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NEURAL SPINE BIFURCATION IN SAUROPOD DINOSAURS OF THE MORRISON FORMATION: ONTOGENETIC AND PHYLOGENETIC IMPLICATIONS

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ABSTRACT

It has recently been argued that neural spine bifurcation increases through ontogeny in several Morrison Formation sauropods, that recognition of ontogenetic transformation in this 'key character' will have sweeping implications for sauropod phylogeny, and that *Suuwassea* and *Haplocanthosaurus* in particular are likely to be juveniles of known diplodocids. However, we find that serial variation in sauropod vertebrae can mimic ontogenetic change and is therefore a powerful confounding factor, especially when dealing with isolated elements whose serial position cannot be determined. When serial position is taken into account, there is no evidence that neural spine bifurcation increased over ontogeny in Morrison Formation diplodocids. Through phylogenetic analysis we show that neural spine bifurcation is not a key character in sauropod phylogeny and that *Suuwassea* and *Haplocanthosaurus* are almost certainly not juveniles of known diplodocids. Skeletochronology based on the sequence of skeletal fusions during ontogeny can provide relative ontogenetic ages for some sauropods. Although such data are sparsely available to date and often inconsistent among sauropod genera they provide another line of evidence for testing hypotheses of ontogenetic synonymy. Data from skeletal fusions suggest that *Suuwassea* and *Haplocanthosaurus* are both valid taxa and that neither is an ontogenetic morph of a known diplodocid.

Introduction

Among tetrapods, sauropod dinosaurs are unusual in that many taxa have deeply bifid neural spines in their presacral vertebrae. Many mammals have shallowly bifid spines in their cervical vertebrae, but usually only the neurapophysis is divided, whereas in sauropods the division is more extensive. In the most extreme cases the midline cleft extends to the roof of the neural canal, completely dividing the neural spine into bilaterally paired metapophyses (figure 1). Bifid presacral neural spines evolved several times independently in sauropods, and are present in some mamenchisaurids, all known diplodocids and dicraeosaurids, the basal macronarian *Camarasaurus*, the basal somphospondyls *Euhelopus*, *Erketu*, and *Qiaowanlong*, and the derived titanosaur *Opisthocoelicaudia* (Wilson & Sereno, 1998; Ksepka & Norell, 2006; You & Li, 2009; figure 2). In addition, the tips of the proximal caudal neural spines are often weakly bifid in diplodocids (*e.g. Diplodocus carnegii* CM 84/94, Hatcher, 1901: plate 9). In contrast, non-pathological bifid neural spines are uncommon in extant tetrapods, and are limited to the

cervical vertebrae in certain large-bodied, long-necked birds (*Rhea*, Tsuihiji, 2004: figure 2b; *Casuarius*, Schwarz *et al.*, 2007: figure 5b; *Dromaius*, Osborn 1898: figure 1; *Theristicus*, Tambussi *et al.*, 2012: 7; also in the recently extinct Dromornithidae, Gastornithidae, and Phorusracidae, Tambussi *et al.* 2012: 7), the thoracic vertebrae in some bovids (*e.g.* zebu *Bos indicus*, Mason & Maule, 1960: 20), and the lumbar vertebrae of sirenians (Kaiser, 1974). Cervical neural spines in humans and many other mammals have paired tubercles at their tips (Kapandji, 2008: 190-191; Cartmill *et al.*, 1987: figure 2-3a; figure 3). They are therefore sometimes described as being bifid (*e.g.* White & Folkens, 2000: 145). The appearance of bifurcation is caused by the outgrowth of bone at the spine tip to anchor the large transversospinalis muscles. This is a different phenomenon from the non-union of the endochondral portions of the vertebral spine, which occurs pathologically in humans (and presumably all other vertebrates) as spina bifida cystica and spina bifida occulta (Barnes, 1994: 46-50 and figures 3.5 and 3.6).

The developmental underpinnings of bifid neural spines in sauropods are not well under-

Figure 1. A cervical vertebra of *Apatosaurus ajax* YPM 1860 showing complete bifurcation of the neural spine into paired metapophyses. In dorsal (top), anterior (left), left lateral (middle), and posterior (right) views.
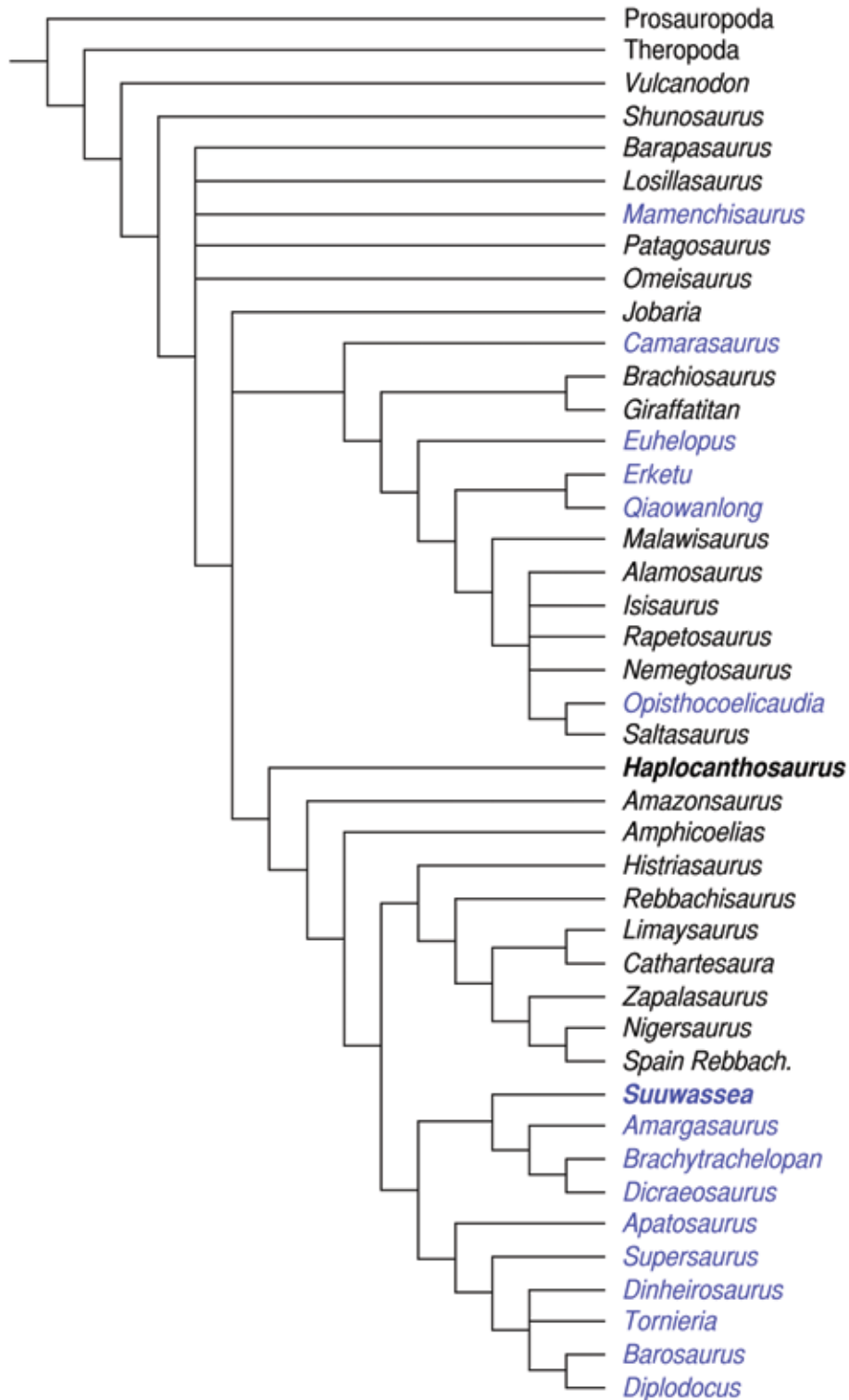
Figure 2. Consensus phylogeny of sauropods based on the strict consensus trees of Taylor (2009), Ksepka & Norell (2010) and Whitlock (2011). The first of these provides the skeleton of the tree including outgroups, basal sauropods and macronarians; the second gives the positions of *Erketu* and *Qiaowanlong*; the last provides a detailed phylogeny of Diplodocoidea. Taxa with bifid neural spines are highlighted in blue. *Haplocanthosaurus* and *Suuwassea*, whose positions are disputed by Woodruff & Fowler (2012) are shown in bold.

Figure 3. A middle cervical vertebra of a human in cranial view showing paired bony processes for the attachment of dorsal muscles to the neural spine. Uncatalogued specimen from the anthropology teaching collection at the University of California, Santa Cruz.

stood. It is possible that in some vertebrae the paired embryonic neural arch elements never fused except to form a roof over the neural canal. In contrast, in the genus *Camarasaurus* it is possible that many of the presacral neural spines were not bifid in young animals, and that the degree of bifurcation increased over the course of ontogeny (see below).

In a recently-published paper, Woodruff & Fowler (2012) argued that the degree of bifurcation of sauropod neural spines was ontogenetically controlled, with the simple, undivided spines of juveniles gradually separating into paired metapophyses over the course of posthatching ontogeny. Based on this inferred ontogenetic trajectory, Woodruff & Fowler (2012) further argued that currently recognized sauropod taxa are oversplit, and that when ontogenetic transformations were taken into account, it would be necessary to synonymize several taxa. In particular, they argued that the Morrison Formation diplodocoid *Suuwassea* was a juvenile of a known diplodocid (*Ibidem*: 6-8), that *Haplocanthosaurus* and *Barosaurus* were likewise suspect (*Ibidem*: 9), and that rebbachisaurids were possibly paedomorphic dicraeosaurids (*Ibidem:* 8-9).

Our goals in this paper are, first, to re-examine the evidence for an ontogenetic increase in neural spine bifurcation in sauropods, and then to evaluate the synonymies proposed by Woodruff & Fowler (2012). Although bifid neural spines also occur in other sauropods, as noted

above, the hypotheses of Woodruff & Fowler (2012) depend on ontogenetic inferences drawn from Morrison Formation sauropod taxa, and therefore we are confining our discussion to those taxa (*e.g. Camarasaurus*, *Haplocanthosaurus*, and the Morrison diplodocoids).

Abbreviations

AMNH, American Museum of Natural History, New York City, New York, USA;
BYU, Earth Sciences Museum, Brigham Young University, Provo, Utah, USA;
CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA;
FMNH, Field Museum of Natural History, Chicago, Illinois, USA;
MB.R., Museum für Naturkunde Berlin, Germany;
NSMT, National Science Museum, Tokyo, Japan;
OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA;
SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany;
USNM, National Museum of Natural History, Washington, D.C., USA;
UWGM, University of Wyoming Geological Museum, Laramie, Wyoming, USA;
WPL, Western Paleontological Laboratories, Lehi, Utah, USA;
YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

Materials and Methods

Neural spine bifurcation in sauropods is a continuum from completely unsplit spines to those that are completely separated down to the roof of the neural canal. For the sake of convenience, in this paper we classify neural spines into four categories based on their degree of bifurcation:
1) Spines that entirely lack any midline indentation are described as *unsplit*;
2) Those with extremely shallow notches in the dorsal margin, whose depth is less than the minimum width of the spine itself, are described as *notched*;
3) Those that are split over less than half the distance from the spine tips to either the postzygapophyses or transverse processes (whichever are higher) are described as *shallowly bifid*;
4) Those split over more than half that distance are described as *deeply bifid* (figure 4).
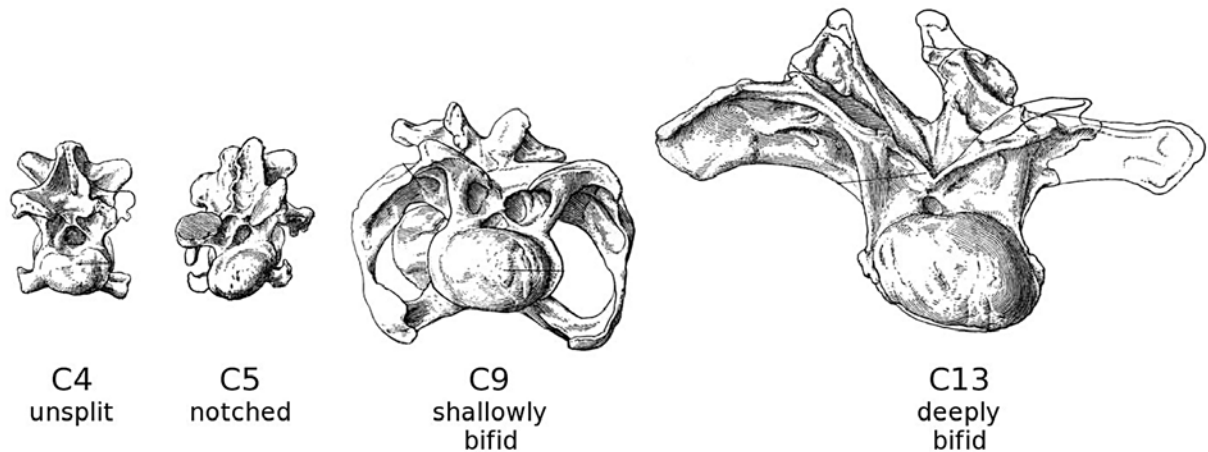
Figure 4. Cervical vertebrae of *Camarasaurus supremus* AMNH 5761 cervical series 1 in anterior view, showing different degrees of bifurcation of the neural spine. Modified from Osborn & Mook (1921: plate 67).

Note that a spine might appear notched either because the two halves of the endochondral bone had not fused or had re-separated during ontogeny, or because of paired bony outgrowths to anchor muscles or ligaments, as in the human cervical vertebra shown in figure 3. It is possible that the two causes of bifurcation could be distinguished histologically, but this has not been attempted to date.

Vertebral proportions vary ontogenetically, serially, and phylogenetically. To compare vertebral proportions we use the elongation index (EI), which is centrum length divided by centrum diameter. It has been measured in different ways. In the original definition of the term, Upchurch (1998) divided the centrum length by the width of the cotyle. Wilson & Sereno (1998) did not use the term 'elongation index' but used centrum length divided by cotyle height as a phylogenetic character. In this paper we follow Wedel *et al.* (2000) in defining EI as the anteroposterior length of the centrum divided by the midsagittal height of the cotyle.

Nearly all of the Morrison Formation material in the OMNH collections comes from Black Mesa in the Oklahoma panhandle (Czaplewski *et al.*, 1994: 3). It was collected in the 1930s by Works Progress Administration crews working under the direction of J. Willis Stovall. Most of the fossils were prepared by unskilled laborers using hammers, chisels, pen-knives, and sandpaper.

Uncommonly for the Morrison, the bones are very similar in color to the rock matrix, and the preparators often failed to realize that they were sanding through bone until they penetrated the cortex and revealed the internal trabeculae. Consequently, many surface features in the OMNH Morrison Formation material were eroded or lost during preparation. This surface damage is a particular problem for interpreting the vertebrae of juvenile sauropods, in which many of the delicate processes on the vertebrae were lost. This will become important later in the paper, when we discuss the possible serial positions of these vertebrae.

Criteria for Assessing Skeletal Maturity in Sauropods

The order and timing of the formation of synostoses in sauropods has been poorly studied. Sauropod growth rates have been investigated using bone histology (*e.g.* Curry, 1999; Sander, 2000; Sander *et al.*, 2004; Klein *et al.*, 2012), but there have been few published attempts to chart macroscopic changes in sauropod skeletons through ontogeny (but see Ikejiri *et al.*, 2005; Tidwell *et al.*, 2005; and Tidwell & Wilhite, 2005). The identification of adult specimens is particularly problematic, given that some very large individual sauropods are not skeletally mature. For example, the holotype individual of *Brachiosaurus altithorax* FMNH P 25107, the paralectotype of *Giraffatitan brancai* MB.R.2181, and the holotype of *Apatosaurus ajax* YPM 1860 all have unfused elements that typically are fused in adult sauropods: in FMNH P 25017 and MB.R.2181 the scapulae and coracoids are not fused, and in YPM 1860 the sacrum and sacricostal yokes involve only three vertebrae instead of the expected five.

Possible criteria for inferring adulthood in sauropods include:

1) Absolute size;
2) Fusion of the vertebral neural arches and centra;
3) Fusion of the sacral vertebrae and formation of the sacricostal yoke;
4) Fusion of the cervical ribs to the neural arches and centra;
5) Ossification of vertebral ligaments and tendons, especially in the dorsals and sacrals
6) Fusion of the scapula and coracoid;
7) Presence of an external fundamental system (EFS) in the cortices of the long bones.

