Why sauropods had long necks; and why giraffes have short necks

The necks of the sauropod dinosaurs reached 15 m in length: six times longer than that of the world record giraffe and five times longer than those of all other terrestrial animals. Several anatomical features enabled this extreme elongation, including: absolutely large body size and quadrupedal stance providing a stable platform for a long neck; a small, light head that did not orally process food; cervical vertebrae that were both numerous and individually elongate; an efficient air-sac-based respiratory system; and distinctive cervical architecture. Relevant features of sauropod cervical vertebrae include: pneumatic chambers that enabled the bone to be positioned in a mechanically efficient way within the envelope; and muscular attachments of varying importance to the neural spines, epipophyses and cervical ribs. Other long-necked tetrapods lacked important features of sauropods, preventing the evolution of longer necks: for example, giraffes have relatively small torsos and large, heavy heads, share the usual mammalian constraint of only seven cervical vertebrae, and lack an air-sac system and pneumatic bones. Among non-sauropods, their saurischian relatives the theropod dinosaurs seem to have been best placed to evolve long necks, and indeed they probably surpassed those of giraffes. But 150 million years of evolution did not suffice for them to exceed a relatively modest 2.5 m.

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INTRODUCTION

The necks of the sauropod dinosaurs were by far the longest of any animal, six times longer than that of the world record giraffe and five times longer than those of all other terrestrial animals. We survey the evolutionary history of long necks in sauropods and other animals, and consider the factors that allowed sauropod necks to grow so long. We then examine the osteology of sauropod necks more closely, comparing their cervical anatomy with that of their nearest extant relatives, the birds and crocodilians, and discussing unusual features of sauropods' cervical vertebrae. Finally we discuss which neck elongation features were absent in non-sauropods, and show why giraffes have such short necks.

Museum Abbreviations

BYU, Earth Sciences Museum, Brigham Young University, Provo, Utah (USA)

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

HMN, Humboldt Museum für Naturkunde, Berlin (Germany)

FMNH, Field Museum of Natural History, Chicago, Illinois (USA)

IGM, Geological Institute of the Mongolian Academy of Sciences, Ulaan Baatar (Mongolia)

ISI, Geology Museum, Indian Statistical Institute, Calcutta (India)

MAL, Malawi Department of Antiquities Collection, Lilongwe and Nguludi (Malawi)

MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (USA)

MIWG, Dinosaur Isle, Sandown, Isle of Wight (UK)

OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma (USA)

PMU, Palaeontological Museum, Uppsala (Sweden**)**

UA, Université d'Antananarivo, Antananarivo (Madagascar)

UJF, University of Jordan Department of Geology Collections, Amman (Jordan**)**

WDC, Wyoming Dinosaur Center, Thermopolis, Wyoming (USA)

ZMNH, Zhejiang Museum of Natural History, Hangzhou (China)

LONG NECKS IN DIFFERENT TAXA

While they reach their apotheosis in sauropods, long necks have evolved repeatedly in several different groups of tetrapods. Although they impose a high structural and metabolic cost, long necks provide evolutionary advantages including an increased browsing range (Cameron and du Toit 2007) and the ability to graze a wide area without locomotion (Martin 1987) and probably played some role in mate attraction (Simmons and Scheepers 1996; Senter 2006; Taylor et al. 2011). Here we survey the longest necked taxa in several groups of extant and extinct animals (Figs. 1, 2).

Extant Animals

Among extant animals, adult bull giraffes can attain 2.4 m (Toon and Toon 2003, p. 399), and no other extant animal exceeds half of this. The typical length of the neck of the ostrich is only 1.0 m (sum of vertebral lengths in Dzemski and Christian 2007, table 1, plus 8% to allow for intervertebral cartilage).

