The neck of *Barosaurus*: longer, wider and weirder than those of *Diplodocus* and other diplodocines

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Barosaurus is a diplodocid sauropod from the Upper Jurassic Morrison Formation of the western United States, and is known for its very long neck. It is closely related to the sympatric *Diplodocus*, and often thought of as more or less identical except with a longer neck. The holotype YPM 429 includes three and a half posterior cervical vertebrae, somewhat distorted and damaged, which are nevertheless very distinctive and quite different from those of *Diplodocus*. The cervicals of the better known and more complete referred *Barosaurus* specimen AMNH 6341 show the same characteristic features as the holotype, though not to the same extent: transversely broad but anteroposteriorly short zygapophyseal facets; prezygapophyses carried on broad, squared-off rami; zygapophyses shifted forward relative to the centrum; diapophyses, parapophyses and neural spines shifted backwards; and broad diapophyseal "wings". These features form a single functional complex, enabling great lateral flexibility, but restricting vertical flexibility. This may indicate that *Barosaurus* used a different feeding style from other sauropods perhaps sweeping out long arcs at ground level. The Morrison Formation contains at least nine diplodocid species in six to eight genera whose relationships are not yet fully understood, but *Barosaurus* remains distinct from its relatives.

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Abstract

Barosaurus is a diplodocid sauropod from the Upper Jurassic Morrison Formation of the western United States, and is known for its very long neck. It is closely related to the sympatric *Diplodocus*, and often thought of as more or less identical except with a longer neck. The holotype YPM 429 includes three and a half posterior cervical vertebrae, somewhat distorted and damaged, which are nevertheless very distinctive and quite different from those of *Diplodocus*. The cervicals of the better known and more complete referred *Barosaurus* specimen AMNH 6341 show the same characteristic features as the holotype, though not to the same extent: transversely broad but anteroposteriorly short zygapophyseal facets; prezygapophyses carried on broad, squared-off rami; zygapophyses shifted forward relative to the centrum; diapophyses, parapophyses and neural spines shifted backwards; and broad diapophyseal “wings”. These features form a single functional complex, enabling great lateral flexibility, but restricting vertical flexibility. This may indicate that *Barosaurus* used a different feeding style from other sauropods perhaps sweeping out long arcs at ground level. The Morrison Formation contains at least nine diplodocid species in six to eight genera whose relationships are not yet fully understood, but *Barosaurus* remains distinct from its relatives.

Keywords: dinosaur, sauropod, *Barosaurus*, *Diplodocus*, neck, cervical vertebrae

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Introduction

Barosaurus is an iconic genus of sauropod dinosaur, a diplodocine diplodocid from the Morrison Formation of Late Jurassic western United States (Marsh 1890, Lull 1919). Even among sauropods, its neck is proportionally and absolutely very long at about 8.5 m (Wedel 2007:194–195) – the same length as the neck of the much bulkier African brachiosaur *Giraffatitan*, and three and a half times as long as that of the world-record giraffe (Toon and Toon 2003:399). As such, it is a staple in popular dinosaur books (e.g. Bartram et al. 1983, Lindsay 1992, Lambert 2000). A mounted cast of a *Barosaurus* skeleton, AMNH 6341, dominates the entrance hall of the American Museum of Natural History, dwarfing the adjacent skeleton of the predatory dinosaur *Allosaurus* (Figure 1). A recently rediscovered *Barosaurus* skeleton, ROM 3670, has been mounted at the Royal Ontario Museum where it provides the centrepiece of the dinosaur gallery. Other specimens are known, but are less complete and in many cases juvenile, so less informative. The complex history of the genus and its principal specimens is helpfully summarised by McIntosh (2005:40–43).

Barosaurus is sometimes thought of as merely *Diplodocus* with a longer neck. In fact, the cervical vertebrae of *Barosaurus* are not merely elongated versions of those of its relative, but morphologically very distinct. Here, we reconsider the cervicals of the holotype specimen, compare them with those of the referred AMNH specimen, recognise distinctive features of the *Barosaurus* neck, and consider their functional implications.

Institutional abbreviations

AMNH – American Museum of Natural History, New York (USA).

ANS – Academy of Natural Sciences, Philadelphia (USA).

MB – Museum für Naturkunde Berlin, Berlin (Germany).

NSMT – National Science Museum, Tokyo (Japan).

ROM – Royal Ontario Museum, Toronto (Canada).

SMA – Sauriermuseum Aathal (Switzerland).

YPM – Yale Peabody Museum, New Haven (USA).

Description

Comparison of *Barosaurus* and *Diplodocus*

As noted by McIntosh (1990:389–390), *Barosaurus* resembles *Diplodocus* in most aspects of its anatomy:

> The genus [*Barosaurus*] is very closely related to *Diplodocus*, and the limb bones are so similar as to be indistinguishable. *Barosaurus* differs from *Diplodocus* in its enormously elongated cervical vertebrae, which are

> relatively 33 percent longer than those of the latter. […] The enormously elongated cervicals are generally similar to those of *Diplodocus* if the latter were stretched.

As such, *Barosaurus* is invariably depicted as virtually identical to *Diplodocus* except for an elongated neck – as for example in the skeletal reconstructions of Paul (2000:406). It has even been tentatively suggested by Senter (2006:46) that *Diplodocus* and *Barosaurus* might be sexual dimorphs, with the longer neck of the latter marking it out as the more flamboyant male. Such possibilities are lent credibility by the close phylogenetic position of the two taxa: every phylogenetic analysis that includes both genera has recovered them as sister taxa, including the sauropod phylogeny in *The Dinosauria, 2nd edition* (Upchurch et al. 2004: fig. 13:18) and the recent diplodocoid phylogenetic analyses of Whitlock (2011: fig. 7) and Mannion et al. (2011: fig. 10).

What is more, autapomorphies of the *Barosaurus* neck have been surprisingly hard to find in the literature. The phylogenetic analysis of Wilson (2002) gives three autapomorphies for *Barosaurus*, but two are in the dorsal vertebrae and one in the caudals. The analysis of Upchurch et al. (2004) also finds two autapomorphies in the dorsals and one in the caudals, though these are different from those of Wilson (2002). In the analysis of Taylor et al. (2011b), based on that of Harris (2006b), four autapomorphies were found, but three were again in the dorsal vertebrae and one in the ischium. No autapomorphies of *Barosaurus* are given by Whitlock (2011) or Mannion et al. (2011). Similarly, McIntosh (2005:39) gave a differential diagnosis separating *Barosaurus* from *Diplodocus*, but the only cervical characters listed are the presumed increase in cervical count, and elongation of the vertebrae. Consequently, and surprisingly, none of these analyses reported any autapomorphies in the neck of *Barosaurus*, its most distinctive feature. This indicates that additional characters, discussed below, should be added to future analyses.

Despite the failure of modern studies to identify differences between the cervicals of the two diplodocines, Lull (1919:20), in his classic descriptive monograph of *Barosaurus*, was cautious regarding the relationship between these genera:

> The preserved elements compare most nearly with those of *Diplodocus*, but differ remarkably in certain proportions. These resemblances may have been in part convergence and merely similar mechanical adjustments of bony tissue to meet similarly disposed strains and stresses, and as such imply no close relationship.

The post-cervical skeletons of *Diplodocus* and *Barosaurus* are indeed very similar, although the latter has only nine rather than ten dorsal vertebra, having apparently recruited the anteriormost dorsal into its neck (McIntosh 2005:44–45), and has a shorter tail (McIntosh 2005:57). However, the widely assumed similarity of the cervical vertebrae between the diplodocines is based almost entirely on lateral views (Figure 2). This is understandable, as the cervical columns of both *Diplodocus* and *Barosaurus* have been illustrated in detail in lateral view – the former as both drawings and photographs by Hatcher (1901: plates III and IV), the latter as photographs only by McIntosh (2005: fig. 2.1). However, the cervical vertebrae of *Diplodocus* have been illustrated in anterior and posterior views only by relatively uninformative photographs

(Hatcher 1901: plates V and VI), and only two cervicals of *Barosaurus* (C8 and 13) have been illustrated in anterior or posterior views (McIntosh 2005: fig. 2.2). Worst of all, the important dorsal view is completely unpublished for *Diplodocus*, and published for only a single vertebra in the *Barosaurus* holotype (Lull 1919: plate II: part 3). The vertebra illustrated by Lull is part of the holotype specimen YPM 429, designated by him as "vertebra R" and considered by him to be the most posterior cervical. It is extremely distinctive and superficially very different from those of *Diplodocus* (Figure 3).

Although the cervical series of *Diplodocus* has not been illustrated in dorsal view, those of three other diplodocids have: *Apatosaurus ajax* (Upchurch et al. 2005: plate I), *Suuwassea* (Harris 2006a: figs. 4–9; note that some recent phylogenies place this at the base of Dicraeosauridae, the sister group to Diplodocidae), and most helpfully *Kaatedocus* (Tschopp and Mateus 2012: unnumbered supplementary figures). The *Kaatedocus* figures of Tschopp and Mateus are full colour, high resolution photographs of all fourteen preserved cervical vertebrae in five cardinal directions, and so provide an invaluable comparative resource – especially as *Kaatedocus* is probably a diplodocine, and so more closely related to *Diplodocus* and *Barosaurus* than *Apatosaurus* and *Suuwassea* are (Taylor and Naish 2005: table 1).

Comparison of the posterior cervicals of these genera in dorsal view (Figure 4) appears to show that *Barosaurus* is dramatically different from the others: for example, it has very broad prezygapophyseal rami that are squared off anteriorly, wide "wings" that sweep back to posteriorly placed diapophyses before cutting back in towards the centrum, and an apparently unsplit neural spine at the junction of an "X" shape formed by the spinoprezygapophyseal and spinopostzygapophyseal laminae.

The neck of the Yale *Barosaurus*

The genus *Barosaurus* has only one species, *B. lentus*, and the holotype specimen, YPM 429, is held at the Yale Peabody Museum. As noted by Lull, this specimen contains material from four posterior cervical vertebrae, which he arbitrarily designated as vertebrae Q, R, S and T. Of these, vertebra T is too incomplete to be informative, but the other three are all informative. Measurements are given in Table 1.

Table 1. Measurement of cervical vertebrae in YPM 492, the *Barosaurus lentus* holotype. Measurements taken from Lull (1919) are suffixed "L"; measurements from photographs are marked "P". Width across parapophyses of vertebra Q based on reconstruction of how the undamaged element would have been. All measurements are in mm.

Vertebra	Vertebra R	Vertebra Q	Vertebra S
Serial position	C?15	C?13	C?12
Total length	960 L	980	1020 L
Total height			560 L
Centrum length	670	820	930 L
Condyle height	180	150	216 L
Condyle width	340	300 L	220 L
Condyle height:width ratio	0.53	0.5	0.98
Cotyle height	195	180	273 L
Cotyle width	370	350	220 L

Vertebra	Vertebra R	Vertebra Q	Vertebra S
Cotyle height:width ratio	0.53	0.51	1.24
Width across prezygapophyses	620		
Width across diapophyses	720	580	
Width across parapophyses	410 P	330 P	200 P
Left prezygapophyseal ramus width (anterior end)	280	182 P	
Right prezygapophyseal ramus width (anterior end)	240		
Left prezygapophyseal facet width		126 P	
Right prezygapophyseal facet width	190		

Vertebra R

Because Lull's vertebra R differs significantly from all other diplodocid vertebrae in dorsal, lateral and anterior views (compare Figure 3 with Figure 2 and with Hatcher 1901: plate V), it is appropriate to consider whether it really is part of the same individual as the rest of YPM 429; and, if so, whether YPM 429 is really a diplodocid at all, and whether AMNH 6341 and other “classic” *Barosaurus* individuals have been incorrectly referred.

