Almost all known sauropod necks are incomplete and distorted

Michael P. Taylor

Department of Earth Sciences, University of Bristol, Bristol, England.
dino@miketaylor.org.uk

Abstract

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

Keywords: sauropod, dinosaur, neck, cervical vertebrae, preservation, distortion, cervicodorsal transition

Table of Contents

Introduction

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

37   Sauropod specimens are rarely found in a form complete enough to allow even relatively
38   rudimentary measurements to be made — for example, neck length or shoulder height. In fact,
39   the problem is more significant than is generally realised. It is not just that we do not have large
40   populations of well-preserved sauropod individuals, capable of being subject to statistical
41   analyses; even individual complete sauropods are extremely rare. This is true especially of the
42   necks, which are composed of large, fragile vertebrae that are prone to disarticulation and
43   distortion.

44   The consequent incompleteness of known sauropod necks, and the ubiquitous distortion of the
45   elements that are available, has negative consequences for taxonomic work (since we are
46   frequently unable to compare overlapping elements of different specimens), phylogenetic
47   analysis (due to loss of character data), developmental studies (as we are frequently unable to
48   determine for example how pneumatic features vary along the neck in patterns mimicking
49   ontogeny), biomechanical function (since we do not have sufficiently precise joint anatomy to
50   accurately model neutral posture or range of motion) and ecological impact (using neck length as
51   a proxy for feeding behaviour). While these problems are appreciated by seasoned campaigners,
52   they are less well understood by newcomers to the field and to those whose specialisms are in
53   adjacent fields such as extant animal anatomy, especially as most people's initial impressions of

54   sauropod are formed by large and apparently complete mounted specimens in public galleries.

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

59   **Institutional Abbreviations**

60   AODF — Australian Age of Dinosaurs Fossil, Winton (Australia)

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

62   CCG V — Chengdu College of Geology, Chengdu (China), vertebrate collection

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

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

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

67   MACN — Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires
68   (Argentina)

69   MAU-Pv — Museo Argentino Urquiza, Rincón de los Sauces, Neuquén (Argentina), vertebrate
70   palaeontology collection

71   MB.R — see MfN

72   MCT — Collection of the Earth Science Museum of the National Department of Mineral
73   Production, Rio de Janeiro (Brazil)

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

76   MNBH — Musée National Boubou Hama, Niamey (Republic of Niger)

77   MOZ-Pv — Museo Provincial de Ciencias Naturales "Dr. Prof. Juan A. Olsacher", Zapala
78   (Argentina), vertebrate palaeontology collection

79   MPEF — Museo Paleontológico Egidio Feruglio, Trelew (Argentina): collection numbers for
80   fossil vertebrates: MPEF PV

81   MPM — Museo Padre Molina, Río Gallegos, Santa Cruz (Argentina): collection numbers for
82   fossil vertebrates: MPM PV

83   MUCPv — Museo de Geologia y Paleontologia de la Universidad Nacional del Comahue,
84   Neuquén (Argentina), vertebrae palaeontology collection

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

86   PMU — Paleontological Museum, Uppsala, Sweden

87   QJGPM — Qijiang Petrified Wood and Dinosaur Footprint National Geological Park Museum,
88   Chongqing (China)

89   SMA — Sauriermuseum Aathal (Switzerland)

90   SSV — Shanshan Geological Museum, Shanshan (China)

91   USNM — National Museum of Natural History, Smithsonian Institution, Washington, D.C.
92   (USA)

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

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

95 Incompleteness

96   A truly complete neck would consist of all vertebrae, each of them individually complete.
97   Unfortunately, it is rarely possible to tell from published descriptions whether a given neck is
98   complete in this sense: necks are sometimes described superficially as "complete" when all that
99   is meant is that some portion of each vertebra is preserved. In the cases of necks that are
100 described in detail, it is almost always apparent that a "complete" neck is complete only in this
101 limited sense: for example, in the *Cathetosaurus lewisi* holotype BYU 9047, McIntosh et al.
102 (1996:76) note that although all 12 cervicals are present, "10–12, particularly 12, have suffered
103 such severe damage that it is impossible to restore them". For the purposes of this paper, then we
104 use "complete" in the unsatisfactory sense that at least a good part of each vertebra is present.

105 The determination of completeness of necks is also hindered by the problem that for many
106 species we do not know how many vertebrae would constitute a complete neck. When necks are
107 not found in articulation but a probably complete set of cervicals is found scattered, the
108 possibility that additional vertebrae were present in life cannot be discounted. The mode of
109 preservation can vary wildly with disarticulated necks, giving us a greater or lesser degree of
110 confidence that all vertebrae are present. At one end of the spectrum, vertebrae may be scattered
111 around, and intermixed with those of other species or even other individuals of the species, as
112 with the numerous cervical vertebrae included in the *Camrasaurus specimen* complex AMNH
113 5761/5761a and assigned somewhat arbitrarily to three sequences (Osborn and Mook 1921:plates
114 LXVII–LXIX). In happier cases, such as that of the *Qijianglong guokr* holotype QJGPM 1001,
115 partial sequences are articulated (in this case C2–11) and other cervicals closely associated.
116 However, even a neck found in articulation may be impossible to evaluate as to its completeness,
117 as with *Lavocatisaurus agrioensis* (see below).

118 With these caveats in mind, I now survey the known complete and nearly-complete sauropod
119 necks.

120 Catalogue of complete necks

121 Unambiguously complete necks are known from published accounts of only a few sauropod
122 specimens. In chronological order of description, the following specimens were found with their
123 necks complete and articulated, and have been adequately described — each of them known to
124 include the posteriormost cervicals because the vertebral column is articulated through into the
125 dorsal region:

126 • CM 11338, a referred specimen of *Camarasaurus lentus* described by Gilmore (1925).
127   This is a juvenile specimen, and thus does not fully represent the adult morphology.
128   (McIntosh et al. 1996:76 claim that this specimen is the holotype, but this is not correct:
129   YPM 1910 is the holotype — see below.)
130 • CM 3018, the holotype of *Apatosaurus louisae*, described by Gilmore (1936). The neck

131   was separated from the torso but articulated from C1–C15, though the last three cervicals
132   were badly crushed: see below for details.
133 • CCG V 20401, the *Mamenchisaurus hochuanensis* holotype, described by Young and
134   Zhao (1972). Each vertebra is broken in half at mid-length, with the posterior part of each
135   adhering to the anterior part of the its successor; and all the vertebrae are badly crushed in
136   an oblique plane.
137 • ZDM T5402, a *Shunosaurus lii* referred specimen, described in Chinese by Zhang
138   (1988), with English figure captions. Their figure 22 depicts the atlas. Unlike the
139   holotype T5401, this specimen is mature.
140 • BYU 9047, the *Cathetosaurus lewisi* holotype, described by Jensen (1988). (Jensen
141   incorrectly gives the specimen number as BYU 974.) This specimen was redescribed, and
142   the species referred to *Camarasaurus*, by McIntosh et al. (1996). Although all 12
143   cervicals are present, "10–12, particularly 12, have suffered such severe damage that it is
144   impossible to restore them" (McIntosh et al. 1996:76).
145 • MACN-N 15, the holotype of *Amargasaurus cazaui* MACN-N 15, described by Salgado
146   and Bonaparte (1991) who described "22 presacral vertebrae articulated with each other
147   and attached to the skull and sacrum, relatively complete" (Salgado and Bonaparte
148   1991:335, translated.
149 • ZDM 0083, the holotype of *Mamenchisaurus youngi*, described in Chinese by Ouyang
150   and Ye (2002) with English figure captions. Their figure 14 depicts the atlas and axis.
151 • MUCPv-323, the holotype of *Futalognkosaurus dukei*, initially described by Calvo et al.
152   2007a and redescribed by Calvo et al. 2007b. The neck was found in two articulated
153   sections which fit together without needing additional vertebrae in between (Jorge O.
154   Calvo, pers. comm., 2021).
155 • SSV12001, the holotype of *Xinjiangtitan shanshanesis*, described by Zhang et al. (2018).
156   The original description of this specimen by Wu et al. 2013 included only the last two
157   cervicals, which were the only ones that had been excavated at that time.

158   A few additional specimens are known to have complete and articulated necks, but have not
159 yet been described:

160 • USNM 13786, a referred subadult specimen of *Camarasaurus lentus* recently mounted at
161   the Smithsonian. The specimen "was almost completely buried before the sinews had
162   allowed the bones to separate" (letter from Earl Douglass to William J. Holland, 22
163   August 1918), and photographs kindly supplied by Andrew Moore show that the atlas
164   was preserved.
165 • MNBH TIG3, the holotype of *Jobaria tiguidensis*. Sereno et al. (1999:1343) assert that
166   this species has 12 cervicals in all and say "One articulated neck was preserved in a fully
167   dorsiflexed, C-shaped posture". Paul C. Sereno (pers. comm., 2021) confirms that the
168   articulated neck is MNBH TIG3
169 • SMA 002, referred to *Camarasaurus* sp. Tschopp et al. (2016), in a description of its feet,
170   say that this specimen "lacks only the vomers, the splenial bones, the distal end of the
171   tail, and one terminal phalanx of the right pes. The bones are preserved in three
172   dimensions and in almost perfect articulation".
173 • MAU-Pv-LI-595, the "La Invernada" Titanosaur. Filippi et al. (2016) give a very brief
174   account in an abstract. Filippi (pers. comm, 2021) says that the entire preserved specimen
175   was articulated.

176   •   MAU-Pv-AC-01, an unnamed titanosaur mentioned in abstracts by Calvo et al. (1997)
177   and Coria and Salgado (1999). The specimen was found in perfect articulation from skull
178   down to the last caudal vertebrae (Rodolfo A. Coria, pers. comm., 2021).

179   The first cervical (the atlas) in sauropods is very different in form from the other vertebrae,
180 and small and fragile. Consequently it is easily lost. Some further specimens have necks that are
181 complete and articulated from C2 (the axis) backwards:

182   •   MB.R.4886, the holotype of *Dicraeosaurus hansemanni*, described by Janensch (1929),
183   has a neck that complete and well preserved from C2 to C12 (the last cervical). Janensch
184   referred to this as "specimen m" and writes "It was found articulated from the 19th
185   caudal vertebra to the 9th cervical vertebra inclusive. The proximal part of the neck from
186   the 8th cervical vertebra up to the axis was bent ventrally and lay at right angles to the
187   distal part of the neck." (Janensch 1929:41).
188   •   PMU 233, the holotype of *Euhelopus zdanskyi*, described by Wiman (1929) as "exemplar
189   a" and redescribed by Wilson and Upchurch (2009).
190   •   ZDM T5401, the subadult holotype of *Shunosaurus lii*, described in Chinese by Zhang et
191   al. 1984. The quarry map (Zhang et al. 1984:figure 1) suggests that the atlas is missing.
192   •   MCT 1487-R, informally known as "DGM Series A", described by Powell (2003).
193   Gomani (2005:9) summarises as "12 cervical vertebrae, except the atlas, preserved in
194   articulation with three proximal dorsal vertebrae".
195   •   GCP-CV-4229, the holotype of *Spinophorosaurus nigerensis*, described by Remes et al.
196   (2009). This species is known from two specimens, of which the holotype was found in
197   very good condition and well articulated from C2 to C13, the last cervical (Figure 1). The
198   atlas seems to be missing (Kristian Remes, pers. comm., 2021; Ralf Kosma, pers. comm.,
199   2021).

200   One other sauropod is complete from the first cervical, but probably not to the last:

201   •   MOZ-Pv1232, the holotype of *Lavocatisaurus agrioensis*, described by Canudo et al.
202   (2018). This is complete from C1–C11. Canudo's guess is that this is the complete neck
203   (Jose I. Canudo, pers. comm, 2021), but the specimen doesn't demand that conclusion
204   and no known eusauropod is definitively known to have fewer than 12 cervicals.
205   However, Upchurch (pers. comm., 2021) notes that the dicraeosaurid neosauropod
206   *Amargasaurus* has 22 presacral vertebrae in total, and difficulties in locating the
207   cervicodorsal junction (see below) make it impossible to state confidently whether it had
208   12 or only 11 cervicals, so caution is warranted here.

209   Other sauropod specimens have necks that are complete and articulated from further back in
210 the cervical sequence:

211   •   YPM 1910, the holotype of *Camarasaurus lentus*, a mounted specimen described by Lull
212   (1930). The neck is complete from C2 or C3, Lull was uncertain which. (It should be
213   possible to clear that up by re-examining the specimen in light of what has subsequently
214   become known about *Camarasaurus lentus*, but this work has not yet been done.)
215   •   SMA 0004, *Kaatedocus siberi*, described by Tschopp and Mateus (2012). Cervicals 3–14
216   are preserved.
217   •   AODF 888 (informally "Judy"), probably referrable to *Diamantinasaurus*, briefly
218   described by Poropat et al. (2019). Preserved from C3 or maybe C4. "One posterior

219   cervical (XIII or XIV) found several metres from articulated series, but appears to slot
220   nicely into the gap between the articulated cervical series and the unprepared thoracic
221   section, which might include at least one additional cervical (XIV or XV)" (Poropat, pers.
222   comm. 2021).