Extinct Mammals

The largest terrestrial mammal of all time was the long-necked rhinoceratoid *Paraceratherium* Forster-Cooper 1911 (= *Baluchitherium* Forster-Cooper 1913, *Indricotherium* Borissiak 1915). The length of its neck can be measured as 1.95 m from the skeletal reconstruction of Granger and Gregory (1936, figure 47), modified here as Fig. 2.1. This length, however, is rather shorter than suggested by the text (pp. 10–20), in which lengths of 39, 39, 36, 29.6 and 18 cm are given for cervicals 1, 2, 4, 6 and 7, even though C2 and C7 are reported as of "size class III". When the lengths of C2 and C7 are multiplied by 1.3 to give lengths of equivalent "size class I" bones (Granger and Gregory 1936, p. 65), their lengths become 50.7 and 23.4 cm. The total length of the preserved cervicals would then be 178.7 cm even though C3 and C5, which were not recovered, are omitted. If these vertebrae are tentatively assigned lengths intermediate between those that preceded and succeeded them (i.e., 43.4 and 32.8 cm) then the total length of all seven centra is 254.9 cm, more than 30% longer than the illustrated length. At any rate, the material available suggests a total neck length in the 2–2.5 m range.

Theropods

At least three lineages of theropod dinosaurs evolved long necks. The lengths of their necks can be estimated from their incomplete remains, though with some uncertainty, as follows.

Therizinosaurus cheloniformis Maleev 1954 is a bizarre, long-necked giant theropod, known from incomplete remains. Measuring from Barsbold (1976, figure 1), its humerus was about 75 cm long. In a skeletal reconstruction of the therizinosauroid *Nanshiungosaurus* Dong 1979 by Paul (1997, p. 145), modified and rescaled here as Fig. 2.2, the neck is 2.9 times the length of the humerus. If *Therizinosaurus* were similarly proportioned, its neck would have been about 2.2 m long.

Another giant theropod, *Deinocheirus mirificus* Osmólska and Roniewicz 1969, is known only from a pair of forelimbs, of which the left humerus is 938 mm long (Osmólska and Roniewicz 1969, p. 9). *Deinocheirus* probably belongs to the long-necked ornithomimid group of theropods (Kobayashi and Barsbold 2006) and thus may have had roughly the same proportions as *Struthiomimus* Osborn 1916. Osborn (1916, pp. 744–745) gives a humerus length of 310 mm for *Struthiomimus*, and a total neck length 2.5 times as long, at 770 mm. If it was similarly proportioned (Fig. 2.3), *Deinocheirus* would have had a neck about 2.35 m long.

A third giant theropod, *Gigantoraptor erlianensis* Xu et al. 2007 belongs to another long-necked group, Oviraptorosauria. Measured from the skeletal reconstruction of Xu et al. (2007, figure 1A), modified here as Fig. 2.4, it appears to have had a neck 2.15 m in length – although this is conjectural as almost no cervical material is known.

Pterosaurs

Although it is often noted in general terms that azhdarchid pterosaurs had long necks (e.g., Howse 1986; Witton and Naish 2008), there are no published numeric estimates of neck length in this group. This is due to the lack of any published azhdarchid specimen with a complete neck (Witton and Habib 2010): *Quetzalcoatlus* specimens at the Texas Memorial Museum may have complete necks, but have been embargoed since the early 1980s (Langston 1981): a monographic description is still awaited. In the absence of a complete neck, all length estimates are uncertain, but it is nevertheless possible to arrive at an approximate length.

The azhdarchid for which the most complete neck has been described is *Zhejiangopterus linhaiensis* Cai and Wei 1994, so we will base our estimates on this species. Cai and Wei (1994, table 7) give the lengths of cervicals 3–7 for three specimens, ZMNH M1323, M1324 and M1328. In all three, C5 is the longest cervical, as is generally true of pterodacyloid pterosaurs including azhdarchids (Howse 1986, p. 323). Cai and Wei (1994) do not give lengths for C1 and C2, stating only that "the atlas-axis is completely fused and extremely short but morphological details are indistinct due to being obscured by the cranium" (p. 183, translation by Will Downs). Their figure 6, a reconstruction of *Zhejiangopterus linhaiensis*, bears this out, showing the atlas-axis as about one quarter the length of C3. Using this ratio to estimate the C1–2 lengths for each specimen, we find by adding the lengths of the individual cervicals that the three specimens had necks measuring approximately 511, 339 and 398 mm. These lengths are 3.60, 4.04 and 4.06 times the lengths of their respective C5s. On average, then, total C1–C7 neck length in known *Zhejiangopterus* specimens was about 3.85 times that of C5.