Vertebra R resembles the cervicals of brachiosaurids and other basal titanosauriforms rather than those of diplodocids in the following respects:

- Its neural arch and spine are much less tall relative to total length, as seen in *Giraffatitan* (Janensch 1950: figs. 14–50), *Brachiosaurus* sp. (BYU 12866, Wedel 2005: fig. 7.2) and especially *Sauroposeidon* (Wedel et al. 2000a, b).
- The articular surfaces of its centrum are anterodorsally inclined, as in the *Giraffatitan* lectotype specimen MB.R.2180 (previously known as HMN SI; Janensch 1950: figs. 17–29).
- The entire neural arch is shifted forward on its centrum, so that the prezygapophyses greatly overhang the anteriormost part of the centrum, and the postzygapophyses (which are broken off) must have been located corresponding forward from the posterior rim of the centrum, as in *Giraffatitan*, *Brachiosaurus*, and *Sauroposeidon*.
- The parapophyses are located more posteriorly than the diapophyses, so that a line joining them is inclined anterodorsally rather than posterodorsally, as in at least some vertebrae of *Giraffatitan* and *Brachiosaurus*.
- The neural spine appears unsplit, rising to a low peak that is buttressed from the four diagonals by zygapophyseal laminae (compare with Figure 5).

On the other hand, vertebra R also has some significant dissimilarities to brachiosaur cervicals:

- Its neural spine appears proportionally lower than in any known posterior vertebra of a sauropod, its condition being perhaps most closely approached by C6 of MB.R.2180 (Janensch 1950: fig. 26).

- The vertebra is very much more proportionally broad than in brachiosaurs, resembling in this respect (though not in others) the vertebrae of some titanosaurs such as *Puertasaurus* (Novas et al. 2005: fig. 1).
- The prezygapophyseal rami are extraordinarily broad, whereas those of brachiosaurs are drawn forward almost to a point, where they bear small oval facets (Figure 5).

The distinctiveness of vertebra R raises important questions about the *Barosaurus* holotype YPM 429. Does it belong to an animal very different from the classical conception of *Barosaurus*, which is derived primarily from AMNH 6341? Or perhaps YPM 429 as a whole is similar to the AMNH specimen, but vertebra R is part of a different animal that was inadvertently referred to the same specimen? The latter seems unlikely, as the quarry map (Lull 1919: fig. 2) shows it closely associated with the other three cervical vertebrae, and surrounded on three sides by other elements belonging to the specimen. The solution to the mystery of vertebra R, then, is to be found in the other cervical vertebrae that are part of YPM 429.

Vertebra Q

Vertebra Q is similar in size to vertebra R: it is 2% longer overall (980 vs. 960 mm), though its centrum is fully 22% longer (820 vs. 670 mm). But it is proportionally narrower: only 80% as broad across the diapophyses (580 vs. 720 mm). Helpfully, it is preserved upside down in its jacket, and so different portions of the vertebra are available for study (Figure 6). Although it is less in overall breadth than vertebra R, it shares some important features that corroborate Lull's assignment of both to the same individual. Most importantly, the left prezygapophysis is preserved and undistorted, and is very broad as in vertebra R. (The prezygapophyses of vertebra R seem to be broader still, but distortion and reconstruction make it difficult to be certain of their true width.) Vertebra Q also has wing-like prezygadiapophyseal laminae that are swept back like those of vertebra R. And, contra Lull (1919:14), the diapophyses of vertebra Q are positioned more anteriorly than its parapophyses, as in vertebra R (Figure 6: top part).

Assuming that the two vertebrae do belong to the same individual, vertebra Q adds important information. Its postzygapophyses are unbroken: they sweep out posterolaterally and upwards from behind the diapophyseal wings and appear triangular in posterior view. The postzygapophyseal facets are difficult to discern precisely, but seem to be very broad, extending almost all the way to the lateral edges of the rami that bear them, and so matching the broad prezygapophyseal facet that is apparent in anterior view (Figure 6: left part).

Most significantly, when viewed in left ventrolateral aspect, vertebra Q can be seen to bear a left metapophysis, broadly similar in shape to what would be expected in a diplodocid: flat and somewhat laminated, anteroposteriorly longer than tall, and with distinct anterodorsal and posterodorsal corners. The right metapophysis is either lost or embedded in the jacket.

Vertebra S

Vertebra S is the longest of the preserved vertebrae: it is 13% longer than vertebra Q in centrum length (930 vs. 820 mm) and 4% longer in total preserved length (1020 vs. 980 mm). Its preservation is very different from that of vertebrae R and Q. While those vertebrae present their dorsal and ventral faces respectively, and have undergone some dorsoventral crushing, vertebra S lies on its left side in its jacket so that the right lateral view is presented (Figure 7), and it appears to have been crushed transversely. Its cotyle height is 124% of its width compared with 53% and 51% for R and Q respectively; and the preserved width across parapophyses is only 200 mm compared with 410 and 330 for R and Q (Figure 8).

Vertebra S provides the clearest evidence of bifid neural spines in YPM 429, as both metapophyses are preserved. These are apparent in dorsal view. The intermetapophyseal cleft is shallow, only about 75 mm deep. In *Barosaurus* the bifurcation of cervical neural spines starts farther back along the neck than it does in Diplodocus, and as far back as C13 in AMNH 6341 only a shallow cleft is present (McIntosh 2005: fig. 2.3A).

Both prezygapophyseal rami are present but incomplete. The better preserved left ramus indicates that despite its much lesser overall broadness, this vertebra had broad prezygapophyses similar in character if not in degree to those of vertebrae R and Q. The right ramus is more distorted, the spinoprezygapophyseal lamina having been displaced in a lateral kink.

The right postzygapophysis is intact. As with vertebra Q, the facet is broad, and is supported by a wide ramus that is strongly triangular in dorsal or ventral view.

The cortex of vertebra S has eroded away from the condyle, revealing a camellate internal structure of many small, irregular pneumatic cells. Similar structure is also visible, though less clearly, in the broken condyle of vertebra Q. Lull (1919:11) noted that the pneumatic fossae in the lateral faces of the centra of *Barosaurus* cervicals are consistently smaller than those in equivalent vertebrae of *Diplodocus*, though no less deep: this external morphology is consistent with that of titanosaur presacrals, which also have camellate to somphospondylous internal structure, suggesting that the internal and external structures are functionally correlated.

Association of the cervical vertebrae

In light of their similar general morphology – overall broadness, prezygapophyses extending well forwards of their centra, very broad prezygapophyseal rami and facets – it is reasonable to assume that vertebrae R and Q belong to the same individual. But vertebra S poses a problem: it is much narrower than the other two vertebrae, and correspondingly taller; and the preserved portions of its prezygapophyses hardly overhang its centrum at all.

However most of these differences can be explained by the different preservation of the three vertebrae. The orientation of the elements in their jackets alone is sufficient to suggest that only vertebra S was found on its side. If it suffered a moderate amount of transverse crushing and the other two were affected by dorsoventral crushing, then all three could have approached an intermediate morphology when fully intact.

The lack of prezygapophyseal overhang in vertebra S can also be explained: an additional bony plate is preserved, above the condyle but unattached (Figure 7: inset). It resembles the flat surfaces of the prezygapophyseal rami of the other vertebrae. It must represent the anterior portion of one of the rami, broken downwards and inwards. So most likely vertebra S did have overhanging prezygapophyses, and therefore had a greater total length when intact.

Other features suggest a relationship between vertebrae Q and S. They share the distinctive triangular shape of the postzygapophyses as seen from below (also seen in *Kaatedocus*), and both have small fossae just below the tip of the metapophysis (also present in *Dinheirosaurus*).

There is little to tie vertebra R directly to S, but Q is a helpful intermediate – both in preservation and possibly in serial position – which is evidently similar to both, and so ties them together.

Interesting differences among the vertebrae remain even after accounting for taphonomic deformation. First, in vertebrae R and Q, but not in S, the diapophyses are more anteriorly positioned than the parapophyses, and this remains true even when vertebra R is corrected for shearing. This can only be interpreted as serial variation between individual vertebrae. Something similar is seen in Hatcher's (1901: plate III) illustration of the cervicals of *Diplodocus carnegii*, in which the diapophysis of C12 is directly above the parapophysis whereas it is more posterior in all the other cervicals.

Second, Lull's (1919: 11) description states, and our observations confirm (Figure 7), that a small midline keel is present on the ventral surface of Vertebra S. Vertebrae R and Q have no trace of a keel. The presence of a ventral keel in the cervical vertebrae is a primitive character for sauropods, and keels are present in *Barapasaurus*, *Shunosaurus*, *Patagosaurus*, *Omeisaurus*, *Mamenchisaurus*, and *Phuwiangosaurus* (Upchurch 1998). Among diplodocoids, ventral keels are present in the cervical vertebrae of *Dicraeosaurus* (Upchurch 1998 and pers. obs.) and they are variably present in *Haplocanthosaurus* (Wedel and Sanders 2002: 2). More delicate ventral ridges appear in some cervical vertebrae at BYU that are probably referable to *Barosaurus* (pers. obs.) and in certain privately held specimens. However, the number and nature of these ridges in diplodocids is highly variable, even between different vertebrae of the same individual. These features may or may not be homologous with the true ventral ridges of basal sauropods and dicraeosaurs, but are probably not diagnostic at the generic level.

Reconstructions of the cervical vertebrae

Vertebra R is probably the most distorted, having evidently undergone not only crushing but also shearing, with the dorsal part of the vertebra shifted anteriorly (Lull 1919:14) which has exaggerated the already substantial prezygapophyseal overhang and shifted the diapophyses further forward of the parapophyses than they would have been.

In addition, both postzygapophyses are missing. These can be reconstructed after those of vertebra Q, but perhaps splaying further laterally than in Q to correspond with

R's broader prezygapophyses.

Because the spinoprezygapophyseal and spinopostzygapophyseal laminae converge to a low point, with ossified ligament attached to its posterior aspect, we were initially inclined to perceive this as the summit of an unusually low neural spine. However, the edges of the laminae do not preserve any finished bone, instead being broken in some places and restored with plaster in others. In light of the clearly bifid spine for vertebra S, and of the single preserved metapophysis of vertebra Q, we now accept the interpretation of Lull (1919:14), that vertebra R in life bore plate-like metapophyses that rose well above the level of the highest preserved point, and the remaining parts of the spinopostzygapophyseal and spinopostzygapophyseal laminae represent the bases of these lost metapophyses (Figure 9).

We initially suspected that the prezygapophyseal rami were broken off and would have extended yet further anteriorly in life. This was based on three things: the assumption that they could not have been so broad at their extremity; the folded profile of the rami in anterior aspect, which could not bear functional articular facets; and the lack of perceptible finished bone along much of the anterior margin. However, all of these points now seem flawed: the broadness of the rami is a genuine osteological feature, corroborated by the similar (though less extreme) morphology in vertebra Q; the rami appear folded because they have indeed been folded by crushing, and would have been straighter in life; and the paucity of good bone along the anterior margin is due to over-enthusiastic restoration work and the liberal application of plaster. So we now feel that the complete zygapophyseal rami are preserved, though badly damaged.

Vertebra Q seems to be less distorted, but it has undergone a complex crushing along a diagonal axis along with some twisting. Although it does not lie in a true upside-down position in its jacket, the ventral aspect shows that most of the element is intact apart from the right anterolateral portion including the right prezygapophysis, parapophysis, and much of the condyle. These can mostly be reconstructed by mirroring from the better left side.

While well preserved in most respects, vertebra S is missing its entire diapophyseal wing and the anterior tips of both prezygapophyses. As a result it is superficially very different from the other two cervicals. However, the anterior part of one prezygapophysis is present, out of position above the centrum; and the missing parts can be tentatively reconstructed by reference to vertebra Q.

Serial position of the cervical vertebrae

Lull (1919:11–15) considered these three vertebrae, together with the fragmentary and uninformative vertebra T, to be the four most posterior cervicals – C12–15 of his usage, since he thought *Barosaurus*, like *Diplodocus*, had 15 cervicals. He placed them in the sequence S, Q, T, R from front to back, “determined in part by the circumference of the posterior articular face of the centrum” (p. 11), but he did not mention any other criteria.