Each criterion is discussed in turn below.

Size alone is an extremely poor indicator of maturity in sauropods, in part because of variation in size at adulthood among closely related taxa. The holotype individuals of *Apatosaurus excelsus* YPM 1980 and *A. ajax* YPM 1860 are

approximately the same size, but the sacrum of the former is fully fused whereas that of the latter is very incompletely united, as mentioned above (figure 5). Some of the *Apatosaurus* material from the Oklahoma panhandle represents individuals that matured at even larger sizes. The dorsal vertebra OMNH 1382 has an unfused neural arch but it is comparable in size to the dorsal vertebrae of *A. louisae* holotype CM 3018. OMNH 1670 is another dorsal vertebra from the same quarry as OMNH 1382 but from a larger and more mature individual. OMNH 1670 is probably D5 based on the location of the parapophyses and the slight degree of neural spine bifurcation, and it is considerably larger (1350 mm total height) than D5 from CM 3018 (1060 mm total height; figure 6). In the genus *Camarasaurus*, the very large individuals of *C. supremus* that make up the composite specimen AMNH 5761 are considerably larger than the holotype individual of *C. lewisi* BYU 9044, but the latter has many age-related changes to the skeleton suggesting that it survived to a very old age, which are absent in AMNH 5761 (Jenson, 1988; McIntosh, Miller *et al.*, 1996).

The previous examples are all of very large individual sauropods that nevertheless had major joints unfused. Conversely, sometimes very small sauropod vertebrae have fully fused neural arches and cervical ribs. BYU 12613 is
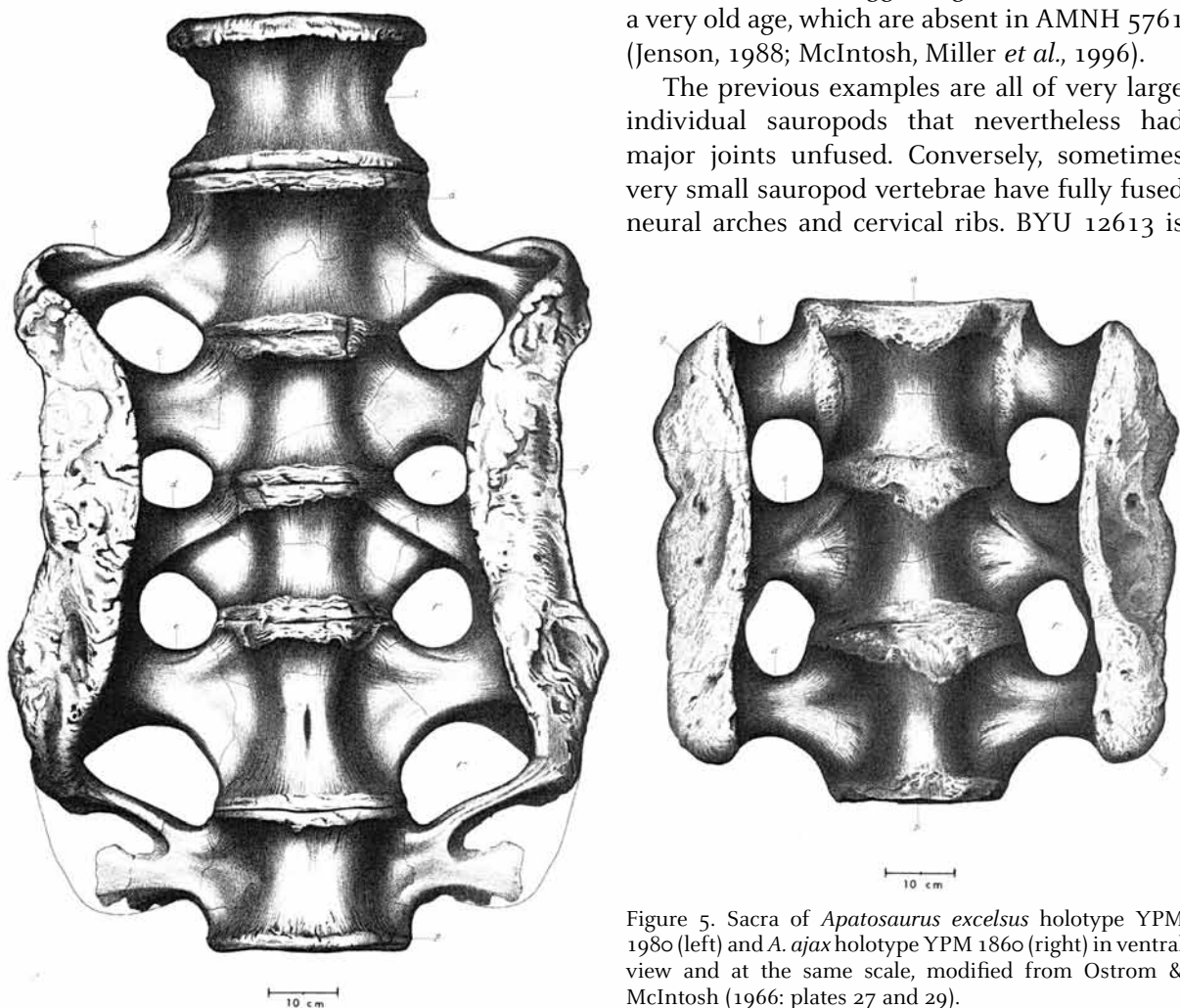

Figure 5. Sacra of *Apatosaurus excelsus* holotype YPM 1980 (left) and *A. ajax* holotype YPM 1860 (right) in ventral view and at the same scale, modified from Ostrom & McIntosh (1966: plates 27 and 29).
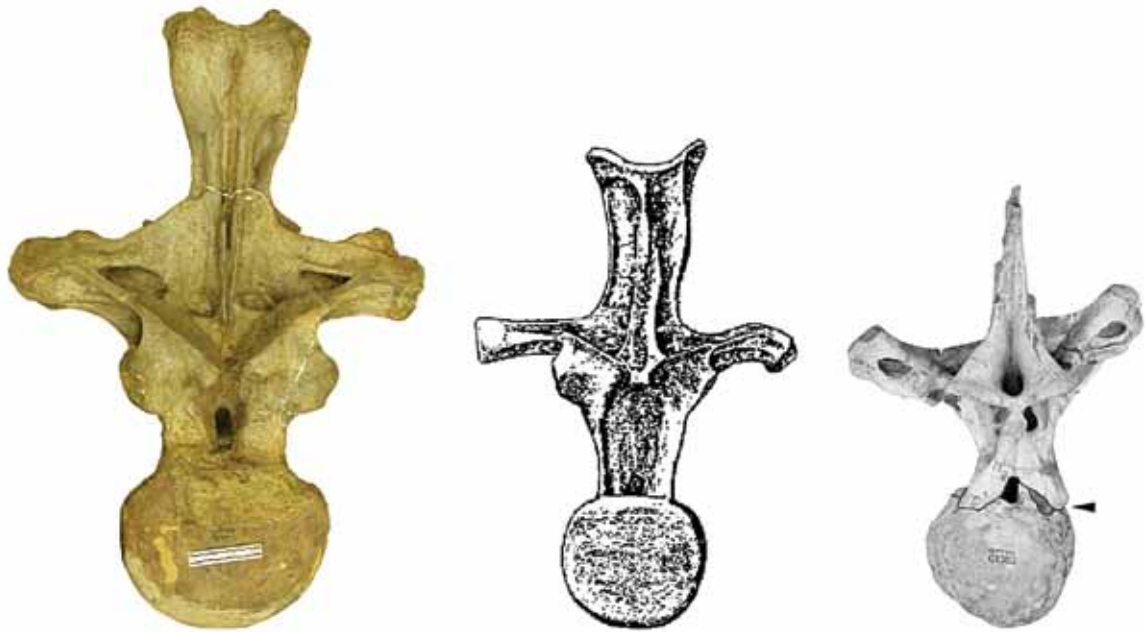
Figure 6. From left to right: *Apatosaurus* sp. OMNH 1670 D?5 in anterior view, *A. louisae* CM 3018 D5 in anterior view, and *A.* sp. OMNH 1382 in posterior view. Total heights of the vertebrae are 1350 mm, 1060 mm, and 950 mm, respectively, although OMNH 1382 would have been somewhat taller when the spine was intact. The arrow next to OMNH 1382 points to the unfused neurocentral synchondrosis.

probably a C14 or C15 of *Diplodocus*, based on the proportions of the centrum and the shape of the neural spine, but with a centrum length of only 270 mm it is less than one half the size of C14 and C15 from *D. carnegii* CM 84/94 (figure 7). The neural arch of BYU 12613 is fully fused and the left cervical rib is fused at the parapophysis; the left rib is broken at the di-

Figure 7. BYU 12613, a posterior cervical of *Diplodocus* or *Kaatedocus* in dorsal (top), left lateral (left), and posterior (right) views. It compares most favourably with C14 of *D. carnegii* CM 84/94 (Hatcher, 1901: plate 3) despite being only 42% as large, with a centrum length of 270 mm compared to 642 mm for C14 of *D. carnegii.*

apophysis and the right rib is also broken. BYU 12613 might represent a small adult *Diplodocus* or *Kaatedocus* (Tschopp & Mateus, 2012) or a subadult in which the neural arch and cervical ribs fused relatively early in ontogeny; current evidence is insufficient to falsify either hypothesis. Nevertheless, it indicates that small individuals of known taxa can have fully fused vertebrae and deeply bifurcated neural spines.

Size can be a particularly misleading indicator of ontogenetic age for isolated vertebrae, because vertebrae change so dramatically in size along the vertebral column in sauropods. In the famous mounted skeleton of *Diplodocus carnegii* CM 84/94, the largest post-axial cervical vertebra, C15, has a posterior centrum diameter more than three and a half times that of C3, the smallest (245 vs 69 mm; Hatcher, 1901: 38; figure 8).

Although open neurocentral joints (properly synchondroses while developing and synostoses when fused) indicate juvenile or subadult status in extant crocodilians (Brochu, 1996; Ikejiri, 2012) and in fossil archosaurs (Irmis, 2007), including sauropods (*e.g.* Peterson & Gilmore, 1902; Myers & Fiorillo, 2009; Remes *et al.*, 2009), it is not clear that the reverse is true. In other words, fused neurocentral synostoses do not necessarily indicate the attainment of either full size or skeletal maturity. Regarding full size, the MB.R.2180 (formerly HM SI) lectotype specimen of *Giraffatitan brancai* is only about 75% the size of the mounted paralectotype MB.R.2181 (formerly HM SII) and only

Figure 8. Third and fifteenth cervical vertebrae of *Diplodocus carnegii* CM 84/94 in posterior view. The cotyle diameters of the vertebrae are 69 and 245 mm, respectively. Modified from Hatcher (1901: plate 6).

66% the size of the largest known individuals of *Giraffatitan* from Tendaguru, but has fully fused neurocentral synostoses throughout the presacral vertebrae. In comparing neurocentral fusion with respect to other markers of skeletal maturity, we note that *Apatosaurus ajax* YPM 1860, *G. brancai* MB.R.2181, and *Diplodocus carnegii* CM 84/94 all have fused neucentral synostoses in all of the vertebrae that can be assessed, but YPM 1860 has a substantially unfused sacrum, MB.R.2181 has an unfused scapulocoracoid joint, and CM 84/94 has unfused cervical ribs in the anterior cervical vertebrae. Fusion of neurocentral synostoses is probably a necessary but not sufficient criterion for inferring adulthood in sauropods.

The sacrum and in particular the sacricostal yokes formed by the fused sacral ribs are the bony interfaces between the axial skeleton and the hindlimbs, so we might expect them to be biomechanically important and for their formation to be closely related to the attainment of adult size. But as criteria for inferring adulthood in sauropods, fusion of the sacral vertebrae and formation of the sacricostal yokes are also problematic.

From a practical standpoint, sacral fusion can be difficult to assess, especially if during preparation matrix is left around the sacrum or between the sacral ribs. As a more biological consideration, the sacrum and sacricostal yokes are not always the last elements to fuse in ontogeny, and the timing of sacral fusion relative to other fusions varies among taxa. *Apatosaurus ajax* YPM 1860 has fused neural arches and cervical ribs but a very incompletely fused sacrum (Ostrom & McIntosh, 1966: plate 29), whereas *Diplodocus carnegii* CM 84/94 has fused scapulocoracoids, the five sacral centra coossified and a sacricostal yoke uniting the ribs of S2-S5 (S1-S4 of Hatcher, 1901, who described S1 as an eleventh dorsal), but the cervical ribs of the anterior cervical vertebrae are unfused (Hatcher, 1901: plate 3). *Brachiosaurus altithorax* FMNH P 25017 has a fully fused sacrum and sacricostal yokes, but the scapulocoracoid joint is still open (Riggs, 1904: plates 73 and 75).

Other macro-scale indicators of skeletochronology in sauropods suffer the same problem of variation among taxa. In *Diplodocus carnegii* CM 84/94 cervical rib fusion apparently followed the incorporation of S5 into the sacrum and fusion of the scapulocoracoid joint. This contrasts
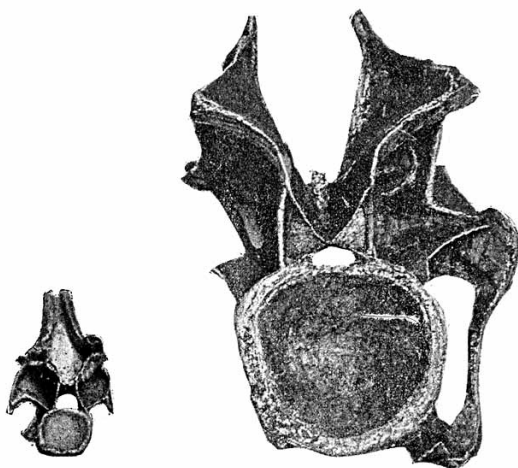
with the pattern in *Apatosaurus ajax* YPM 1860, in which the cervical ribs are fused but S1 and S5 are not fused to the sacrum, and in *Giraffatitan brancai* MB.R.2181, in which the cervical ribs are all fused but the scapulocoracoid joint is open. MB.R.2181 also has plates of ossified interspinous ligaments between the neural spines of D11 and D12 (Janensch, 1950: figure 62), so even the ossification of these ligaments, which in other cases has been taken as a sign of advanced age (McIntosh, Miller, *et al.*, 1996), may not always indicate adulthood. The inconsistent sequencing of all of these macro-scale skeletal changes in sauropod skeletons is summarized in table 1.

The most reliable method for determining cessation of growth is the formation of an external fundamental system (EFS) in the outer cortex of a bone (Sander *et al.*, 2004). However, it is possible that not all sauropods formed an EFS, or, if an EFS formed, it may have been quickly remodelled to the point of being unidentifiable (Klein *et al.*, 2012). Even if an EFS is present, it can only be assessed by histological sectioning, which requires destructive sampling (even if only drilling cores), is time-consuming, and has been done for few individual sauropods.

The implication of the foregoing discussion is that the readily available ways of determining adulthood in sauropods are all inexact and frequently conflict with each other. For the purposes of this paper we will refer to the large mounted skeletons – *Apatosaurus louisae* CM 3018, *Diplodocus carne-gii* CM 84/94, *Giraffatitan brancai* MB.R.2181, and others – and individuals of like size as 'adults' because they are latest ontogenetic stages that are well-represented by existing fossils, and as such they form the de facto comparative basis for our understanding of these taxa. It is possible that when complete skeletons become available for even larger individuals, such as the *Apatosaurus* represented by OMNH 1670, we will have to revise our idea of what constitutes adult morphology for certain taxa. We refer to the large mounted skeletons as adults without implying that they had finished growing or had developed external fundamental systems, or that smaller individuals were necessarily subadult. 'Adult' is used herein as a term of convenience, not a biological fact.

Data from Descriptive Monographs

Before examining the data from Woodruff & Fowler (2012), it will be useful to review previously published observations on neural spine bifurcation in the Morrison Formation sauropods (figure 9). We include *Suuwassea emilieae* in this compilation, although its status as an independent source of data depends on whether it is a valid taxon or a juvenile of a known diplodocid, as argued by Woodruff & Fowler (2012). We will revisit this point in detail in a later section; for now we are merely reviewing the data available before the publication of Woodruff & Fowler (2012), and drawing what inferences we can.