The azhdarchid *Arambourgiania philadelphiae* (Arambourg 1959) is the largest pterosaur for which cervical material has been described. Its type specimen, UJF VF1, is a single cervical vertebra. It was nearly complete when found, but has since been damaged and is now missing its central portion, but plaster replicas made before the damage indicate the extent of the missing portion. The preserved part of the vertebra was 620 mm long before the damage, and when complete it would have been about 780 mm long (Martill et al. 1998, p. 72). Assuming that the preserved element is C5, as considered likely by Howse (1986, p. 318) and Frey and Martill (1996, p. 240), the length of the C1–C7 region of the neck can be estimated as 3.85 times that length, which is 3.0 m.

The total number of cervical vertebrae in *Zhejiangopterus* is not clear: Cai and Wei (1994) imply that there are seven, and their illustrations (figures 5, 6) indicate that in at least one specimen the vertebral column is complete. However, at least some azhdarchids seem to have have nine cervical vertebrae (e.g., *Phosphatodraco*, Pereda Suberbiola et al. 2003), although the ninth "cervical" bears a long vertically oriented rib and must have contributed to the length of the torso rather than the neck. Bearing this in mind, the total neck length of *Arambourgiania* may have somewhat exceeded 3.0 m. In azhdarchids, C8 may be between 20% and 50% the length of C5 (Pereda Suberbiola et al. 2003, p. 86), which might amount to 16–39 cm in *Arambourgiania.*

Another azhdarchid, *Hatzegopteryx thambema* Buffetaut et al. 2002a, may have been even larger than *Arambourgiania*, but no cervical material is known. Since its skull was much more robust that those of other azhdarchids (Buffetaut et al. 2002a, p. 183), it was probably carried on a proportionally shorter and stronger neck.

Plesiosaurs

As marine reptiles, plesiosaurs benefited from the support of water and so lived under a wholly different biomechanical regime than terrestrial animals. The long necks of elasmosaurid plesiosaurs were constructed very differently from those of sauropods, consisting of many very short cervicals – 76 in the neck of *Albertonectes vanderveldei* Kubo et al. 2012 and 71 in *Elasmosaurus platyurus* Cope 1868 (Sachs 2005, p. 92). Despite their marine lifestyle and very numerous cervicals, elasmosaurids did not attain neck lengths even half those of the longest-necked sauropods. According to Kubo et al. (2012, p. 570), "The approximately 7 m long neck of *Albertonectes* is the longest known for elasmosaurs (equal to 62% of total postcranial length)." Since the neck of *Albertonectes* was found articulated, the reported total neck length presumably includes the invertebral cartilage. Other elasmosaurs may have had equally long necks. The cervical vertebrae of *Elasmosaurus platyurus* holotype ANSP 10081 sum to 610.5 cm, based on individual vertebral lengths listed by Sachs (2005, p. 95). For other plesiosaurs, Evans (1993) estimated that the thickness of intercervical cartilage amounted to 14% of centrum length in *Muraenosaurus* Seeley 1874 and 20% in *Cryptoclidus* Seeley 1892. Using the average of 17% for *Elasmosaurus*, we can estimate its total neck length as 7.1 m (Fig. 2.5). This is within 6% of Leidy's (1870) estimate of "almost twenty-two feet", or about 6.7 m, and approximately equal to the 7-m neck length reported for *Albertonectes* by Kubo et al. (2012).

Sauropods

The necks of sauropod dinosaurs greatly exceeded in length those of all other animals (Wedel 2006a). Furthermore, very long necks evolved in at least four distinct sauropod lineages (Fig. 3).

The basal eusauropod *Mamenchisaurus* Young 1954 is known from several species. One, *M. hochuanensis* Young and Zhao 1972, is known from an individual with a complete neck that is 9.5 m in length (personal measurement, MPT). Another species, *M. sinocanadorum* Russell and Zheng 1993 is known only from skull elements and anterior cervical vertebrae, but by comparing this material with the corresponding elements of *M. hochuanensis*, its neck can be estimated to have been about 12 m long.