Lull's relative positions for the three adequately preserved vertebrae are corroborated by their progressively decreasing length and increasing broadness across the parapophyses (Table 1; Figure 8): compare with Janensch's (1950: fig. 50) illustration of the ventral view of vertebrae C10–C13 and D1–D2 of *Giraffatitan*; and with Upchurch et al.'s (2005: plate 1) illustration of the dorsal views of cervical vertebrae of *Apatosaurus*. Even allowing for some transverse crushing of vertebra S, it must have been narrower than vertebra Q when intact. The featureless ventral surface of vertebra R also corroborates its position as the most posterior of the preserved cervicals, as this condition is often seen in posterior cervicals and in dorsals.

The absolute positions of the vertebrae are harder to judge. The centra appear rather elongate to be the most posterior cervicals as suggested by Lull: specifically, vertebra R, probably the most posterior of the three, is somewhat longer than the last cervical of the AMNH specimen (960 vs. 750 mm). However, the vertebrae are evidently close to the back of the neck. They were found in association with an anterior dorsal (considered D1 by Lull, but reassigned as D2 by McIntosh 2005:48), which does suggest that there were probably not many intervening vertebrae. Accordingly, we tentatively consider these to be three of the four cervicals before the last, i.e. C12–C15. Another possibility is that the broken vertebra T – of which only the most posterior part remains – was the last cervical, C16, and S, Q and R are C13–C15. But Lull (1919:14–15) points out that the cotyle circumference of vertebra T is intermediate between that of vertebrae Q and R. So our preferred interpretation is that S is C12, Q is C13, T is C14, R is C15, and C16 and D1 are missing.

The neck of the AMNH *Barosaurus*

Comparisons between the referred *Barosaurus* individual AMNH 6341 and the holotype YPM 429 have been hampered by the lack of published illustrations of the AMNH material. McIntosh (2005: fig. 2.1) illustrated the preserved cervicals (C8–C16) but only with small, poorly reproduced monochrome photographs of the left lateral view. Two of the vertebrae are also illustrated in anterior or posterior view – C8 in fig. 2.2A and C13 in fig. 2.3A, but the remainder are not. None are illustrated in dorsal view.

Unfortunately these vertebrae are now inaccessible for study: they are on display in the Hall of Saurischian Dinosaurs at the American Museum of Natural History, but inconveniently located underneath a glass walkway which is scuffed by the feet of visitors. As a result, photography is very difficult. Nevertheless, because there are currently no published dorsal-view illustrations, we have made our best effort to capture the vertebrae from above and to clean the resulting images (Figures 10, 11).

It is now apparent that the penultimate cervical of the AMNH specimen bears important similarities, not previously apparent, to vertebra R (Figure 12):

- While not as broad as those of vertebra R, the prezygapophyseal rami of the AMNH vertebra are much broader and squarer in dorsal view than in other sauropods: compare with Figure 4.
- The prezygadiapophyseal laminae form broad horizontal wings, which sweep inwards towards the centrum behind the diapophysis.
- The bases of the metapophyses converge at the midline and form an “X” composed of the spinozygapophyseal laminae, as in vertebra R, corroborating the interpretation that this vertebra originally bore metapophyses that have since been lost.

These similarities suffice to confirm the referral of the AMNH material to *Barosaurus*: the remaining differences in proportion between vertebra R and the AMNH cervical can mostly be understood as the result of individual variation or differences in preservation. The similarities between C15 of the AMNH material and vertebra R of the YPM series lend credence to the idea that the latter series really does represent C12–15, as outlined above.

In some of the dorsal-view photographs of the AMNH cervicals, the prezygapophyseal facets can be discerned, verifying that they are both transversely broad, occupying almost the whole width of the rami, and anteroposteriorly short. It is not possible to determine prezygapophyseal facet extent directly from the Yale material due to poor preservation and over-enthusiastic reconstruction of this area in vertebra R, but it must be assumed to resemble the condition in the AMNH material.

Discussion

Fusion of vertebral elements

The diapophyses and left parapophysis of vertebra Q preserve articular surfaces, indicating that the cervical ribs were unfused in this individual despite its great size – surprisingly, as McIntosh (2005:48) says that in the similarly sized or slightly smaller AMNH 6341 “The cervical ribs are firmly coalesced to all the cervicals”. Parapophyseal and diapophyseal facets are also present in vertebra R, though poorly preserved and difficult to interpret. They are lost in vertebra S.

Hatcher (1901: plate III) shows vertebrae in C6–C15 of *Diplodocus carnegii* CM 84 with their ribs fused to them (though broken in C10). Therefore, either YPM 429 was considerably less mature than CM 84, despite being of comparable size, or *Barosaurus* and *Diplodocus* did not follow the same ontogenetic trajectory of fusions. This represents another example of the increasingly recognised inconsistency in the timing of fusions in sauropod ontogeny (Wedel and Taylor 2013: table 1; Hone et al. 2016). The discrepancies between ontogenetic progression in YPM 429, AMNH 6341 and CM 84 are further evidence that lumping multiple taxa together in analyses of ontogenetic change (e.g. Woodruff and Fowler 2012) is unwise.

Functional implications of *Barosaurus* neck anatomy

Functional implications follow from the unique anatomy of the Yale *Barosaurus* material. The short anteroposterior extent of the zygapophyseal facets together with the anterior displacement of the zygapophyseal articulations relative to those of the centra suggest that the neck may have been limited in vertical flexibility. On the other hand, the extreme transverse width of the facets seems to indicate an unusual degree of lateral flexibility. Lull (1919:13) recognised the latter, but did not comment on the former.

The broad diapophyseal wings of *Barosaurus*, the posterior migration of the diapophyses and parapophyses, and the anterior extension of the zygapophyses would also have had implications for lateral movement of the neck. The broadness of the wings shifted the lateral muscles away from the midline, allowing them to act with greater mechanical advantage. Each of the other changes contributed to extending the length of the ansae costotransversariae, or cervical rib loops, which provided the attachment area for the long lateral flexors. Assuming that these muscles were laid out as they are in birds (see Wedel and Sanders 2002), the Mm. cervicalis ascendens originated on the prezygadiapophyseal laminae and inserted on the epipophyses of more anterior vertebrae; and the Mm. flexor colli lateralis originated on the anterior aspect of the rib, including its anterior projection. Both these areas were proportionally larger in *Barosaurus* than in other diplodocines (Figure 13).

The parapophyses and diapophyses migrate progressively backwards in the posterior vertebrae of *Diplodocus* (Hatcher 1901: plate III) as well as in *Barosaurus*; but the migration seems to begin more anteriorly in *Barosaurus* (Lull 1919:12) and reaches its extreme in vertebra R, where the prezygadiapophyseal laminae run half the entire length of the vertebra. By contrast the diapophyses and parapophyses do not migrate backwards in the posterior cervicals of *Kaatedocus* (Tschopp and Mateus: unnumbered supplementary figures), and together with the mediolateral narrowness of the *Kaatedocus* cervicals this may indicate that lateral neck motion was less important in this taxon (although this narrowness is increased by transverse compression in SMA 0004).

So the broad zygapophyseal facets, diapophyseal wings and posterior migration of the cervical rib loop in *Barosaurus* are all aspects of a single functional complex related to lateral neck movement: the facets enable lateral flexibility and the other features provide both expanded attachment area and mechanical advantage to the muscles that produce it. Not only was the neck of *Barosaurus* absolutely and proportionally long even among sauropods, it was also uniquely adapted for lateral sweeping: no other sauropod shows the same degree of development of the relevant characters.

Like the diapophyses and parapophyses, the neural spine is also located more posteriorly in *Barosaurus* than in other diplodocids. Two groups of muscles are inferred to originate on the spine (Wedel and Sanders 2002): the Mm. interspinales, which insert on the posterior aspect of the next spine, and so are invariably the length of a single vertebra; and the Mm. longus colli dorsalis, which span many vertebrae, so that posterior displacement of the origin within a single vertebra would have very little mechanical effect. We are therefore unable to determine what purpose if any the posterior location of the neural spine served, although we note that the apex of the neural spine is also located quite far back in posterior cervicals of *Giraffatitan* and *Sauroposeidon* (Janensch 1950, Wedel et al. 2000a, b), so this character seems to be correlated with neck elongation.

Behavioural implications

How did *Barosaurus* use its unique neck? Martin (1987) proposed, and Stevens and Parrish (1999) and Ruxton and Wilkinson (2011) developed, a “vacuum-cleaner” feeding hypothesis for sauropods: that they spent much of their time standing stationary and feeding at ground level, sweeping out a broad area with their long necks. Although we have been sceptical that this feeding model was common for sauropods (Taylor et al. 2009, 2011a), we recognise that *Barosaurus*, with its limited dorsoventral flexibility at the base of the neck and its suite of lateral-sweep adaptations, is a prime candidate for such behaviour.

Most work on niche partitioning among Morrison sauropods has focused on their jaws and teeth (e.g. Barrett and Upchurch 1994, Fiorillo 1998, Button et al. 2013). Browsing height has also been mentioned in connection with niche partitioning (e.g. Paul 1998). However, beyond the general discussion of Stevens and Parrish (2005a, 2005b), the role of neck behaviour has so far been little studied. But sauropod heads were, to a first approximation, simple food scoops; and their necks were almost certainly adapted primarily for food gathering (Sander et al. 2010, Taylor et al. 2011a). Given these baseline similarities it seems likely that different sauropod taxa were using their necks in different ways.

Morphological trends in the necks of diplodocines

Barosaurus is not just a stretch-limo remix of *Diplodocus*. Not only is the morphology of its neck different in functionally significant ways, but as noted by Lull (1919:34–36), the pubis of the type specimen is significantly larger than that of the similar-sized *Diplodocus carnegii*. (Lull also described additional appendicular elements of the *Barosaurus* holotype, all larger or more robust than their counterparts in Diplodocus. But McIntosh (2005:40–41) says that these are from a different site, a fact that Lull singularly fails to record, and says that there is no reason to believe they belong to YPM 429, or to *Barosaurus* at all. The pubis is the only appendicular element shown in the quarry map of Lull 1919: fig. 2, and the only one that can be confidently associated with the holotype.)

The cervical vertebrae of the Morrison-Formation diplodocines *Diplodocus*, *Kaatedocus*, AMNH *Barosaurus* and Yale *Barosaurus* seem to form a continuum: each stage in the sequence has more elongate centra, its zygapophyses shifted further forward with respect to the centrum, its neural spine further back, its diapophyseal wings broader and its prezygapophyseal rami broader and more squared off in dorsal view.

Differences remain between the Yale and AMNH *Barosaurus* cervical material, even when allowing for differences in preservation. The trend towards broadening the zygapophyses and the diapophyseal wings is taken to an extreme in the Yale material. This is best seen by comparing vertebra Q, which we tentatively identify as C13, with C12 of the AMNH specimen. When scaled to the same total length, the Yale vertebra is 23% wider across the diapophyses and 95% wider across the postzygapophyses. This could possibly indicate that the two specimens represent different species; it could be sexual dimorphism, with the male exhibiting a flamboyant neck; or it might simply be individual variation.

It is also possible that the differences between the necks of the Yale and AMNH *Barosaurus* specimens represent changes through evolutionary time. Unfortunately, this possibility cannot be meaningfully evaluated, as the stratigraphic context of the YPM specimen is not well constrained. As explained by Foster (2013), limited exposure of the Morrison Formation in the region of the quarry makes it unclear whether the YPM specimen is older or more recent than the AMNH one.

Diplodocid diversity in the Morrison Formation

With the recent addition of *Kaatedocus* to the roster, the diversity of diplodocids in the Morrison Formation has become yet more impressive: as well as the diplodocines *Diplodocus, Galeamopus* (probably two species), *Barosaurus* and *Kaatedocus*, there are at least four species of *Apatosaurus* (Upchurch et al. 2005: fig 15), *Supersaurus*, and possibly *Eobrontosaurus*, which awaits restudy. Other diplodocoids are also present in the Morrison Formation: *Suuwassea*, which is now thought to be a dicraeosaurid (Whitlock 2011); probably *Amphicoelias* (Whitlock 2011, Mannion et al. 2011); and possibly *Haplocanthosaurus*, which was recovered as a basal diplodocoid in the analyses of Wilson (2002), Whitlock (2011) and Mannion et al. (2011).