	S1S	S4S	S1C	S5C	S1R	S5R	CR	SC	LO
A. ajax YPM 1860			no	no	no	no	yes	no	no
A. excelsus YPM 1981			yes	no	yes	no			
A. excelsus YPM 1980	no	yes	yes	yes	yes	yes	yes	no	no
D. carnegii CM 84/94	no	no	yes	yes	no	yes	no	yes	no
H. delfsi CM 879	yes	yes	no	no	no	no	no	no	no
H. delfsi CM 572	yes	no	yes	yes	yes	yes	yes		no
B. altithorax FMNH P 25107	no	no	yes	yes	yes	yes		no	no
G. brancai MB.R.2181*	yes	yes				yes	yes	no	yes

* The sacral vertebrae are not preserved in MB.R.2181, but are already fused in the smaller specimen 'Aa' (see Janensch, 1950: figures 74 and 75).

Table 1. The timing of macroscopic changes in sauropod skeletons over ontogeny is not consistent among taxa. Although this may not be surprising from an evolutionary standpoint, it complicates attempts to determine the relative ontogenetic age of sauropods with non-histological methods. Some of these differences may reflect taxonomic rather than ontogenetic variation; the larger point is that most of these specimens are taken to represent the adult morphology of their respective taxa, but every one has at least one major joint unfused. 'yes' indicates fusion, 'no' indicates lack of fusion, and empty cells indicate that the relevant material is not preserved. Abbreviations: S1S, sacral 1 spine fused to other spines; S4S, sacral 4 spine fused to other spines; S1C, sacral 1 centrum fused to other sacral centra; S5C, sacral 5 centrum fused to other sacral centra; S1R, sacral 1 rib fused to sacricostal yoke; S5R, sacral 5 rib fused to sacricostal yoke; CR, all available cervical ribs fused; SC, scapula and coracoid fused; LO, ligaments ossified in at least some dorsal neural spines.
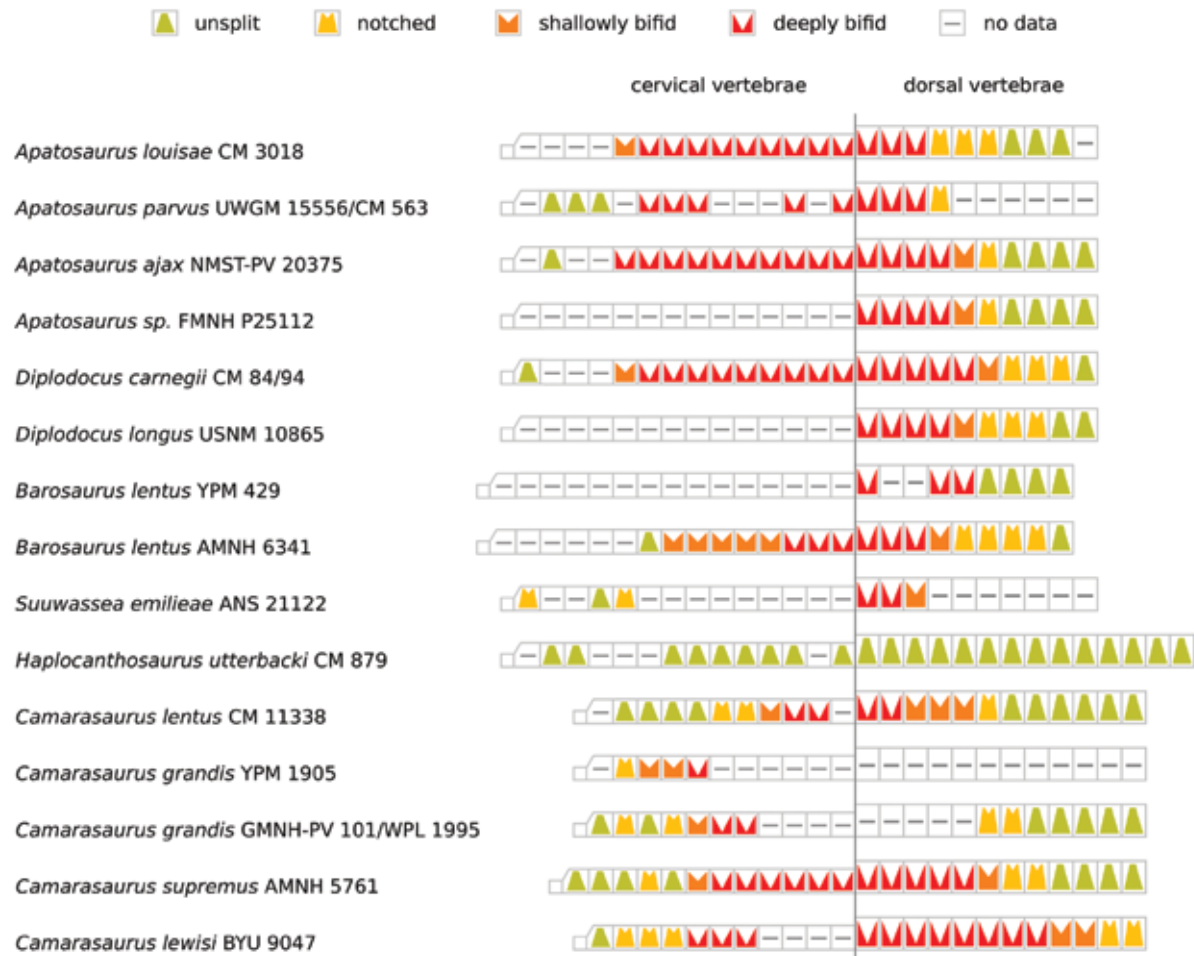
Figure 9. Degree of neural spine bifurcation of presacral vertebrae in well-preserved Morrison Formation sauropod specimens representing several taxonomic groups. In all taxa with deep bifurcations, these are concentrated around the cervico-dorsal transition. 'No data' markers may mean that the vertebrae are not preserved (*e.g.,* posterior dorsals of *Suuwassea emilieae* ANS 21122), that the degree of bifurcation cannot be assessed (*e.g.,* anterior cervicals of *Diplodocus carnegii* CM 84/94), or that the serial positions of the vertebrae are uncertain so they contribute no information on serial changes in bifurcation (*e.g.,* the four cervical vertebrae known for *Barosaurus lentus* YPM 429). The *Camarasaurus* specimens are roughly in ontogenetic order: *C. lentus* CM 11338 is a juvenile, *C. grandis* YPM 1905 and GMNH-PV 101/WPL 1995, and *C. supremus* AMNH 5761 are adults, and *C. lewisi* BYU 9047 is geriatric. See text for sources of data.

The presacral vertebral formulae are assumed to be as follows: 15 cervicals and 10 dorsals in *Apatosaurus* and *Diplodocus*, 16 cervicals and 9 dorsals in *Barosaurus*, and 12 cervicals and 12 dorsals in *Camarasaurus*. In each group, only the informative specimens are listed; for example, the cervical vertebrae of *Barosaurus lentus* YPM 429 are of uncertain serial position, so this specimen is not included in the descriptions of cervical vertebrae.

A note on preservation: when material is broken or incomplete, it is easier to detect deep bifurcations than shallow ones. The neural spine tips are usually narrow, fragile, and easily broken or lost. If a vertebra is missing the top half of its spine but the bottom half is not split, it is impossible to say whether the complete vertebra was bifid or not. But if the spine is deeply bifurcated, even a small piece of bone from the base of the trough or one of the metapophyses is enough to confirm that it was bifid.

Cervical Vertebrae
Apatosaurus louisae CM 3018 (Gilmore, 1936: 195 and plate 24) – Impossible to assess in C2-C5, at least shallowly bifid in C6, deeply bifid in C7-C15. According to Gilmore (1936: 195): "Unfortunately the type of *A. louisae* lacks most of the spine tops, only those of cervicals eight, ten and twelve being complete; thus the point of change from single to bifid spines cannot be determined in this specimen." However, Gilmore (1936: plate 24) shows the base of the cleft preserved in C6 and C7, indicating that those ver-

tebrae were bifid even if, as Gilmore noted, the position of the first bifid vertebra is uncertain.

Apatosaurus parvus UWGM 15556 (originally described and catalogued as *A. excelsus* CM 563, Gilmore 1936: plate 31) – Unsplit in C3-C5, deeply bifid in C7-C9, 13?, and 15 (other cervical vertebrae missing; figure 10).

Apatosaurus ajax NMST-PV 20375 (Upchurch *et al.,* 2005: 27-28 and plates 1 and 2) – Unsplit in C3, C4 missing, impossible to assess in C5, deeply bifid in C6 and more posterior cervicals.

Diplodocus carnegii CM 84/94 (the mounted skeleton is a composite of two individuals; Hatcher 1901: plates 3-6) – Unsplit in C2, impossible to assess in C3-C5 but reconstructed as notched or shallowly bifid (Hatcher, 1901: 21), shallowly bifid in C6, deeply bifid in C7-C15.

Barosaurus lentus AMNH 6341 (McIntosh, 2005: 47-48, figures 2.1, 2.2, and 2.3) – Cervicals 2-7 missing, unsplit in C8, shallowly bifid in C9-C13, deeply bifid in C14-C16.

Suuwassea emilieae ANS 21122 (Harris, 2006c: 1094-1101, text-figures 4-7) – Notched in C2, impossible to determine in C3, C4 missing, C5 unsplit, notched in C6, impossible to assess in more posterior cervicals. Note that Woodruff &

Fowler (2012: fig. 9C) include C5 in a group of "weakly bifurcated neural spines", but the spine of C5 is not bifid but broken. According to Harris (2006c: 1099), "the spinous process expands mediolaterally toward its apex, attaining maximal width just proximal to its terminus. A long, narrow crack at the distal end gives the appearance of bifurcation, but the collinear dorsal margin indicates that no true split was present."

Camarasaurus grandis YPM 1905 (Ostrom & McIntosh, 1966: plates 9-11; McIntosh, Miller, *et al.,* 1996: 76) – "The cleft in cervical 3 of *C. grandis* (YPM 1905) is barely perceptible, very modest in numbers 4 and 5, and distinct in 6".

Camarasaurus grandis GMNH-PV 101 (formerly WPL 1995; McIntosh, Miles, *et al.,* 1996: pages 11-12, figures 24-30) – Unsplit in C2, notched in C3, unsplit in C4, notched in C5, shallowly bifid in C6, deeply bifid in C7-C8. More posterior cervicals are missing.

Camarasaurus lentus CM 11338 (Gilmore, 1925: 369) – Unsplit in C3-C6, notched in C7, grading to deeply bifid at C11.

Camarasaurus lentus YPM 1910 (McIntosh, Miller *et al.,* 1996: 76) – "A small depression is present in cervical 5 of the holotype (YPM 1910)".
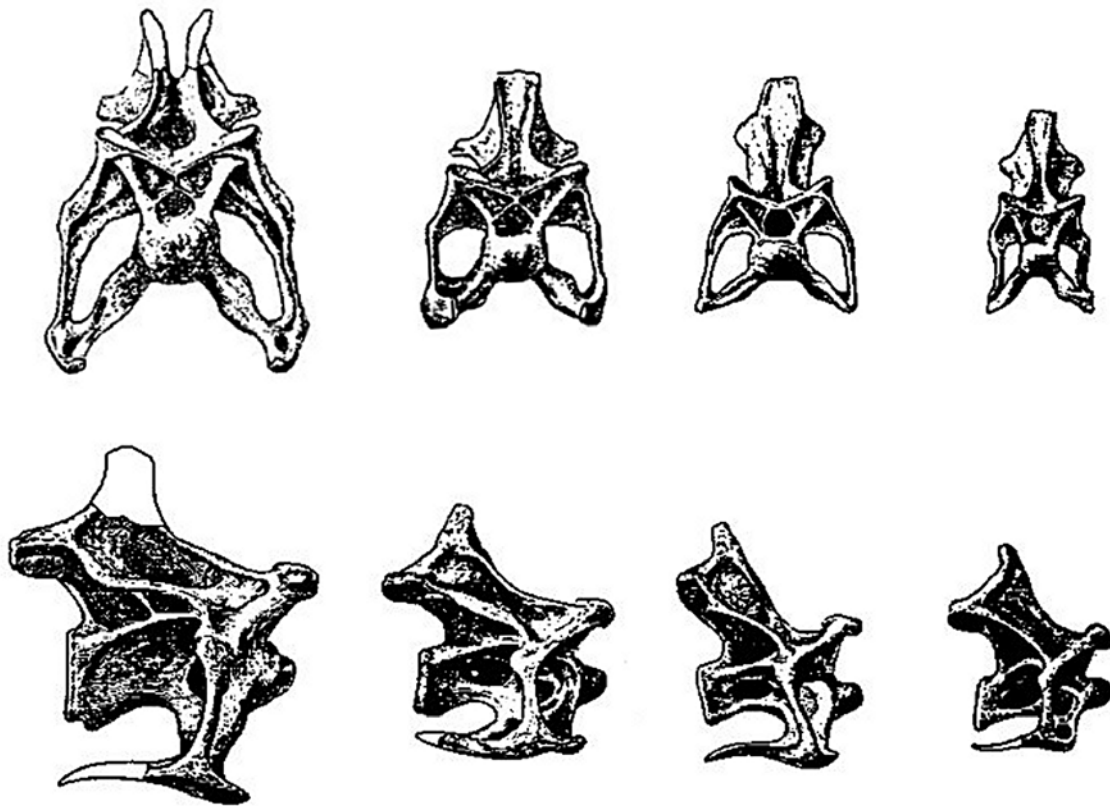

Figure 10. *Apatosaurus parvus* UWGM 15556 (formerly *A. excelsus* CM 563) cervicals 7, 5, 4 and 3 in anterior (top) and right lateral views, showing that neural spines of anterior cervicals are unsplit even in adult diplodocids. From Gilmore (1936: plate 31).

Camarasaurus supremus AMNH 5761 (Osborn & Mook, 1921: 294, plates 67-69) – Unsplit in C2-C4, notched in C5, shallowly bifid in C7, deeply bifid in C8-C13. C6 is problematic; according to Osborn & Mook (1921: 294): "in C. 6 the characters of the spine are obscure owing to the poorly preserved condition of the two specimens of this member of the series." However, their plate 67 shows the C6 from cervical series I with an unsplit spine.

Camarasaurus lewisi BYU 9047 (McIntosh, Miller *et al.*, 1996: 76, plates 1-4) – Unsplit in C2, notched in C3-C5, deeply bifid in C6-C8, impossible to assess in C9-C12.

Inferences on Bifurcation in Cervicals

1) There is no evidence in any of the North American diplodocoids of a bifid spine farther forward than C6. The bifid spines in C3-C5 of *Diplodocus carnegii* CM 84/94 are sculptures; Hatcher was doing his best with imperfect fossils and limited information, as no other reasonably complete cervical series of a diplodocid had yet been described. The appearance of a split spine in C5 of *Suuwassea* is caused by a vertical crack and a small amount of missing bone (Harris, 2006c: 1099). In the very large AMNH 6341 *Barosaurus*, the first notched spine is on C9 (McIntosh, 2005);

2) Adult sauropods can show unsplit spines, notched spines, shallowly bifid spines, and deeply bifid spines serially in the same individual. This is true even in very large individuals (*e.g. Apatosaurus* parvus UWGM 15556, *Barosaurus lentus* AMNH 6341, *Camarasaurus supremus* AMNH 5761), so it cannot be interpreted as an artifact of ontogeny. Therefore single spines do not always indicate juveniles, bifid spines do not always indicate adults, and incompletely bifid spines did not always become fully bifid–in most of the specimens listed above, the most anterior bifid spines are only notched or shallowly divided. We should describe vertebrae with shallow splits as 'incompletely' bifid rather than 'incipiently' bifid; the latter term implies that the bifurcation was going to deepen with time, which did not always happen depending on serial position;

3) The evidence from *Camarasaurus* is consistent with an ontogenetic increase in bifurcation. The juvenile *C. lentus* described by

Gilmore (1925) has the first incompletely bifurcated spine at C7, whereas the larger, presumably adult individual of the same species represented by YPM 1910 has the first split at C5, as do the individuals that make up *C. supremus* AMNH 5761 (although in those individuals, Osborn and Mook's assignments of serial position are tentative). In *C. lewisi* BYU 9047 and *C. grandis* YPM 1905, and arguably in *C. grandis* GMNH-PV 101 the first spine to be partially split is C3. It is tempting to interpret the difference between adult *C. lentus* and *C. supremus* on one hand (first split at C5) and *C. lewisi* and *C. grandis* on the other (first split at C3) as interspecific variation, but it is not possible to rule out individual variation given the small sample sizes involved.

