence of cervical vertebrae. However, each vertebra is broken in half at mid-length, and the vertebrae are badly crushed in an oblique plane.
- *Shunosaurus lii* was described by Dong et al. (1983), based on a specimen, IVPP V.9065, from which only five cervicals are known, all of them poorly preserved. However, Zhang et al. (1984) indicates that multiple additional specimens are known, and their figure 1 is a quarry map showing a very complete specimen ZDM T5401 with all vertebrae from cervical 2 to caudal 7 in articulation. Zhang (1988: figure 2) illustrated a different complete specimen ZDM T5402 as excavated. Chatterjee and Zheng (2002) also confirmed that *Shunosaurus* is known from several complete skeletons.
- *Mamenchisaurus youngi* was described by Ouyang and Ye (2002) based on ZDM 0083, a complete specimen containing a vertebral column that is perfectly articulated from skull to anterior caudals. The quarry is illustrated in their figure 2 and photographed in plate 1, and all 18 cervicals are illustrated.
- *Spinophorosaurus nigerensis* (Remes et al. 2009) is known from two specimens, of which the holotype was found in very good condition and well articulated (Figure 1). The description is not explicit, but implies that the skeleton of the neck is complete.

The total number of sauropods for which even one complete neck has been described is a tiny proportion of all the sauropods that have been named. As best we can tell, only one sauropod – *Shunosaurus* – is known from more than a single complete neck; and those multiple specimens have not been described. So while in theory it might be possible to determine whether there is a bimodal distribution in the length of *Shunosaurus lii* necks, the data doesn't exist to do this work.



Figure 1. *Spinophorosaurus nigerensis* holotype GCP-CV-4229 in situ during excavation in the region of Aderbissinat, Thirozerine Dept., Agadez Region, Republic of Niger. Reproduced from Remes et al. (2009: figure 1).

Several well-known sauropod specimens are often thought of as having complete, undamaged necks, but this is not the case. I now survey these specimens.

***Diplodocus carnegii* CM 84**

The Carnegie *Diplodocus* is one of the most recognised dinosaurs in the world: not only is the original specimen, CM 84, on display as a mounted skeleton in the Carnegie Museum, but casts are displayed in many other major museums (e.g. the Natural History Museum in London, the Museum für Naturkunde Berlin and the Muséum National d'Histoire Naturelle in Paris.) The neck appears complete, with fifteen cervical vertebrae, in these mounted skeletons, and is illustrated as such by Hatcher (1901: plate 8); Figure 2.

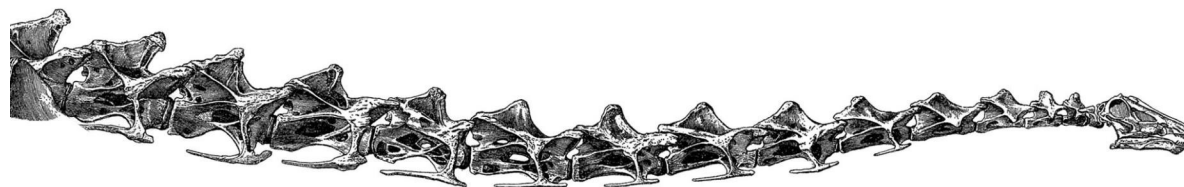


Figure 2. Neck of *Diplodocus carnegii* holotype CM 84, as reconstructed by Hatcher (1901: plate XIII), with fifteen undamaged cervical vertebrae.

However, the situation is not as clear as it appears in these exhibits.

Holland (1900:816), in the first published account of the Carnegie *Diplodocus*, assigned to it only eleven cervicals, noting (on p. 817) that:

The cervicals were for the most part interarticulated, all lying in such position as to show the serial order [...] Eleven are found in the specimen at the Carnegie Museum, atlas and axis being as yet undiscovered.

Allowing for the missing atlas and axis, Holland concluded only that the cervical count was “at least 13”.

However, Hatcher (1900:828–829) corrected this count later the same year:

About 45 feet (14 meters) of the vertebral column is preserved in our specimen. When discovered the vertebrae did not lie in a connected and unbroken series, yet there can be little doubt that they all pertain to the same individual [...] Unfortunately no diagram was made, at the time of exhuming the remains, showing the relative position of each of the vertebrae in the quarry [...] Early last spring, at the request of the writer, Mr. W. H. Reed (who assisted in unearthing the skeleton), while again on the ground, made a diagram of the quarry, showing the relative positions, as he remembered them, of the various bones of the skeleton.