It's interesting that of the 13 or so diplodocoid species currently known from the Morrison Formation, 10 are diplodocids. As noted by Taylor (2006), the clade Diplodocidae was limited in time and space: more diplodocids are known from the Morrison Formation than from the rest of the global Mesozoic put together. Yet in the one time and place when Diplodocidae flourished, its diversity was much greater than that of other sauropod groups. By comparison the other diplodocoid clades, Rebbachisauridae and Dicraeosauridae, were less speciose at any given time but longer lived.

The very high diversity of sauropods in the Morrison Formation gives us a picture of an amazing ecosystem positively abundant with numerous species of giant animals bigger than anything alive on land today. It could be argued that the extremity of such an ecosystem constitutes evidence that Morrison sauropods are oversplit. But this argument from incredulity would be mistaken. We must assess taxonomy on its own grounds, based on what the fossil morphology tells us; only then can we determine what the resulting species roll-call tells us about the ecosystem. Mesozoic ecosystem were simply not like modern ones (see e.g. O'Gorman and Hone 2012), and sauropod possessed a suite of key adaptations that have not been combined in any other clade of organisms. We must resist the insidious temptation to assume that what we would have seen in the Late Jurassic is somehow analogous to what we see today on the Serengeti.

Trends in sauropod descriptive monographs

The classic descriptive monographs on sauropods remain influential and useful (e.g. Hatcher 1901 on *Diplodocus*, Lull 1919 on *Barosaurus*, Gilmore 1936 on *Apatosaurus*, Janensch 1950 and other papers on *Giraffatitan*). However, they are showing their age, and due for revision. They were mostly written at a time when only a tiny fraction of presently recognised sauropod diversity was known, and without phylogenetic context. The illustrations in these monographs, while aesthetically beautiful, are often less scientifically uninformative than those of modern descriptions, depicting elements in only one or two orientations, invariably in monochrome, and often at small sizes.

With the increasing accessibility of digital photography and online publishing, fossils should now be routinely illustrated from as many of the cardinal directions as possible, in full colour and at high resolution. The excellent multi-view photographs of the *Kaatedocus* cervicals provided with the description of Tschopp and Mateus (2012) demonstrate what is now possible, and set a new bar for descriptive illustration – though it is unfortunate that they are not part of the main paper, but relegated to second-class status as unnumbered supplementary figures.

Conclusions

Barosaurus is a valid genus of diplodocine sauropod, and the specimen AMNH 6341 from which it is principally known is closely related to the holotype YPM 429. *Barosaurus* is distinguished from all other sauropods by the nature of its cervical vertebrae. These bear uniquely broad and anteroposteriorly short prezygapophyseal facets on uniquely broad prezygapophyseal rami, which merge into broad, wing-like, horizontal prezygadiapophyseal laminae. This suggests that the neck of *Barosaurus* was mechanically optimised for wide, sweeping horizontal movements, but may have been less mobile vertically.

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Figure captions

Figure 1. Mounted cast skeleton of *Barosaurus* referred specimen AMNH 6341, in the entrance hall of the American Museum of Natural History. *Homo sapiens* (MPT) for scale. Photograph by MJW.

Figure 2. Posterior cervical vertebrae (C13) of diplodocine sauropods in lateral view, showing proportional differences. Top left, *Kaatedocus*, from Tschopp and Mateus (2012: unnumbered supplementary figure tjsp_a_746589_sup_30912151.tif); top right, *Barosaurus* referred specimen AMNH 6341, left lateral, reversed (photo by MJW); bottom left, *Diplodocus*, from Hatcher (1901: plate III); bottom right, *Diplodocus* elongated by 33%. *Kaatedocus* and *Barosaurus* scaled to the same centrum length as original *Diplodocus* and elongated *Diplodocus* respectively. In lateral view, the widely assumed similarity between the cervicals of *Barosaurus* and elongated *Diplodocus* is largely borne out: the principal differences in *Barosaurus* are the less prominent and more posteriorly positioned neural spine (**ns**), the more prominent ventrolateral flanges (**vlf**), and the reduced pneumatic fossa (**pf**) in the centrum. Scale bars = 100 mm.

Figure 3. *Barosaurus lentus* holotype YPM 429, vertebra R, C?15. Top row, left to right: posterior, dorsal and anterior views; middle row: right lateral view; bottom row: ventral view, from Lull (1919: plate II). Note the apparently very low, undivided neural spine at the intersection of the PRSLs and POSLs, forward-shifted neural arch, broad prezygapophyses, broad, wing-like prezygadiapophyseal laminae, and great width across the diapophyses and across the parapophyses. Abbreviations: **dia**, diapophysis; **para**, parapophysis; **prz**, prezygapophysis; **prdl**, prezygadiapophyseal lamina; **spol**, spinopostzygapophyseal lamina; **sprl**, spinoprezygapophyseal lamina. Scale bar = 500 mm.

Figure 4. Diplodocid posterior vertebrae in dorsal view, scaled to equal total length, with neural spines highlighted. Left column, from top to bottom: *Apatosaurus ajax* Tokyo specimen NSMT-PV 20375, C12 (From Upchurch et al. 2005: plate I, part I), centrum length 380 mm; *Barosaurus lentus* holotype YPM 429, vertebra R (C?15), total length 960 mm. Right column, from top to bottom: *Apatosaurus ajax* holotype YPM 1860, C?11, centrum length unknown but probably about 500 mm; *Suuwassea emilieae* holotype ANS 21122, C7 (photograph supplied by Jerry Harris), centrum length 284 mm; *Kaatedocus siberi* holotype SMA 004, C13 (from unnumbered supplementary figure in Tschopp and Mateus 2012), total length 309 mm. *Diplodocus* is not pictured due to the lack of published illustrations. The vertebrae of *Apatosaurus* and *Barosaurus* are proportionally much wider than those of *Suuwassea* and *Kaatedocus*, and the bifurcation of the neural spine is far wider in both *Apatosaurus* specimens than in *Suuwassea* or *Kaatedocus*. No bifurcation is apparent in *Barosaurus*, which appears to have a low unsplit spine at the summit of four converging laminae, but this is a preservational artefact: see text. Scale bars = 100 mm.

Figure 5. *Giraffatitan brancai* lectotype MB.R.2180, fifth cervical vertebra. Top row: left lateral view. Second row: dorsal view, with anterior to the right. Third row (from left to right): anterior, right lateral and posterior views. Bottom row: ventral view, with anterior to the right. Scale bar = 500 mm.

Figure 6. *Barosaurus lentus* holotype YPM 429, Vertebra Q (C?13). Top row: left ventrolateral view. Middle row, from left to right: anterior view, with ventral to the right; ventral view; posterior view, with ventral to the left. Bottom row: right lateral view, inverted. Inset shows diapophyseal facet on right side of vertebra, indicating that the cervical ribs were unfused in this individual despite its great size. Note the broad, flat prezygapophyseal facet visible in anterior view. Scale

bar = 500 mm.

Figure 7. *Barosaurus lentus* holotype YPM 429, Vertebra S (C?12). Left column from top to bottom: dorsal, right lateral and ventral views; right column: anterior view. Inset shows displaced fragment of broken prezygapophysis. Note the narrow span across the parapophyses in ventral view. Scale bar = 500 mm.

Figure 8. *Barosaurus lentus* holotype YPM 429, cervical vertebrae in ventral view. From top to bottom: vertebra R (from Lull 1919: plate II), vertebra Q, vertebra S. Probably from more posterior to more anterior. Scale bar = 500 mm.

Figure 9. Partial restoration of the *Barosaurus lentus* holotype YPM 429, cervical vertebra R, approximating its undamaged state by allowing for dorsoventral crushing, shearing and loss of some extremities. Anterior and posterior views scaled to 125% of uncorrected height and 80% of uncorrected width. Dorsal view scaled to 80% of uncorrected width; condyle moved forward and cotyle scaled to 50% of uncorrected width to allow for shearing. Lateral view scaled to 125% of uncorrected height, and sheared backwards 15 degrees. Lateral processes sheered upwards in anterior and posterior views. Metapophyses and postzygapophyses drawn in multiple views based on vertebrae Q and S, and C14–16 of AMNH 6341. Scale bar = 500 mm.

Figure 10. *Barosaurus* AMNH 6341, cervical vertebrae in dorsal view, to scale. Left column, from top to bottom: C9–C12. Right column, from top to bottom: C14–C16. Extensive image manipulation was necessary to bring out the information in these photographs, due to to poor photography conditions. C16 is sheered to the right, so the aspect is slightly left dorsolateral rather than true dorsal. C8 is on display in the gallery with these vertebrae, but the structure of the display makes it impossible to photograph in dorsal view. C13 is on a shelf in collections, apart from the other cervicals, and we were not able to photograph it in dorsal view. Scale bar = 500 mm.

Figure 11. *Barosaurus* AMNH 6341, cervical vertebrae C8–C16 in dorsal (where available) and lateral views, to scale. Lateral views except C13 from McIntosh (2005: fig. 2.1). Scale bar = 500 mm.

Figure 12. Similarities between *Barosaurus lentus* holotype YPM 429, cervical vertebra R (C?15, left) and referred specimen AMNH 6341, C15 (right), scaled to same total length. Green brackets show width of prezygapophyseal rami, omitting apparent reconstruction on left anterolateral corner of YPM 429. Red outlines indicate margins of diapophyseal wings. Blue outlines show posterior fillets of diapophyseal wings. Orange “X” on AMNH 6341 indicates base of metapophyses, extended from prezygadiapophyseal and postzygadiapophyseal laminae and forming a diagonal cross similar to that of vertebra R. Prezygapophyseal facets of AMNH 6341 highlighted in yellow: the right facet is fairly clear in the photograph (see Figure 10); the exact margin of the left facet is less certain. Zygapophyseal facets cannot be directly recognised in vertebra R due to poor preservation and overzealous reconstruction. Scale bars = 500 mm.

Figure 13. Attachments of the lateral flexor muscles of the neck in *Kaatedocus* and *Barosaurus*. On the left, C11 of *Kaatedocus siberi* holotype SMA 0004 (traced from Tschopp and Mateus 2012: fig. 10C2) in dorsal (top) and right lateral (bottom) views, with simplified versions of the lateral flexor muscles included, based on those of birds (see Wedel and Sanders 2002, and Taylor and Wedel 2013). The M. longus colli dorsalis and M. cervicalis ascendens insert together on the epipophysis (= torus dorsalis of birds), and the M. flexor colli lateralis and M. longus colli ventralis (ventral and medial, not shown) insert together on the cervical rib. The pre-epipophysis (*sensu* Tschopp and Mateus 2012) and the head of the cervical rib may have served as expanded attachments for M. cervicalis ascendens and M. flexor colli lateralis, respectively. The actual muscles were probably much more complex than those drawn here,

with numerous slips connecting multiple vertebrae: for a similar condition in birds, see Zweers et al. (1987) and van der Leeuw et al. (2001: fig. 2). On the right, C15 of *Barosaurus* AMNH 6341, scaled to the same total length as C11 of *Kaatedocus*. Actual total lengths for the two vertebrae are 840 mm for C15 of *Barosaurus* (McIntosh 2005: table 2.1) and 324 mm for C11 of *Kaatedocus* (Tschopp and Mateus 2012: table 1). In *Barosaurus*, the ansae costotransversariae or cervical rib loops are taller, wider and more posteriorly located than in *Kaatedocus*, providing a larger attachment area for the lateral flexor muscles (blue arcs) and lending them greater mechanical advantage (red lines). In this respect, *Barosaurus* is more similar to *Apatosaurus* than to the narrow-necked *Diplodocus*, although the cervical ribs of *Barosaurus* are much less robust than those of *Apatosaurus*.

Figure 1

Mounted cast skeleton of *Barosaurus* referred specimen AMNH 634.