223   Several necks are probably nearly complete, but it is not possible to knew due to their not
224 being found in articulation:

225   • CM 84, the holotype of *Diplodocus carnegii*, described by Hatcher (1901). C2–C15 are
226   preserved, though not all in articulation; C11 may be an intrusion: see below for details.
227   • ZDM T5701, the holotype of *Omeisaurus tianfuensis*, described by He et al. (1988). The
228   neck was not articulated (He et al. 1988:figure 1), and was missing "two elements or so"
229   (He et al. 1988:120).
230   • QJGPM 1001, the holotype of *Qijianglong guokr*, described by Xing et al. (2015). On
231   page 8, the authors say "The axis to the 11th cervical vertebra were fully articulated in
232   the quarry. The atlas intercentrum and the 12th–17th cervical vertebrae were closely
233   associated with the series."
234   • MNBH TIG9, a referred specimen of *Jobaria tiguidensis*. Wilson (2012:103) writes that
235   this specimen "includes a partially articulated series of 19 vertebrae starting from the axis
236   and extending through the mid-dorsal vertebrae."
237   • MNBH TIG6, another referred specimen of *Jobaria tiguidensis*, which has not been
238   mentioned in the literature. Paul C. Sereno (pers. comm., 2021) says that it is "a subadult
239   partial skeleton with excellent neck" and that "the sequence was articulated from C2–11.
240   Most of the ribs were attached as well."

241   **Note.** The *Jobaria tiguidensis* individuals previously had specimen numbers beginning MNN,
242 but the Musee National du Niger changed its name to Musée National Boubou Hama and the
243 specimen numbers have changed with it.

244   The breakdown of these complete and near-complete necks is interesting (Figure 2). Non-
245 neosauropods are relatively well represented, both inside and outside of Mamenchisauridae —
246 although it is unfortunate many of these specimens are not well well described in English: two of
247 the ten are of *Jobaria*, for which the cursory summary of Sereno et al. (1999) remains the only
248 published description, and some of the Chinese sauropods are described only in Chinese.

249   Diplodocoids are surprisingly poorly represented, with only a single specimen in each of
250 Dicraeosauridae and Diplodocidae that is complete. Brachiosaurids have absolutely no
251 representation — see below on how unconvincing the neck of *Giraffatitan* is. More advanced
252 titanosauriforms are better represented, but there is still only one with a complete neck,
253 *Futalognkosaurus dukei*. By contrast, the single genus *Camarasaurus* is very well represented,
254 with five specimens of which four are fully complete (though only two of those have been
255 described). Probably this does not indicate a taxon-specific taphonomic signal, but follows from
256 the sheer abundance of *Camarasaurus* specimens — an abundance likely influenced by over-
257 lumping of multiple rather different species into a single genus.

258   It is surprising, though, that the second and third best represented sauropods in museums,
259 *Diplodocus* and *Apatosaurus*, are both barely represented in terms of complete necks. And while
260 the number of complete and nearly-complete necks among somphospondyls, including
261 titanosaurs, is encouraging, it is disappointing that so many of them are not yet described.

262   At the time of writing (21 December 2021), the Paleobiology Database
263   (https://paleobiodb.org/) lists 342 sauropod species. The nine unambiguously complete and
264   articulated necks therefore represent only one in 38 known sauropod species — and recall that
265   even these are mostly "complete" only in the weak sense of preserving some part of each
266   cervical vertebra.

267   As best we can tell, only one sauropod species, *Camarasaurus lentus*, is known from more
268   than a single complete neck. Of the two individuals, CM 11338 is a juvenile and USNM 13786 is
269   a subadult, so the mature morphology is unknown. If we allow necks missing the atlas, then there
270   are also two individuals of *Shunosaurus lii*: ZDM T5401, the subadult holotype, which is
271   missing its atlas; and ZDM T5402, an adult referred specimen whose neck is complete. (These
272   specimens have not been described in English.) With sample sizes this small, it is not possible
273   even in principle to determine whether there is a bimodal distribution in the length of any
274   sauropod's neck.

275   Several well-known sauropod specimens are often thought of as having complete, undamaged
276   necks, but in each case the truth is less clear. I now discuss three important specimens.

Diplodocus carnegii CM 84

278   The Carnegie *Diplodocus* is one of the most recognised dinosaurs in the world: not only is the
279   original specimen, CM 84, on display as a mounted skeleton in the Carnegie Museum in
280   Pittsburgh, but casts are displayed in many other major museums (e.g. the Natural History
281   Museum in London, the Museum für Naturkunde Berlin and the Muséum National d'Histoire
282   Naturelle in Paris.) The neck appears complete in these mounted skeletons, with fifteen cervical
283   vertebrae, and is illustrated as such by Hatcher (1901: plate 8); Figure 3. However, the situation
284   is not as clear as it appears in these exhibits.

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

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

290   Allowing for the missing atlas and axis, Holland concluded only that the cervical count was
291   "at least 13".

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

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

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

302   "In all 41 vertebrae are represented, including 14 cervicals (all but the atlas) […]

303   Assuming that no vertebrae are missing from our series the vertebral formula of
304   *Diplodocus* should now be written as follows: Cervicals, 15 […] The number of
305   cervical vertebrae in *Diplodocus* is definitely fixed at at least 15."

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

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

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

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

324   [The] last (fifteenth) cervical was considerably removed from the succeeding dorsals
325   and less so from the preceding cervicals. Commencing with the next vertebra
326   (cervical fourteen), the direction of the entire cervical series was altered so that it lay
327   with its axis almost at right angles to that of the dorsal series. The cervicals extended
328   in an almost straight line from the fourteenth to the fifth, but there was a considerable
329   gap between cervicals eleven and ten, while the axis and cervicals three, four and
330   five were doubled back under the succeeding vertebrae.

331   This account almost explains why Holland underestimated the number of cervicals: the
332 anteriormost four, lying under more posterior cervicals, had not yet been found. However, if ten
333 cervicals (C6–C15) had been found and the atlas and axis were both missing, Holland
334 (1900:816) would surely have stated "Ten are found in the specimen at the Carnegie Museum,
335 atlas and axis being as yet undiscovered" rather than eleven. Some mystery remains: perhaps
336 Holland was aware of one of the anteriormost four preserved cervicals.

337   Coggeshall's description is somewhat corroborated by Reed's quarry map, which is included
338 as Plate 1 of Hatcher's (1901) monograph (Figure 4). However, the map is in some respects at
339 odds with the description: for example, it shows all 13 vertebrae C2–C14 in a single straight line
340 rather than indicating that C2–C5 were doubled back; and it shows gaps both between C10 and
341 C11 (as stated), and also between C11 and C12 (not mentioned in the text).

342   Regarding the vertebra that might pertain to "a second individual belonging perhaps to a
343 distinct genus", Hatcher (1901:22) explained: "*Eleventh Cervical.*—This vertebra is so unlike
344 either the immediately preceding or succeeding vertebrae that if it had been found isolated it
345 would have been unhesitatingly referred to a different genus. Mr. Coggeshall, however, assures

346 me that it was interlocked with the succeeding, or twelfth cervical." Yet, as noted, the quarry
347 map suggests that there was some distance between C11 and C12, perhaps invalidating
348 Coggeshall's assertion. It is to be lamented that both the map and the description were created
349 some time after the excavation actually took place, by which time memories had evidently
350 become unreliable.

351   In conclusion, *Diplodocus carnegii* most likely had fifteen cervicals, but may have had more
352 (if some vertebrae were not recovered), or maybe fewer (if C11 was misassigned). Furthermore,
353 the anterior cervicals are damaged in a way that is not at all apparent from Hatcher's drawings
354 (plate III) or photographs (plate IV) because they were restored before these illustrations were
355 prepared. As Hatcher (1901:23) noted, "The work of freeing these vertebrae from the matrix and
356 restoring them was for the most part done during my absence in the field. Unfortunately no
357 drawings or photographs were taken prior to the process of restoring with colored plaster." (In
358 the early 20th Century, it was routine to restore damaged fossils in ways that completely
359 obscured the degree of damage: see Figure 5.)

Apatosaurus louisae CM 3018

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

364   The specimen was collected by Earl Douglass in 1909 and 1910, from what was then known
365 as the Carnegie Museum Dinosaur Quarry near Jensen, Utah, and is now Dinosaur National
366 Monument. It was mounted for exhibition in 1913, and somewhat belatedly named the type of a
367 new species in a brief initial description by Holland (1915). He noted that "the specimen consists
368 of a series of vertebrae, complete from the atlas to nearly the end of the tail" and appendicular
369 material; but also that "the cervical vertebrae had been separated from the dorsals and shifted,
370 but the entire series was found articulated in regular order" (p. 143). (Holland's description also
371 mentioned that "a skull, which judging by its location, belongs to the specimen, was found
372 within eleven feet of the atlas. It does not differ greatly in form from the skull which belongs to
373 *Diplodocus*". Had Holland stuck to his guns, *Apatosaurus* could have been restored with its
374 correct skull 63 years before Berman and McIntosh (1978) corrected Marsh's long-standing and
375 influential misapprehension that it had a *Camarasaurus*-like skull.)

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

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

390 from badly crushed originals, and should be used with caution." It is also evident from this plate
391 that most of C5 is also missing, although this is not acknowledged in the text. As noted by
392 Upchurch (2000), the poor condition of the posterior cervical vertebrae, and their replacement by
393 plaster models in the mounted skeleton, compromise the validity of biomechanical modelling
394 based on this specimen, such as that of Stevens and Parrish (1999).

395 In conclusion, while the articulation of the cervical sequence of CM 3018 leaves little doubt
396 that all cervicals are present and in the correct order, the crucial posterior cervicals are largely
397 uninformative.

398 ### *Giraffatitan brancai* MB.R.2181

399 This specimen is the paralectotype of *Giraffatitan brancai* (= "*Brachiosaurus*" *brancai*).
400 Much of the material is incorporated in the mounted skeleton in the atrium of the Museum für
401 Naturkunde Berlin, which remains the largest substantially real mounted skeleton of a terrestrial
402 animal anywhere in the world. (There are larger mounts of sauropods, such as the skeletons of
403 *Patagotitan* at the AMNH and FMNH, but these are casts and sculptures, not real material.)
404 While most of the material of the Berlin brachiosaur mount is real fossil bones, the presacral
405 vertebrae are too heavy and fragile to mount: instead, high quality sculptures are used, and the
406 vertebrae themselves are held in collections.

407 The presacrals in the mount are based on real bones that are from two specimens — the
408 lectotype MB.R.2180 (formerly known as SI) and the paralectotype MB.R.2181 (formerly SII).
409 The former includes cervicals 2–7, an assignment that can be accepted with some confidence if
410 the vertebrae indeed form a sequence because the axis, C2, in sauropods is very distinctive,
411 having a completely different anterior articular surface from all the subsequent cervicals (see e.g.
412 Janensch 1950:figs. 9–16, cf. figs. 17–48.) MB.R.2181 includes cervicals assigned by Janensch
413 to positions 3–13 (although almost all of them are damaged, some very severely).

414 However, the two individuals MB.R.2180 and MB.R.2181 were found together in a single
415 quarry (designated Quarry S). Bones of the two individuals were jumbled up together, with little
416 articulation, as shown in the quarry map, redrawn by Heinrich (1999: figure 16; Figure 6) from
417 an original drawn in the field by Werner Janensch. Any reconstruction — or even assignment of
418 individual vertebrae to one specimen or the other — must be considered provisional.

419 I have previously suggested (Taylor 2009:800–801) that the distinctively high-spined dorsal
420 vertebra usually considered the fourth of MB.R.2181 may not actually belong to that specimen,
421 or even that taxon. Instead, this unusually tall vertebra may belong to an animal more closely
422 resembling the Tendaguru titanosauriform briefly described by Migeod (1931) and which I am in
423 the process of redescribing (Taylor 2005, Taylor in prep at
424 https://github.com/MikeTaylor/palaeo-archbishop/). If this vertebra is indeed not part of
425 MB.R.2181 then the most likely inference is that it is part of MB.R.2180. This would be
426 unfortunate if these two specimens were indeed representatives of different taxa. The smaller and
427 less complete MB.R.2180, rather than the larger, more complete and better known MB.R.2181,
428 is the lectotype (Janensch 1935–1936). Therefore, the ICZN rules dictate that the name
429 *Giraffatitan brancai* would adhere to MB.R.2180, and that a new name would be required for the
430 better-known MB.R.2181. Since this species was thought until relatively recently to be a species
431 of the North American genus *Brachiosaurus* (see Taylor 2009), a further reassignment would
432 mean that this charismatic and iconic specimen would become known by a third different name
433 in not much more than a decade. To avoid this outcome, an ICZN petition may be warranted.

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

> 436 The vertebrae from the 3rd to 15th presacrals [of MB.R.2181] lay in articulation in a
> 437 consolidated lime sandstone lens; of them, the 3rd to 5th vertebrae are tolerably
> 438 complete, the remaining 10 vertebrae were articulated with one another, with one
> 439 interruption that arose when the 8th presacral vertebra rotated out of the series and
> 440 was displaced. [Translation by Gerhard Maier.]

441 Janensch's words are somewhat at odds with the quarry map, which shows cervical material
442 scattered around the northeastern part of the quarry (Figure 6). Other quarry sketches drawn by
443 Janensch, including one reproduced by Heinrich (1999: figure 18), certainly show at least some
444 cervicals having been found in articulation, but it is not clear what the correspondence is between
445 the field numbers on these sketches and subsequently assigned element identifications.

446 So it is possible, though unlikely, that there might have been other displaced cervicals, before
447 or after the one designated "8th", that were not recovered. Neither can we be wholly confident
448 that the anteriormost preserved cervical in the MB.R.2181 series is really C3. Its identification is
449 based on the overlap with vertebrae of MB.R.2180, but we cannot be certain that MB.R.2180 is a
450 member of the same species as MB.R.2181. Perhaps the anteriormost preserved cervical is really
451 C4? Or perhaps some of the "MB.R.2181" cervicals really belong to MB.R.2180. This is not
452 particularly likely, as Janensch pointed out, due to the difference in size between the two
453 specimens — the MB.R.2181 cervical centra are about 30–40% longer than those assigned the
454 same serial position in MB.R.2180. But the size difference cannot be considered a conclusive
455 argument, especially given the uncertainty in serial-position assignments in both specimens.