Despite this uncertainty, Hatcher asserted (p. 828–829):

“In all 41 vertebrae are represented, including 14 cervicals (all but the atlas) [...] Assuming that no vertebrae are missing from our series the vertebral formula of *Diplodocus* should now be written as follows: 15 cervicals [...] The number of cervical vertebrae in *Diplodocus* is definitely fixed at at least 15.”

Hatcher's 1900 paper is unsatisfactory in that it gives no reason for his revision of the cervical count. Hatcher also hedged by leaving open the possibility of there being more than 15 cervicals. The lack of a reliable quarry map is unfortunate.

In his subsequent monograph, Hatcher (1901:4) expanded on the completeness and condition of the material as follows:

[*Diplodocus carnegii* holotype CM 84] has been entirely freed from the matrix and is found to consist of [appendicular material and] forty-one vertebrae divided as follows: fourteen cervicals including the axis, eleven dorsals, four sacrals, and twelve caudals. These vertebrae are for the most part fairly complete, though unfortunately the sacrals and **anterior cervicals are more or less injured**. This series of forty-one vertebrae are believed to pertain to one individual and to form an unbroken series from the axis to the twelfth caudal, although as was shown in a previous paper, **there is some evidence that there are perhaps one or more interruptions in the series and that one or more vertebrae are missing**. On the other hand, as will appear later, **it is not entirely impossible that at least one vertebra of this supposed series pertains to a second individual** belonging perhaps to a distinct genus. [Emphasis added.]

Hatcher (1901:11) went on to quote a statement from A. S. Coggeshall, who had assisted in the excavation, explaining in more detail how the elements of the neck were discovered:

[The] last (fifteenth) cervical was considerably removed from the succeeding dorsals and less so from the preceding cervicals. Commencing with the next vertebra (cervical fourteen), the direction of the entire cervical series was altered

so that it lay with its axis almost at right angles to that of the dorsal series. The cervicals extended in an almost straight line from the fourteenth to the fifth, but there was a considerable gap between cervicals eleven and ten, while the axis and cervicals three, four and five were doubled back under the succeeding vertebrae.

This account almost explains why Holland underestimated the number of cervicals: the anteriormost four, lying under more posterior cervicals, had not yet been found. However, if ten cervicals (C6–C15) had been found and the atlas and axis were both missing, Holland would surely have stated that there were in total at least twelve cervicals, not at least eleven. Some mystery remains: perhaps Holland was not counting C11 (see below) as part of the specimen.

Coggeshall's description is largely corroborated by Reed's quarry map, which is included as Plate 1 of Hatcher's (1901) monograph (Figure 3). However, the map is in some respects at odds with the description: for example, it shows all 13 vertebrae C2–C14 in a single straight line, and shows gaps both between C10 and C11 (as stated), and also between C11 and C12 (not mentioned in the text).