Mounted cast skeleton of *Barosaurus* referred specimen AMNH 6341, in the entrance hall of the American Museum of Natural History. *Homo sapiens* (MPT) for scale. Photograph by MJW.


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Figure 2

Posterior cervical vertebrae (C13) of diplodocine sauropods in lateral view, showing proportional differences.

Posterior cervical vertebrae (C13) of diplodocine sauropods in lateral view, showing proportional differences. Top left, *Kaatedocus*, from Tschopp and Mateus (2012: unnumbered supplementary figure tjsp_a_746589_sup_30912151.tif); top right, *Barosaurus* referred specimen AMNH 6341, left lateral, reversed (photo by MJW); bottom left, *Diplodocus*, from Hatcher (1901: plate III); bottom right, *Diplodocus* elongated by 33%. *Kaatedocus* and *Barosaurus* scaled to the same centrum length as original *Diplodocus* and elongated *Diplodocus* respectively. In lateral view, the widely assumed similarity between the cervicals of *Barosaurus* and elongated *Diplodocus* is largely borne out: the principal differences in *Barosaurus* are the less prominent and more posteriorly positioned neural spine (**ns**), the more prominent ventrolateral flanges (**vlf**), and the reduced pneumatic fossa (**pf**) in the centrum. Scale bars = 100 mm.

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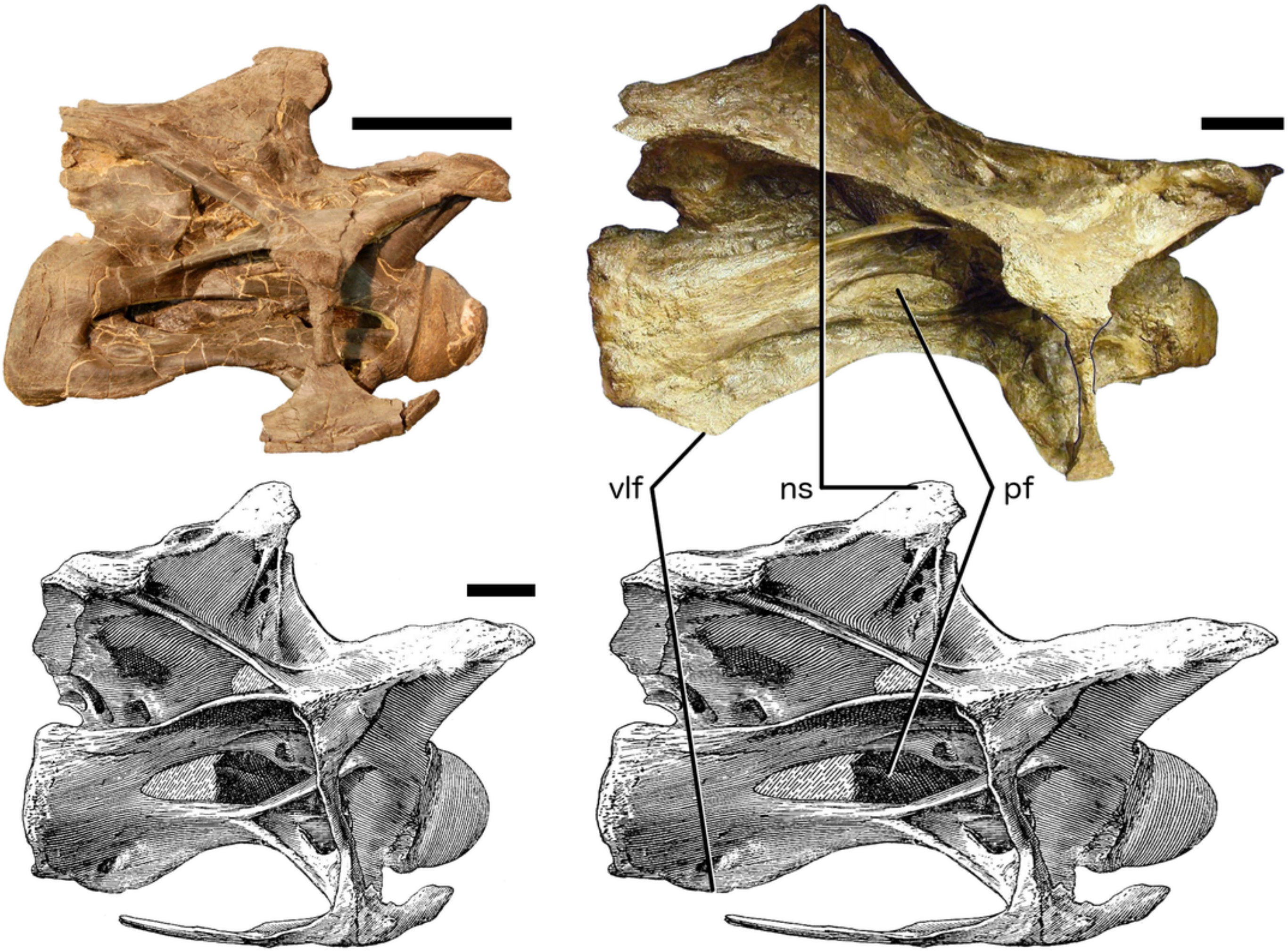
vlf
ns
pf

Figure 3

Barosaurus lentus holotype YPM 429, vertebra R, C?15.

Barosaurus lentus holotype YPM 429, vertebra R, C?15. Top row, left to right: posterior, dorsal and anterior views; middle row: right lateral view; bottom row: ventral view, from Lull (1919: plate II). Note the apparently very low, undivided neural spine at the intersection of the PRSLs and POSLs, forward-shifted neural arch, broad prezygapophyses, broad, wing-like prezygadiapophyseal laminae, and great width across the diapophyses and across the parapophyses. Abbreviations: **dia**, diapophysis; **para**, parapophysis; **prz**, prezygapophysis; **prdl**, prezygadiapophyseal lamina; **spol**, spinopostzygapophyseal lamina; **sprl**, spinoprezygapophyseal lamina. Scale bar = 500 mm.

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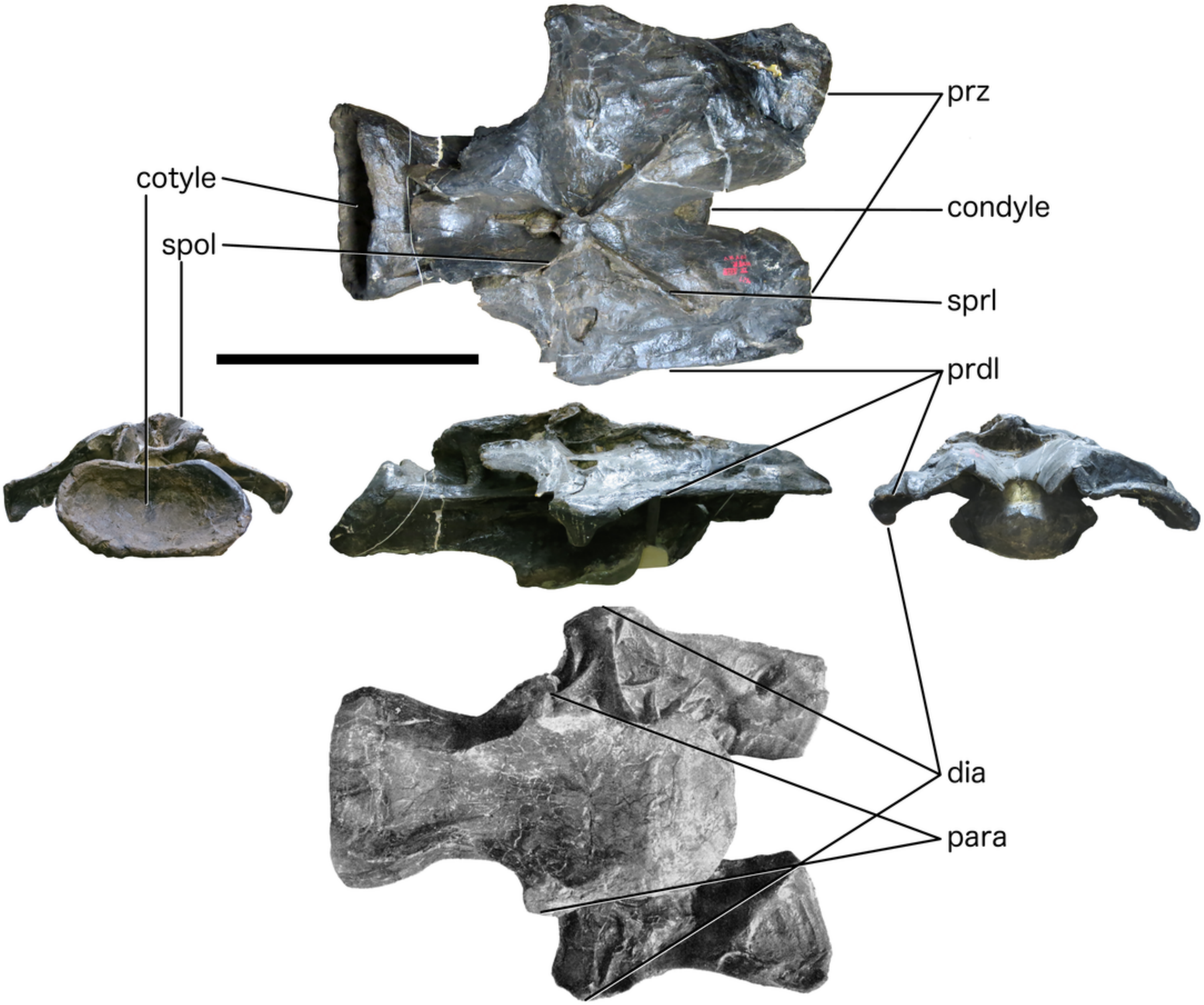
cotyle
spol
prz
condyle
sprl
prdl
dia
para

Figure 4

Diplodocid posterior vertebrae in dorsal view, scaled to equal total length, with neural spines highlighted.

Diplodocid posterior vertebrae in dorsal view, scaled to equal total length, with neural spines highlighted. Left column, from top to bottom: *Apatosaurus ajax* Tokyo specimen NSMT-PV 20375, C12 (From Upchurch et al. 2005: plate I, part I), centrum length 380 mm; *Barosaurus lentus* holotype YPM 429, vertebra R (C?15), total length 960 mm. Right column, from top to bottom: *Apatosaurus ajax* holotype YPM 1860, C?11, centrum length unknown but probably about 500 mm; *Suuwassea emilieae* holotype ANS 21122, C7 (photograph supplied by Jerry Harris), centrum length 284 mm; *Kaatedocus siberi* holotype SMA 004, C13 (from unnumbered supplementary figure in Tschopp and Mateus 2012), total length 309 mm. *Diplodocus* is not pictured due to the lack of published illustrations. The vertebrae of *Apatosaurus* and *Barosaurus* are proportionally much wider than those of *Suuwassea* and *Kaatedocus*, and the bifurcation of the neural spine is far wider in both *Apatosaurus* specimens than in *Suuwassea* or *Kaatedocus*. No bifurcation is apparent in *Barosaurus*, which appears to have a low unsplit spine at the summit of four converging laminae, but this is a preservational artefact: see text. Scale bars = 100 mm.