456 In conclusion: *Giraffatitan brancai* probably had thirteen cervicals, but may have had more,
457 or possibly less; and the neural arches are only known for cervicals 3, 4, 5 and 8 in MB.R.2181
458 (if these are the correct serial positions for those vertebrae). If MB.R.2180 is indeed a member of
459 the same species then cervicals 2–7 are known from well-preserved elements, but no more. All
460 of this uncertainty is exacerbated by the problem that no complete or even nearly complete neck
461 of any other brachiosaur has been described.

462 To summarise this section, not only are complete sauropod necks in very short supply, even
463 those that are considered complete cannot generally be confidently considered so, and
464 complexities of interpretation bedevil the best-known specimens.

465 ## Distortion

466 Even in necks where most or all of the vertebrae are present and largely complete, extensive
467 distortion is common. This is difficult to quantify, even in principle, given the very complex
468 shapes of sauropod cervicals. But we can take tentative steps towards recognising the extent of
469 the problem by considering one simple aspect: the shapes of the cotyles of consecutive vertebrae.

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

476 In extant animals, including birds, crocodilians, lizards and mammals, the articular facets of
477 consecutive vertebrae are of much the same shape, varying only gradually along the neck. In
478 particular, the aspect ratio of the facet — its width:height ratio — remains constant or nearly so
479 (Figures 7–10). However, in the fossilised necks of sauropods, it's not unusual for even
480 consecutive vertebrae to be crushed in opposite directions, giving their cotyles (apparently)
481 wildly different aspect ratios.

482 Consider for example the *Giraffatitan brancai* lectotype MB.R.2180 (formerly HMN SI), one
483 of the best preserved sauropod neck series. Cervicals 4 and 6 of this specimen are shown in
484 posterior view in Figure 11. (The intermediate cervical 5 has part of its cotyle rim broken off,
485 and cannot be reliably measured.) Measuring from the photos, the width:height ratio of C4 (on
486 the left) is 683/722 pixels = 0.95, and that of C6 (on the right) is 1190/820 pixels = 1.45. So
487 these two vertebrae — from the same neck, and with only one other vertebrae coming in between
488 them — differ in preserved cotyle aspect ratio by a factor of 1.53.

489 As a second example, consider the single most studied sauropod neck specimen in the world,
490 that of the *Diplodocus carnegii* holotype CM 84. Figure 12 shows adjacent cervicals 13 and 14,
491 in posterior view. Note that the posterior part of the neck was considered well preserved by
492 Hatcher (1901), with only anterior vertebrae noted as having been damaged. Measuring from
493 Hatcher's photos, the width:height for C14 (on the left) is 342/245 pixels = 1.40. For C13 (on the
494 right), it is 264/256 pixels = 1.03. So C14 is apparently 35% broader than its immediate
495 predecessor.

496 There is no established metric for quantifying change in a measure, such as the aspect ratio of
497 articular surfaces, along a vertebral column. Table 1 offers two candidate metrics and shows how
498 they are worked out for six of the seven specimens discussed in this section. (The cat has too few
499 available vertebrae for the metric to be meaningful.) Using the first metric, average difference
500 between aspect ratios in consecutive vertebrae, the young juvenile giraffe, the monitor lizard, the
501 alligator and the ostrich all score in the range 4.2–6.3, while the two sauropods score 9.1 and
502 16.3. Using the second metric, average ratio between aspect ratios of consecutive vertebrae, the
503 four extant animals score in the range 6.7–8.9, and the sauropods 12.0 and 22.1. It would be
504 useful in future to calculate these metrics for larger sets of extant and fossil vertebrates, and to
505 see whether it is generally the case that the variation metrics are higher for fossils than for extant
506 vertebrates. For now, though, this tentative initial analysis corroborates the "eye-test" conclusion
507 that variation is significantly greater along sauropod necks.

508 It might be argued that variation on cotyle shape in sauropod necks arises from mechanical
509 factors. Since their necks were elongate, segmented cantilevers, they become broader towards
510 their base, and this could be reflected in cotyle shape. However, we would expect mechanical
511 influences such as this to produce gradual monotonic variation — cotyles either becoming
512 consistently broader or consistently taller towards the base of the neck. But this is not what we
513 observe: instead, the preserved aspect ratios of sauropod condyles vary erratically along the
514 neck. Such extreme variation in apparent aspect ratio of the cotyles of adjacent and near-adjacent
515 cervical vertebrae can only be the result of extensive and unpredictable crushing.

516 This variation in preservation of aspect ratios has implications for calculating the elongation
517 index (EI) of vertebrae, a calculated character widely used in phylogenetic analyses and
518 elsewhere. For example, Janensch's (1950:39) table of measurements for the *Giraffatitan*
519 *brancai* lectotype MB.R.2180 (formerly HMN SI) gives the centrum length and cotyle height of

520 C4 as 45.7 and 13.8 cm, for an EI *sensu* Wedel et al. (2000:346) of 3.31. For C6, he gives
521 centrum length and cotyle height as 69.1 and 15.0, for a much greater EI of 4.6. But if the true
522 cotyle proportions of C6 were the same as those of C4, then the cotyle height corresponding to
523 its width of 22.1 would be a much taller 23.1 cm, yielding an EI of only 3.0. Some recent work
524 uses the aEI of Chure et al. (2010), in which the centrum length is divided not by cotyle height,
525 but by the average of cotyle height and width. This goes some way towards mitigating the
526 confounding effects of crushing, but cannot fully allow for its unpredictable effects: for example,
527 oblique crushing may increase both maximum height and width of the cotyle, yielding a
528 misleadingly low aEI. At the very least, we need to be circumspect in our use of elongation
529 indices as phylogenetic characters or ecological correlates.

530   Deformation of the articular cotyle is only one example of the many ways in which sauropod
531 vertebrae, with their complex and fragile anatomy are subject to crushing, It is certain that other
532 parts of the vertebrae, especially the delicate lateral processes and zygapophyseal rami, were also
533 often distorted, and it is generally not possible to reliably restore to their undistorted state.

534   In addition to such distortions of individual processes of vertebrae, systematic distortion of
535 entire vertebrae is common. For example, in CCG V 20401, the holotype specimen of
536 *Mamenchisaurus hochuanensis* for which the neck is complete and articulated, every vertebra of
537 the neck and trunk is sheared and rotated such that the left side is displaced downwards (Taylor
538 2004, personal observation of mounted casts in Copenhagen, Denmark; Trzic, Slovenia; and
539 Chicago, USA). This distortion is illustrated for dorsal vertebra 2 by Young and Zhao
540 (1972:figure 6); although they do not illustrate it for a cervical vertebra, it is present throughout
541 the column.

542   While the *Mamenchisaurus hochuanensis* distortion is very apparent, subtler distortions are
543 ubiquitous but easier to overlook. For example, the *Giraffatitan brancai* holotype cervical
544 vertebrae MB.R.2180 (formerly HMN SI) appear undistorted to the naked eye, but manual
545 articulation of C2 and C3 demonstrates that sufficient distortion has occurred to prevent the
546 bones being posed in ways that the live animal surely could have achieved (Figure 13).

Location of cervicodorsal junction

548   One further issue impedes our ability to analyse and compare the necks of different
549 sauropods, and that is the difficulty of identifying the last cervical vertebra — and therefore of
550 defining how many vertebrae make up the neck (and how many make up the dorsal series). In
551 general it is easy to tell cervical and dorsal vertebrae apart: for example, compare C13 and D3 of
552 the *Diplodocus carnegii* holotype CM 84 (Hatcher 1901:plates III and VII). The cervical vertebra
553 is relatively low, its centrum is elongated, its neural spine is roughly triangular and its
554 parapophysis hangs down below the centrum and has a cervical rib fused to it and the
555 diapophysis (though this latter character is not consistent in sauropods: see below). By contrast,
556 the dorsal vertebra is tall, its centrum is short, its neural spine is anteroposteriorly compressed its
557 parapophysis is up on the dorsal half of the centrum, and no rib is fused to it. But the change in
558 these characters is gradual, and at the transition it is much more difficult to distinguish between
559 cervical and dorsal vertebrae. Compare C15 and D1 of CM 84 (Hatcher 1901:plates III and VII
560 once more). Had Hatcher classified his C15 as the first dorsal, or his D1 as the last cervical, it
561 would not be obvious that this was incorrect. Similarly, Wilson and Upchurch (2009:20) found it
562 difficult to unambiguously identify the first dorsal vertebra even when dealing with the relatively

563   complete and well-preserved presacral sequence of *Euhelpus zdanskyi*.

564   The difficulty of locating the cervicodorsal junction is exacerbated by the lack of a single
565   standard definition. Several exist:

- 566 **Rib fusion.** Hatcher (1901:25) writes "The dorsals are distinguished from the cervicals
567   by supporting free instead of fixed ribs …"

- 568 **Ventral centrum shape.** Hatcher (1901:25–26) continues "… and in having the inferior
569   surface of the centra regularly convex transversely instead of concave in either direction".

- 570 **Scapular support.** In his description of *Haplocanthosaurus* two years later, Hatcher
571   (1903:8) uses a completely different definition: "That [D1] was a dorsal is conclusively
572   shown not by the presence of tubercular and capitular rib facets showing that it supported
573   on either side a free rib […] The character in this vertebra distinguishing it as a dorsal is
574   the broadly expanded external border of the anterior branch of the horizontal lamina [i.e.
575   what we would now call the prezygadiapophyseal lamina …] to give greater surface for
576   the attachment of the powerful muscles necessary for the support of the scapula." (See
577   Figure 14.)

- 578 **Parapophysis location.** Hatcher (1901:16) notes "In the fifth dorsal the capitular facet is
579   on the middle of the neural arch, while in dorsals four and three it has shifted down to the
580   centrum and encroached upon the pleurocentral cavities of these vertebrae. In dorsals two
581   and one it lies wholly inferior to that cavity", and his illustrations show that it is well
582   below the centrum in all cervical vertebrae.

- 583 **Gene expression.** Wilson (2002:226) notes that "the cervicodorsal transition in many
584   tetrapods, for instance, appears to be defined by the expression boundary of the *Hoxc-6*
585   gene".

586   However none of these definitions is wholly satisfactory.

- 587 Rib fusion is not a reliable criterion, as Hatcher (1903:8) notes: "there are in our
588   collections of sauropods, skeletons of other dinosaurs fully adult but, with the posterior
589   cervical, bearing free cervical ribs articulating by both tubercular and capitular facets as
590   do the ribs of the dorsal region". As one example, the *Mamenchisaurus hochuanensis*
591   holotype CCG V 20401 has free ribs on its last three cervicals (Young and Zhao 1972;
592   personal observation). It may be argued that those last three cervicals are really dorsals,
593   but while a case could possibly be made for the last one, the rib shafts of the previous two
594   are much too horizontally oriented to sustain such an interpretation.

- 595 Ventral centrum shape is highly variable between different sauropod taxa — and, as
596   noted above, centra are prone to distortion, though this is probably less prevalent in the
597   relatively robust ventral part of the centrum than in the more fragile cotyle.

- 598 The presence of a scapular support facet on the lateral face of the CPRL is difficult to
599   detect, and evidently not trusted by Hatcher himself as he noted of C15 of *Diplodocus*
600   CM 84 that "the superior of the anterior blades of the horizontal lamina has its external
601   surface somewhat expanded and rugose. It no doubt served as a support for the muscular
602   attachment of the heavy scapular arch" (Hatcher 1901:25).

- 603 While the parapophysis migrates dorsally across the centrum to the arch in successive

604 vertebrae of all sauropods, this migration typically does not commence until after the first
605 dorsal, making it useless to determining the location of the junction.

606 • The genetic definition is obviously useless for fossil organisms.

607 In practice, most workers seem to use a combination of multiple criteria, often not explicitly
608 specified. For example, in considering the dorsal count of *Barosaurus*, McIntosh (2005:45)
609 writes "The eighth presacral [counting forward from the sacrum] is unquestionably a dorsal and
610 the tenth a cervical", but does not explain why he makes these designations. He continues, "But
611 what is the ninth? At first glance it certainly appears to be a cervical — the parapophysis projects
612 from the very bottom of the centrum well below the pleurocoel. However […] neither rib is co-
613 ossified to the parapophyses and diapophyses as in the cervical vertebrae anterior to it. Largely
614 for this reason, I have concluded that it is the first dorsal." Here, McIntosh is making a
615 judgement on the contradictory evidence of the rib-fusion and parapophysis-location criteria,
616 while not using ventral centrum shape (perhaps because the ventral view of the centrum is not
617 available) or scapular-support facets (perhaps due to preservational problems making it
618 impossible to assess). This example is instructive, as it illustrates pervasive difficulties when
619 dealing with bones as large, fragile and difficult to manipulate as sauropod presacrals: very few
620 such bones can be inspected from all cardinal directions, and as noted above distortion and
621 damage is ubiquitous.

622 Perhaps, then, the best we can hope for in identifying the cervicodorsal junction is to use a
623 combination of criteria according to what is available for study in the specimen in question, but
624 to be explicit about which criteria are used. As McIntosh's example demonstrates, this
625 identification is important, as it determines the number of cervical vertebrae deemed to belong to
626 a neck: even in those very rare cases when a presacral vertebral sequence is complete and
627 undistorted, it is still to some degree a matter of judgement how many cervical vertebra
628 constitute the neck.

629 (In some older papers (e.g. Migeod 1931), a "shoulder vertebra" is referenced, an intermediate
630 between the last cervical and the first dorsal, but this terminology is not used in modern
631 literature. However, introducing this concept does not aid the quest for consensus over how the
632 junction is located: the issue simply becomes the problem of locating the shoulder vertebra,
633 rather than locating the first dorsal.)