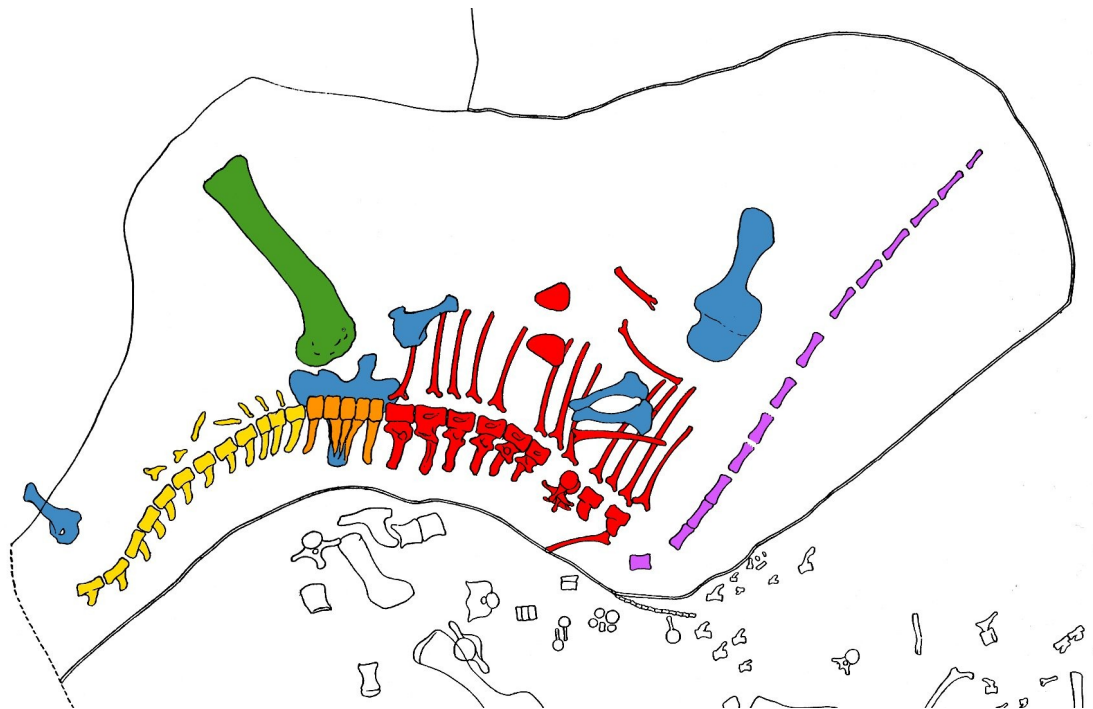


Figure 3. W. H. Reed's diagram of Quarry C near Camp Carnegie on Sheep Creek, in Albany County, Wyoming. The coloured bones belong to CM 84, the holotype of *Diplodocus carnegii*; other bones belong to other individuals, chiefly of *Brontosaurus*, *Camarasaurus* and *Stegosaurus*. Modified (cropped and coloured) from Hatcher (1901: plate I). Cervical vertebrae are purple (and greatly simplified in outline), dorsals are red, the sacrum is orange, caudals are yellow, limb girdle elements are blue, and limb bones are green.

Regarding the vertebra that might belong to a different genus, Hatcher (1901:22) explained: “*Eleventh Cervical*.—This vertebra is so unlike either the immediately preceding or succeeding vertebrae that if it had been found isolated it would have been unhesitatingly referred to a different genus. Mr. Coggeshall, however, assures me that it was interlocked with the succeeding, or twelfth cervical.” Yet, as noted, the quarry map suggests that there was some distance between C11 and C12, perhaps invalidating Coggeshall's assertion. It is to be lamented that both the map and the description were created some time after the excavation

actually took place, by which time memories had evidently become unreliable.

In conclusion, *Diplodocus carnegii* most likely had fifteen cervicals, but may have had more (if some vertebrae were not recovered), or maybe fewer (if C11 was misassigned). Furthermore, the anterior cervicals are damaged in a way that is not at all apparent from Hatcher's drawings (plate III) or photographs (plate IV) because they were restored before these illustrations were prepared. As Hatcher (1901:23) noted, "The work of freeing these vertebrae from the matrix and restoring them was for the most part done during my absence in the field. Unfortunately no drawings or photographs were taken prior to the process of restoring with colored plaster." (In the early 20th Century, it was routine to restore damaged fossils in ways that completely obscured the degree of damage: see Figure 4.)