Dorsal Vertebrae

Apatosaurus louisae CM 3018 (Gilmore, 1936: plate 25) – Deeply bifid in D1-D3, notched in D4-D6, unsplit in D7-D9, D10 spine missing.

Apatosaurus parvus CM 563/UWGM 15556 (Gilmore, 1936: plate 32) – Deeply bifid in D1-D3, notched in D4, D5-D10 spines missing (figure 11).

Apatosaurus ajax NMST-PV 20375 (Upchurch *et al.*, 2005: 29-35 and plate 3) – Deeply bifid in D1-D4, shallowly bifid in D5, notched in D6, unsplit in D7-D10.

Apatosaurus sp. FMNH P25112 (Riggs, 1903: 174 and plate 46) – Deeply bifid in D-D3, shallowly bifid in D4, notched in D5-D6, unsplit in D7-D10.

Diplodocus carnegii CM 84/94 (Hatcher, 1901: plate 8) – Deeply bifid in D1-D5, shallowly bifid in D6, notched in D7-D9, unsplit in D10.

Diplodocus longus USNM 10865 (Gilmore, 1932: plate 5) – Deeply bifid in D1-D4, shallowly bifid in D5, notched in D6-D8, unsplit in D9-D10.

Barosaurus lentus YPM 429 (Lull, 1919: 15-21 and plates 3-4) – Deeply bifid in D1, D4, and D5, unsplit in D6-D9 (NB: Lull interpreted the latter as D7-D10 on the expectation of 10 dorsals, based on *Diplodocus*).

Barosaurus lentus AMNH 6341 (McIntosh, 2005: 51 and figure 2.5) – Deeply bifid in D1-D3, shallowly bifid in D4, notched in D5-D8, unsplit in D9.

Camarasaurus grandis GMNH-PV 101 (formerly WPL 1995; McIntosh, Miles, *et al.*, 1996:
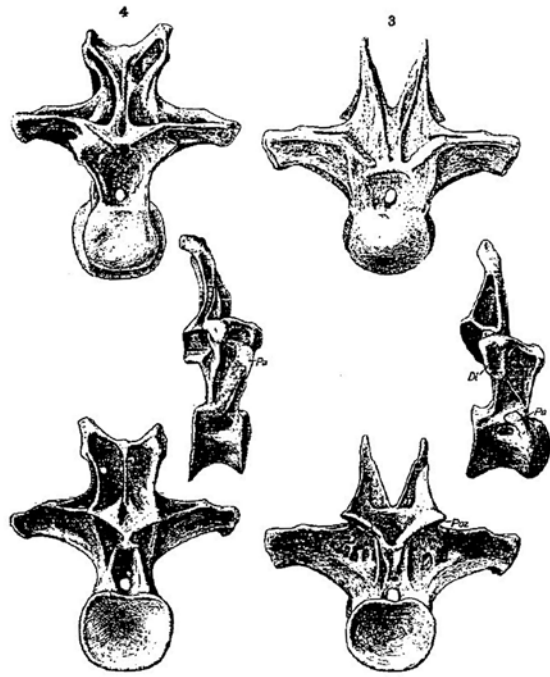
Figure 11. *Apatosaurus parvus* UWGM 15556 D4 (left) and D3 (right) in anterior (top), right lateral, and posterior views, showing that neural spine bifurcation generally does not persist farther back than the mid-dorsals even in adult diplodocids. From Gilmore (1936: plate 32).

11-13 and figures 31-37) – D1-D5 missing, notched in D6-D7, unsplit in D8-D12.

Camarasaurus lentus CM 11338 (Gilmore, 1925: 370) – Deeply bifid in D1 grading to notched in D6, unsplit in D7-D12.

Camarasaurus supremus AMNH 5761 (Osborn & Mook, 1921: 300 and plates 70-73) – In the four dorsal series included in the composite specimen, all have deeply bifid spines in D1-D5, D6 is shallowly bifid or notched, and the more posterior dorsals are either notched or unsplit. Notching of the spine persists as far back as the dorsosacral (Osborn & Mook, 1921: plate 73).

Camarasaurus lewisi BYU 9047 (McIntosh, Miller, *et al.*, 1996: 79 and plate 5) – Deeply bifid in D1-D8, shallowly bifid in D9-D10, notched in D11-D12.

Inferences on Bifurcations in Dorsals
1) As with the cervicals, most adult sauropods have deeply bifid, shallowly bifid, and unsplit spines in serially adjacent vertebrae. In the diplodocids, the spines of D6-D10 (or D9 in *Barosaurus*) are always either unsplit or notched at the tips;
2) The diplodocid genera show some interesting differences. In *Apatosaurus* the last four

dorsals are always unsplit. In *Diplodocus* the spines are at least shallowly indented as far back as D8 or D9. *Barosaurus* shows variation among specimens, with YPM 429 having unsplit spines in the four most posterior dorsals, and AMNH 6341 having an entirely unsplit spine only in the last dorsal;
3) In the diplodocids, deeply bifid spines are always confined to the first half of the dorsal series (D1-D5), and these are usually followed by a long run of vertebrae with very shallowly notched spine tips. The exception is *Barosaurus* YPM 429, which – if the vertebrae are truly consecutive (the series is missing at least two) – has a deep split in D5 and unsplit spines in D6-D9;
4) As with the cervicals, the evidence from *Camarasaurus* does not rule out an ontogenetic increase in bifurcation. In the juvenile *C. lentus* CM 11338, the spines are only bifid as far back as D6; in the adult *C. supremus* AMNH 5761 and in the old *C. lewisi* BYU 9047 even the most posterior dorsals have notched spines. If these differences represent ontogenetic changes rather than interspecific differences (which also cannot be ruled out at this point), it is interesting that there is at leaust as much difference between the adult *C. supremus* and the old *C. lewisi* as between the juvenile *C. lentus* and the adult *C. supremus*: in other words, significant changes took place after adulthood was attained.

Implications of Serial Changes in Bifurcation for Isolated Elements

In the Morrison Formation diplodocids, adults are expected to have unsplit spines as far back as C5, C6 may be only incompletely bifid (*e.g. D. carnegii* CM 84/94), and the spines in the posterior dorsals are expected to be either very shallowly notched at the tip or completely unsplit. Therefore it is impossible to say that an isolated vertebra belongs to a juvenile individual on the basis of neural spine bifurcation alone. Depending on how one defines 'anterior cervical', one half to one third of anterior cervicals are expected to have unsplit spines even in adults.

In *Camarasaurus* the picture is less clear (figure 12). The immense *C. supremus* AMNH 5761 has unsplit spines in C3-C4, and the most posterior dorsals have unsplit or notched spines, with little consistency among the four individu-
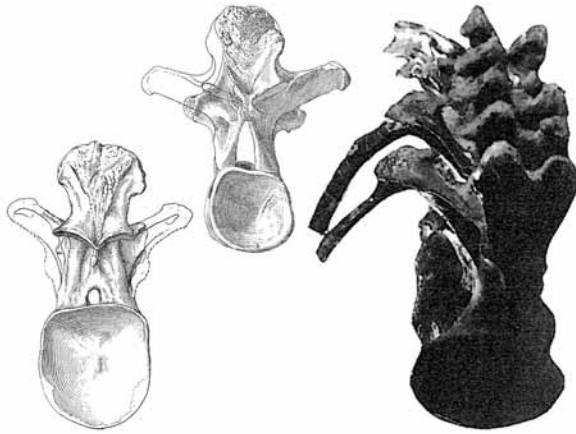
Figure 12. Serially comparable dorsal vertebrae in different *Camarasaurus* species or ontogenetic stages. Left: dorsal vertebra 7 (top) and dorso-sacral (= D11) (bottom) of *C. supremus* AMNH 5760 and 5761 "Dorsal Series II" both in posterior view, with unsplit neural spines. Modified from Osborn & Mook (1921: plate 71). Right: dorsal vertebrae 7-11 of *C. lewisi* holotype BYU 9047 in posterodorsal view, with split spines. From McIntosh, Miller *et al.* (1996: plate 5). Scaled so that the height of D11 is roughly equivalent in the two specimens.

als that make up the specimen. In the geriatric *C. lewisi* BYU 9047 all of the post-axial presacral neural spines are at least notched, and most are shallowly or deeply bifid. Even in the very posterior dorsals there is still a distinct V-shaped notch in the neural spine, deeper and more dis-

tinctive than the very slightly bilobed spine tips in the posterior dorsals of *C. supremus* AMNH 5761. Either the difference between the specimens is individual or interspecific variation, or some amount of ontogenetic bifurcation happened well into adulthood; current evidence is insufficient to falsify either hypothesis.

'Primitive' Morphology can be an Effect of Serial Position

Even in 'adult' sauropods like the big mounted *Apatosaurus* and *Diplodocus* skeletons (*e.g. A. louisae* CM 3018, *D. carnegii* CM 84/94), the anterior cervicals are less complex than the posterior ones. Compared to posterior cervicals, anterior cervicals tend to have simpler pneumatic fossae and foramina, fewer laminae, and unsplit rather than bifid spines (Gilmore, 1936: plate 24; Hatcher, 1901: plate 3; figure 13). In all of these characters the anterior cervicals are similar to those of juveniles of the same taxa, and to those of adults of more basal taxa. So serial position recapitulates both ontogeny and phylogeny. This is also true in prosauropods – in *Plateosaurus engelhardti* SMNS 13200, the diapophyseal laminae develop in a stepwise fashion in successive cervical vertebrae (figure 14).
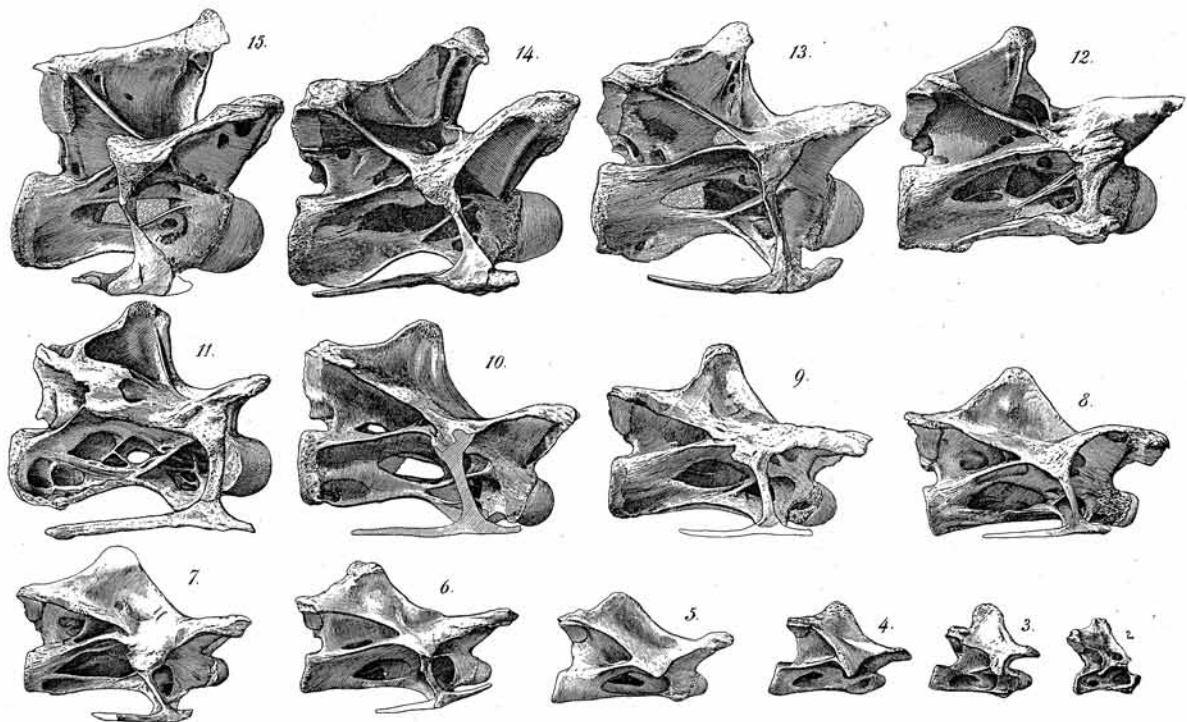

Figure 13. Cervical vertebrae of *Diplodocus carnegii* CM 84/94 in right lateral view. Note the increasing complexity of the laminae and pneumatic cavities in successively posterior cervicals. From Hatcher (1901: plate 3).
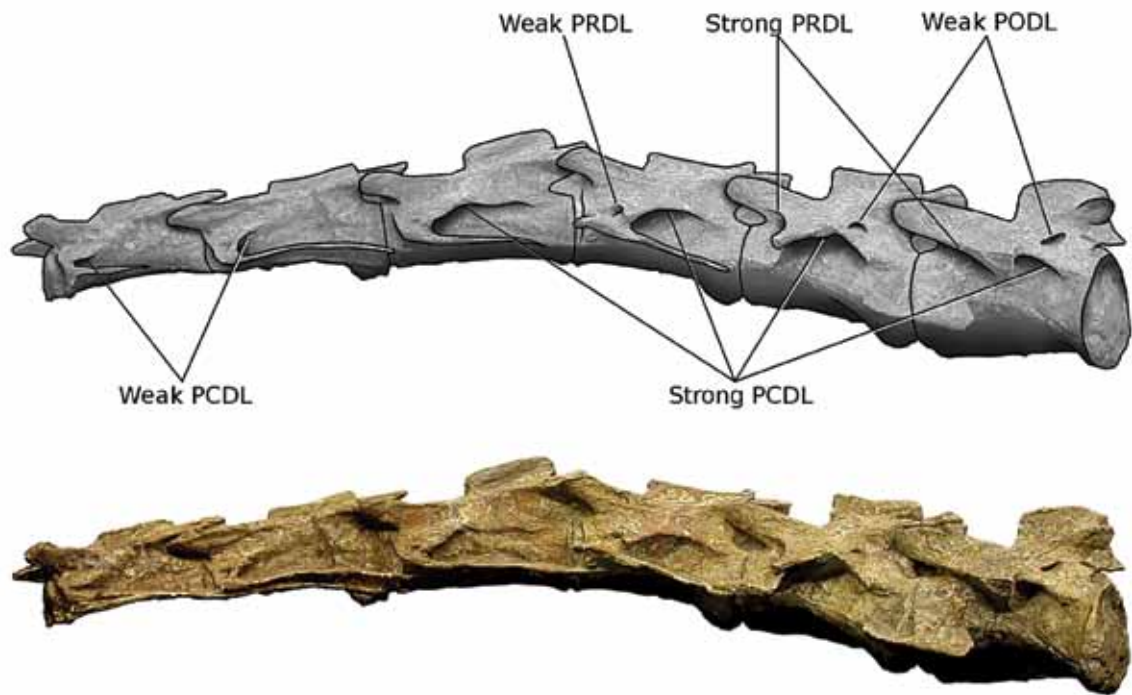
Figure 14. *Plateosaurus engelhardti* (originally *P. trossingensis*) SMNS 13200 cervical vertebrae 3-8 in left lateral view, showing the gradual acquisition of diapophyseal laminae in successively posterior cervicals. The PODL becomes strongly developed in the dorsal vertebrae. C8 is roughly 15 cm long. Abbreviations (after Wilson, 1999): PCDL, posterior centrodiapophyseal lamina; PODL, postzygodiapophyseal lamina; PRDL, prezygodiapophyseal lamina.

Woodruff & Fowler (2012: figure 2) compare an adult *Mamenchisaurus* cervical, an isolated cervical of a putative juvenile *Diplodocus* (MOR 790 8-10-96-204), and a cervical of *D. carnegii* CM 84/94. The serial position of the *D. carnegii* cervical is not stated but by reference to Hatcher (1901: plate 3) it is C12. The point of the figure is to show that the isolated 'juvenile' vertebra is more similar in gross form to the *Mamenchisaurus* cervical than to the adult *D. carnegii* cervical.