Discussion

Taphonomic factors

636 All of the problems with sauropod neck preservation arise from the nature of the animals and
637 the general procedures of taphonomy.

638 First, sauropods are big. This is a recipe for incompleteness of preservation: small skeletons
639 are more easily destroyed by taphonomic processes, but if they survive are more easily preserved
640 whole, while large skeletons less rarely survive intact (Brocklehurst et al. 2012). It is no accident
641 that the most completely preserved sauropods are small individuals such as CM 11338, the cow-
642 sized juvenile *Camarasaurus lentus* described by Gilmore (1925). For an organism to be
643 fossilised, it is necessary for the carcass to be swiftly buried in mud, ash or some other substrate.
644 This can happen relatively easily to small animals, such as the many finely preserved small

645 theropods from the Yixian Formation in China, but is much less possible with a large animal
646 (Mannion 2010:284).

647   Cleary et al. (2015:528 and figure 6) showed that medium-sized ichthyosaurs preserve more
648 completely than either small or large individuals, but since these are aquatic animals their
649 preservational context is not applicable to the case of sauropods. Brown et al. (2012) found that
650 in the Dinosaur Park Formation, "large-bodied" dinosaurs preserved more completely than
651 smaller ones, but their sample contained no sauropods, their threshold for "large" was only 60
652 kg, and the largest animals included were 4.5-tonne hadrosaurs. It may be that if the methods of
653 Brown et al. (2012) were used to analyse the sauropod-bearing Morrison or Tendaguru
654 formations, the result would be similar to those of Cleary et al. (2015), with medium-sized
655 animals having the most complete preservation. At a larger scale, Cashmore et al. (2020:963)
656 found only a weak, and weakly significant, correlation between sauropod body mass and
657 specimen completeness ($R^2 = 0.03$; $p = 0.04$), using the SCM2 skeletal completeness metric of
658 Mannion & Upchurch (2010). However, analysis of their figure 5A, plotting log body mass
659 against log completeness shows a rapid falling away in completeness above body masses with
660 log 10 — presumably natural log, representing about 22 tonnes.

661   It is also possible that the light construction of highly pneumatic cervical vertebrae would
662 have rendered them particularly prone to water transport, disarticulating and scrambling the
663 necks of even some otherwise adequately preserved specimens.

664   Except in truly exceptional circumstances, sediments simply are not deposited quickly enough
665 in terrestrial environments to cover a 25 meter, 30 tonne animal with a light neck skeleton before
666 it is broken apart by scavenging, decay and water transport. Fossilisation of the very largest
667 sauropods tends to produce even more fragmentary remains. In light of this, it is not surprising
668 that the very longest sauropod necks are usually known from particularly inadequate specimens.
669 The longest neck for which we have direct evidence is that of the diplodocid *Supersaurus*,
670 possibly 15 m long, but the only cervical material of the largest specimen is a single 1.4 m
671 cervical (BYU 9024, formerly BYU 5003; Jensen 1985, 1987). Similarly, the giant basal
672 titanosauriform *Sauroposeidon* probably had a neck about 11 m long, but the only definite
673 material belonging to it is a sequence of three and a half cervicals from the middle of the neck
674 (OMNH 53062; Wedel et al. 2000). The longest known titanosaur necks are probably those of
675 *Patagotitan*, *Puertasaurus* and *Dreadnoughtus*, all at around 9–10 m, but the cervical material
676 from which they are known is meagre: only three vertebrae in the *Patagotitan* holotype MPEF-
677 PV 3400, of which the longest is 120 cm long (supplementary information to Carballido et al.
678 2007); a single 118 cm *Puertasaurus* vertebra, MPM-PV 10002 (Novas et al. 2005); and a single
679 113 cm vertebra of *Dreadnoughtus* MPM-PV 1156 (Lacovara et al. 2014).

680   Secondly, even when complete sauropod skeletons are preserved, or at least complete necks,
681 distortion of the preserved cervical vertebrae is almost inevitable because of their uniquely
682 fragile construction. As in modern birds, the cervical vertebrae were lightened by extensive
683 pneumatisation, so that they were more air than bone (Taylor and Wedel 2013a: figure 4), with
684 the air-space proportion typically in the region of 60–70% and sometimes reaching as high as
685 89% (Taylor and Wedel 2013a: table 2; Wedel 2005: figure 7.4C). While this construction
686 enabled the vertebrae to withstand great stresses for a given mass of bone, it nevertheless left
687 them prone to crushing, shearing and torsion when removed from their protective layer of soft
688 tissue. For highly pneumatized cervicals in particular, the chance of the shape surviving through
689 taphonomy, fossilisation and subsequent deformation would be tiny.

Possible mitigations

690

691 Some information about sauropods necks that is not directly observable can be inferred from
692 phylogenetic bracketing: the observation that if two close outgroups to an organism of interest
693 both have a feature, then the null hypothesis is that the organism of interest inherited that feature
694 from the common ancestor (see Witmer 1995). For example, the neck of *Sauroposeidon proteles*
695 is known only from a sequence of four vertebrae (Wedel et al 2000). But as a brachiosaurid it is
696 bracketed by *Giraffatitan brancai*, which is thought on reasonable evidence (see above) to have
697 had 13 cervicals, and *Camarasaurus lentus*, which is known from complete specimens to have
698 had 12 cervicals (Gilmore 1925:367). It is therefore parsimonious on this basis to conclude that
699 the most recent common ancestor of *Giraffatitan* and *Camarasaurus* probably had 12–13
700 cervical vertebrae, and that *Sauroposeidon proteles* likewise also had 12–13 cervicals.

701 While this level of inference is better than no information, the present example illustrates
702 three problems with the use of phylogenetic bracketing for sauropod morphology. First, due to
703 incomplete knowledge of most sauropods, it is often necessary to move some way down the tree
704 from the organism of interest before reaching specimens for which morphology is sufficiently
705 known. In this example, while *Giraffatitan* is probably close to *Sauroposeidon*, *Camarasaurus* is
706 some way basal to it — but more closely related brachiosaurids such as *Abydosaurus* and
707 *Europasaurus*, while possessing good cervical material, do not have anything close to a complete
708 neck, and so cannot be used in bracketing. As a result, the *Giraffatitan–Camarasaurus* bracket
709 used in this example is broader than we would wish. Second, the phylogenetic context in which
710 we interpret brackets is not always well established. In the present example, I have been
711 following Wedel et al.'s (2000) referral of *Sauroposeidon* to the clade Brachiosauridae; but if
712 D'Emic and Foreman (2012) are correct in their assessment that *Sauroposeidon* in fact a
713 somphospondylian, then it would be more appropriate to bracket it between *Giraffatitan brancai*
714 and *Euhelopus zdanskyi* — which has 17 cervical vertebrae (Wiman 1929:7), suggesting a
715 significantly higher cervical count of 13–17 for *Sauroposeidon*. Third, in the case of sauropods,
716 the morphology of the bracketing taxa is often not as solidly established as we might wish. In
717 this case, while the cervical counts of *Camarasarus lentus* and *Euhelopus zdanskyi* are well
718 established, that of *Giraffatitan brancai* is less so, as documented above, rendering the cervical-
719 count ranges for *Sauroposeidon* even more uncertain. In conclusion, while phylogenetic
720 bracketing remains a useful tool, it must be used with care.

721 The problem of distortion in individual vertebrae can be addressed to some extent through
722 retrodeformation (e.g. Schlager et al. 2018). This term encompasses a suite of techniques in
723 which mathematical processes are applied to virtual models of fossils in an attempt to restore
724 them to the shape they had before their deformation in matrix. Various methods have been
725 proposed in the literature, largely based on an assumption of symmetry. Most of the early
726 methods were designed for 2D transformations on morphologically simple invertebrate fossils
727 (e.g. Cooper 1990), but more recent developments have yielded methods more capable of
728 handling complex 3D shapes (e.g. the Single Axis Method of Kazhdan et al. 2009). Application
729 of these techniques to sauropod vertebrae has so far been limited, but Tschopp et al. (2013)
730 conducted experiments on cervical vertebrae of the diplodocid *Kaatedocus siberi* using an
731 artificially deformed model of a dodo cervical as a control. They found that while the
732 retrodeformation techniques they tested were capable of restoring symmetry to a deformed
733 vertebra, they often did so at the expense of artificially making the vertebra shorter, broader or
734 thinner than it should be. Surprisingly, they also found that applying the same process twice to a

735   vertebra first made it more robust than the original, then more slender. At this stage it seems that
736   more sophisticated techniques, preserving more aspects of the 3D geometry, will be necessary
737   before retrodeformed sauropod cervicals can be taken at face value.

738   But this does not mean that other strategies cannot help in dealing with distorted material. For
739   example, Hedrick and Dodson (2013) used 3D geometric morphometric techniques to better
740   understand individual and taphonomic variation in a set of 30 skulls representing three nominal
741   species of *Psittacosaurus*. They showed that the apparent morphological variation between these
742   "species" actually represent the results of different taphonomic processes, and that all 30 skulls
743   in fact represent members of the same species. It may be possible to use similar techniques on
744   sauropod vertebrae, although modifications would be required to deal with the additional
745   complexity introduced by serial variation in vertebral morphology.

746   One thing that is apparent in all this is the necessity of careful documentation on how
747   specimens were found, in what states of articulation, in what kinds of matrix, and under what
748   strains: for example, Angielczyk and Sheets (2007) use strain measurements to quantify
749   deformation. These descriptions should where possible be accompanied by quarry maps, and
750   ideally by photos and even 3D models of the excavation — something that is increasingly
751   possible given the unlimited capacity for online supplementary information in many journals.
752   Such additional documentation may not materially increase our understanding of the specimens
753   but does at least make it more explicit what we do and do not know, yielding rigidly defined
754   areas of doubt and uncertainty. Similarly, when fossils are restored, it should be done in such a
755   way that it is apparent what parts of the restored specimen are real bone and which are
756   reconstructed. Happily, modern palaeontologists are much better in all these respects than our
757   predecessors were. Some "golden age" palaeontologists were concerned primarily with what
758   would constitute a spectacular museum mount: it is for this reason that O. C. Marsh had YPM
759   1980, the holotype of *Brontosaurus excelsus*, so enthusiastically "restored" that it is now
760   impossible to determine which parts of the cervical vertebrae are real (pers. obs., Barbour 1890).
761   But these days are mostly behind us, and nearly all modern specimens are prepared in a form that
762   accurately conveys what was actually preserved.

763   **Implications**

764   Both the incompleteness and distortion of sauropod necks have grave consequences for our
765   ability to reason about sauropods. As noted above, the very small sample of complete necks
766   makes it quite impossible to perform meaningful statistical analyses. This incomplete
767   information also impedes our ability to understand the evolution of sauropod necks, making it
768   difficult to determine the plesiomorphic cervical morphology and vertebral counts at the bases of
769   clades. Similarly, the frequent, unpredictable and sometimes dramatic distortion of what
770   vertebrae we do have renders mechanical analysis of neutral poses and ranges of motion
771   extremely problematic. For vertebrae small and robust enough to be manipulated by hand, this
772   can be readily observed in physical space (Figure 13). There is no reason to think that computer
773   modelling of vertebrae and their articulations (e.g. Stevens and Parrish 1999) should yield
774   models any more informative than the distorted fossils that they are based on.

775   On a more positive note, the lack of complete necks does not mean that we are without
776   information. For many sauropods that lack complete necks, enough vertebrae are preserved with
777   enough fidelity that we can have a good idea how morphology varies between anterior, middle
778   and posterior cervicals, even if precise identification of the vertebrae is not possible. Crucially,

779 this degree of completeness suffices for the majority of characters to be scored in phylogenetic
780 analyses: apart from a few characters specific to the atlas or axis, most such characters pertain
781 only to anterior, middle or posterior cervicals.

782 Conclusion

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

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

794 None of this is necessarily disastrous, so long as we properly acknowledge the degree of
795 uncertainty that afflicts our work. Problems arise when studies such as that of Stevens and
796 Parrish (1999) draw apparently firm conclusions about sauropod neck posture based on
797 specimens that are deficient in respects not acknowledged in the text, lending the results a veneer
798 of definitiveness that they do not merit.

799 Acknowledgments

800 An earlier version of this manuscript was reviewed in 2015 by Paul Barrett, Paul Upchurch
801 and Jeffrey Wilson; the present version was reviewed by Oliver Rauhut, Paul Upchurch (again)
802 and Veronica Diez-Diaz. This final version is much stronger for having been updated in response
803 to their comments. I also thank Brandon Hedrick for his editorial handing of the manuscript, and
804 my wife, Fiona, for motivating me to finally get the revisions done on this long overdue paper.

805 After the first version of this manuscript was published as a preprint, numerous people
806 reminded me of additional complete and near-complete sauropod necks. These include (in
807 alphabetical order) Lee Braithwaite, John D'Angelo, Vahe Demirjian, Oliver Demuth, Daniel
808 Gonçalves, Stephen Gunnell, Rutger Jansma, Matt Lamanna, Stefan Reiss, Emmanuel Tschopp,
809 Justin Tweet and Paul Upchurch.

810 I thank Jorge O. Calvo, Paul C. Sereno, Leonardo S. Filippi, Rodolfo A. Coria, Kristian
811 Remes, Ralf Kosma, Jose I. Canudo and Stephen F. Poropat for permission to cite personal
812 communications.