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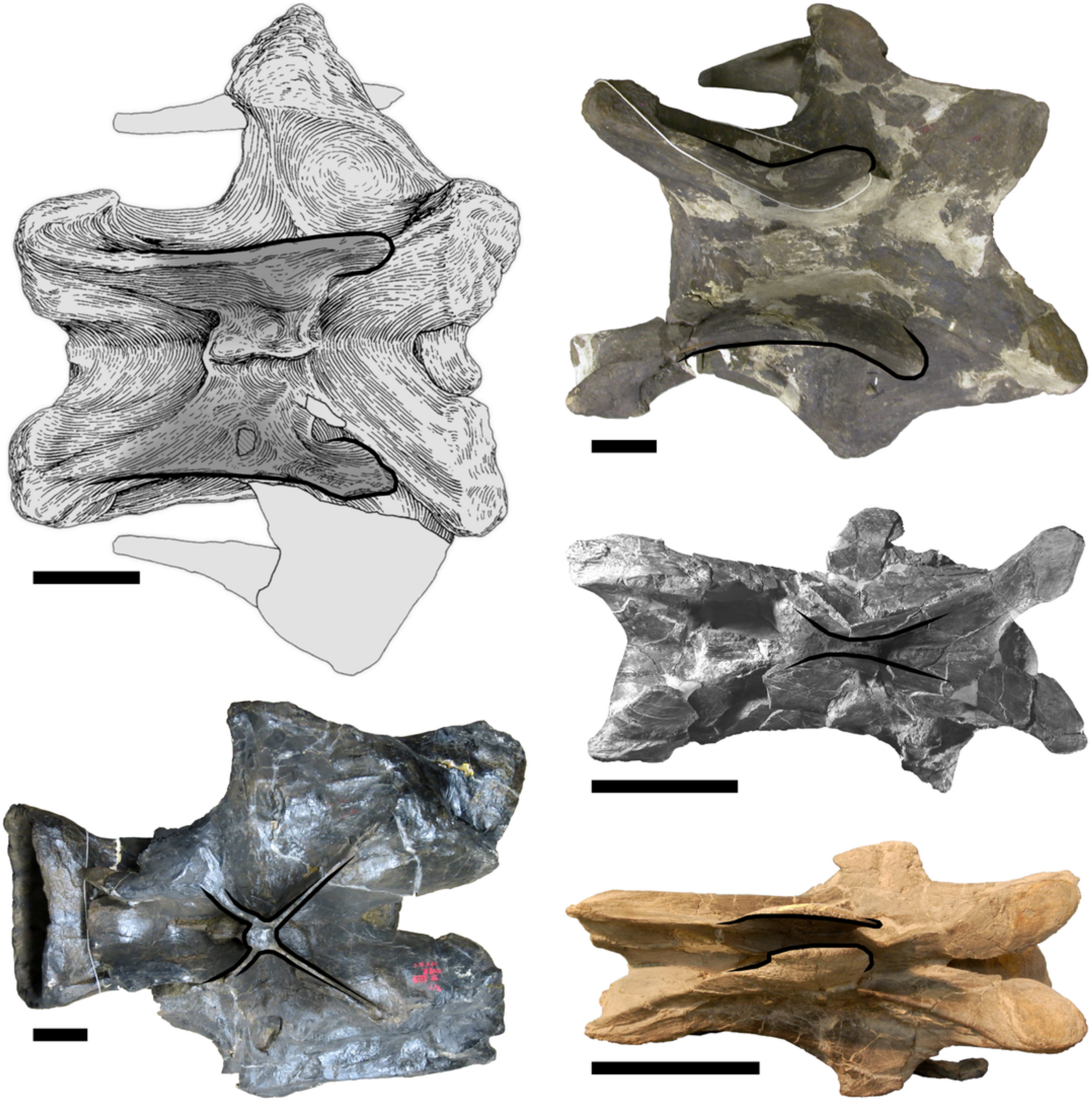

Figure 5

Giraffatitan brancai lectotype MB.R.2180, fifth cervical vertebra.

Giraffatitan brancai lectotype MB.R.2180, fifth cervical vertebra. Top row: left lateral view. Second row: dorsal view, with anterior to the right. Third row (from left to right): anterior, right lateral and posterior views. Bottom row: ventral view, with anterior to the right. Scale bar = 500 mm.

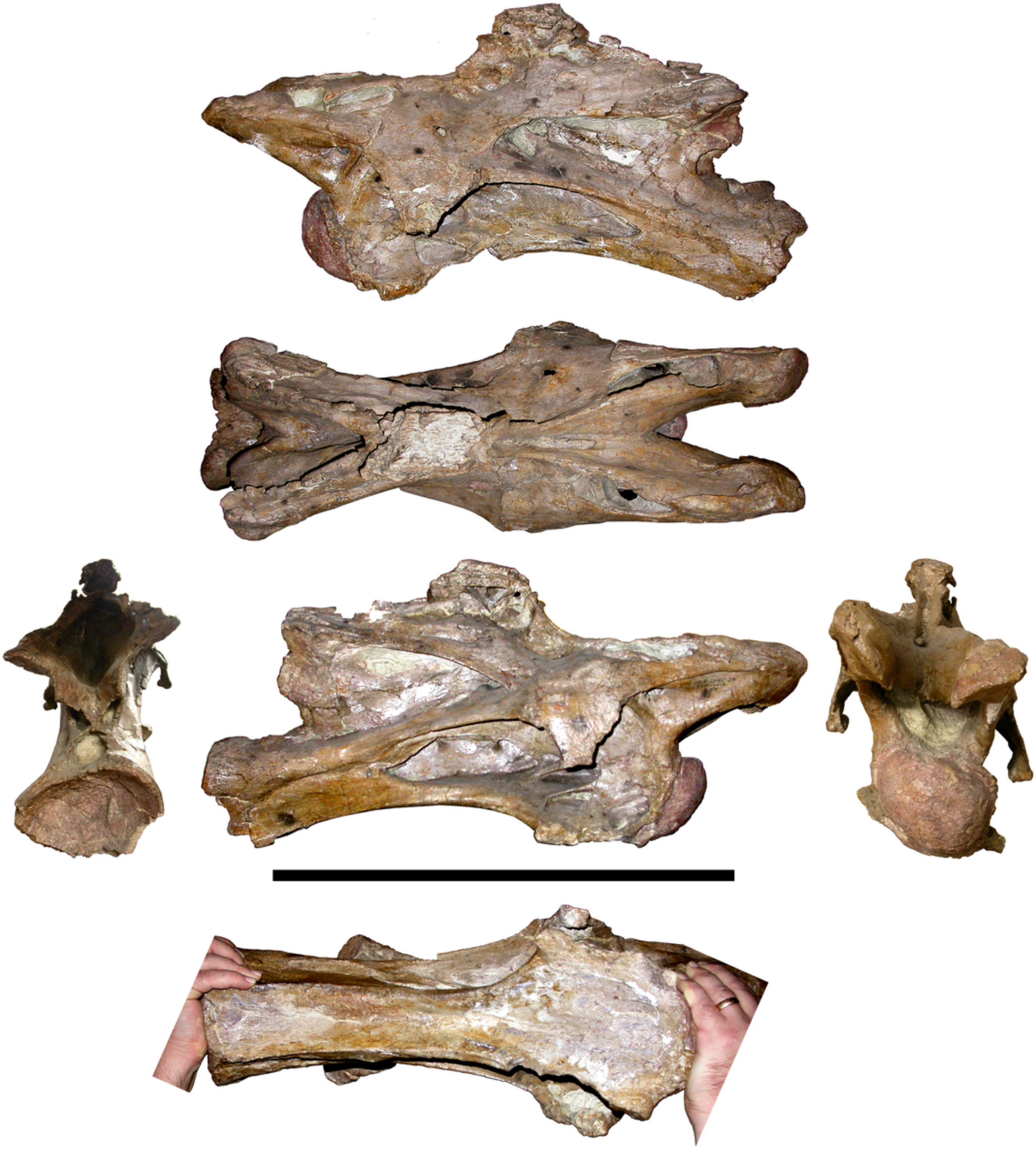

Figure 6

Barosaurus lentus holotype YPM 429, Vertebra Q (C?13).

Barosaurus lentus holotype YPM 429, Vertebra Q (C?13). Top row: left ventrolateral view. Middle row, from left to right: anterior view, with ventral to the right; ventral view; posterior view, with ventral to the left. Bottom row: right lateral view, inverted. Inset shows diapophyseal facet on right side of vertebra, indicating that the cervical ribs were unfused in this individual despite its great size. Note the broad, flat prezygapophyseal facet visible in anterior view. Scale bar = 500 mm.

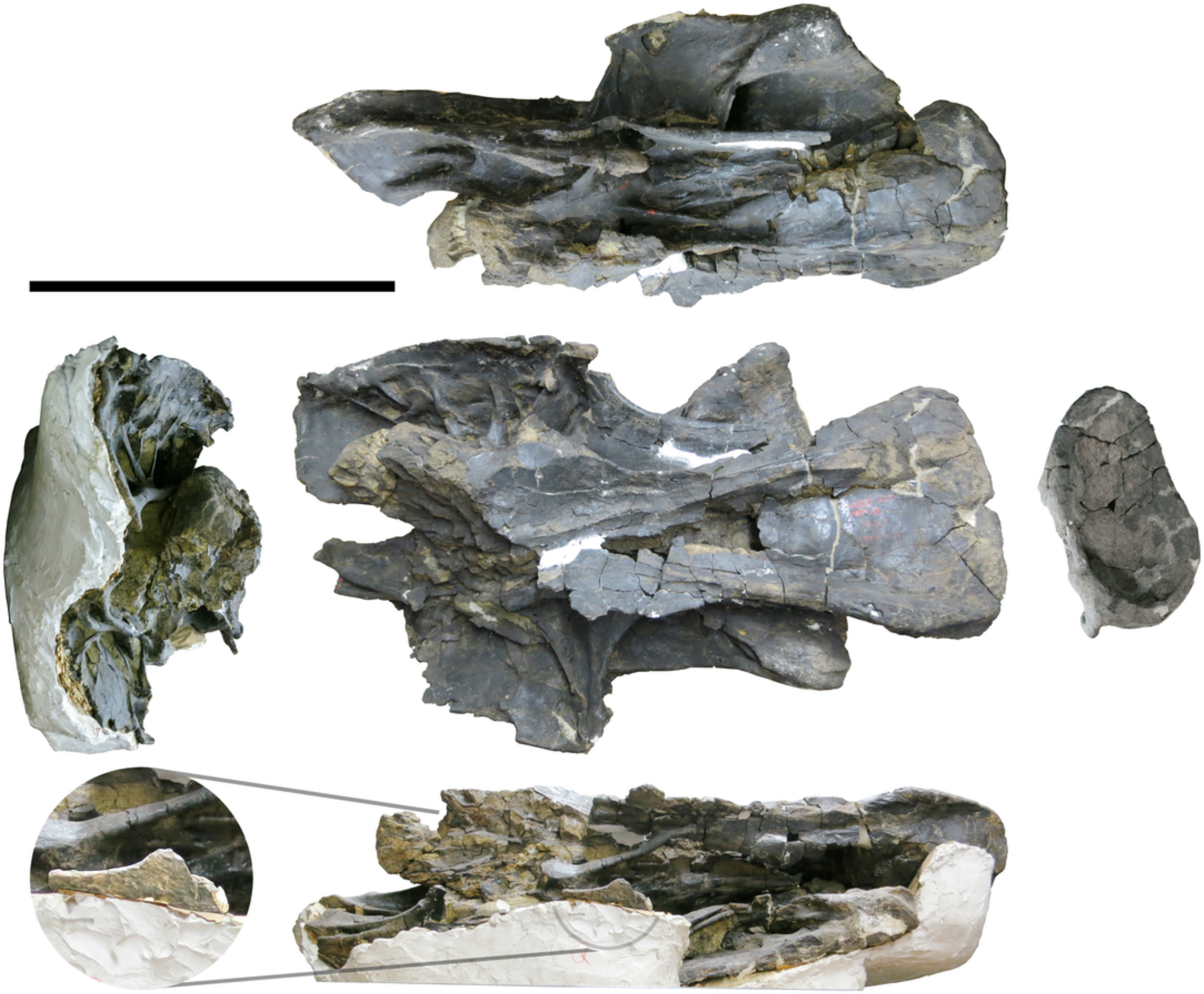

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Figure 7

Barosaurus lentus holotype YPM 429, Vertebra S (C?12).

Barosaurus lentus holotype YPM 429, Vertebra S (C?12). Left column from top to bottom: dorsal, right lateral and ventral views; right column: anterior view. Inset shows displaced fragment of broken prezygapophysis. Note the narrow span across the parapophyses in ventral view. Scale bar = 500 mm.

Figure 8

Barosaurus lentus holotype YPM 429, cervical vertebrae in ventral view.