However, MOR 790 8-10-96-204 more closely resembles C5 of *D. carnegii* than C12, in the possession of overhanging prezygapophyses, non-overhanging postzygapophyses, centrum proportions (EI), anterodorsal inclination of the cotyle margin, and lack of anterior deflection of the diapophyses (figure 15). The biggest differences between the MOR vertebra and C5 of *D. carnegii* are the shape of the neural spine and the sinuous profile of the ventral centrum margin in lateral view. Both characters are highly variable serially within an individual, among individuals in a species, and among species in the Morrison Formation diplodocids (see, *e.g.* Hatcher, 1901: plate 3; Gilmore, 1936: plates 24 and 31; and McIntosh, 2005: figure 2.1), so it is unwise to attach much weight to them.

This raises an additional problem. MOR 790 8-10-96-204 is used as an example of juvenile morphology by Woodruff & Fowler (2012), both in their figure 2 and in their ontogenetic series of anterior cervical vertebrae (Woodruff & Fowler 2012: figure 3). However, as we have just shown, the morphology of MOR 790 8-10-96-204 is indistinguishable from the morphol-

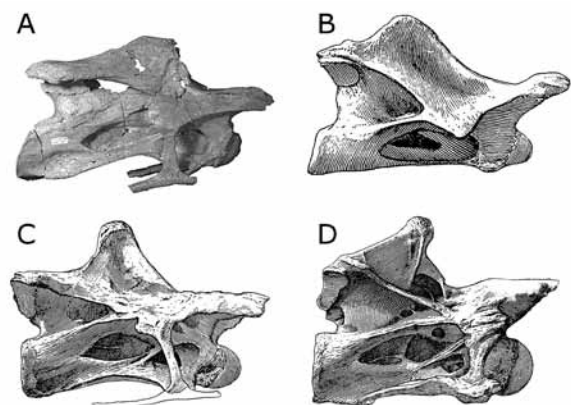Figure 15. An isolated cervical of *cf. Diplodocus* MOR 790 8-10-96-204 (A) compared to *D. carnegii* CM 84/94 C5 (B), C9 (C), and C12 (D), all scaled to the same centrum length. Actual centrum lengths are 280 mm, 372 mm, 525 mm, and 627 mm for A-D respectively. MOR 790 8-10-96-204 modified from Woodruff & Fowler (2012: figure 2B), reversed left to right for ease of comparison; *D. carnegii* vertebrae from Hatcher (1901: plate 3).

ogy of an anterior cervical vertebra in an adult, and it compares especially well to C4 and C5 of *D. carnegii* CM 84/94. The apparent centrum length (measured from the scale bar in the figure) of MOR 790 8-10-96-204 is 28 cm, compared to 29 cm and 37 cm for C4 and C5 of *D. carnegii* CM 84/94, respectively. So MOR 790 8-10-96-204 is roughly the same size as the adult C4 and about 80% of the size of the adult C5. Furthermore, its neural arch appears to be fused and its cervical ribs are fused to the neural arch and centrum, whereas the cervical ribs of the 'adult' *D. carnegii* CM 84/94 are not yet fused in C2-C5.

In sum, the isolated MOR vertebra shown in Woodruff & Fowler (2012: figure 2) is most likely a C4 or C5 of an adult *Diplodocus* similar in size to *D. carnegii* CM 84/94, and based on cervical rib fusion it may be from an individual that is actually more mature than CM 84/94. All of the differences between that vertebra and the *D. carnegii* C12 shown in the same figure are more easily explained as consequences of serial, rather than ontogenetic, variation. The implications of this apparently adult vertebra being found in the Mother's Day Quarry are explored below in the Discussion.

Ontogenetic Series of Woodruff & Fowler (2012) Reassessed

In the Materials and Methods, Woodruff & Fowler (2012: 2) stated: "Study specimens comprise 38 cervical, eight dorsal, and two caudal vertebrae from 18 immature and one adult diplodocid (*Diplodocus* sp., *Apatosaurus* sp., and *Barosaurus* sp.), and two immature macronarians (both *Camarasaurus* sp.)."

However, their Table 1 and Supplementary Information list only 15 specimens, not 18. Of the 15, one is probably not a diplodocid (SMA 0009 'Baby Toni'; Woodruff & Fowler (2012: Supplementary Information, pp. 5-6). Of the remaining 14 specimens, 11 are isolated vertebrae, so only three represent reasonably complete probably-diplodocoid series (MOR 592, AMNH 7535, and CM 555). From *Apatosaurus* CM 555 they discuss only one vertebra, the sixth cervical. AMNH 7535 is not mentioned at all outside of Table 1 and a passing mention the Supplementary Information, so the subadult diplodocid data actually used in the paper consist of isolated vertebrae and only a single articulated series, MOR 592.

The affinities of MOR 592 are uncertain. Wilson & Smith (1996) provisionally referred it to *Amphicoelias*. Whitlock (2011: 890, table 8) provisionally referred it to Dicraeosauridae, writing: "A partial braincase, skull roof, and dentary (MOR 592), previously referred to the basal diplodocoid *Amphicoelias* (Wilson & Smith, 1996), appear to belong instead to a dicraeosaurid. A sharp crest on the supraoccipital (character 45) and the presence of a tuberosity near the dentary symphysis (character 61) both suggest dicraeosaurid affinities, although the dentary symphysis is intermediate between the subtriangular dicraeosaurid and the ovate diplodocid conditions. This and other minor differences between these elements and *Suuwassea emilieae* (Harris, 2006a) preclude referral of MOR 592 to that taxon, but it is probable that the two are closely related."

Woodruff & Fowler (2012: table 1) referred MOR 592 to Diplodocinae, implying that it is more closely related to *Diplodocus* and *Barosaurus* than to *Apatosaurus* or the dicraeosaurids. However, they provided no rationale for this referral, and did not discuss the dicraeosaurid referral of Whitlock (2011), although they cited that paper. At present, the hypothesis of Whitlock (2011) that MOR 592 represents a dicraeosaurid has not been falsified. Therefore the data used by Woodruff & Fowler (2012) do not include any articulated subadult diplodocids (*i.e.* from CM 555 they used only one vertebra, and MOR 592 is probably not a diplodocid).

Woodruff & Fowler (2012) did not state what criteria they used to infer age in their specimens. Neural arch fusion is discussed in general terms in the Supplementary Information, but in the text and in the figures specimens are ordered and discussed simply in terms of size. This is problematic because size is a notoriously unreliable criterion of age; MOR 790 8-10-96-204 from figure 2 in Woodruff & Fowler (2012) also appears in their figure 3 as the second-smallest vertebra in this 'ontogenetic' series, despite most likely coming from a well-fused adult approximately the same size as the *D. carnegii* individual that represents the end of the series. So without any evidence other than sheer size (if that size overlaps with the adult size range) and degree of neural spine bifurcation (which cannot help but overlap with the adult range, since the adult range encompasses all possible states), simply picking small vertebrae with un-

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split spines and calling them juvenile is unsupported and logically circular.

We suggest that the confounding effects of size, serial position, and ontogeny in the data of Woodruff & Fowler (2012) are not controlled for, and therefore their conclusions are suspect. To explore this possibility, we will review each of the putative ontogenetic series presented in the paper.

Anterior cervical vertebrae
The proposed ontogenetic series used by Woodruff & Fowler (2012: 2-3 and figure 3) for anterior cervical vertebrae consists of:

- CMC VP7944, an isolated ?*Diplodocus* vertebra from the Mother's Day site, which is described in the text but not pictured;
- MOR 790 7-30-96-132, an isolated vertebra from the same site;
- MOR 790 8-10-96-204, another isolated vertebra from the same site;
- MOR 592, from a partial cervical series of a subadult *Diplodocus* but with the serial position unspecified;
- ANS 21122, C6 of *Suuwassea* (included in figure 3, but not discussed as evidence in the accompanying text);
- CM 555, C6 of a nearly complete (C2-C14) cervical series of a subadult *Apatosaurus*;
- CM 84/94, C7 of *Diplodocus carnegii*.

CMC VP7944 is not pictured, but based on the description in the text it is plausible that it represents a C3, C4, or C5, all of which have undivided spines even in adult diplodocids. It therefore contributes no information: the hypothesis that the spine is undivided because of ontogeny is not yet demonstrated, and the hypothesis that the spine is undivided because of serial position is not yet falsified.

MOR 790 7-30-96-132 is shown only from the front, so the centrum proportions and the shape of the neural spine cannot be assessed. The neural arch appears to be fused, but the cervical ribs are not. Again, we cannot rule out the possibility that it comes from a very anterior cervical and therefore its undivided spine could be an artifact of its serial position. It therefore contributes no information on possible ontogenetic changes in neural spine bifurcation.

As shown above, MOR 790 8-10-96-204 is probably a C4 or C5 of an adult or near-adult *Di-*

plodocus about the same size as or only slightly smaller than *D. carnegii* CM 84/94. It is small and has an undivided spine because it is an anterior cervical, not because it is from a juvenile. It therefore contributes no support to the ontogenetic bifurcation hypothesis.

The pictured vertebra of MOR 592 has a shallow notch in the tip of the spine, which is expected in C6 in *Apatosaurus* and *Diplodocus* and in C9 and C10 in *Barosaurus*. The serial position of the vertebra is not stated in the paper, but about half of the anterior cervicals even in an adult diplodocid are expected to have unsplit or shallowly split spines based on serial position alone. Based on the evidence presented, we cannot rule out the possibility that the shallow cleft in the pictured vertebra is an artifact of serial position rather than ontogeny. It therefore contributes no support to the ontogenetic bifurcation hypothesis.

In ANS 21122 and CM 555 the sixth cervical has an incompletely divided neural spine, which is in fact expected for the sixth cervical in adult diplodocids as shown by *A. parvus* CM 563/UWGM (in which C6 is missing but C5 has an unsplit spine and C7 a deeply bifid spine) and *D. carnegii* CM 84/94 (in which C6 is also shallowly bifid). *A. ajax* NMST-PV 20375 has a wider split in the spine of C6, but the exact point of splitting appears to vary by a position or two among diplodocids. The hypothesis that the spine of C6 in ANS 21122 and CM 555 is already as split as it would ever have become cannot be falsified on the basis of the available evidence. Note that in ANS 21122 the neural arch and cervical ribs are fused in C6, and in C6 of CM 555 they are not.

CM 84/94 C7 has a deeply split spine, but this is expected at that position. C6 of the same series has a much shallower cleft, and C5 would be predicted to have no cleft at all (recall that according to Hatcher [1901: 20-21] the neural spines of C3-C5 of this specimen are sculptures). So any trend toward increasing bifurcation is highly dependent on serial position; if serial position cannot be specified then it is not possible to say anything useful about the degree of bifurcation in a given vertebra.

Summary – CMC VP7944 and MOR 790 7-30-96-132 could be very anterior vertebrae, C3-C5, in which bifurcation is not expected even in adults. Since they are isolated elements, that hypothesis is very difficult to falsify. MOR

790 8-10-96-204 is almost certainly a C4 or C5 of an adult or near-adult *Diplodocus*. C6 in ANS 21122 and CM 555 are incompletely divided, as expected for vertebrae in that position even in adults. CM 84/94 has a shallowly divided spine in C6 and more deeply bifid spines from C7 onward, just like CM 555, and as expected for adult diplodocids. Therefore, no ontogenetic change has been demonstrated.

Posterior cervical vertebrae
The proposed ontogenetic series (Woodruff & Fowler 2012: 3-4 and figure 4) includes:

- OMNH 1267 and 1270;
- MOR 790 7-26-96-89;
- MOR 592;
- CM 84/94.

OMNH 1267 and 1270 are isolated neural arches of baby sauropods from the Black Mesa quarries. OMNH 1267 does not appear to be bifurcated, but it has a very low neural spine and it was abraded during preparation (MJW pers. obs.), so some material might have been lost. OMNH 1270 actually shows a bifurcation – Woodruff & Fowler (2012: 3) describe it as having "a small excavated area" – but again it is not clear that the spines are as intact now as they were in life. More seriously, since these are isolated elements their serial position cannot be determined with any accuracy, and therefore they are not much use in determining ontogenetic change. Although they are anteroposteriorly short, that does not necessarily make them posterior cervicals. The cervical vertebrae of all sauropods that have been examined grow proportionally longer over ontogeny (Wedel *et al.*, 2000: 368-369), and the possibility that these are actually from anterior cervicals–not all of which are expected to have bifurcations–is impossible to rule out.

The other three vertebrae in the series have deeply bifurcated spines. In the text, Woodruff & Fowler (2012: 3) make the case that the bifurcation in MOR 592 is deeper than in the preceding vertebra, MOR 790 7-26-96-89. However, the proportions of the two vertebrae are very different, suggesting that they are from different serial positions, and the centrum of MOR 790 7-26-96-89 is actually larger in diameter than that of the representative vertebra from MOR 592. So unless centrum size decreased through

ontogeny, these vertebrae are not comparable. The serial position of MOR 790 7-26-96-89 is unknown, but nothing presented in Woodruff & Fowler (2012) rules out possibility that is actually an anterior cervical, and in fact the very low neural spines suggest that that is the case.

Allowing for lateral crushing, the vertebra from MOR 592 (the serial position is presumably known but not stated) looks very similar to the *D. carnegii* CM 84/94 vertebra (C15, by comparison with Hatcher [1901: plate 3]), and is probably from a similar position in the neck. In comparing the two, Woodruff & Fowler (2012: 4) stated that in CM 84/94, "the bifurcated area has broadened considerably", but this clearly an illusion caused by the lateral compression of the MOR 592 vertebra – its centrum is also only half as wide proportionally as in the CM 84/94 vertebra.

Summary – The OMNH vertebrae are of unknown serial position and probably lost at least some surface bone during preparation, so their original degree of bifurcation is hard to determine. The other three vertebrae in the series all have deeply bifid spines, but they are out of order by centrum size, MOR 790 7-26-96-89 might be an anterior cervical based on its low neural spines, and the 'broadening' of the trough between MOR 792 and CM 84/94 is an artifact of crushing. Therefore, no ontogenetic change has been demonstrated.

Anterior dorsal vertebrae
THe ontogenetic series (Woodruff & Fowler, 2012: 4 and figure 5) consists of:

- MOR 790 7-17-96-45;
- MOR 592;
- CM 84/94.

The serial position of the MOR 592 vertebra is presumably known but not stated in the paper. The serial position of the *D. carnegii* CM 84/94 vertebra is likewise not stated, but by reference to Hatcher (1901: plate 8) it is D4. Comparisons to the MOR 592 vertebra are not helped by the fact that it is shown in oblique posterior view. Nevertheless, the two vertebrae are strikingly similar, which is interesting in light of the dicraeosaurid affinities of the specimen proposed by Whitlock (2011). The spines in the larger two vertebrae are equally bifurcated, so the inference of

ontogenetic increase in bifurcation rests on the smallest of the three vertebrae, MOR 790 7-17-96-45.

MOR 790 7-17-96-45 is an isolated unfused neural arch, clearly from a juvenile (figure 16). Its serial position is hard to determine, but it is probably not from as far back as D4 or D5 because it appears to lack a hypantrum and shows no sign of the parapophyses, which migrate up onto the neural arch through the cervico-dorsal transition.

Given that MOR 7-17-96-45 lacks a hypantrum and parapophyses, it is not directly comparable to the two larger vertebrae. Although we cannot determine its serial position, its spine is shallowly bifurcated, to about half the distance from the metapophyses to the postzygapophyses.

In *Apatosaurus louisae* CM 3018, the notch in D3 is about equally deep, and in C15 it is only slightly deeper, still ending above the level of postzygapophyses. So there is some variation in the depth of the bifurcation in the posterior cervicals and anterior dorsals in the North American diplodocids. Without knowing the precise serial position of MOR 7-17-96-45, it is difficult to derive inferences about the ontogeny of neural spine bifurcation.

What this element does conclusively demonstrate is that the neural arches of posterior cervicals or anterior dorsals in even small, unfused juvenile diplodocids were in fact bifurcated to a degree intermediate between D3 and D4 in the large adult *Apatosaurus louisae* CM3018 – in fact, so far as neural cleft depth is concerned, MOR 7-17-96-45 makes rather a nice intermediate between them. It differs in other respects, most notable that it is proportionally broad (possibly a result of ontogeny) and lacks a hypantrum and parapophyses.

Figure 16. Diplodocid anterior dorsal vertebrae. Left and right, dorsal vertebrae 3 and 4 of adult *Apatosaurus louisae* holotype CM 3018, from Gilmore (1936: plate 25). Center, juvenile neural arch MOR 790 7-17-96-45, modified from Woodruff & Fowler (2012: figure 5B), corrected for shearing and scaled up.