813 I thank Mathew J. Wedel for his observations on the phylogenetic distribution of complete
814 and near-complete necks, and for providing the juvenile alligator neck illustrated in Figure 8.
815 Matt Cobley provided the ostrich neck illustrated in Figure 7. Andrew Moore supplied
816 photographs of the neck of the *Camarasaurus lentus* specimen USNM 13786. Daniela Schwarz
817 provided high-resolution scans of Werner Janensch's site maps of "Quarry S", where important
818 *Giraffatitan* material was found. Gerhardt Maier provided the translation of Janensch (1950).
819 This translation, and others that I referred to, are freely available from the Polyglot

820   Paleontologist web-site at http://paleoglot.org/

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

824   References

825   Angielczyk, Kenneth D., and H. David Sheets. 2007. Investigation of simulated tectonic
826   deformation in fossils using geometric morphometrics. *Paleobiology* **33(1)**:125–148.
827   doi:10.1666/06007.1

828   Barbour, Erwin H. 1890. Scientific News: 5. Notes on the Paleontological Laboratory of the
829   United States Geological Survey under Professor Marsh. *The American Naturalist*
830   **24(280)**:388–400.

831   Berman, David S., and John S. McIntosh. 1978. Skull and relationships of the Upper Jurassic
832   sauropod *Apatosaurus* (Reptilia, Saurischia). *Bulletin of the Carnegie Museum* **8**. 35 pages.

833   Brocklehurst, Neil, Paul Upchurch, Philip D. Mannion and Jingmai O'Connor. 2012. The
834   completeness of the fossil record of Mesozoic birds: implications for early avian evolution.
835   *PLOS ONE* **7(6)**:e39056. doi:10.1371/journal.pone.0039056

836   Brown, Caleb M., David C. Evans, Nicolás E. Campione, Lorna J. O'Brien and David A. Eberth.
837   2012. Evidence for taphonomic size bias in the Dinosaur Park Formation (Campanian,
838   Alberta), a model Mesozoic terrestrial alluvial-paralic system. *Palaeogeography,*
839   *Palaeoclimatology, Palaeoecology* **372**:108–122. doi:10.1016/j.palaeo.2012.06.027

840   Calvo, Jorge O., Rodolfo. A. Coria, and Leonardo Salgado. 1997. Uno de los más completos
841   titanosáuridos (Dinosauria-Sauropoda) registrados en el mundo [One of the most complete
842   titanosaurids (Dinosauria-Sauropoda) recorded in the world]. *Ameghiniana* **34**:534.

843   Calvo, Jorge O., Juan D. Porfiri, Bernardo J. González-Riga and Alexander W. A. Kellner.
844   2007a. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new
845   sauropod dinosaur. *Anais da Academia Brasileira de Ciências* **79(3)**:529–541.

846   Calvo, Jorge O., Juan D. Porfiri, Bernardo J. González Riga and Alexander W. A. Kellner.
847   2007b. Anatomy of *Futalognkosaurus dukei* Calvo, Porfiri, González Riga & Kellner, 2007
848   (Dinosauria, Titanosauridae) from the Neuquén Group (Late Cretaceous), Patagonia,
849   Argentina. *Arquivos do Museu Nacional, Rio de Janeiro* **65(4)**:511–526.

850   Canudo, José, Jose Carballido, Alberto Garrido and Leonardo Salgado. 2018. A new
851   rebbachisaurid sauropod from the Aptian–Albian, Lower Cretaceous Rayoso Formation,
852   Neuquén, Argentina. *Acta Palaeontologica Polonica* **63(4)**:679–691.
853   doi:10.4202/app.00524.2018. ISSN 0567-7920.

854   Carballido, José L., Diego Pol, Alejandro Otero, Ignacio A. Cerda, Leonardo Salgado, Alberto C.
855   Garrido, Jahandar Ramezani, Néstor R. Cúneo, and Javier M. Krause. 2007. A new giant
856   titanosaur sheds light on body mass evolution among sauropod dinosaurs. *Proceedings of the*
857   *Royal Society B*. doi:10.1098/rspb.2017.1219

858   Cashmore, Daniel D., Philip D. Mannion, Paul Upchurch and Richard J. Butler. 2020. Ten more
859   years of discovery: revisiting the quality of the sauropodomorph dinosaur fossil record.

860   *Palaeontology* **63(6)**:951–978. doi:10.1111/pala.12496

861   Chure, Daniel, Brooks B. Britt, John A. Whitlock and Jeffrey A. Wilson. 2010. First complete
862   sauropod dinosaur skull from the Cretaceous of the Americas and the evolution of sauropod
863   dentition. *Naturwissenschaften* **97(4)**:379–91. doi:10.1007/s00114-010-0650-6

864   Cleary, Terri J., Benjamin C. Moon, Alexander M. Dunhill and Michael J. Benton. 2015. The
865   fossil record of ichthyosaurs, completeness metrics and sampling biases. *Palaeontology*
866   **58(3)**:521–536. doi:10.1111/pala.12158

867   Cooper, R. A. 1990. Interpretation of tectonically deformed fossils. *New Zealand Journal of*
868   *Geology and Geophysics* **33(2)**:321–332.

869   Coria, Rodolfo A., and Leonardo Salgado. 1999. Nuevos aportes a la anatomía craneana de los
870   saurópodos titanosáuridos [New reports on the cranial anatomy of titanosaurid sauropods].
871   *Ameghiniana* **36**:98.

872   D'Emic, Michael D., and Brady Z. Foreman. 2012. The beginning of the sauropod dinosaur
873   hiatus in North America: insights from the Lower Cretaceous Cloverly Formation of
874   Wyoming. *Journal of Vertebrate Paleontology* **32(4)**:883–902.
875   doi:10.1080/02724634.2012.671204

876   Filippi, Leonardo. S., Rubén D. Juárez Valieri, Pablo A. Gallina, Ariel H. Méndez, Federico A.
877   Gianechini and Alberto C. Garrido. 2016. A new titanosaur specimen with highly derived
878   skull from the Santonian of northern Patagonia, Argentina. 11° Congreso de la Asociación
879   Paleontológica Argentina, Gral. Roca, Río Negro, Argentina.

880   Gilmore, Charles W. 1925. A nearly complete articulated skeleton of *Camarasaurus*, a
881   saurischian dinosaur from the Dinosaur National Monument, Utah. *Memoirs of the Carnegie*
882   *Museum* **10**:347–384 and plates XIII–XVII.

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

885   Gomani, Elizabeth M. 2005. Sauropod dinosaurs from the Early Cretaceous of Malawi, Africa.
886   *Palaeontologia Electronica* **8(1)**:27A (37 pp.)

887   Hatcher, Jonathan B. 1900. Vertebral formula of *Diplodocus* (Marsh). *Science* **12**:828–830.
888   doi:10.1126/science.12.309.828

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

891   Hatcher, J. B. 1903. Osteology of *Haplocanthosaurus* with description of a new species, and
892   remarks on the probable habits of the Sauropoda and the age and origin of the Atlantosaurus
893   beds; additional remarks on *Diplodocus*. *Memoirs of the Carnegie Museum* **2**:1–75 and plates
894   I–VI.

895   He Xinlu, Li Kui and Cai Kaiji. 1988. The Middle Jurassic dinosaur fauna from Dashanpu,
896   Zigong, Sichuan, vol. IV: sauropod dinosaurs (2): *Omeisaurus tianfuensis*. Sichuan
897   Publishing House of Science and Technology, Chengdu, China. 143 pp. + 20 plates.

898   Heinrich, Wolf-Dieter. 1999. The taphonomy of dinosaurs from the Upper Jurassic of
899   Tendaguru, Tanzania (East Africa), based on field sketches of the German Tendaguru

900   expedition (1909–1913). *Mitteilungen aus dem Museum für Naturkunde in Berlin,*
901   *Geowissenschaftliche Reihe* **2**:25–61.

902   Hedrick, Brandon P., and Peter Dodson. 2013. Lujiatun psittacosaurids: understanding individual
903   and taphonomic variation using 3D geometric morphometrics. *PLOS ONE* **8(8)**:e69265.
904   doi:10.1371/journal.pone.0069265

905   Holland, W. J. 1900. The vertebral formula in *Diplodocus*, Marsh. *Science* **11**:816–818.

906   Holland, William. J. 1915. A new species of *Apatosaurus*. *Annals of the Carnegie Museum*
907   **10**:143–145.

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

910   Janensch, Werner. 1935–1936. Die Schadel der Sauropoden *Brachiosaurus*, *Barosaurus* und
911   *Dicraeosaurus* aus den Tendaguru-Schichten Deutsch-Ostafrikas. *Palaeontographica* (Suppl.
912   7) **2**:147–298 and plates IX–XIII.

913   Janensch, Werner. 1950. Die Wirbelsaule von *Brachiosaurus brancai*. *Palaeontographica*
914   (Suppl. 7) **3**:27–93 and plates I–V. English translation at
915   http://www.paleoglot.org/files/Janensch%2050.pdf

916   Jensen, James A. 1985. Three new sauropod dinosaurs from the Upper Jurassic of Colorado.
917   *Great Basin Naturalist* **45(4)**:697–709.

918   Jensen, James A. 1987. New brachiosaur material from the Late Jurassic of Utah and Colorado.
919   *Great Basin Naturalist* **47(4)**:592–608.

920   Jensen, James A. 1988. A fourth new sauropod dinosaur from the Upper Jurassic of the Colorado
921   Plateau and sauropod bipedalism. *Great Basin Naturalist* **48(2)**:121–145.

922   Kazhdan, Misha, Nina Amenta, Shengyin Gu, David F. Wiley and Bernd Hamann. 2009. 21st
923   Canadian Conference on Computational Geometry, Vancouver, British Columbia, Canada. 4
924   pages, unpaginated.

925   Lacovara, Kenneth J, Matthew C. Lamanna, Lucio M. Ibiricu, Jason C. Poole, Elena R.
926   Schroeter, Paul V. Ullmann, Kristyn K. Voegele, Zachary M. Boles, Aja M. Carter, Emma K.
927   Fowler, Victoria M. Egerton, Alison E. Moyer, Christopher L. Coughenour, Jason P. Schein,
928   Jerald D. Harris, Rubén D. Martínez and Fernando E. Novas. 2014. A gigantic, exceptionally
929   complete titanosaurian sauropod dinosaur from Southern Patagonia, Argentina. *Scientific*
930   *Reports* **4(6196)**. doi:10.1038/srep06196

931   Lull, Richard S. 1930. Skeleton of *Camarasaurus lentus* recently mounted at Yale. *American*
932   *Journal of Science*, 5th series, **19(109)**:1–5.

933   Mannion, Philip David. 2010. Environmental and geological controls on the diversity and
934   distribution of the Sauropodomorpha. Ph.D dissertation, University College London. 349
935   pages.

936   Mannion, Philip D., and Paul Upchurch. 2010. Completeness metrics and the quality of the
937   sauropodomorph fossil record through geological and historical time. *Paleobiology* 36:283–
938   302. doi:10.1666/09008.1

939   McIntosh, John S. 2005. The genus *Barosaurus* Marsh (Sauropoda, Diplodocidae). pp. 38–77 in:

940   Virginia Tidwell and Ken Carpenter (eds.), *Thunder Lizards: the Sauropodomorph*
941   *Dinosaurs*. Indiana University Press, Bloomington, Indiana. 495 pp.

942 McIntosh, John S., Wade E. Miller, Kenneth L. Stadtman and David D. Gillette. 1996. The
943   osteology of *Camarasaurus lewisi* (Jensen, 1988). *BYU Geology Studies* **41**:73–115.

944 Migeod, Frederick W. H. 1931. British Museum East Africa Expedition: account of the work
945   done in 1930. *Natural History Magazine* **3(19)**:87–103.

946 Novas, Fernando E., Leonardo Salgado, Jorge Calvo and Federico Agnolin. 2005. Giant
947   titanosaur (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia. *Revista del Museo*
948   *Argentino de Ciencias Naturales*, new series **7(1)**:37–41.

949 Osborn, Henry Fairfield, and Charles C. Mook. 1921. *Camarasaurus*, *Amphicoelias* and other
950   sauropods of Cope. *Memoirs of the American Museum of Natural History*, n.s. **3**:247–387,
951   and plates LX–LXXXV.

952 Ouyang Hui and Ye Yong. 2002. The first mamenchisaurian skeleton with complete skull:
953   *Mamenchisaurus youngi*. 111 pages and 20 plates. Sichuan Science and Technology Press,
954   Chengdu.

955 Poropat, Stephen F., Philip D. Mannion, Paul Upchurch and David A. Elliott. 2019. New
956   sauropod dinosaur discoveries in the lower Upper Cretaceous Winton Formation
957   (Cenomanian–Lower Turonian) of Queensland, Australia: implications for titanosaurian
958   evolution. Society of Vertebrate Paleontology, *Program and Abstracts, 2019*:171–172.

959 Powell, Jaime E. 2003. Revision of South American Titanosaurid dinosaurs: palaeobiological,
960   palaeobiogeographical and phylogenetic aspects. *Records of the Queen Victoria Museum*
961   **111**:1–94.

962 Remes, Kristian, Francisco Ortega, Ignacio Fierro, Ulrich Joger, Ralf Kosma, Jose Manuel Marin
963   Ferrer, for the Project PALDES, for the Niger Project SNHM, Oumarou Amadou Ide, and
964   Abdoulaye Maga. 2009. A new basal sauropod dinosaur from the Middle Jurassic of Niger
965   and the early evolution of Sauropoda. *PLOS ONE* **4(9)**:e6924.
966   doi:10.1371/journal.pone.0006924

967 Riggs, Elmer S. 1904. Structure and relationships of opisthocoelian dinosaurs. Part II, the
968   Brachiosauridae. *Field Columbian Museum, Geological Series* **2(6)**:229–247 and plates
969   LXXI–LXXV.