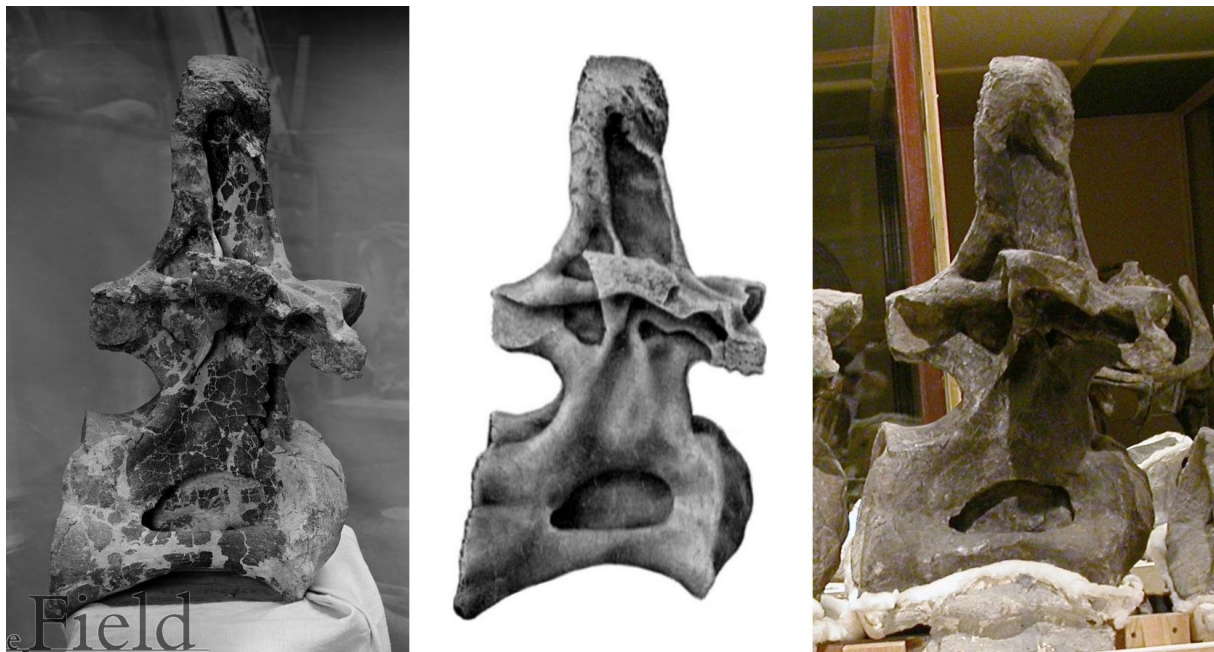


Figure 4. Three images of presacral vertebra 6 (probably dorsal 7) of *Brachiosaurus altithorax* holotype FMNH P25107, in right lateral view, showing misleading restoration. **Left:** Field Museum photograph CS GEO16166, photographer Charles Carpenter, taken in 1905, the year after Riggs's (1904) descriptive monograph. Note the "crazy-paving" effect of the many cracks and missing areas of bone surface. **Middle:** Illustration of the same vertebra in Riggs (1904: plate LXXII). Note that the damage to the vertebral surface is not depicted. **Right:** photograph of the same vertebra, taken by the author in 2005. Note that the damage apparent in the 1905 photograph is no longer visible: the vertebra seems to have been painted to conceal its incompleteness.

***Apatosaurus louisae* CM 3018**

Apatosaurus louisae is the best known species of *Apatosaurus*, since its holotype CM 3018 is much more complete and better preserved than that of the type species *A. ajax* (YPM 1680), or that of the closely related *Brontosaurus excelsus* (YPM 1980).

The specimen was collected by Earl Douglass in 1909 and 1910, from what was then known as the Carnegie Museum Dinosaur Quarry near Jensen, Utah, and is now Dinosaur National Monument. It was mounted for exhibition in 1913, and somewhat belatedly named the type of a new species in a brief initial description by Holland (1915). He noted that "the specimen consists of a series of vertebrae, complete from the atlas to nearly the end of the tail" and appendicular material; but also that "the cervical vertebrae had been separated from the dorsals and shifted, but the entire series was found articulated in regular order" (p. 143).

(Holland's description also mentioned that “a skull, which judging by its location, belongs to the specimen, was found within eleven feet of the atlas. It does not differ greatly in form from the skull which belongs to *Diplodocus*”. Had Holland stuck to his guns, *Apatosaurus* could have been restored with its correct skull 63 years before Berman and McIntosh (1978) corrected Marsh's long-standing and influential misapprehension that it had a *Camarasaurus*-like skull.)

Holland stated (p. 144) that he had “in preparation a large monographic paper relating to the genus, based in part upon [CM 3018]”. However, completion was long delayed, and Holland died in 1932 before it was ready to be published. It was eventually brought to completion by Gilmore (1936) and it is from this monograph that the species is primarily known.

Gilmore's monograph explains that all is not as it seems in the neck of his specimen. He notes (p. 191) that “there was some distortion due to the compression to which [the cervicals] had been subject, but this has been largely corrected during preparation” – a questionable decision, as it means that the shapes of the vertebrae as originally found are now lost, and cannot be subjected to more modern retrodeformation techniques (e.g. Tschopp et al. 2013). He continues “Cervicals thirteen, fourteen, and fifteen, however, were so badly crushed that it was thought best to replace them in the mounted skeleton by plaster restorations of these vertebrae”, although he does claim that “they are, however, sufficiently well preserved so that most of their important characteristics can be determined”. The caption to Gilmore's plate XXIV reads “Cervical vertebrae of *Apatosaurus louisae*. Type, No. 3018 [...] Cervicals 13, 14 and 15 have been much restored from badly crushed originals, and should be used with caution.” It is evident from the plate that most of C5 is also missing, although this is not acknowledged in the text.

In conclusion, while the articulation of the cervical sequence of CM 3018 leaves no doubt that all cervicals are present and in the correct order, the crucial posterior cervicals are largely uninformative.

***Giraffatitan brancai* MB.R.2181**

This specimen is the paralectotype of *Giraffatitan brancai* (= “*Brachiosaurus*” *brancai*). Much of the material is incorporated in the mounted skeleton in the atrium of the Museum für Naturkunde, which is the largest mounted skeleton of a terrestrial animal anywhere in the world. The presacral vertebrae, however, are too heavy and fragile to mount: instead, high quality sculptures are used, and the vertebrae themselves are held in collections.

The real bones that the presacrals in the mount are based on are those of two specimens – the lectotype MB.R.2180 (previously known as SI) and the paralectotype MB.R.2181 (previously SII). The former includes cervicals 2–7, an assignment that can be accepted with some confidence because C2 in sauropods is very distinctive, having a completely different anterior articular surface from all the subsequent cervicals. The latter includes cervicals 3–13 (although almost all of them are damaged, some very severely).