Barosaurus lentus holotype YPM 429, cervical vertebrae in ventral view. From top to bottom: vertebra R (from Lull 1919: plate II), vertebra Q, vertebra S. Probably from more posterior to more anterior. Scale bar = 500 mm.

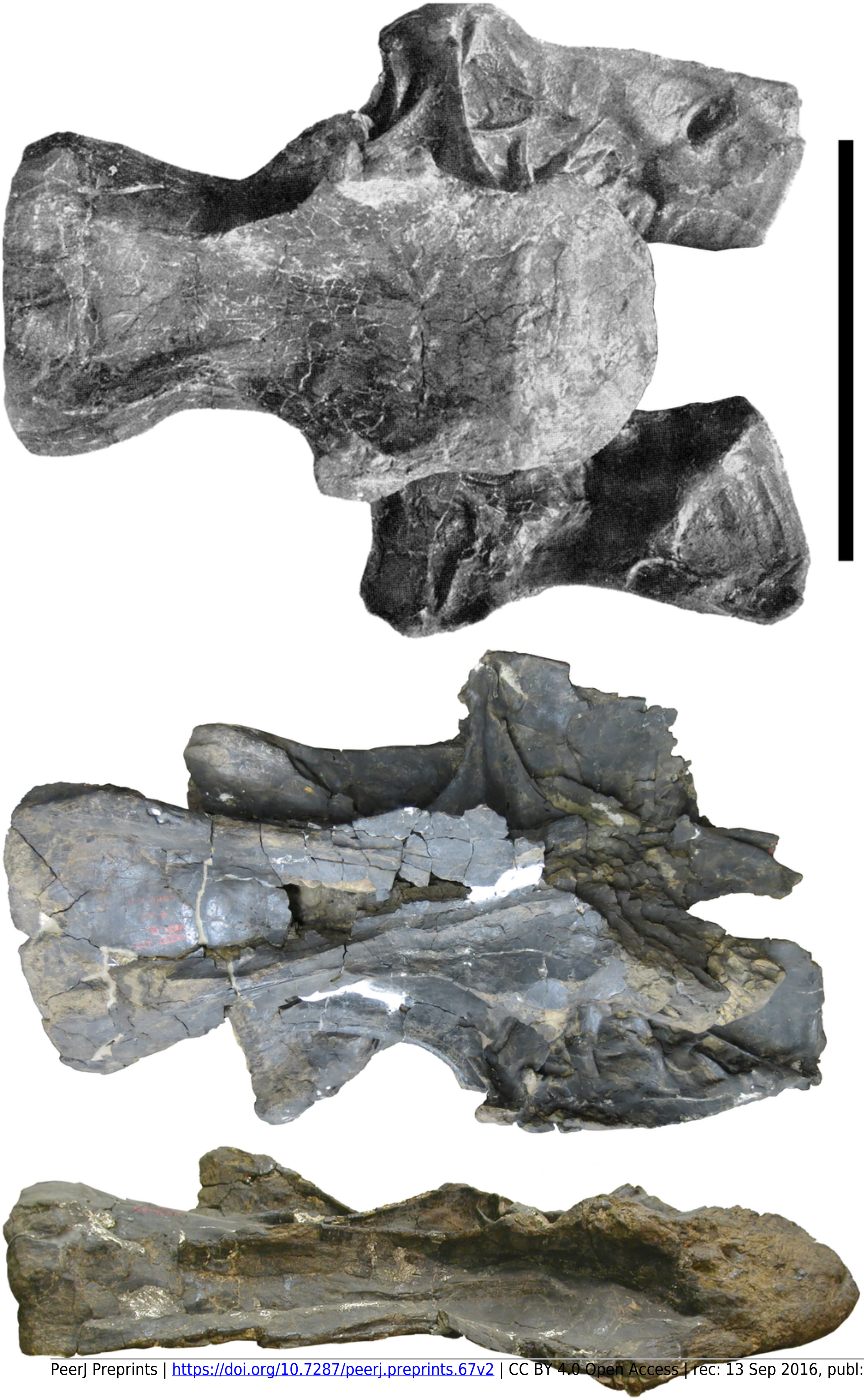

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Figure 9

Partial restoration of the *Barosaurus lentus* holotype YPM 429.

Partial restoration of the *Barosaurus lentus* holotype YPM 429, cervical vertebra R, approximating its undamaged state by allowing for dorsoventral crushing, shearing and loss of some extremities. Anterior and posterior views scaled to 125% of uncorrected height and 80% of uncorrected width. Dorsal view scaled to 80% of uncorrected width; condyle moved forward and cotyle scaled to 50% of uncorrected width to allow for shearing. Lateral view scaled to 125% of uncorrected height, and sheared backwards 15 degrees. Lateral processes sheered upwards in anterior and posterior views. Metapophyses and postzygapophyses drawn in multiple views based on vertebrae Q and S, and C14–16 of AMNH 6341. Scale bar = 500 mm.

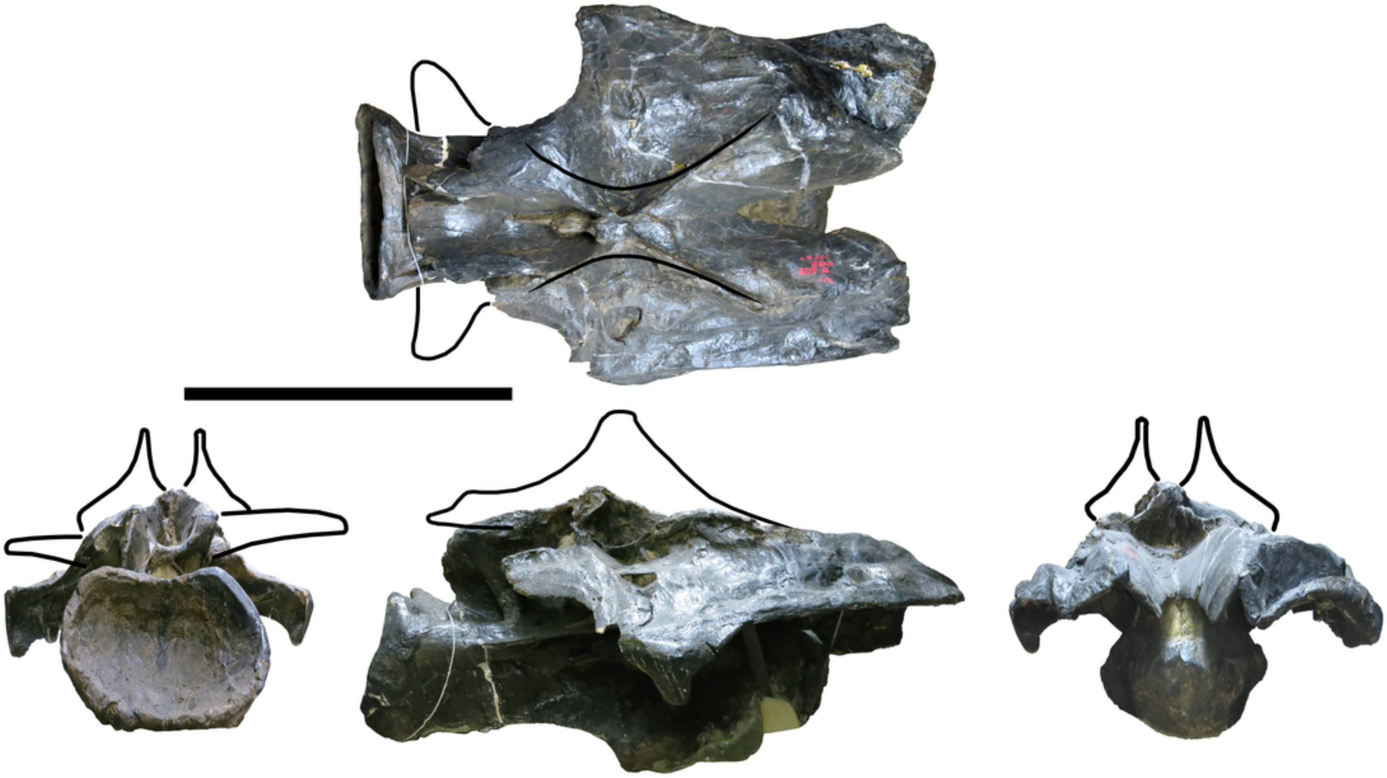

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Figure 10

Barosaurus AMNH 6341, cervical vertebrae in dorsal view, to scale. *Barosaurus* AMNH 6341, cervical vertebrae in dorsal view, to scale. Left column, from top to bottom: C9–C12. Right column, from top to bottom: C14–C16. Extensive image m

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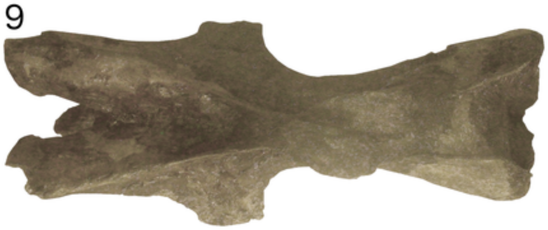

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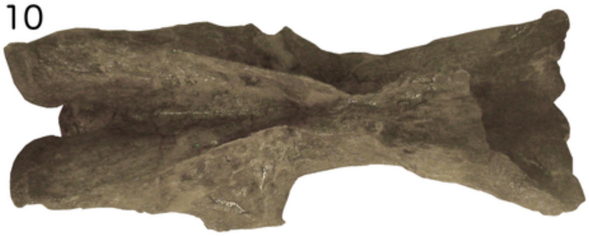

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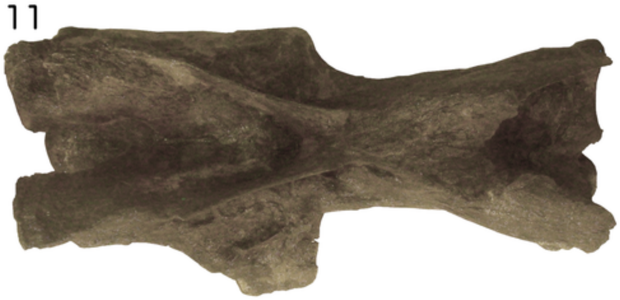

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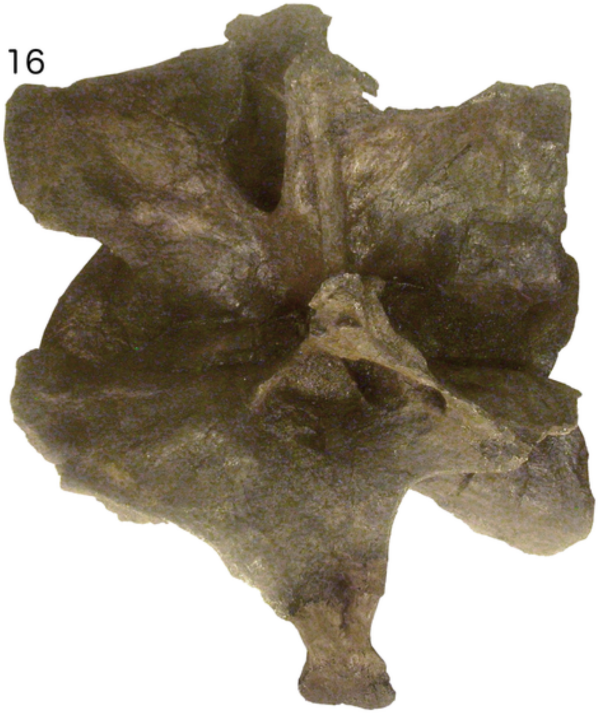

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Figure 11

Barosaurus AMNH 6341, cervical vertebrae C8–C16 in dorsal (where available) and lateral views, to scale.

Barosaurus AMNH 6341, cervical vertebrae C8–C16 in dorsal (where available) and lateral views, to scale. Lateral views except C13 from McIntosh (2005: fig. 2.1). Scale bar = 500 mm.