970 Salgado, Leonardo, and José F. Bonaparte. 1991. Un nuevo sauropodo Dicraeosauridae,
971   *Amargasaurus cazaui* gen. et sp. nov., de la Formacion La Amarga, Neocomiano de la
972   Provincia del Neuquén, Argentina [*Amargasaurus cazaui* gen. et sp. nov. from the Late
973   Neocomian beds of La Amarga Formation of the Neuquén Basin, Argentina]. *Ameghiniana*
974   **28(3–4)**:333–346.

975 Schlager, Sterfan, Antonio Profico, Fabio Di Vincenzo and Giorgio Manzi. 2018.
976   Retrodeformation of fossil specimens based on 3D bilateral semi-landmarks: Implementation
977   in the R package "Morpho". *PLOS ONE* **13(3)**:e0194073. doi:10.1371/journal.pone.0194073

978 Sereno, Paul C., Allison L. Beck, Didier. B. Dutheil, Hans C. E. Larsson, Gabrielle. H. Lyon,
979   Bourahima Moussa, Rudyard W. Sadleir, Christian A. Sidor, David J. Varricchio, Gregory P.
980   Wilson and Jeffrey A. Wilson. 1999. Cretaceous sauropods from the Sahara and the uneven

981   rate of skeletal evolution among dinosaurs. *Science* **282**:1342–1347.

982   Stevens, Kent A., and J. Michael Parrish. 1999. Neck posture and feeding habits of two Jurassic
983   sauropod dinosaurs. *Science* **284**:798–800. doi: 10.1126/science.284.5415.798

984   Taylor, Michael P. 2004. The Copenhagen *Mamenchisaurus* (photographs with commentary).
985   http://www.miketaylor.org.uk/dino/mamenchi/ accessed on 28 May 2021. Archived at
986   https://web.archive.org/web/20210528083543/http://www.miketaylor.org.uk/dino/mamenchi/

987   Taylor, Michael P. 2005. Sweet seventy-five and never been kissed: the Natural History
988   Museum's Tendaguru brachiosaur. p. 25 in Paul M. Barrett (ed.), *Abstracts volume for 53rd*
989   *Symposium of Vertebrate Palaeontology and Comparative Anatomy, The Natural History*
990   *Museum, London, 7th–9th September 2005*. 41 pp. Slides at
991   http://www.miketaylor.org.uk/dino/pubs/svpca2005/Taylor2005-tendaguru-brachiosaur.ppt

992   Taylor, Michael P. 2009. A re-evaluation of *Brachiosaurus altithorax* Riggs 1903 (Dinosauria,
993   Sauropoda) and its generic separation from *Giraffatitan brancai* (Janensch 1914). *Journal of*
994   *Vertebrate Paleontology* **29(3)**:787–806.

995   Taylor Michael P. 2011. How long was the neck of *Diplodocus*? Blog post on *Sauropod*
996   *Vertebra Picture of the Week*, 19 May 2011. http://svpow.com/2011/05/19/how-long-was-the-
997   neck-of-diplodocus/. Archived at http://www.webcitation.org/6c312pREN on 5 October 2015.

998   Taylor Michael P. 2013. Measuring the elongation of vertebrae. Blog post on *Sauropod Vertebra*
999   *Picture of the Week*, 20 September 2013. http://svpow.com/2013/09/20/measuring-the-
1000   elongation-of-vertebrae/. Archived at http://www.webcitation.org/6c31BeoTd on 5 October
1001   2015.

1002   Taylor Michael P. 2014. The Field Museum's photo-archives tumblr, featuring: airbrushing
1003   dorsals. Blog post on *Sauropod Vertebra Picture of the Week*, 4 June 2014.
1004   http://svpow.com/2014/06/04/the-field-museums-photo-archives-tumblr-featuring-
1005   airbrushing-dorsals/. Archived at http://www.webcitation.org/6c31Hh5Xb on 5 October 2015.

1006   Taylor Michael P., and Mathew J. Wedel. 2011. Sauropod necks: how much do we really know?.
1007   p. 20 in Richard Forrest (ed.), *Abstracts of Presentations, 59th Annual Symposium of*
1008   *Vertebrate Palaeontology and Comparative Anatomy, Lyme Regis, Dorset, UK, September*
1009   *12th–17th 2011*. 37 pp. Slides at
1010   http://www.miketaylor.org.uk/dino/pubs/svpca2011/TaylorWedel2011-what-do-we-really-
1011   know.ppt

1012   Taylor, Michael P., and Mathew J. Wedel. 2013a. Why sauropods had long necks; and why
1013   giraffes have short necks. *PeerJ* **1:e36**. 41 pages. doi:10.7717/peerj.36

1014   Taylor, Michael P., and Mathew J. Wedel. 2013b. The effect of intervertebral cartilage on neutral
1015   posture and range of motion in the necks of sauropod dinosaurs. *PLOS ONE* **8(10)**:e78214. 17
1016   pages. doi:10.1371/journal.pone.0078214

1017   Taylor, Michael P., David W. E. Hone, Mathew J. Wedel and Darren Naish. 2011. The long
1018   necks of sauropods did not evolve primarily through sexual selection. *Journal of Zoology*
1019   **285(2)**:150–161. doi:10.1111/j.1469-7998.2011.00824.x

1020   Tschopp, Emanuel, and Octávio Mateus. 2012. The skull and neck of a new flagellicaudatan
1021   sauropod from the Morrison Formation and its implication for the evolution and ontogeny of

1022   diplodocid dinosaurs. *Journal of Systematic Palaeontology* **11(7)**:853–888.
1023   doi:10.1080/14772019.2012.746589

1024   Tschopp, Emanuel, João Russo and Gordon Dzemski. 2013. Retrodeformation as a test for the
1025   validity of phylogenetic characters: an example from diplodocid sauropod vertebrae.
1026   *Palaeontologia Electronica* **16(1)**:2T. 23 pages.

1027   Tschopp, Emanuel, Oliver Wings, Thomas Frauenfelder, and Bruce M. Rothschild. 2016.
1028   Pathological phalanges in a camarasaurid dinosaur and implications on behaviour. *Acta
1029   Palaeontologica Polonica* **61(1)**:125–134. doi:10.4202/app.00119.2014

1030   Upchurch, Paul. 2000. Neck posture of sauropod dinosaurs [response to Stevens and Parrish
1031   1999]. *Science* **287**:547b. doi:10.1126/science.287.5453.547b

1032   Wedel, Mathew J. 2005. Postcranial skeletal pneumaticity in sauropods and its implications for
1033   mass estimates. pp. 201–228 in J. A. Wilson and K. Curry-Rogers (eds.), *The Sauropods:
1034   Evolution and Paleobiology*. University of California Press, Berkeley.

1035   Wedel, Mathew J, Richard L. Cifelli and R. Kent Sanders. 2000. Osteology, paleobiology, and
1036   relationships of the sauropod dinosaur *Sauroposeidon*. *Acta Palaeontologica Polonica*
1037   **45**:343–388.

1038   Wilson, Jeffrey A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis.
1039   *Zoological Journal of the Linnean Society* **136**:217–276.

1040   Wilson, Jeffrey A. 2012. New vertebral laminae and patterns of serial variation in vertebral
1041   laminae of sauropod dinosaurs. *Contributions from the Museum of Paleontology, University
1042   of Michigan* **32(7)**:91–110. http://hdl.handle.net/2027.42/92460

1043   Wilson, Jeffrey A. and Paul Upchurch. 2009. Redescription and reassessment of the phylogenetic
1044   affinities of *Euhelopus zdanskyi* (Dinosauria — Sauropoda) from the Early Cretaceous of
1045   China. *Journal of Systematic Palaeontology* **7**:199–239. doi:10.1017/S1477201908002691

1046   Wiman, Carl. 1929. Die Kreide-Dinosaurier aus Shantung. [The Cretaceous dinosaurs of
1047   Shantung]. *Palaeontologia Sinica* Series C, **6**:1–67.

1048   Witmer, Lawrence M. 1995.The extant phylogenetic bracket and the importance of
1049   reconstructing soft tissues in fossils. pp: 19–33 in: J. J. Thomason (ed)., *Functional
1050   Morphology in Vertebrate Paleontology*. Cambridge University Press, New York.

1051   Wu Wen-hao, Zhou Chang-Fu, Oliver Wings, Toru Sekiya and Dong Zhi-ming. 2013. A new
1052   gigantic sauropod dinosaur from the Middle Jurassic of Shanshan, Xinjiang [in Chinese].
1053   *Global Geology* **32(3)**:437–446. doi:10.3969/j.issn.1004-5589.2013.03.002.

1054   Xing Lida, Tetsuto Miyashita, Jianping Zhang, Daqing Li, Yong Ye, Toru Sekiya, Fengping
1055   Wang and Philip J. Currie. 2015. A new sauropod dinosaur from the Late Jurassic of China
1056   and the diversity, distribution, and relationships of mamenchisaurids. *Journal of Vertebrate
1057   Paleontology* **35**, e889701. doi:10.1080/02724634.2014.889701

1058   Young, Chung-Chien, and X. Zhao. 1972. [Chinese title. Paper is a description of the type
1059   material of *Mamenchisaurus hochuanensis*]. *Institute of Vertebrate Paleontology and
1060   Paleoanthropology Monograph Series I*, **8**:1–30.

1061   Zhang Yihong. 1988. The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan, vol.

1062   1: sauropod dinosaur (I): *Shunosaurus*. Sichuan Publishing House of Science and Technology,
1063   Chengdu, China.

1064 Zhang Yihong, Yang Daihuan and Peng Guangchao. 1984. New material of *Shunosaurus* from
1065   Middle Jurassic of Dashanpu, Zigong, Sichuan. *Journal of Chengdu College of Geology*
1066   supplement 2:1–12 and plates I–II.

1067 Zhang, Xiao-Qin, Li Da-Qing, Xied Yan and You Hai-Lu. 2018. Redescription of the cervical
1068   vertebrae of the mamenchisaurid sauropod *Xinjiangtitan shanshanesis* Wu et al. 2013.
1069   *Historical Biology* **32(6)**:803–822. doi:10.1080/08912963.2018.1539970

Table Captions

1071 **Table 1.** Serial variation in preserved aspect ratios of consecutive cervical vertebrae in extant
1072   animals and sauropods from several major amniote clades. Mammalia: giraffe *Giraffa*
1073   *camelopardalis*, young juvenile specimen, C2–C7. Lacertilia: savannah monitor, *Varanus*
1074   *exanthematicus*, C3–C7. Crocodylia: alligator *Alligator mississippiensis*, juvenile specimen,
1075   C5–D2; Aves: ostrich *Struthio camelus*. C5–C11. Sauropoda: *Diplodocus carnegii* holotype
1076   CM84 and *Giraffatitan brancai* lectotype MN.R.2180 (formerly HMN SI). **Vertical** and
1077   **horizontal** columns contain measurements of the posterior articular surfaces of the vertebrae,
1078   except for the procoelous alligator vertebrae for which anterior articular surface was used. For
1079   the saddle-shaped ostrich cervicals, the maximum height and width of the posterior articular
1080   surface was used, rather than the shorter midline distances. Measurements are in arbitrary
1081   units (e.g. mm or pixels in a photograph) but consistent within any one specimen. **V/H** is the
1082   aspect ratio of the measured surface, the ratio of the vertical and horizontal measurements, so
1083   that values less than 1.0 indicate a surface wider than tall, and values greater than 1.0 indicate
1084   a surface taller than wide. Note that this ratio is independent of the measurement units. **1st**
1085   **diff** measures the absolute value of the difference between the V/H ratios of each vertebra and
1086   its successor. **Max diff** is the highest value of 1st diff for each specimen, and **Avg diff** is the
1087   average value; **×100** is this value times 100, a measure of the serial variation along the
1088   column. **1st ratio** is the "absolute ratio" of the V/H values of one vertebra and its successor,
1089   normalized so that when the ratio is less than 1.0 its inverse is used. **Max ratio** is the highest
1090   value of 1st ratio for each specimen, and **Avg ratio** is the average value; **–1×100** is this value
1091   minus one, multiplied by 100, another measure of the serial variation along the column. Note
1092   that by both measures, the variation is articular surface aspect ratios is greater in the two
1093   sauropods than in any of the extant animals, even though these are among the best preserved
1094   sauropod necks.

Figure Captions

1096 **Figure 1.** *Spinophorosaurus nigerensis* holotype GCP-CV-4229 in situ during excavation in the
1097   region of Aderbissinat, Thirozerine Dept., Agadez Region, Republic of Niger. Reproduced
1098   from Remes et al. (2009: figure 1).

1099 **Figure 2**. Simplified phylogeny of Sauropoda, showing counts of complete and near-complete
1100   necks. Captions: **C**, complete and described; **U**, complete but undescribed; **–1**, missing the
1101   atlas but otherwise complete; **O**, other near-complete necks (see text for details); **T**, total.

1102 **Figure 3.** Neck of *Diplodocus carnegii* holotype CM 84, as reconstructed by Hatcher (1901:

1103   plate XIII), with fifteen undamaged cervical vertebrae.

1104   **Figure 4.** W. H. Reed's diagram of Quarry C near Camp Carnegie on Sheep Creek, in Albany
1105   County, Wyoming. The coloured bones belong to CM 84, the holotype of *Diplodocus*
1106   *carnegii*; other bones belong to other individuals, chiefly of *Brontosaurus*, *Camarasaurus* and
1107   *Stegosaurus*. Modified (cropped and coloured) from Hatcher (1901: plate I). Cervical
1108   vertebrae are purple (and greatly simplified in outline by Reed), dorsals are red, the sacrum is
1109   orange, caudals are yellow, limb girdle elements are blue, and limb bones are green.