Summary -- The two larger specimens in the 'ontogenetic series' are from similar serial positions and show the same degree of bifurcation. MOR 7-17-96-45 is from a more anterior position, based on its lack of hypantrum and parapophyses. Although it is a juvenile, its degree of bifurcation is similar to that of anterior dorsal vertebrae in adult *Apatosaurus* (and that of C15 in *A. louisae* CM 3018). Therefore, no ontogenetic change has been demonstrated.

Posterior dorsal vertebrae
The ontogenetic sereis (Woodruff & Fowler, 2012: 4 and figure 6) consists of:

- OMNH 1261;
- MOR 592;
- CM 84/94.

The *D. carnegii* CM 84/94 vertebra is D6, and based on its almost identical morphology the MOR 592 vertebra is probably from the same serial position. They show equivalent degrees of bifurcation.

OMNH 1261 is another isolated juvenile neural arch. The portion of the spine that remains is unbifurcated. However, the spine is very short and it is possible that some material is missing from the tip. More importantly, the last 3-4 dorsals in *Apatosaurus*, *Diplodocus*, and *Barosaurus* typically have extremely shallow notches in the neural spines or no notches at all. If OMNH 1261 is a very posterior dorsal, it would not be expected to show a notch even when fully mature. Therefore, no ontogenetic change has been demonstrated.

Caudal vertebrae
The ontogenetic series (Woodruff & Fowler, 2012: 4-5 and figure 7) consists of:

- MOR 592;
- CM 84/94.

The 'bifurcation' in MOR 592 is at right angles to that in the proximal caudals of *D. carnegii* CM 84/94, so the one can hardly be antecedent to the other. More importantly, antero-posterior 'bifurcations' like that in MOR 592 are occasionally seen in the caudal vertebrae of adult sauropods. Figure 17 shows two examples, caudals 7 and 8 of *A. parvus* CM 563/UWGM 15556. So in this character MOR
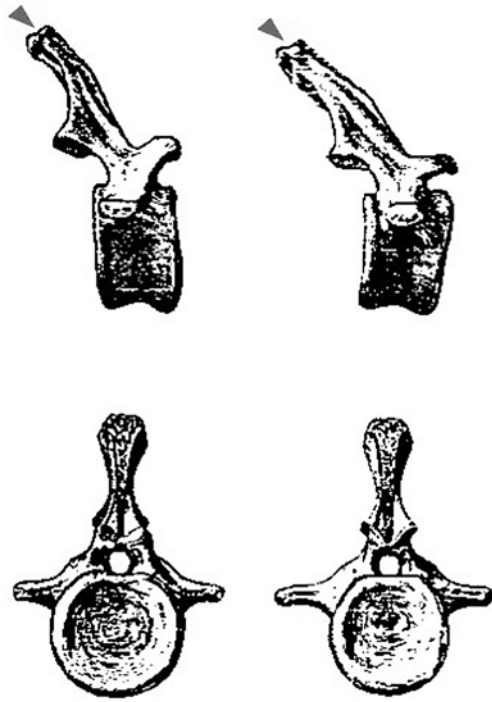
Figure 17. *Apatosaurus parvus* CM 563/UWGM 15556 caudals 8 and 7 in right lateral (top) and posterior view, from Gilmore (1936: plate 33). Arrows highlight shallow antero-posterior notches in the tips of the neural spines.

592 already displays adult morphology. Therefore, no ontogenetic change has been demonstrated.

Camarasaurus
The ontogenetic series (Woodruff & Fowler, 2012: 5 and figure 8) consists of:

• OMNH 1417;
• AMNH 5761.

OMNH 1417 is an isolated cervical neural spine, and the pictured vertebra of *Camarasaurus supremus* AMNH 5761 is a posterior cervical. In *C. grandis* and *C. lewisi*, all of the cervical vertebrae eventually develop at least a shallow notch in the tip of the neural spine, but as discussed above there seems to be some variation between *Camarasaurus* species, and, likely, between individuals.

In the absence of information about its serial position and the species to which it belonged, the lack of bifurcation in OMNH 1417 is uninformative; it could belong to an anterior cervical of *C. supremus* that would not be expected to develop a bifurcation. Therefore, no ontogenetic change has been demonstrated.

strated. There is evidence that neural spine bifurcation developed ontogenetically in *Camarasaurus*, but it comes from the juvenile *C. lentus* CM 11338, described by Gilmore (1925), and the geriatric *C. lewisi*, described by McIntosh, Miller *et al.* (1996) – see above for discussion.

Summary
The 'ontogenetic' series of Woodruff & Fowler (2012) cannot parsimoniously be interpreted as ontogenetic series. In all of the diplodocid presacral vertebrae and in *Camarasaurus*, the smallest elements in the series are isolated vertebrae or neural arches for which the serial position is almost impossible to determine and even the taxonomic identifications are suspect (*e.g.* the OMNH juvenile material – the criteria for reliably distinguishing the neural arches of *Apatosaurus* and *Camarasaurus* are not stated). The larger vertebrae in the presacral series are all compromised in various ways: one includes a probable adult masquerading as a juvenile (MOR 790 8-10-96-204 in the anterior cervicals), one is out of order by centrum size (MOR 790 7-26-96-89 and MOR 592 in the posterior cervicals), and two show no change in degree of bifurcation from the middle of the series to the upper end (MOR 592 and CM 84/94 in the anterior and posterior dorsals). The shallow longitudinal bifurcation in the MOR 592 caudal vertebra is similar to those found in caudal vertebrae of adult diplodocids, and is not antecedent to the transverse bifurcations discussed in the rest of the paper.

To the extent that the taxonomic hypotheses of Woodruff & Fowler (2012) rely on an ontogenetic increase in bifurcation in diplodocids, they are suspect. That will be the subject of the next two sections.

Is *Suuwassea* a Juvenile of a Known Diplodocid?

In the abstract, Woodruff & Fowler (2012:1) wrote: "On the basis of shallow bifurcation of its cervical and dorsal neural spines, the small diplodocid *Suuwassea* is more parsimoniously interpreted as an immature specimen of an already recognized diplodocid taxon."

We test this hypothesis in two ways. In this section we consider whether it is plausible, based on comparative morphology, that *Suu-*

wassea emilieae ANS 21122 is a juvenile of a known diplodocid. In the section 'Phylogenetic Analysis of Suggested Synonymies', below, we further investigate the hypothesis by constraining *Suuwassea* to be the sister taxon of a known diplodocid in two phylogenetic analyses.

The material of *Suuwassea* includes cranial, axial, and appendicular material, which has been exhaustively described and compared to known sauropod taxa by Harris & Dodson (2004), Harris (2006a; b; c; 2007), and Whitlock & Harris (2010). Rather than go through all of the known elements of *Suuwassea* and compare them with those of known Morrison diplodocids, here we will focus on a more limited problem. Given that Woodruff & Fowler (2012) focus on the presacral vertebrae, especially the cervicals, we ask whether the cervical morphology of *Suuwassea* can plausibly be explained as an ontogenetic stage of one of the known Morrison diplodocids.

Diplodocids from the Morrison Formation include *Apatosaurus*, *Amphicoelias*, *Barosaurus*, *Diplodocus*, *Eobrontosaurus*, and *Supersaurus*. No cervical material is available for *Amphicoelias* altus or the possibly synonymous *A. fragillimus*, and the cervical vertebrae of *Eobrontosaurus* have not yet been described in detail or illustrated. The extremely elongate, low-spined cervical vertebrae of *Barosaurus* and *Supersaurus* (figure 18) are obviously poor matches for the vertebrae of *Suuwassea*, so we will not consider them further. If *Suuwassea* cannot plausibly be interpreted as a juvenile of *Apatosaurus* or *Diplodocus*, then there is no reason to suspect that it is belongs to one of these long-necked taxa, to which it is even less similar. That leaves *Apatosaurus* and *Diplodocus* as potential adults of *Suuwassea*.

Diplodocus – The mid-cervicals of *Suuwassea* and *Diplodocus* differ considerably in centrum proportions (figure 19). C6 of *S. emilieae* has a centrum length of 257 mm, a cotyle diameter of 75 mm, and so an EI of 3.4. C6 of *D. carnegii* has a centrum length of 442 mm, a cotyle diameter of 99 mm, and an EI of 4.5. So the *Diplodocus* vertebra is one third more elongate than the equivalent vertebra of *Suuwassea*. It is true that sauropod cervicals elongate through ontogeny, as discussed above, but the *Suuwassea* holotype is a decent-sized animal, and would be expected to have attained adult proportions even if it was not fully

Figure 18. Middle cervical vertebrae of *Barosaurus* AMNH 6341 (top) and *Supersaurus* BYU 9024 (bottom) in left lateral view, scaled to the same centrum length. The actual centrum lengths are 850 mm and 1380 mm, respectively. BYU 9024 is the longest single vertebra of any known animal.

adult. We know from the juvenile *Sauroposeidon* vertebra YPM 5294 (Wedel *et al.*, 2000: 372; referred to *Sauroposeidon* by D'Emic & Foreman, 2012) that subadult sauropod cervicals could be very elongate: YPM 5294 is from an animal young enough to have had an unfused neural arch but it has an EI exceeding 5.0.

Neural spine shape also differs strikingly between *Suuwassea* and *Diplodocus*. Neural spine shape is quite variable serially, and some posterior cervical vertebrae of *Diplodocus* have forward-leaning neural spine tips, but those are very posterior cervicals and the shapes of the spines are still quite different.

Also note that the prezygapophyses of the *D. carnegii* C6 strongly overhang the condyle but are only slightly elevated, whereas those of *S. emilieae* are right above the condyle but strongly elevated, so that the prezygapophyseal rami might fairly be called pedestals. Such pedestaling of the prezygapophyses is present in some cervicals of *Apatosaurus*, although perhaps not to the same extreme. Some *Apa-*

Figure 19. The sixth cervical vertebrae of *Diplodocus carnegii* CM 84/94, *Suuwassea emilieae* ANS 21122, and *Apatosaurus* sp. CM 555 in left lateral view, scaled to the same centrum length. Actual centrum lengths are 442 mm, 258 mm, and 327 mm, respectively. *Diplodocus carnegii* modified from Hatcher (1901: plate 3), reversed left to right for ease of comparison. *Suuwassea emilieae* from a photo provided by Jerry Harris; the same photo also appears as Harris (2006c: text-figure 7B). *Apatosaurus* photographs by Mathew Wedel, digitally composited by Michael Taylor.

tosaurus cervicals also have tall, narrow neural spine tips that somewhat resemble those of *Suuwassea*.

Summary – The cervical vertebrae of *Suuwassea* differ from those of *Diplodocus* in almost every detail, and there is no evidence from presacral morphology that *Suuwassea* is a juvenile of *Diplodocus*.

Apatosaurus – According to Gilmore (1936: 196), C6 of *A. louisae* CM 3018 has a centrum length of 440 mm and a cotyle diameter of 150 mm, and therefore an EI of 2.9. C6 of *A. parvus* UWGM 15556 was not preserved, but C5 and C7 have EIs of 2.6 and 2.4, respectively (Gilmore, 1936: 196). The vertebrae between the fifth and seventh positions in *Apatosaurus* are therefore consistently shorter than C6 in *Suuwassea* (EI of 3.4), but more similar in proportions than the equivalent vertebrae in *Diplodocus*. As noted above, some cervical vertebrae of *Apatosaurus* have prezygapophyseal rami shaped like anterodorsally-projecting pedestals, and forward-leaning, chimney-shaped neural spine tips (Gilmore, 1936: plates 24 and 31), but in no known vertebrae of *Apatosaurus* do these characters reach the same degree of expression as in *Suuwassea*. Note that Lovelace *et al.* (2008) recovered *Suuwassea* as an apatosaurine, but not as *Apatosaurus*. The most striking difference between *Suuwassea* and *Apatosaurus* is that *Suuwassea* lacks the immense, low-hanging cervical ribs that are diagnostic for *Apatosaurus* (see Upchurch *et al.*, 2005: 80-81). The cervical ribs of *Suuwassea* are short, as in other diplodocoids, and do not extend past the end of the centrum of the vertebra on which they

originate, but they are neither enlarged nor set well below the centrum as in *Apatosaurus*. This cannot be explained as an result of ontogeny because vertebrae of subadult *Apatosaurus* with unfused neural arches and cervical ribs nevertheless have greatly enlarged parapophyses to support the latter (figure 18).

Summary – The cervical vertebrae of *Suuwassea* are more similar to those of *Apatosaurus* than those of *Diplodocus*, but they differ in several important characters that cannot be interpreted as ontogenetically labile. On gross morphology alone, it is very unlikely that *Suuwassea* represents a juvenile of either taxon. The case for synonymy grows even worse when skeletochronology is considered, as discussed in the next section.

Ontogenetic status of *Suuwassea* – The *Suuwassea* holotype ANS 21122 can be assessed for four of the non-histological criteria of skeletal maturity discussed above:

1) Sheer size;
2) Fusion of the neural arches and centra;
3) Fusion of the cervical ribs to their respective vertebrae;
4) Fusion of the scapula and coracoid.

We will ignore sheer size for reasons explained above, and discuss the other evidence in turn.

The neural arches are fused in the cervicals and dorsals but unfused in most of the caudals. Harris (2006c: 1107): "Of all the caudal vertebrae preserved in ANS 21122, only the distal, 'whiplash' caudals are complete. All the remaining vertebrae consist only of vertebral bodies

[*i.e.* centra] that lack all phylogenetically informative portions of their respective arches. On the proximal and middle caudals, this absence is due to lack of fusion as evidenced by the deeply fluted articular surfaces for the arches on the bodies. In contrast, the arches on the most distal vertebrae that retain them are seamlessly fused, but everything dorsal to the bases of the corporozygapophyseal [*i.e.* centrozygapophyseal] laminae are broken."

It is interesting that the unfused arches in the proximal and middle caudals are bracketed by fused arches both anteriorly (in the dorsals) and posteriorly (in the distal caudals). This shows that neural arch fusion in *Suuwassea* was not a simple "zipper" that ran from back to front, as in crocodilians (Brochu, 1996) and phytosaurs (Irmis, 2007), or front to back. The sequence of neural arch fusion cannot be determined based on the one available skeleton of *Suuwassea*, but clearly the anterior and middle caudals would have fused last, at least in this individual.

The cervical neural arches are all fused, but some of the cervical ribs are partly fused or unfused (Harris, 2006c). In C3, the left cervical rib is not attached, and the right one is attached at the parapophysis but not fused. In C5, the ribs are attached, not fused at the parapophyses, and fused at the diapophyses (this may be the first time that anyone has documented which of the two attachment points fused first within a single cervical rib in a sauropod). In C6, the ribs are fused at both attachment points. C7 lacks the ribs, but their absence appears to be caused by breakage rather than lack of fusion. One fragmentary posterior cervical of uncertain position is missing the diapophyses but has one rib fused at the parapophysis.

Finally, the scapula-coracoid joint is unfused (Harris, 2007), but that is often the case even for substantially 'adult' sauropods such as *Giraffatitan brancai* MB.R.2181 and *Apatosaurus excelsus* YPM 1980.

Based on the lack of fusion in the caudal neural arches, anterior cervical ribs, and scapulocoracoid joint, *Suuwassea* holotype ANS 21122 was not fully mature. However – and this is absolutely crucial for the synonymization hypothesis – the *Suuwassea* specimen already has a greater degree of cervical element fusion than *Diplodocus carnegii* holotype CM 84/94 (which has unfused ribs back to C5) and *Apatosaurus* CM 555 (which has unfused arches back to C8 and unfused ribs

throughout), both of which have attained essentially 'adult' morphology. So if Woodruff & Fowler (2012) are correct in identifying *Suuwassea* as a juvenile of a known diplodocid, the ontogenetic clock has to run forward from CM 555 and CM 84/94, through a *Suuwassea*-like stage, and then back to normal *Apatosaurus* or *Diplodocus* morphology. This is sufficiently unlikely to not warrant further consideration.

The unfused arches in the *Suuwassea* caudals are especially interesting because most of the cervical ribs are fused. This is in contrast to *D. carnegii* CM 84/94, in which all the neural arches are fused but the anterior cervical ribs are not. So the developmental timing in *Suuwassea* is dramatically different than in *D. carnegii*, which is a further problem for the synonymization hypothesis: *Suuwassea* doesn't belong in the same ontogenetic series as *Diplodocus*, contra Woodruff & Fowler (2012: figures 3 and 9) – if the timing of the various fusions differs between the taxa, there is no basis for assuming that the hypothetical ontogenetic bifurcation would follow the same rules.