The known material of the diplodocid *Supersaurus* Jensen 1985 includes a cervical vertebra whose centrum is 138 cm long. Comparing this with the lengths of similar vertebrae from the closely related *Barosaurus* Marsh 1890, for which much more complete necks are known, suggests a complete neck length in the region of 15 m (Wedel 2007a, p. 197).

Sauroposeidon Wedel et al. 2000a is a large brachiosaurid known only from a sequence of four articulated cervical vertebrae. The whole neck of the related brachiosaurid *Giraffatitan* Paul 1988 is known, and measures 8.5 m. The *Sauroposeidon* cervicals are on average 37% longer than the corresponding vertebrae of its relative, indicating a complete neck length of about 11.5 m.

Puertasaurus Novas et al. 2005 is the largest titanosaur for which cervical material has been described. The single known cervical vertebra is 118 cm in total length, including overhanging prezygapophyses, and its incomplete centrum can be reconstructed after related titanosaurs as having been 105 cm long. Cross-scaling with the related *Malawisaurus* Jacobset al. 1993 yields a total neck length of 9 m.

Table 1 lists a selection of sauropods, mostly known from complete or nearly complete necks,

showing how they vary in length, cervical count, centrum length, cervical rib length, and maximum elongation index.

FACTORS ENABLING LONG NECKS

Discounting the aquatic plesiosaurs, whose necks were subject to different forces from those of terrestrial animals, neck-length limits in the range of two to three meters seem to apply to every group except sauropods, which exceeded this limit by a factor of five. Whatever mechanical barriers prevented the evolution of truly long necks in other terrestrial vertebrates, sauropods did not just break that barrier – they smashed it. Since four separate sauropod lineages evolved necks three or four times longer than those of any of their rivals, it seems likely that sauropods shared a suite of features that facilitated the evolution of such long necks. What were these features?

Absolutely Large Body Size

It is obviously impossible for a terrestrial animal with a torso the size of a giraffe's to carry a 10 m neck. Sheer size is probably a necessary, but not sufficient, condition for evolving an absolutely long neck. Mere isometric scaling would of course suffice for larger animals to have longer necks, but Parrish (2006, p. 213) found a stronger result: that neck length is positively allometric with respect to body size in sauropods, varying with torso length to the power 1.35. This suggests that the necks of super-giant sauropods may have been even longer than imagined: Carpenter (2006, p. 133) estimated the neck length of the apocryphal giant *Amphicoelias fragillimus* Cope 1878 as 16.75 m, 2.21 times the length of 7.5 m used for *Diplodocus*, but if Parrish's allometric curve pertained then the true value would have been $2.21^{1.35} = 2.92$ times as long as the neck of *Diplodocus*, or 21.9 m; and the longest single vertebra would have been 187 cm long.

The allometric equation of Parrish (2006) is descriptive, but does not in itself suggest a causal link between size and neck length. As noted by Wedel et al. (2000b, p. 377), one possible explanation is that, because of their size, sauropods were under strong selection for larger feeding envelopes, which drove them to evolve longer necks.

Quadrupedal Stance

One of the key innovations in the evolution of sauropods was quadrupedality, facilitated by characters such as forelimb elongation, columnar limbs and short metapodials (Wilson and Sereno 1998, p. 24). As well as providing a platform for the evolution of large body size, the stability of the quadrupedal posture also enabled the evolution of longer necks: although progressive elongation displaced the centre of mass forwards from above the hindlimbs, it remained in the stable region between fore and hindlimbs.

Computer modelling shows that theropod dinosaurs such as *Tyrannosaurus rex* Osborn 1905 attained masses of 7 or even 10 tonnes (Hutchinson et al. 2011), and other giant theropods including *Therizinosaurus*, *Deinocheirus* and *Gigantorapor* were probably of comparable size. However, they did not evolve necks as long as those of sauropods with similar mass, probably in part for this reason: the increased moment caused by neck elongation in a biped must be

counteracted by an equal moment caused by a longer or more massive tail, increasing the physiological cost.