1110   **Figure 5.** Three images of presacral vertebra 6 (probably dorsal 7) of *Brachiosaurus altithorax*
1111   holotype FMNH P25107, in right lateral view, showing misleading restoration. **Left:** Field
1112   Museum photograph CSGEO16166, photographer Charles Carpenter, taken in 1905, the year
1113   after Riggs's (1904) descriptive monograph. Note the "crazy-paving" effect of the many
1114   cracks and missing areas of bone surface. **Middle:** Illustration of the same vertebra in Riggs
1115   (1904: plate LXXII). Note that the damage to the vertebral surface is not depicted. **Right:**
1116   photograph of the same vertebra, taken by the author in 2005. Note that the damage apparent
1117   in the 1905 photograph is no longer visible: the vertebra seems to have been painted to
1118   conceal its incompleteness.

1119   **Figure 6.** Quarry map of Tendaguru Site S, Tanzania, showing incomplete and jumbled
1120   skeletons of *Giraffatitan brancai* specimens MB.R.2180 (the lectotype, formerly HMN SI)
1121   and MB.R.2181 (the paralectotype, formerly HMN SII). Cervical material is highlighted in
1122   strong yellow, while the remaining elements are desaturated. Anatomical identifications of
1123   MB.R.2181 are underlined. Elements of MB.R.2180 could not be identified on the map with
1124   certainty. Modified from Heinrich (1999: figure 16), which was itself redrawn by Heinrich
1125   from an original field sketch by Werner Janensch. Heinrich's version Copyright Wiley-VCH
1126   Verlag GmbH & Co. KGaA. Reproduced with permission.

1127   **Figure 7.** Cervical vertebrae 5–11 of an ostrich, *Struthio camelus*, in posterior view, showing
1128   that articular facet shape remains similar along the column. Specimen kindly provided by
1129   Matt Cobley.

1130   **Figure 8.** Cervical and dorsal vertebrae (C5–9 and D1–2) of a juvenile alligator, *Alligator*
1131   *mississippiensis*, in anterior view, showing that articular facet shape remains similar along the
1132   column. Specimen kindly provided by Matthew J. Wedel.

1133   **Figure 9.** Sequences of cervical vertebrae of extant animals, showing that articular facet shape
1134   remains similar along the column. **Top.** Cervical vertebrae 3–7 of a mature savannah monitor
1135   lizard, *Varanus exanthematicus*, in anterior view. (The cervicals of monitor lizards, unlike
1136   those of sauropods and most mammals, are procoelous, with the anterior facet being concave
1137   and the posterior convex.) **Bottom.** cervical vertebrae 2–5 of a mature house-cat, *Felis catus*,
1138   in posterior view.

1139   **Figure 10.** Cervical vertebrae of a baby giraffe, *Giraffa camelopardalis*, in posterior view,
1140   showing that articular facet shape remains similar along the column. Top row, left to right:
1141   cervicals 7, 6 and 5; bottom row, left to right: cervicals 4, 3 and 2. Despite changes in the
1142   vertebrae along the column, the flattened inverted pentagon shape of the articular facets
1143   remains similar along the sequence. (Note that extensive cartilage caps existed on the articular
1144   facets of this very young specimen, but were lost in preparation.)

1145   **Figure 11.** Cervical vertebrae 4 (left) and 6 (right) of *Giraffatitan brancai* lectotype MB.R.2180

1146   (formerly HMN SI), in posterior view. Note the dramatically different aspect ratios of their
1147   cotyles, indicating that extensive and unpredictable crushing has taken place. Photographs by
1148   the author.

1149 **Figure 12.** Cervical vertebrae 14 (left) and 13 (right) of *Diplodocus carnegii* holotype CM 84, in
1150   posterior view. Note the dramatically different aspect ratios of their cotyles, indicating that
1151   extensive and unpredictable crushing has taken place.

1152 **Figure 13.** Manipulation of consecutive sauropod vertebrae by hand. Cervicals 2 and 3 of
1153   *Giraffatitan brancai* lectotype MB.R.2181 (formerly HMN SI). I attempted to articulate these
1154   two vertebrae, and empirically determine the feasible range of motion. Due to subtle
1155   distortion of the zygapophyses of these vertebrae, it was not possible to articulate C2 in a
1156   more extended position relative to C3 than shown here. Photograph by Mathew J. Wedel.

1157 **Figure 14.** Cervicodorsal transition of *Haplocanthosaurus priscus* holotype CM 572. Top row,
1158   right lateral view; bottom row, anterior view. From left to right, D1, C15 and C14. Pink
1159   highlights indicate the expanded lateral surface of the prezygadiapophyseal lamina, anchoring
1160   the supporting muscles of the scapula, which Hatcher considered diagnostic of the 1st dorsal
1161   vertebra. Modified from Hatcher (1903: plate I).

1162

Serial variation in preserved aspect ratios of consecutive cervical vertebrae in extant animals and sauropods from several major amniote clades.

Mammalia: giraffe *Giraffa camelopardalis*, young juvenile specimen, C2–C7. Lacertilia: savannah monitor, *Varanus exanthematicus*, C3–C7. Crocodylia: alligator *Alligator mississippiensis*, juvenile specimen, C5–D2; Aves: ostrich *Struthio camelus*. C5–C11. Sauropoda: *Diplodocus carnegii* holotype CM84 and *Giraffatitan brancai* lectotype MN.R.2180 (formerly HMN SI). **Vertical** and **horizontal** columns contain measurements of the posterior articular surfaces of the vertebrae, except for the procoelous alligator vertebrae for which anterior articular surface was used. For the saddle-shaped ostrich cervicals, the maximum height and width of the posterior articular surface was used, rather than the shorter midline distances. Measurements are in arbitrary units (e.g. mm or pixels in a photograph) but consistent within any one specimen. **V/H** is the aspect ratio of the measured surface, the ratio of the vertical and horizontal measurements, so that values less than 1.0 indicate a surface wider than tall, and values greater than 1.0 indicate a surface taller than wide. Note that this ratio is independent of the measurement units. **1st diff** measures the absolute value of the difference between the V/H ratios of each vertebra and its successor. **Max diff** is the highest value of 1st diff for each specimen, and **Avg diff** is the average value; **×100** is this value times 100, a measure of the serial variation along the column. **1st ratio** is the "absolute ratio" of the V/H values of one vertebra and its successor, normalized so that when the ratio is less than 1.0 its inverse is used. **Max ratio** is the highest value of 1st ratio for each specimen, and **Avg ratio** is the average value; **–1×100** is this value minus one, multiplied by 100, another measure of the serial variation along the column. Note that by both measures, the variation is articular surface aspect ratios is greater in the two sauropods than in any of the extant animals, even though these are among the best preserved

sauropod necks.

	Vertebra	Vertical	Horizontal	V/H	1st diff	Max diff	Avg diff	×100	1st ratio	Max ratio	Avg ratio	−1×100
Giraffe												
	C2	437	638	0.685	0.086	0.151	0.062	6.201	1.126	1.208	1.086	8.636
	C3	499	647	0.771	0.014				1.018			
	C4	471	600	0.785	0.014				1.018			
	C5	513	665	0.771	0.045				1.062			
	C6	531	731	0.726	0.151				1.208			
	C7	510	581	0.878								
				0.769								
Monitor												
	C3	155	255	0.608	0.020	0.081	0.043	4.270	1.034	1.137	1.071	7.113
	C4	181	308	0.588	0.007				1.012			
	C5	179	301	0.595	0.081				1.137			
	C6	194	287	0.676	0.062				1.102			
	C7	189	308	0.614								
				0.616								
Alligator												
	C5	202	217	0.931	0.060	0.121	0.055	5.546	1.068	1.159	1.070	6.986
	C6	203	233	0.871	0.016				1.019			
	C7	213	240	0.888	0.121				1.159			
	C8	203	265	0.766	0.073				1.095			
	D1	198	236	0.839	0.007				1.008			
	D2	203	244	0.832								
				0.854								
Ostrich (Measuring maximum distances)												
	C5	156	207	0.754	0.036	0.092	0.063	6.298	1.048	1.135	1.089	8.903
	C6	173	219	0.790	0.027				1.035			
	C7	177	232	0.763	0.084				1.123			
	C8	161	237	0.679	0.092				1.135			
	C9	172	223	0.771	0.048				1.066			
	C10	170	235	0.723	0.091				1.126			
	C11	180	221	0.814								
				0.756								
***Diplodocus* (CM 82)**												
	C2	33	36	0.917	0.087	0.243	0.091	9.130	1.105	1.139	1.120	11.955
	C3	39	47	0.830	0.116				1.139			

C4	52	55	0.945	0.107				1.127				
C5	52	62	0.839	0.045				1.054				
C6	61	69	0.884	0.009				1.010				
C7	70	80	0.875	0.032				1.036				
C8	68	75	0.907	0.032				1.036				
C9	91	104	0.875	0.061				1.069				
C10	102	109	0.936	0.123				1.152				
C11	117	144	0.813	0.056				1.069				
C12	139	160	0.869	0.048				1.055				
C13	143	156	0.917	0.243				1.361				
C14	134	199	0.673	0.228				1.339				
C15	156	173	0.902									
			0.870									

Giraffatitan (MB.R.2180)

C2	864	717	1.205	0.180	0.378	0.163	16.288	1.176	1.568	1.221	22.100
C3	695	678	1.025	0.018				1.018			
C4	672	644	1.043	0.378				1.568			
C5	675	1014	0.666	0.031				1.047			
C6	828	1188	0.697	0.207				1.297			
C7	640	708	0.904								
			0.923								

Figure 1

Spinophorosaurus nigerensis holotype GCP-CV-4229 in situ during excavation in the region of Aderbissinat, Thirozerine Dept., Agadez Region, Republic of Niger.

Reproduced from Remes et al. (2009: figure 1).

Figure 2

Simplified phylogeny of Sauropoda, showing counts of complete and near-complete necks.

Captions: **C**, complete and described; **U**, complete but undescribed; **–1**, missing the atlas but otherwise complete; **O**, other near-complete necks (see text for details); **T**, total.

	C	U	-1	O	T
Basal eusauropods	1	1	2	1	5
Mamenchisaurids	3			2	5
Rebbachisaurids				1	1
Dicraeosaurids	1		1		2
Diplodocids	1			2	3
Basal macronarians	2	2		1	5
Brachiosaurids					0
Somphospondyls	1	2	2	1	6
TOTAL	**9**	**5**	**5**	**8**	**27**
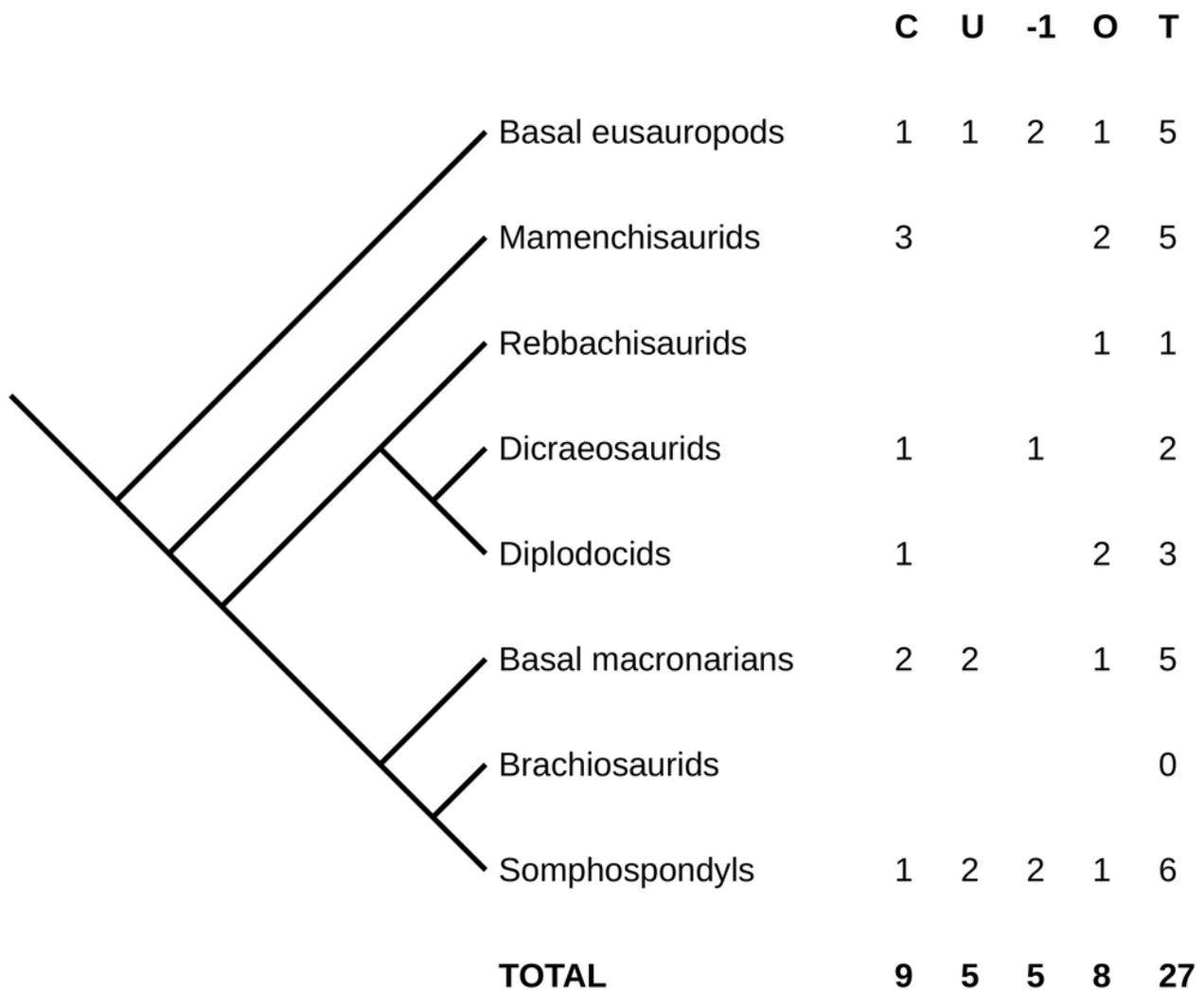
Figure 3