In summary, the entire rationale for the taxonomic arguments of Woodruff & Fowler (2012) – that *Suuwassea* has incompletely bifurcated neural spines because it is a juvenile – turns out be an illusion caused by not taking serial variation into account. *Suuwassea* ANS 21122 probably is a subadult, based on the unfused caudal neural arches, but its cervical vertebrae already show the expected adult morphology in neural arch fusion, cervical rib fusion (except the most anterior), and – most importantly – neural spine bifurcation. The taxonomic distinctness of *Suuwassea* and the nearly adult stage of the holotype are further supported by the histological work of Hedrick *et al.* (In Press).

Is *Haplocanthosaurus* a Juvenile of a Known Diplodocid?

Although Woodruff & Fowler (2012) argue at length that *Suuwassea* is a juvenile of another taxon, they also suggest that the same might be true of other Morrison Formation sauropods. From their Conclusions section (*Ibidem*: 9): "Just as particularly large diplodocid specimens (*e.g. Seismosaurus*; Gillette, 1991) have been more recently recognized as large and potentially older individuals of already recognized taxa (*Diplodocus*; Lucas *et al.*, 2006; Lovelace *et al.*,
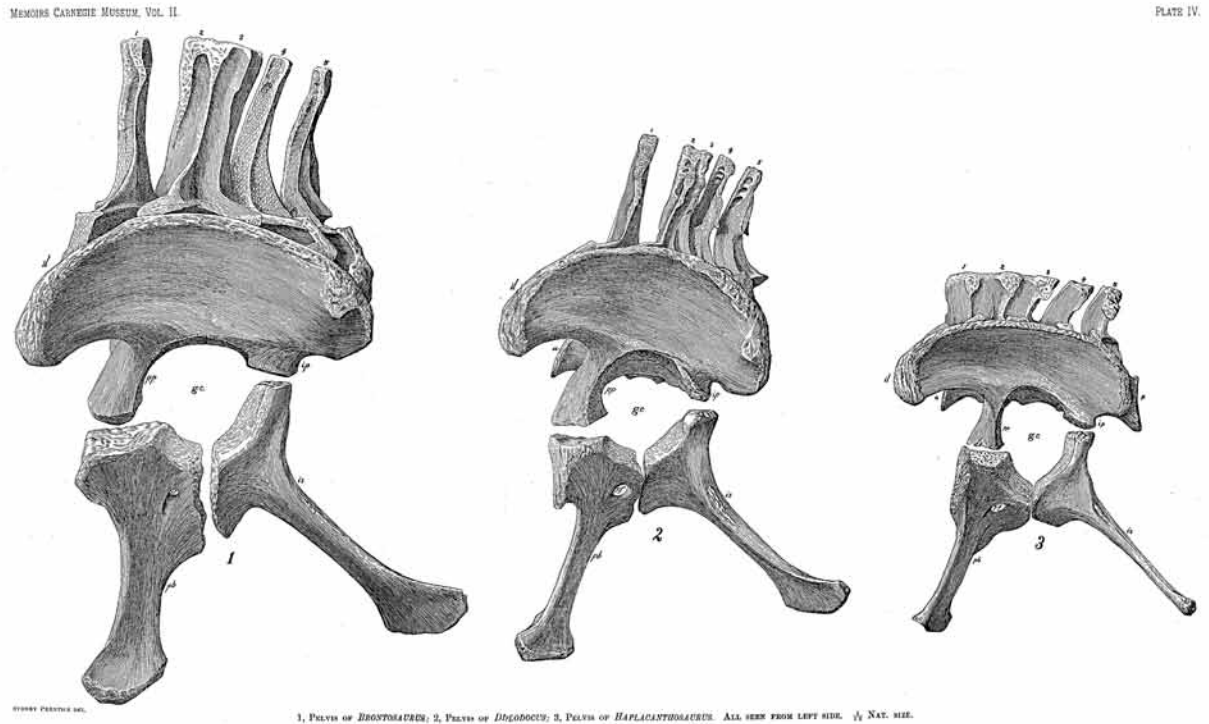
Figure 20. Pelves of diplodocids and *Haplocanthosaurus*. From left to right: *Apatosaurus excelsus* CM 568, *Diplodocus carnegii* CM 84/94, and *Haplocanthosaurus priscus* CM 572. All in left lateral view. From Hatcher (1903: plate 4).

2007), taxa defined on small specimens (such as *Suuwassea*, but also potentially *Barosaurus*, *Haplocanthosaurus*, and ''*Brontodiplodocus*'' [*sic* – the problematic "*Amphicoelias brontodiplodocus*" has been publicized by Galiano & Albersdörfer (2010), but not formally published, so it is currently a nomen nudum]), might represent immature forms of *Diplodocus* or *Apatosaurus*."

In this section we use comparative osteology to test the hypothesis that *Haplocanthosaurus* is a juvenile diplodocid.

Pelvis – Hatcher (1903: plate 4) illustrated the pelvis and sacrum of *Haplocanthosaurus* alongside those of the well-known Morrison diplodocids (figure 20). The pelvis of *Haplocanthosaurus* differs from those of the diplodocids in having a proportionally lower ilium, in the absence of the laterally facing rugosity on the posterodorsal margin of the ilium, in the very small distal expansion of the pubis and in the almost non-existent distal expansion of the ischium. These are all characters of the limb-girdle elements, which do not change greatly through ontogeny in sauropods.

But the evidence from the sacral vertebrae is just as significant: the neural spines in the sacral area are less than half as tall as in the diplodocids – and this in an animal whose dorsal neural spines are conspicuously tall. The spines are also more anteroposteriorly elongate and plate-like. Furthermore, sacral spines 1, 2 and 3 have fused into a single plate in *Haplocanthosaurus*, while the spine of S1 remains well separated from 2 and 3 in the diplodocids. If *Haplocanthosaurus* were a juvenile of *Apatosaurus* or *Diplodocus*, then, its sacral neural spines would have to become less fused through ontogeny.

Cervical vertebrae – It is immediately apparent that the *Haplocanthosaurus* cervicals have less extensive pneumatic features than those of the diplodocids (figure 21), but pneumaticity is known to vary ontogenetically. There are other differences: for example, the cervical ribs in *Haplocanthosaurus* are level with the ventral margin of the centrum rather than hanging below. Nevertheless, in lateral view the *Haplocanthosaurus* cervicals do look like possible juveniles of *Diplodocus*.

In posterior view, however, there are significant differences (figure 22):

- *Haplocanthosaurus* has unsplit neural spines. It is true that Woodruff & Fowler (2012) have argued that it could be ontogenetic, but these are vertebrae from the most
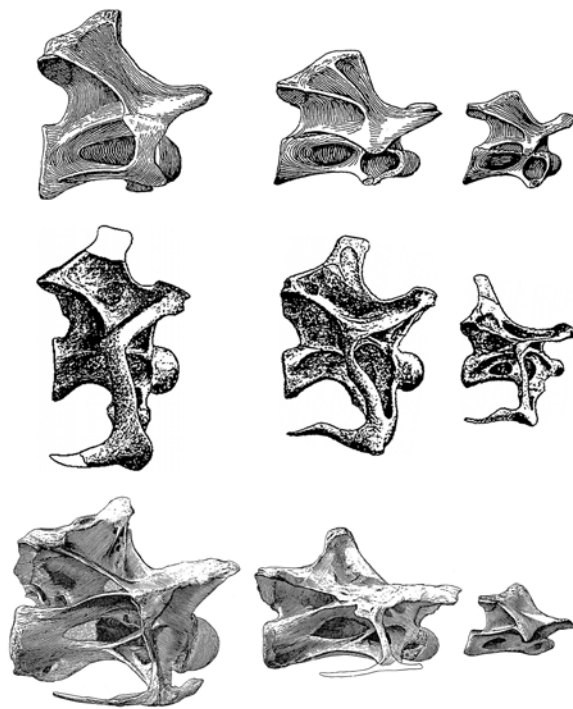
Figure 21. Posterior, mid and anterior cervical vertebrae, in right lateral view, of (top to bottom), *Haplocanthosaurus*, *Apatosaurus louisae* CM 3018 (from Gilmore, 1936: plate 24, reversed for ease of comparison) and *Diplodocus carnegii* CM 84/94 (from Hatcher, 1901: plate 3), scaled to roughly the same size. For the diplodocids, we illustrate C13, C9 and C4. For *Haplocanthosaurus*, we illustrate C14 of *H. priscus* (from Hatcher, 1903: plate 1) and C9 and C4 of *H. utterbacki* (from plate 2).
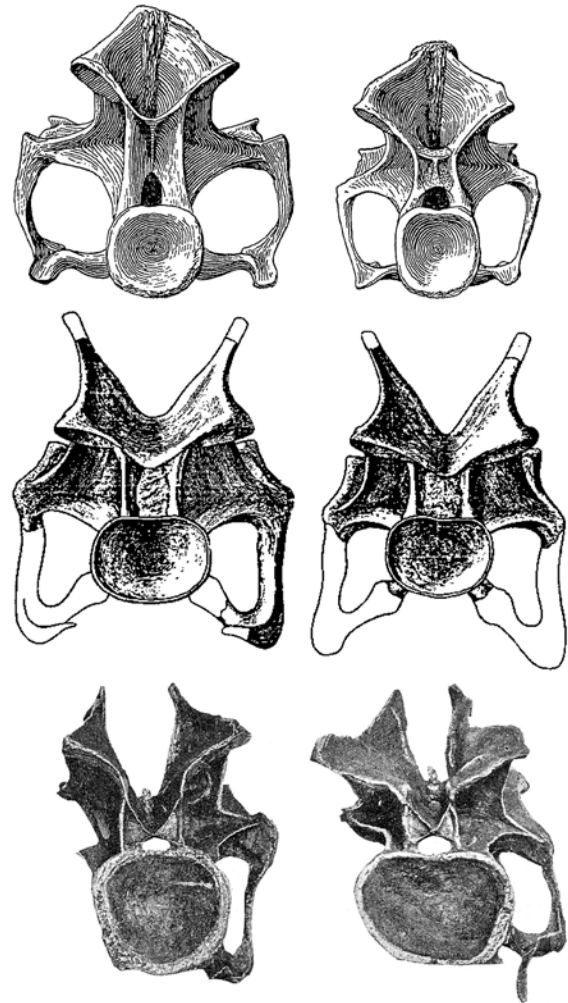

Figure 22. Posterior cervical vertebrae C15 and C14, in posterior view, of (top to bottom), *Haplocanthosaurus priscus* CM 572 (from Hatcher, 1903: plate 1), *Apatosaurus louisae* CM 3018 (from Gilmore, 1936: plate 24) and *Diplodocus carnegii* CM 84/94 (from Hatcher, 1901: plate 6), scaled to the same centrum-to-neural-spine height (these are the only *Haplocanthosaurus* cervical vertebrae that Hatcher illustrated in posterior view.)

deeply bifurcated region of a diplodocid neck, in a good-sized animal, and there are no features that even hint at incipient bifurcation;

- The large, prominent ligament scar running down the back (and also the front, not pictured) of the neural spine. There is nothing like this in any diplodocid – neither on the metapophyses nor running though the intermetapophyseal trough. Ligament scars like these tend to become more, not less, prominent through ontogeny, so their absence from the diplodocids cannot be interpreted as an adult feature;
- The postzygapophyses-to-centrum height is taller in *Haplocanthosaurus* – much taller in the case of C15;
- The bony plates running out to the diapophyses are less dorsoventrally expanded in *Haplocanthosaurus*;
- The centrum is smaller in *Haplocanthosaurus* as a proportion of total height – especially, much smaller than in *Diplodocus*;

- The parapophyses of *Haplocanthosaurus* extend directly laterally rather than ventrolaterally (hence the position of the cervical ribs level with the ventral margin of the centrum).

Dorsal vertebrae – *Haplocanthosaurus* has dorsolaterally inclined diapophyses, a prominent spinodiapophyseal lamina in posterior dorsals, and no infraparapophyseal lamination (figure 23). Also, the dorsal vertebrae have reached their full height by the middle of the series (in fact the last nine dorsals are strikingly similar in proportions), whereas in diplodocids, total height continues to increase posteriorly.

In posterior view (figure 24), the *Haplocanthosaurus* dorsals differ from those of the diplodocids in almost every respect:
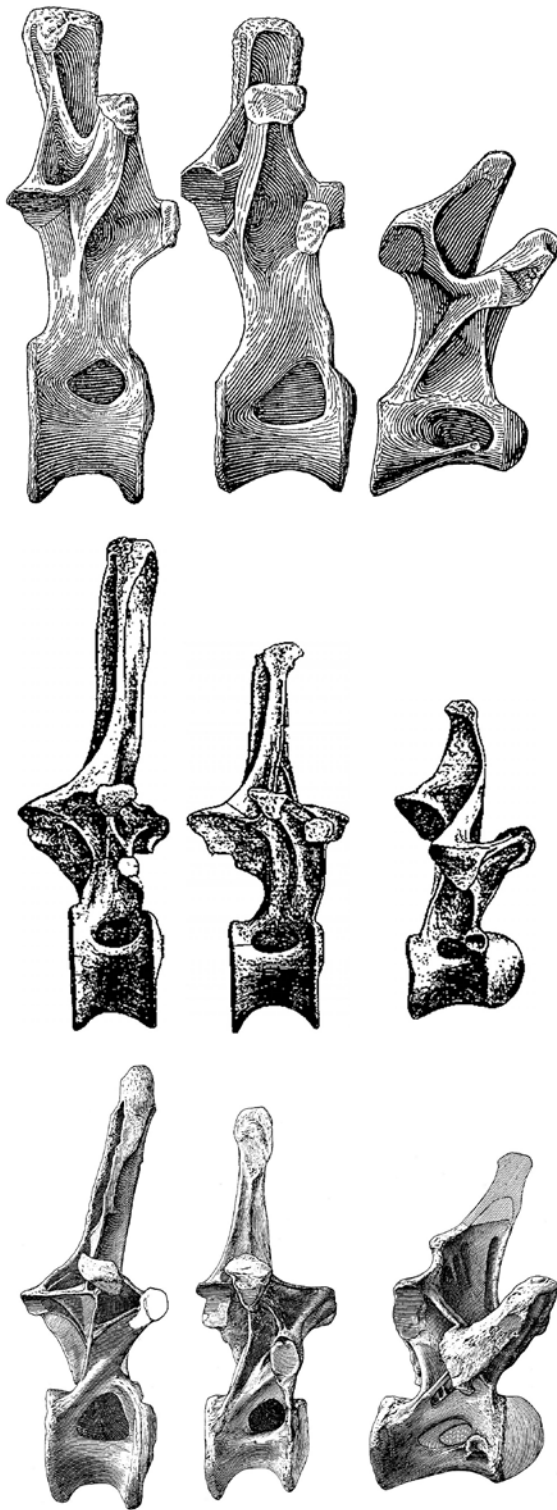

Figure 23. Posterior, middle and anterior dorsal vertebrae, in right lateral view, of (top to bottom), *Haplocanthosaurus, Apatosaurus louisae* CM 3018 (from Gilmore, 1936: plate 25, reversed for ease of comparison) and *Diplodocus carnegii* CM 84/94 (from Hatcher, 1901: plate 7), scaled to roughly the same size. For the diplodocids, we illustrate D9, D5 and D2. For *Haplocanthosaurus*, which has four more dorsals, we illustrate D13 and D7 of *H. priscus* (from Hatcher, 1903: plate 1) and D2 of *H. utterbacki* (from plate 2).

- The neural spine of the anterior dorsal in *Haplocanthosaurus* is non-bifd, as well as the more posterior dorsals;
- The neurapophyses of the *Haplocanthosaurus* dorsals are rounded in posterior view, rather than square as in the non-bifid spines in the diplodocids;
- In the *Haplocanthosaurus* posterior dorsal, the neural spine has laterally directed triangular processes near the top;
- All three *Haplocanthosaurus* neural spines have broad, rugose ligament scars, whereas those of the diplodocids have narrow, smooth postspinal laminae;
- The neural spines (measured from the diapophyses upwards) are much shorter than in the diplodocids;
- The neural arches (measured from the centrum up to the diapophyses) are much taller;
- The diapophyses have distinct club-like rugosities at their tips;
- the diapophyses of the mid and posterior dorsals are inclined strongly upwards;
- The hyposphenes of mid and posterior dorsals have very long centropostzygapophyseal laminae curving up in a gentle arch;
- The centra of the *Haplocanthosaurus* dorsals are proportionally smaller than those of *Apatosaurus* and *Diplodocus*.