Small Head

The heads of sauropods were small relative to body mass. In many clades, they were further lightened by reduced dentition, because unlike other large-bodied animals such as hadrosaurs, ceratopsians and elephants, sauropods did not orally process their food. Sauropod heads were simple cropping devices with a brain and sense organs, and did not require special equipment for obtaining food, such as the long beaks of azhdarchids (Chure et al. 2010, pp. 388–389). The reduction in head weight would have reduced the required lifting power of the necks that carried them, and therefore the muscle and ligament mass could be reduced, allowing the necks to be longer than would have been possible with heavier heads. Other groups of large-bodied animals have not evolved long necks, instead either developing large heads on short necks (ceratopsians, proboscideans, tyrannosaurs) or a compromise of a medium-sized head on a medium-length neck (hadrosaurs, indricotheres)

Numerous Cervical Vertebrae

Many groups of animals seem to be constrained as to the number of cervical vertebrae they can evolve. With the exceptions of sloths and sirenians, mammals are all limited to exactly seven cervicals; azdarchids are variously reported as having seven to nine cervical vertebrae, but never more; non-avian theropods do not seem to have exceeded the 13 or perhaps 14 cervicals of *Neimongosaurus* Zhang et al. 2001, with eleven or fewer being more typical.

By contrast, sauropods repeatedly increased the number of their cervical vertebrae, attaining as many as 19 in *Mamenchisaurus hochuanensis* (Young and Zhao 1972, p. 3–7). Modern swans have up to 25 cervical vertebrae, and as noted above the marine reptile *Albertonectes* had 76 cervical vertebrae. Multiplication of cervical vertebrae obviously contributes to neck elongation.

Elongate Cervical Vertebrae

The shape of cervical vertebrae is quantified by the elongation index (EI), defined by Wedel et al. (2000b, p. 346) as the anteroposterior length of the centrum divided by the midline height of its posterior articular face. As shown in Table 1, EI in sauropods routinely exceeded 4.0, and in some cases exceeded 6.0: *Sauroposeidon* C6 attained 6.1, and *Erketu* Ksepka and Norell 2006 C5 attained 7.0.

A similar degree of elongation is approached by the ostrich, in which C12 can attain an EI of 4.4 (measured from Mivart 1874, figure 29), and by the giraffe, in which the axis can attain an EI of 4.71 (personal measurement of FMNH 34426). It is greatly exceeded by azhdarchid pterosaurs, among which C5 of *Quetzalcoatlus* Lawson 1975 can attain an astonishing 12.4 (measured from Witton and Naish 2008, figure 4c) and an isolated cervical from the Hell Creek Formation might have achieved 15 (measured from Henderson and Peterson 2006, figure 3).

But other long-necked groups are more limited in their elongation of individual vertebrae. *Paraceratherium* seems have been limited to about 3.3 for C2 (measured from Granger and Gregory 1936, figure 7) and much less for the other vertebrae. Elongation indexes of

therizinosaurs such as *Therizinosaurus* probably did not greatly exceed 1.0 (measured for *Nanshiungosaurus* from Dong 1979, figures 1–2); those of ornithomimosaurs such as (probably) *Deinocheirus*, 2.5 (measured for *Struthiomimus* from Osborn 1916, plate XXIV); those of oviraptorosaurs such as *Gigantoraptor*, 2.0 (measured from a photograph by MJW of referred specimen IGM 100/1002 of *Khaan mckennai* Clark et al. 2001). The very numerous vertebrae of *Elasmosaurus* are not very elongate, mostly having an EI around 1.0 and not exceeding about 1.4 (measured from Sachs 2005, figure 4).

Air-Sac System

One limiting factor on neck length is the difficulty of breathing through a long trachea. If the trachea is narrow, then it is difficult to inhale sufficient air quickly – a problem exacerbated by friction of inhaled air against the tracheal wall. But if the trachea is wider, its volume is increased, and a larger quantity of used air in the "tracheal dead space" is re-inhaled in each breath, reducing the oxygen content of each breath.