Neck of *Diplodocus carnegii* holotype CM 84, as reconstructed by Hatcher (1901: plate XIII), with fifteen undamaged cervical vertebrae.
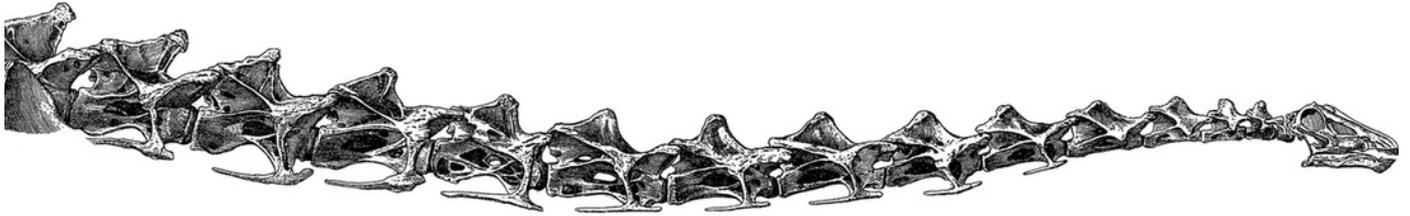
Figure 4

W. H. Reed's diagram of Quarry C near Camp Carnegie on Sheep Creek, in Albany County, Wyoming.

The coloured bones belong to CM 84, the holotype of *Diplodocus carnegii*; other bones belong to other individuals, chiefly of *Brontosaurus*, *Camarasaurus* and *Stegosaurus*. Modified (cropped and coloured) from Hatcher (1901: plate I). Cervical vertebrae are purple (and greatly simplified in outline by Reed), dorsals are red, the sacrum is orange, caudals are yellow, limb girdle elements are blue, and limb bones are green.
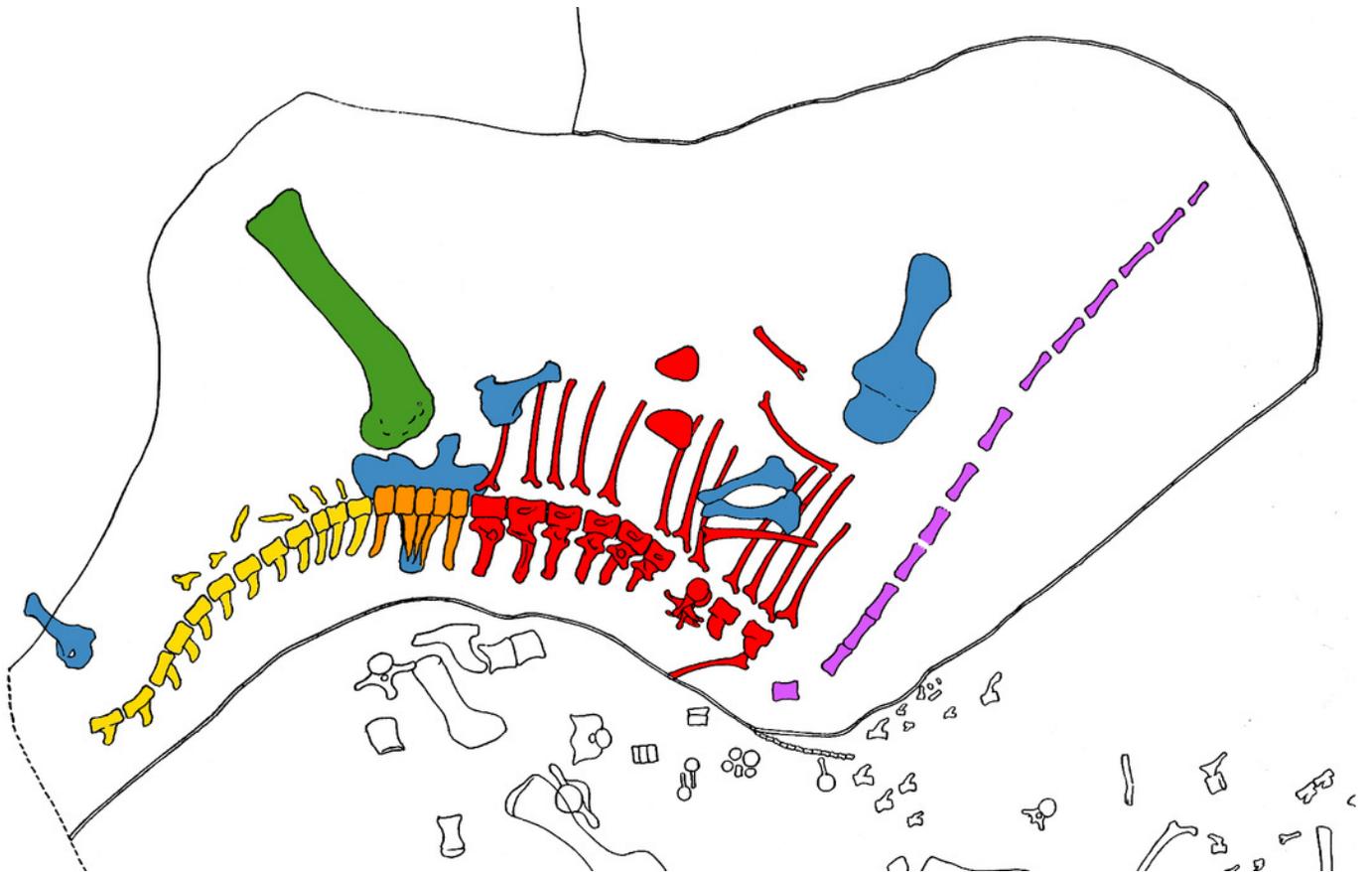
Figure 5

Three images of presacral vertebra 6 (probably dorsal 7) of *Brachiosaurus altithorax* holotype FMNH P25107, in right lateral view, showing misleading restoration.

Left: Field Museum photograph CSGEO16166, photographer Charles Carpenter, taken in 1905, the year after Riggs's (1904) descriptive monograph. Note the "crazy-paving" effect of the many cracks and missing areas of bone surface. **Middle:** Illustration of the same vertebra in Riggs (1904: plate LXXII). Note that the damage to the vertebral surface is not depicted. **Right:** photograph of the same vertebra, taken by the author in 2005. Note that the damage apparent in the 1905 photograph is no longer visible: the vertebra seems to have been painted to conceal its incompleteness.

Figure 6

Quarry map of Tendaguru Site S, Tanzania, showing incomplete and jumbled skeletons of *Giraffatitan brancai* specimens MB.R.2180 (the lectotype, formerly HMN SI) and MB.R.2181 (the paralectotype, formerly HMN SII).

Cervical material is highlighted in strong yellow, while the remaining elements are desaturated. Anatomical identifications of MB.R.2181 are underlined. Elements of MB.R.2180 could not be identified on the map with certainty. Modified from Heinrich (1999: figure 16), which was itself redrawn by Heinrich from an original field sketch by Werner Janensch.

Figure 7

Cervical vertebrae 5–11 of an ostrich, *Struthio camelus*, in posterior view, showing that articular facet shape remains similar along the column.

Specimen kindly provided by Matt Cobley.

Figure 8

Cervical and dorsal vertebrae (C5–9 and D1–2) of a juvenile alligator, *Alligator mississippiensis*, in anterior view, showing that articular facet shape remains similar along the column.

Specimen kindly provided by Matthew J. Wedel.

Figure 9

Sequences of cervical vertebrae of extant animals, showing that articular facet shape remains similar along the column.

Top. Cervical vertebrae 3–7 of a mature savannah monitor lizard, *Varanus exanthematicus*, in anterior view. (The cervicals of monitor lizards, unlike those of sauropods and most mammals, are procoelous, with the anterior facet being concave and the posterior convex.)
Bottom. cervical vertebrae 2–5 of a mature house-cat, *Felis catus*, in posterior view.

Figure 10

Cervical vertebrae of a baby giraffe, *Giraffa camelopardalis*, in posterior view, showing that articular facet shape remains similar along the column.

Top row, left to right: cervicals 7, 6 and 5; bottom row, left to right: cervicals 4, 3 and 2.

Despite changes in the vertebrae along the column, the flattened inverted pentagon shape of the articular facets remains similar along the sequence. (Note that extensive cartilage caps existed on the articular facets of this very young specimen, but were lost in preparation.)

Figure 11

Cervical vertebrae 4 (left) and 6 (right) of *Giraffatitan brancai* lectotype MB.R.2180 (formerly HMN SI), in posterior view.

Note the dramatically different aspect ratios of their cotyles, indicating that extensive and unpredictable crushing has taken place. Photographs by the author.

Figure 12

Cervical vertebrae 14 (left) and 13 (right) of *Diplodocus carnegii* holotype CM 84, in posterior view.

Note the dramatically different aspect ratios of their cotyles, indicating that extensive and unpredictable crushing has taken place.
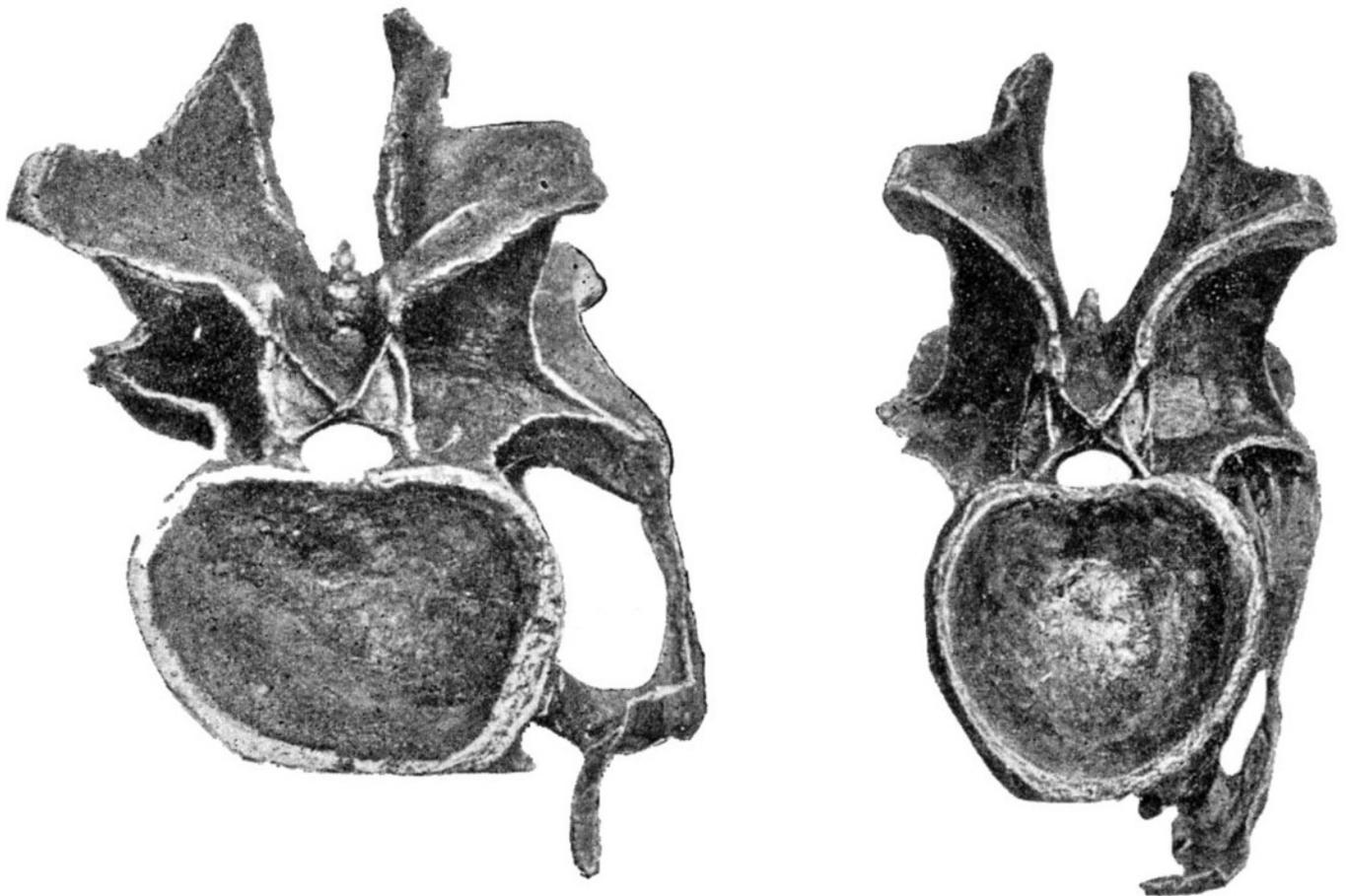
Figure 13

Manipulation of consecutive sauropod vertebrae by hand. Cervicals 2 and 3 of *Giraffatitan brancai* lectotype MB.R.2181 (formerly HMN SI).

I attempted to articulate these two vertebrae, and empirically determine the feasible range of motion. Due to subtle distortion of the zygapophyses of these vertebrae, it was not possible to articulate C2 in a more extended position relative to C3 than shown here. Photograph by Mathew J. Wedel.

Figure 14

Cervicodorsal transition of *Haplocanthosaurus priscus* holotype CM 572.

Top row, right lateral view; bottom row, anterior view. From left to right, D1, C15 and C14. Pink highlights indicate the expanded lateral surface of the prezygadiapophyseal lamina, anchoring the supporting muscles of the scapula, which Hatcher considered diagnostic of the 1st dorsal vertebra. Modified from Hatcher (1903: plate I).