It is interesting how very different the D5s of *Apatosaurus* and *Diplodocus* are. Since both are from presumably adult or near-adult specimens, bifurcation was evidently very different between these genera.

Ontogenetic status of *Haplocanthosaurus* – Woodruff & Fowler (2012: 9) contend that *Haplocanthosaurus* is a juvenile of a different, already recognized taxon, but the type specimen of the type species – *H. priscus* CM 572 – is an adult. As Hatcher (1903: 3) explains: "The type No. 572 of the present genus consists of the two posterior cervicals, ten dorsals, five sacrals, nineteen caudals, both ilia, ischia and pubes, two chevrons, a femur and a nearly complete series of ribs, all in an excellent state of preservation and pertaining to an individual fully adult as is shown by the coössified neural spines and centra."

Woodruff & Fowler may have been misled because the second species that Hatcher describes, *H. utterbacki*, is based on the subadult specimen CM 879. Where possible in the composite illustrations
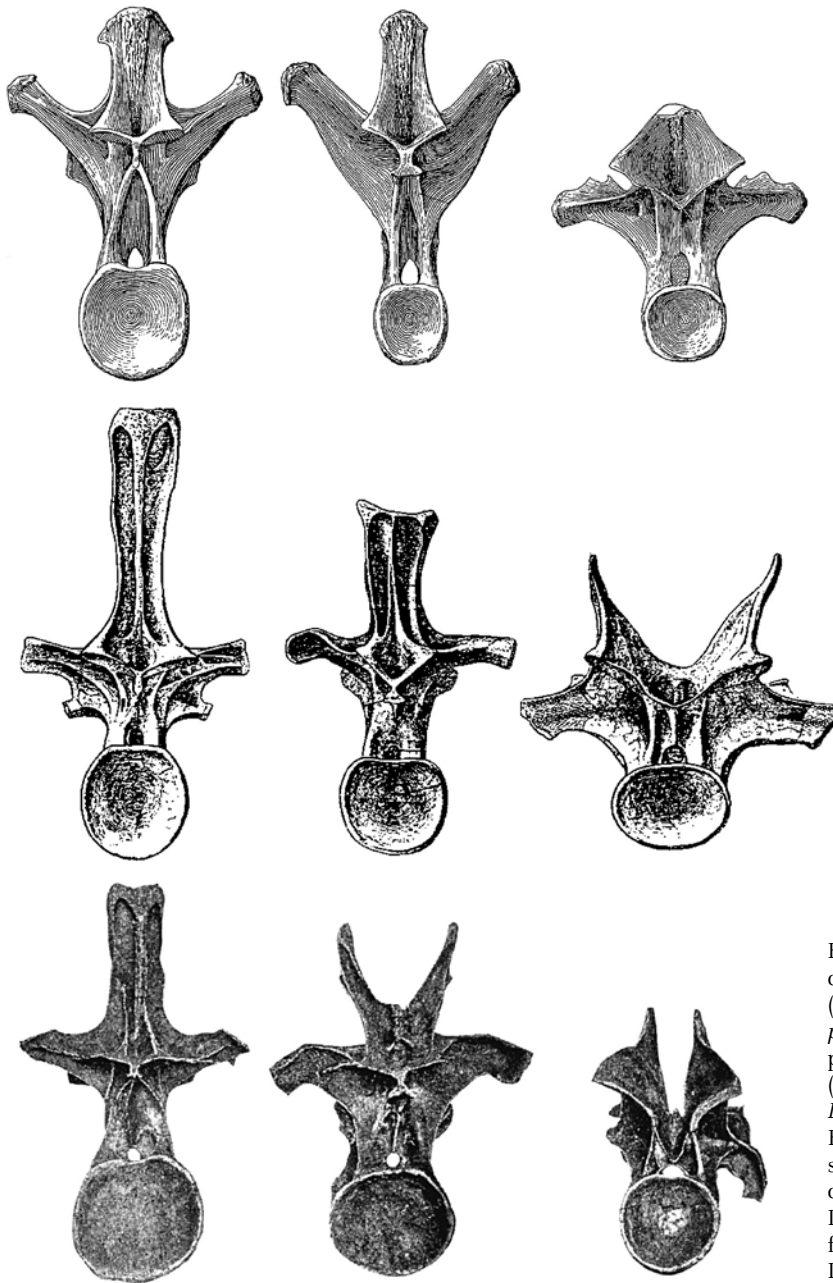
Figure 24. Posterior, mid and anterior dorsal vertebrae, in posterior view, of (top to bottom), *Haplocanthosaurus priscus* CM 572 (from Hatcher, 1903: plate 1), *Apatosaurus louisae* CM 3018 (from Gilmore, 1936: plate 25) and *Diplodocus carnegii* CM 84/94 (from Hatcher, 1901: plate 7), scaled to the same height of the mid dorsal. For the diplodocids, we illustrate D9, D5 and D1. For *Haplocanthosaurus*, which has four more dorsals, we illustrate D13, D6 and D1.

we have used illustrations of the adult *H. priscus*, so that the comparisons are of adult with adult. The exceptions are the two anterior cervicals and the first dorsal, which are known only from *H. utterbacki*. These illustrations, and the Hatcher plates from which they are drawn, show that in these vertebrae and only these vertebrae, the neurocentral junction is shown – because it was not yet fused. The difference in ontogenetic status between these two specimens is also illustrated in figure 25.

So *H. utterbacki* CM 879 certainly is an immature form of something; but that something is *Haplocanthosaurus*, most likely *H. priscus*. As shown by McIntosh & Williams (1988: 22),

the characters which Hatcher used to separate the two species are not very convincing.

Summary – The hypothesis that *Haplocanthosaurus* is a juvenile diplodocid is not supported by either comparative anatomy or skeletochronology.

Phylogenetic Evaluation of Suggested Synonymies

Woodruff & Fowler (2012: 1) claimed that "on the basis of shallow bifurcation of its cervical and dorsal neural spines, the small diplodocid *Suuwassea* is more parsimoniously interpreted as an immature specimen of an already

Figure 25. Neurocentral fusion in *Haplocanthosaurus*. A, B. Posterior cervical vertebra C?12 of sub-adult H. utterbacki holotype CM 879: A, X-ray in right lateral view; B, transverse CT slice showing separate ossificaton of centrum and neural arch. C, D. Mid-dorsal vertebra D6 of adult *H. priscus* holotype CM 572: X-rays in (C) right lateral and (D) posterior view, showing fully fused neural arch. Modified from Wedel (2009: figure 6).

recognized diplodocid taxon". In studies of evolution, the word 'parsimony' has a specific meaning: it refers to minimising the number of character-state changes.

We evaluated the parsimony of the hypothesis that *Suuwassea* or *Haplocanthosaurus* – also mentioned by Woodruff & Fowler (2012: 9) as a candidate for synonymy – was the juvenile form of one of the previously known diplodocids. For the purpose of this analysis we ignored the evidence that both these genera are known from adult individuals, and considered how many additional steps would be needed to make them the sister taxa of one of the diplodocids, or some other Morrison Formation sauropod. The method was as follows:

- Begin with the character-taxon matrix from a previously published peer-reviewed phylogenetic analysis;
- Re-run the matrix to verify that the results are the same as in the published paper based on it. This step re-establishes the null hypothesis and demonstrates that the matrix is being run correctly.
- For each candidate synonymy, impose a constraint that the synonymous taxa are in a sister-group relationship – for example, that

Suuwassea and *Apatosaurus* are more closely related to each other than to any other OTU. Note that the characters, taxa and codings are not modified;
- Run the matrix again, with the constraint in place, and note the length of the most parsimonious trees. The difference between this and the original tree-length is a measure of how unparsimonious the proposed synonymy is;
- Repeat as needed with other constraints to evaluate other phylogenetic hypotheses.

We performed this exercise twice: first with the matrix of Taylor (2009), as the only available study that treated the Morrison Formation brachiosaurid *Brachiosaurus* as a distinct taxon; and second with that of Whitlock (2011), which was focussed particularly on the sauropod subclade Diplodocoidea. The results are given in table 2.

In the analysis of Taylor (2009), *Suuwassea* is separated from *Apatosaurus* by only two steps (and by eight or more steps from the other taxa). However, the separation between these two taxa leaps to 21 steps in Whitlock's (2011) analysis. *Suuwassea*'s separation from the other dipldococids is similarly increased in Whitlock's analysis, because this contains more characters that are parsimony-informative within Diplodocoidea. The more closely we look at *Suuwassea*, the less closely it resembles diplodocids.

In the case of *Haplocanthosaurus*, the numbers of additional steps required are much more similar between the two analyses. In both analyses, it is very widely separated from the diplodocids (from 24–37 steps), but much less separated from the basal macronarian *Camarasaurus*. Taylor (2009) recovered *Haplocanthosaurus* as just outside Neosauropoda, so equally distant from Diplodocoidea and Macronaria, whereas Whitlock (2011) recovered it as the most basal diplodocoid. The large number of steps required to move it further down inside Diplodocoidea in Whitlock's analysis are partly due to that study's focus on characters that are informative within Dipodocoidea, but also reflects how close to the base of Neosauropoda both *Haplocanthosaurus* and *Camarasaurus* are.

The nexus files used in this analysis are available as supplementary information: doi:

	Compared with Taylor (2009)		Compared with Whitlock (2011)	
Proposed relationship	Tree length	Extra steps	Tree length	Extra steps
No constraint imposed	791		273	
Suuwassea sister to:				
Apatosaurus	793	2	294	21
Diplodocus	799	8	299	26
Barosaurus	799	8	299	26
Camarasaurus	811	20	304	31
Brachiosaurus	804	13		
Giraffatitan			309	36
Haplocanthosaurus sister to:				
Apatosaurus	817	26	298	25
Diplodocus	825	34	310	37
Barosaurus	815	24	310	37
Camarasaurus	793	2	278	5
Brachiosaurus	797	6		
Giraffatitan			283	10

Table 2. Results of the phylogenetic analyses, showing the number of extra steps required to force *Suuwassea* and *Haplocanthosaurus* into sister-group relationships with well-represented Morrison Formation sauropods. The analysis of Whitlock (2011) did not include the Morrison Formation taxon *Brachiosaurus altithorax*. It did contain an OTU labelled *Brachiosaurus,* but it was coded from the African species *"Brachioaurus" brancai,* now recognised as the separate genus *Giraffatitan*. We considered possible synonymies with this genus as it is the only brachiosaurid in Whitlock's analysis.

10.6084/m9.figshare.643806 (Nexus file based on Taylor, 2009 matrix), and doi: 10.6084/m9.figshare.643805 (Nexus file based on Whitlock, 2011 matrix).

Discussion

MOR 790 8-10-96-204 and the Mother's Day Quarry

MOR 790 8-10-96-204 is presented by Woodruff & Fowler (2012) as a posterior cervical of a juvenile *Diplodocus*. For reasons explained above, we think it is an anterior cervical from an adult or near-adult. MOR 790 8-10-96-204 is from the Mother's Day Quarry (Woodruff & Fowler 2012: table 1), which until now was only known to contain juvenile and subadult sauropods (Myers & Storrs, 2007; Myers & Fiorillo, 2009). Myers & Fiorillo (2009: 99) wrote: "The quarry has a strikingly low taxonomic diversity, with one sauropod taxon and one theropod taxon present. However, the relative abundance of elements from these taxa is so uneven – diplodocoid sauropod material comprises 99% of the recovered bones – that the quarry is effectively monospecific (Myers and Storrs, 2007). The theropod material consists of isolated teeth only and is probably related to scavenging of the sauropod carcasses. All identifiable sauropod elements belong to either juvenile or subadult individuals (Fig. 2); none is attributable to a fully-adult individual (Myers and Storrs, 2007)."

Figure 2 from Myers & Fiorillo (2009) shows two sauropod centra, a dorsal and a caudal, both with unfused neural arches. In contrast, MOR 790 8-10-96-204 is similar in size and morphology to the anterior cervicals of *D. carnegii* CM 84/94, and appears to have closed neurocentral synostoses and fused cervical ribs. In all aspects, the morphology of MOR 790 8-10-96-204 is consistent with that of an adult or nearly adult animal, which implies that the Mother's Day Quarry includes at least one adult or near-adult *Diplodocus*. If MOR 790 8-10-96-204 represents an adult, it is the only adult *Diplodocus* element identified from the Mother's Day Quarry to date, and its presence in the quarry does not necessarily imply social interaction between the adult individual and the numerous subadults. The inferences that the quarry is dominated by juveniles (Myers & Storrs, 2007) that represent an age-segregated herd (Myers & Fiorillo 2009) are not falsified.

Did neural spine bifurcation increase over ontogeny in Morrison Formation sauropods?
When information on size and serial position are taken into account, none of the 'ontogenetic series' in Woodruff & Fowler (2012) shows any convincing evidence that neural spine bifurcation increases over ontogeny. The best evidence that bifurcation does increase over ontogeny comes from *Camarasaurus*, specifically the juvenile *C. lentus* CM 11338 described by Gilmore (1925) and geriatric *C. lewisi* BYU 9047 described by McIntosh, Miller, *et al.* (1996), it was already recognized prior to Woodruff & Fowler (2012), and it has not caused any taxonomic confusion.

To demonstrate that bifurcation develops over ontogeny, it is necessary to falsify all of the competing hypotheses: serial, intraspecific, or interspecific variation, taphonomy, damage during preparation, and so on. This could only be done by finding a presacral vertebral column that is (1) articulated, (2) from an individual that is clearly juvenile based on criteria other than size and degree of bifurcation, which (3) can be confidently referred to one of the known genera, and then show that it has unbifurcated spines in the same serial positions where adult vertebrae have bifurcated spines. Isolated vertebrae, bones from non-juveniles, and juvenile bones that might pertain to new taxa (*e.g.* MOR 592) are all insufficient if not actively misleading. It may be that demonstrating an ontogenetic increase in bifurcation in diplodocids is not yet possible because the necessary fossils have not been found or described yet. The ontogenetic hypothesis of neural spine bifurcation in diplodocoids is not unreasonable, especially given the evidence from *Camarasaurus*, but it has not yet been demonstrated.

Is histology the only solution?
In their conclusion, Woodruff & Fowler (2012: 9) argued: "Taxa defined on small specimens (such as *Suuwassea*, but also potentially *Barosaurus*, *Haplocanthosaurus*, and "*Brontodiplodocus*"), might represent immature forms of *Diplodocus* or *Apatosaurus*. Such hypotheses can only be properly tested by histological analysis." We agree that histological analysis of ontogenetic age is desirable, but we disagree that histology is the only proper test of hypotheses of ontogenetic synonymy. Such hypotheses can also be tested in at least two other ways. First, the

plausibility of proposed synonymies can be explored through phylogenetic analysis, as we have done for both *Suuwassea* and *Haplocanthosaurus*. In both cases the proposed synonymies with known diplodocids are exceptionally unparsimonious, contra Woodruff & Fowler (2012). Second, skeletal fusions may only be able to provide relative, as opposed to absolute, measures of ontogenetic age, but this may be enough to falsify proposed synonymies. As discussed above, the *Suuwassea* holotype ANS 21122 actually has a greater degree of neural spine and cervical rib fusion than *Diplodocus carnegii* CM 84/94 and *Apatosaurus* CM 555, so it is highly unlikely that it could be a juvenile of either taxon.

Histological analysis may be able to provide a greater level of precision than comparing relative age criteria such as skeletal fusions, but the latter method does not involve destructive sampling and requires no equipment, although a notebook and camera may be useful. To some extent the field of sauropod paleobiology suffers from 'monograph tunnel vision', in which our knowledge of most taxa is derived from a handful of specimens described decades ago (*e.g. Diplodocus carnegii* CM 84/94). Recent work by McIntosh (2005), Upchurch *et al.* (2005), and Harris (2006a, b, c, 2007) is a welcome antidote to this malady, but several of the taxa discussed herein are represented by many more specimens that have not been adequately described or assessed. A comprehensive program to document skeletal fusions and body size in all known specimens of, say, *Camarasaurus*, or *Diplodocus*, could be undertaken for relatively little cost (other than travel expenses, and even these could be offset through collaboration) and would add immeasurably to our knowledge of sauropod ontogeny.

Acknowledgements

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