However, the two individuals SI and SII were found together in a single quarry (designated Quarry S). Bones of the two individuals were jumbled up together, with little articulation, as shown in the quarry map, redrawn by Heinrich (1999: figure 16; Figure 5) from an original drawn in the field by Werner Janensch. Any reconstruction – or even assignment of individual vertebrae to one specimen or the other – must be considered provisional.

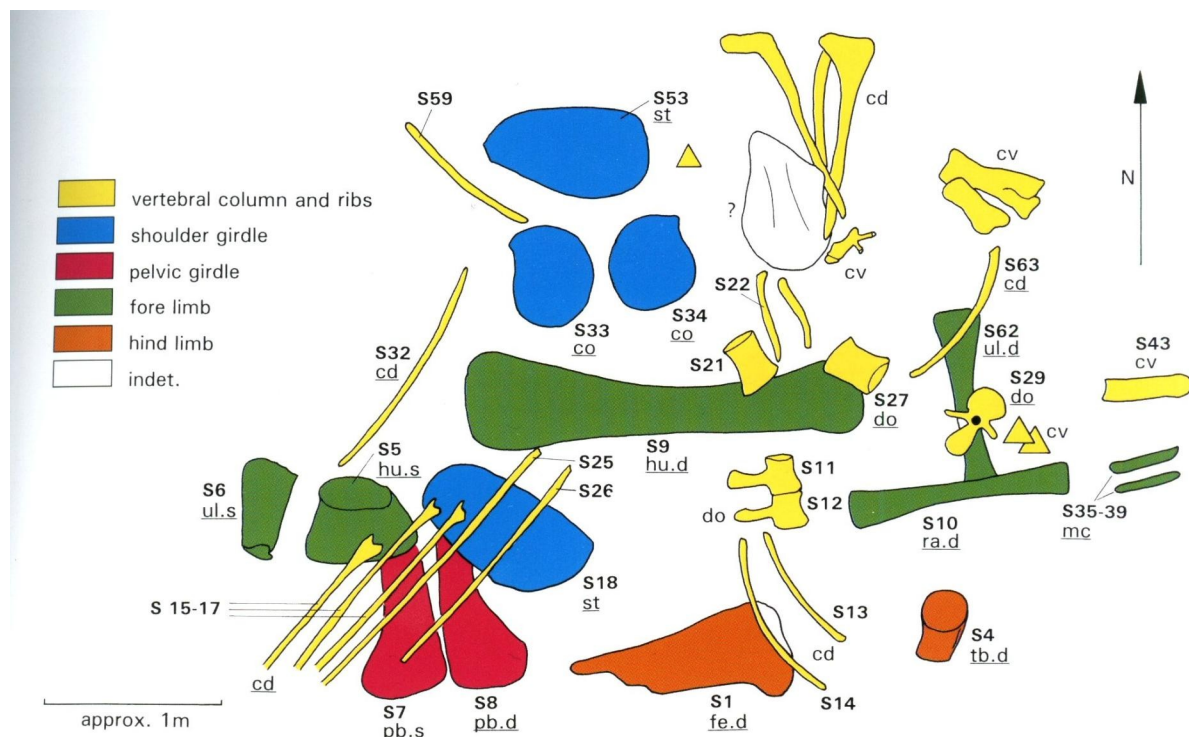


Fig. 16. Incomplete skeletons of *Brachiosaurus brancai* from Tendaguru Site S. Anatomical identifications of skeleton SII are underlined. Elements of skeleton SI could not be identified with certainty. The measured length of the humerus S9 (213.0 cm) was used to calculate the scale for the quarry map. Redrawn after a field sketch from W. Janensch

Figure 5. Quarry map of Tendaguru Site S, Tanzania, showing incomplete and jumbled skeletons of *Giraffatitan brancai* specimens MB.R.2180 (the lectotype, formerly HMN SI) and MB.R.2181 (the paralectotype, formerly HMN SII). Anatomical identifications of SII are underlined. Elements of SI could not be identified with certainty. From Heinrich (1999: figure 16), redrawn from an original field sketch by Werner Janensch.