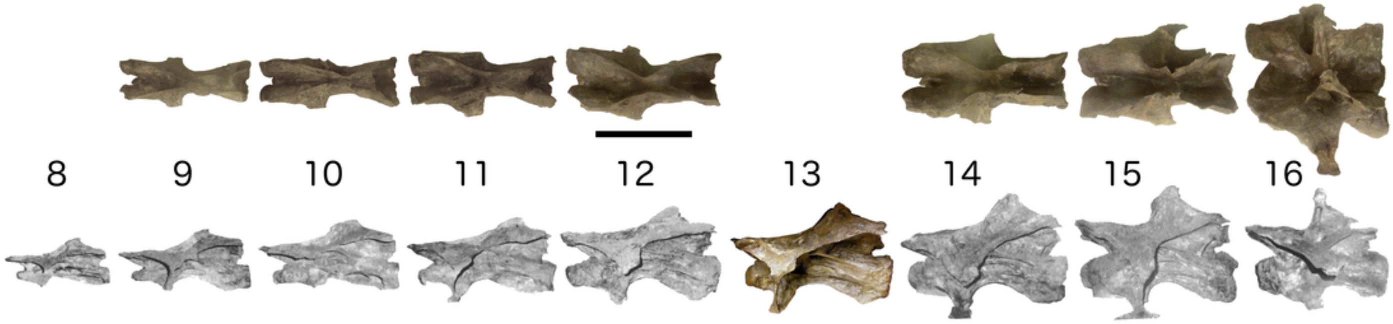

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Figure 12

Similarities between *Barosaurus lentus* holotype YPM 429, cervical vertebra R (C?15) and referred specimen AMNH 6341, C15.

Similarities between *Barosaurus lentus* holotype YPM 429, cervical vertebra R (C?15, left) and referred specimen AMNH 6341, C15 (right), scaled to same total length. Green brackets show width of prezygapophyseal rami, omitting apparent reconstruction on left anterolateral corner of YPM 429. Red outlines indicate margins of diapophyseal wings. Blue outlines show posterior fillets of diapophyseal wings. Orange "X" on AMNH 6341 indicates base of metapophyses, extended from prezygadiapophyseal and postzygadiapophyseal laminae and forming a diagonal cross similar to that of vertebra R. Prezygapophyseal facets of AMNH 6341 highlighted in yellow: the right facet is fairly clear in the photograph (see Figure 10); the exact margin of the left facet is less certain. Zygapophyseal facets cannot be directly recognised in vertebra R due to poor preservation and overzealous reconstruction. Scale bars = 500 mm.

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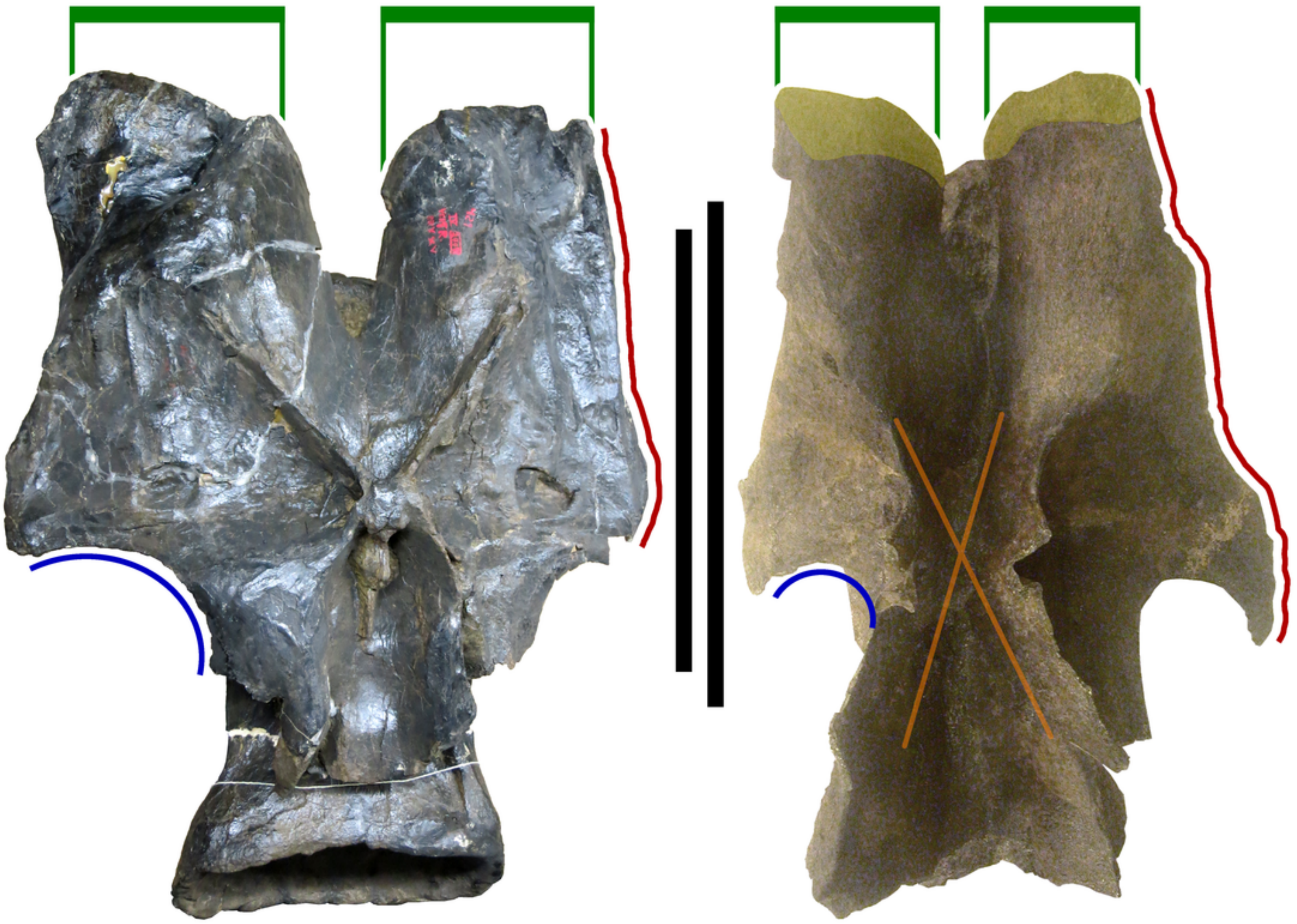

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Figure 13

Attachments of the lateral flexor muscles of the neck in *Kaatedocus* and *Barosaurus*.

Attachments of the lateral flexor muscles of the neck in *Kaatedocus* and *Barosaurus*. On the left, C11 of *Kaatedocus siberi* holotype SMA 0004 (traced from Tschopp and Mateus 2012: fig. 10C2) in dorsal (top) and right lateral (bottom) views, with simplified versions of the lateral flexor muscles included, based on those of birds (see Wedel and Sanders 2002, and Taylor and Wedel 2013). The M. longus colli dorsalis and M. cervicalis ascendens insert together on the epipophysis (= torus dorsalis of birds), and the M. flexor colli lateralis and M. longus colli ventralis (ventral and medial, not shown) insert together on the cervical rib. The pre-epipophysis (*sensu* Tschopp and Mateus 2012) and the head of the cervical rib may have served as expanded attachments for M. cervicalis ascendens and M. flexor colli lateralis, respectively. The actual muscles were probably much more complex than those drawn here, with numerous slips connecting multiple vertebrae: for a similar condition in birds, see Zweers et al. (1987) and van der Leeuw et al. (2001: fig. 2). On the right, C15 of *Barosaurus* AMNH 6341, scaled to the same total length as C11 of *Kaatedocus*. Actual total lengths for the two vertebrae are 840 mm for C15 of *Barosaurus* (McIntosh 2005: table 2.1) and 324 mm for C11 of *Kaatedocus* (Tschopp and Mateus 2012: table 1). In *Barosaurus*, the ansae costotransversariae or cervical rib loops are taller, wider and more posteriorly located than in *Kaatedocus*, providing a larger attachment area for the lateral flexor muscles (blue arcs) and lending them greater mechanical advantage (red lines). In this respect, *Barosaurus* is more similar to *Apatosaurus* than to the narrow-necked *Diplodocus*, although the cervical ribs of *Barosaurus* are much less robust than those of *Apatosaurus*.

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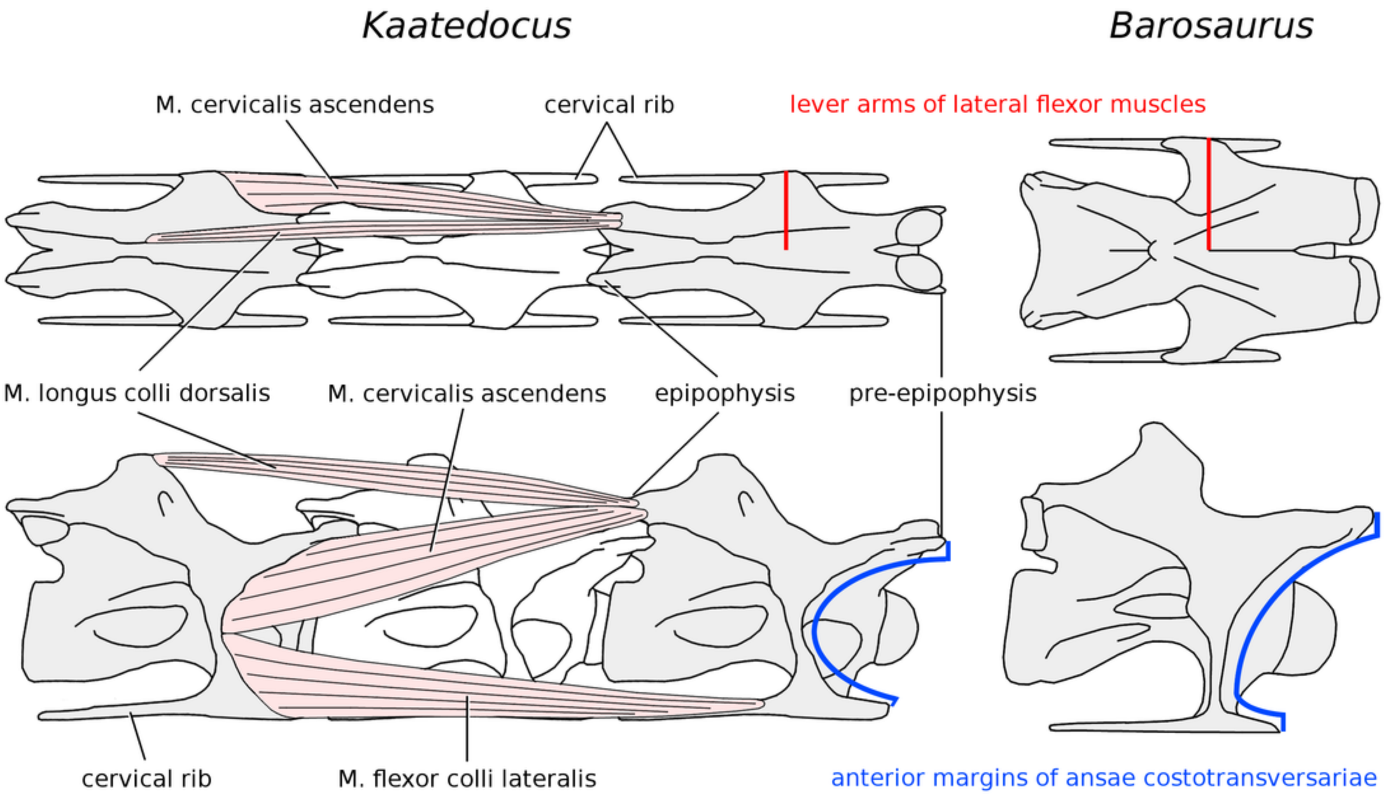
Kaatedocus
Barosaurus
M. cervicalis ascendens
cervical rib
lever arms of lateral flexor muscles
M. longus colli dorsalis
M. cervicalis ascendens
epipophysis
pre-epipophysis
cervical rib
M. flexor colli lateralis
anterior margins of ansae costotransversariae