I have previously suggested (Taylor 2009:800–801) that the distinctively high-spined dorsal vertebra usually considered the fourth of SII may not actually belong to that specimen, or even that taxon. Instead, this unusually tall vertebra may belong to an animal more closely resembling the Tendaguru brachiosaur briefly described by Migeod (1931) and which I plan to redescribe (Taylor 2005, Taylor in prep). If this vertebra is indeed not part of SII then the most likely consequence is that it is part of SI. This would be unfortunate if so. The smaller and less complete SI, rather than the larger, more complete and better known SII, is the lectotype (Janensch 1935–1936). Therefore, the ICZN rules dictate that the name *Giraffatitan brancai* would adhere to SI, and that a new name would be required for the better-known SII. Since this species was thought until relatively recently to be a species of the North American genus *Brachiosaurus* (see Taylor 2009), a further reassignment would mean that this charismatic and characteristic specimen would become known by a third different name in less than a decade. To avoid this outcome, an ICZN petition may be warranted.

Janensch (1950:33) indicates that the confusion of the cervical vertebrae is not as bad as that of the dorsals, but the situation is still far from clear:

The vertebrae from the 3rd to 15th presacrals [of SII] lay in articulation in a consolidated lime sandstone lens; of them, the 3rd to 5th vertebrae are tolerably complete, the remaining 10 vertebrae were articulated with one another, with one interruption that arose when the 8th presacral vertebra rotated out of the series and

was displaced. [Translation by Gerhard Maier.]

So there might have been other displaced cervicals, before or after the one designated “8th”, that were not recovered. Neither can we be wholly confident that the anteriormost preserved cervical in the SII series is really C3. Its identification is based on the overlap with vertebrae of SI, but we cannot be certain that SI is a member of the same species as SII. Perhaps the anteriormost preserved cervical is really C4? Or perhaps some of the “SII” cervicals really belong to SI.

In conclusion: *Giraffatitan brancai* probably had thirteen cervicals, but may have had more, or possibly less; and the neural arches are only certainly known for cervicals 3, 4, 5 and 8 in SII (if these are the correct serial positions for those vertebrae). If SI is indeed a member of the same species then cervicals 2–7 are known from well-preserved elements, but no more. All of this uncertainty is exacerbated by the problem that no complete neck of any other brachiosaur has been described.

Distortion

Even in necks where most or all of the vertebrae are present and largely complete, extensive distortion is common. This is difficult or impossible to quantify, especially as we do not in general know what the original, undistorted shapes are. But we can take tentative steps towards recognising the extent of the problem by considering the shapes of the cotyles of consecutive vertebrae.

In sauropod cervical vertebrae (and most dorsal vertebrae), the posterior articular face of the centrum is called the cotyle, due to its distinctive hollow shape. The anterior articular face is convex, and so is called the condyle. The cotyle of one vertebra and the condyle of the succeeding one form a ball-and-socket joint (see Taylor and Wedel 2013b: figures 2–3), similar to the condition in extant horses and camels (see Taylor and Wedel 2013b: figures 20–21) among other animals.



Figure 6. Sequences of cervical vertebrae of extant animals, showing that articular facet shape remains similar along the column. **Top.** Cervical vertebrae 3–7 of a mature savannah monitor lizard, *Varanus exanthematicus*, in anterior view. (The cervicals of monitor lizards, unlike those of sauropods and most mammals, are procoelous, with the anterior facet being concave and the posterior convex.) **Bottom.** cervical vertebrae 2–5 of a mature house-cat, *Felis catus*, in posterior view. All photographs by the author, of specimens in his personal collection.

In extant animals, the articular facets of consecutive vertebrae are of much the same shape, varying only gradually along the neck. In particular, the aspect ratio of the facet – its width:height ratio – remains constant or nearly so (Figures 6 and 7). However, in the fossilised necks of sauropods, it's not unusual for even consecutive vertebrae to be crushed in opposite directions, giving their cotyles (apparently) wildly different aspect ratios.



Figure 7. Cervical vertebrae of a baby giraffe, *Giraffa camelopardalis*, in posterior view. Top row, left to right: cervicals 7, 6 and 5; bottom row, left to right: cervicals 4, 3 and 2. Despite changes in the vertebrae along the column, the flattened pentagon shape of the articular facets remains similar along the sequence. (Note that extensive cartilage caps existed on the articular facets of this very young specimen, but were lost in preparation.) Photograph by the author, of a specimen in his personal collection.

Consider for example the *Giraffatitan brancai* lectotype MB.R.2180 (formerly HMN SI), one of the best preserved sauropod neck series. Cervicals 4 and 6 of this specimen are shown in posterior view in Figure 8. (The intermediate cervical 5 has part of its cotyle rim broken off, and cannot be reliably measured.) Measuring from the photos, the width:height ratio of C4 (on the left) is $683/722$ pixels = 0.95, and that of C6 (on the right) is $1190/820$ pixels = 1.45. So these two vertebrae – from the same neck, and with only one other vertebrae coming in between them – differ in preserved cotyle aspect ratio by a factor of 1.53.



Figure 8. Cervical vertebrae 4 (left) and 6 (right) of *Giraffatitan brancai* lectotype MB.R.2180 (previously HMN SI), in posterior view. Note the dramatically different aspect ratios of their cotyles, indicating that extensive and unpredictable crushing has taken place. Photographs by author.

As a second example, consider the single most studied sauropod neck specimen in the world, that of the *Diplodocus carnegii* holotype CM 84. Figure 9 shows adjacent cervicals 13 and 14, in posterior view. Note that the posterior part of the neck was considered well preserved by Hatcher (1901), with only anterior vertebrae noted as having been damaged. Measuring from Hatcher's photos, the width:height for C14 (on the left) is $342/245$ pixels = 1.40. For C13 (on the right), it is $264/256$ pixels = 1.03. So C14 is apparently 35% broader than its immediate predecessor.

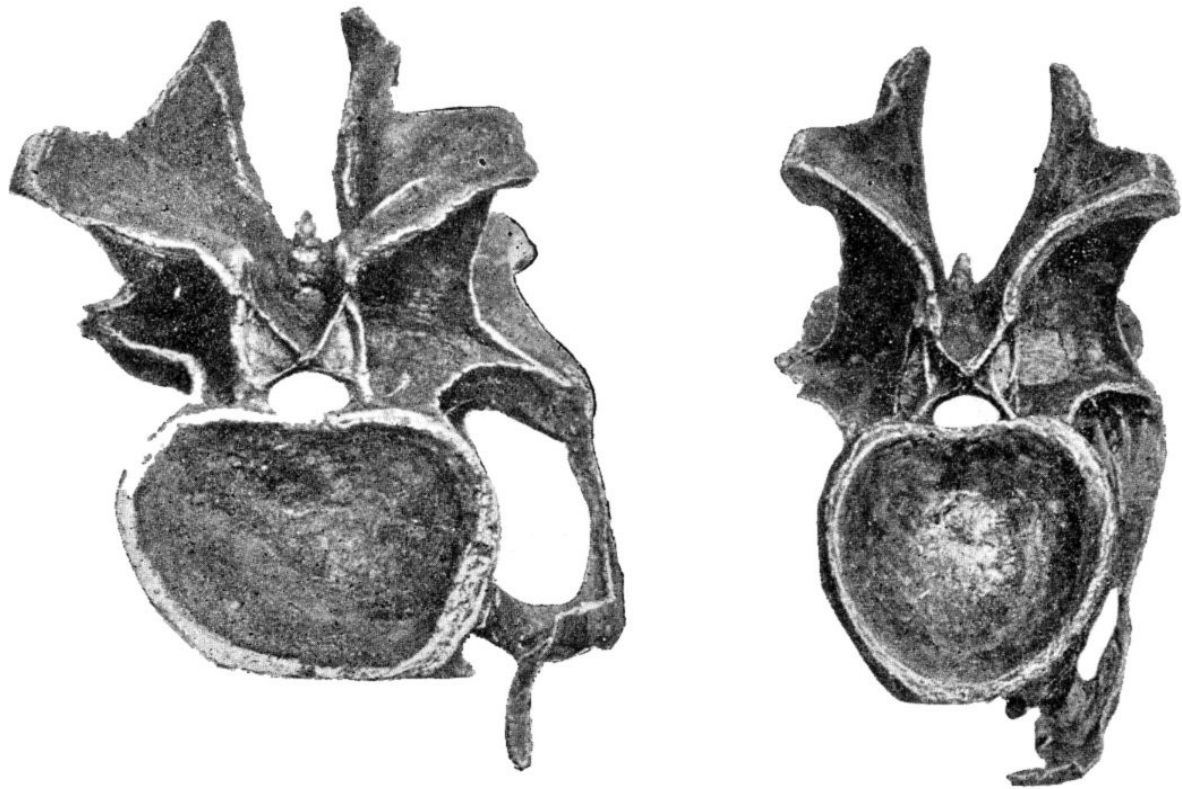


Figure 9. Cervical vertebrae 14 (left) and 13 (right) of *Diplodocus carnegii* holotype CM 84, in posterior view. Note the dramatically different aspect ratios of their cotyles, indicating that extensive and unpredictable crushing has taken place.

Such extreme variation in apparent aspect ratio of the cotyles of adjacent and near-adjacent cervical vertebrae can only be the result of extensive and unpredictable crushing. It is certain that other parts of the vertebrae, especially the fragile lateral processes and zygapophyseal rami, were also distorted, and impossible to reliably restore the undistorted state.

Discussion

All of the problems with sauropod neck preservation arise from the nature of the animals.

First, sauropods are big. This is a recipe for incompleteness of preservation. (It is no accident that the most completely preserved individuals are small individuals such as CM 11338, the cow-sized juvenile *Camarasaurus lentus* described by Gilmore, 1925). For an organism to be fossilised, it is necessary for the carcass to be swiftly buried in mud, ash or some other substrate. This can happen relatively easily to small animals, such as the many finely preserved small theropods from the Yixian Formation in China, but is virtually impossible with a large animal. Except in truly exceptional circumstances, sediments simply are not deposited quickly enough to cover a 25 meter, 20 tonne animal before it is broken apart by scavenging, decay and water transport.

In light of this, it is not surprising that the very longest sauropods necks are generally known from particularly inadequate necks. The longest neck for which we have direct evidence is that of the diplodocid *Supersaurus*, possibly 15 m long, but the only cervical

material of the largest specimen is a single 1.4 m cervical (BYU 9024, formerly BYU 5003; Jensen 1985, 1987). Similarly, the giant basal titanosauriform *Sauroposeidon* probably had a neck about 11 m long, but the only definite material belonging to it is a sequence of three and a half cervicals from the middle of the neck (OMNH 53062; Wedel et al. 2000). The longest known titanosaur neck is probably that of *Puertasaurus*, at around 9m, but the only known cervical material is a single 118 cm vertebra, MPM 10002 (Novas et al. 2005).

Secondly, even when complete sauropods are preserved, or at least complete necks, distortion of the preserved cervical vertebrae is almost inevitable because of their uniquely fragile construction. As in modern birds, the cervical vertebrae were lightened by extensive pneumatization, so that they were more air than bone (Taylor and Wedel 2013a: figure 4), with the air-space proportion typically in the region of 60–70% and sometimes reaching as high as 89% (Taylor and Wedel 2013a: table 2; Wedel 2005: figure 7.4C). While this construction enabled the vertebrae to withstand great stresses for a given mass of bone, it nevertheless left them prone to crushing, shearing and torsion when removed from their protective layer of soft tissue. For large cervicals in particular, the chance of the shape surviving through taphonomy, fossilisation and subsequent deformation would be tiny.

Both the incompleteness and distortion of sauropod necks have grave consequences for our ability to reason about sauropods. As noted above, the very small sample of complete necks makes it quite impossible to perform meaningful statistical analyses. Similarly, the frequent, unpredictable and sometimes dramatic distortion of what vertebrae we do have renders analysis of neutral poses and ranges of motion extremely problematic. For vertebrae small and robust enough to be manipulated by hand, this can be readily observed in physical space (Figure 10). There is no reason to think that computer modelling of vertebrae and their articulations (e.g. Stevens and Parrish 1999) should yield models any more meaningful than the distorted fossils that they are based on.



Figure 10. Manipulation of consecutive sauropod vertebrae by hand. Cervicals 2 and 3 of *Giraffatitan brancai* lectotype MB.R.2181 (formerly HMN SI). I attempted to articulate these two vertebrae, and empirically determine the feasible range of motion. Due to subtle distortion of the zygapophyses of these vertebrae, it was not possible to articulate C2 in a more extended position relative to C3 than shown here. Photograph by Mathew J. Wedel.

Conclusion

What does it all mean? Only this: we don't know as much as we think we do. We don't even know how many cervical vertebrae well-known sauropods such as *Diplodocus* and *Giraffatitan* had. We don't have complete necks for either of these sauropods, nor for almost any others. Even those we do have are in some cases badly crushed (e.g. *Mamenchisaurus hochuanensis*). We are woefully short of sauropod necks.

As scientists, we need to avoid blithely asserting factoids such as “*Diplodocus* had 15 cervicals and *Giraffatitan* only 13”. We simply don't know whether this is true. Evidence supports it as a hypothesis – these numbers are certainly the best guesses for the taxa in question – but a hypothesis is all it is. Hypotheses of neck posture and flexibility should be held even more lightly, since they are based on inferences drawn from distorted elements whose true shapes we may never know.

None of this is necessarily disastrous, so long as we properly acknowledge the degree of uncertainty that afflicts our work.

Acknowledgments

Gerhardt Maier provided the translation of Janensch (1950). This translation, and others that I referred to, are freely available from the Polyglot Paleontologist web-site at <http://paleoglot.org/>

This paper is based in part on three blog-posts from *Sauropod Vertebra Picture of the Week* (Taylor 2011, Taylor 2013, Taylor 2014), and also on part of a talk at the Symposium on Vertebrate Palaeontology and Comparative Anatomy (Taylor and Wedel 2011).

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