For this reason, it would be reasonable to expect animals to evolve the shortest possible trachea. However, in one clade – birds – an elongate trachea is not unusual, having evolved in swans (Banko 1960), cranes (Johnsgard 1983), moas (Worthy and Holdaway 2002), birds-of-paradise (Frith 1994) and several other groups. This trend reaches is apotheosis in the trumpet manucode *Phonygammus keraudrrenii* (Clench 1978). In some mature males, the trachea coils back on itself so many times that its total length exceeds 800 mm, nearly three times the total body length of approx. 30 cm. Alone among extant animals, birds are able to cope with such extreme tracheal elongation, due to their very efficient lungs and the large tidal volume of the whole respiratory system on account of the voluminous air-sacs.

It is now well established that sauropods had an air-sac system similar to that of extant birds (Wedel 2003), and most likely a similarly efficient flow-through lung (Wedel 2009). These features would have greatly eased the problem of tracheal dead space, facilitating the evolution of longer necks. The air-sac system, including cervical air-sacs and extensive cervical diverticula running the full length of the neck, would also have served to lighten long necks.

Among other long-necked animals, theropods (including *Therizinosaurus*, *Deinocheirus* and *Gigantoraptor*) and pterosaurs also had had air-sac systems; but the mammals (giraffes, *Paraceratherium*) did not. However, it is unlikely that the evolution of long necks in terrestrial mammals has been limited by tracheal dead space. In a male sperm whale (*Physeter*) with a total body length of 16 m, the length of the head is 5.6 m (Nishiwaki et al. 1963, cited in Cranford 1999, table 1). The largest sperm whales are up to 20 m in total body length (Gosho et al. 1984), which would give a head length of 7 m if these largest individuals scaled isometrically with the 16-m whales. However, the head length of sperm whales is positively allometric and increases with age even in adults (Cranford 1999, p. 1141 and figure 4), so a 20-m adult might well have a head slightly more than 7 m long. As in all cetaceans, the skull of a sperm whale is separated from the ribcage by the highly compressed cervical series. Finally, the nasal airways in sperm whales do not take a direct path from the blowhole to the lungs but describe sinuous curves through the head (Cranford 1999, figures 1 and 3). In a sperm whale with a 7-m head, the internal convolution of the nasal airways and the addition of the trachea spanning from the head to the trunk would give the path from blowhole to lungs a total length of perhaps 9 m, showing that

trachea at least that long are possible without an air sac system.

Vertebral Architecture

Aside from the factors previously discussed, the elongation of sauropod necks was made possible by the distinctive architecture of their cervical vertebrae. The various aspects of their architecture are discussed in detail in the next section.

ARCHITECTURE OF SAUROPOD NECKS

Pneumaticity of Cervical Vertebrae

Not only did sauropods have a soft-tissue diverticular system, but the diverticula often invaded the vertebrae, leaving extensive excavations and other traces (e.g., Janensch 1947; Wedel et al. 2000b). Indeed, it is from the latter that we are able to infer the former.

The air space proportion (ASP) of a bone is the proportion of its volume taken up by pneumatic cavities (Wedel 2005). Dicraeosaurids (*Dicraeosaurus*, *Amargasaurus*, and related taxa) had reduced postcranial pneumaticity compared to other neosauropods, both in terms of the number of presacral vertebrae that were pneumatized, and in the air space proportion (Schwarz and Fritsch 2006). The presacral vertebrae of most neosauropod taxa had ASPs between 0.50 and 0.70 (Table 2) – as lightly built as the pneumatic bones of most birds (Wedel 2005). Basal sauropods outside or near the base of Neosauropoda, such as *Cetiosaurus*, *Jobaria*, and *Haplocanthosaurus*, had much lower ASPs, around 0.40. (ASPs of *Cetiosaurus* and *Jobaria* are estimates based on personal observations of the holotypes and referred specimens).

The effects of pneumatization on the mass of the cervical series have been little explored. The centrum walls, laminae, septae, and struts that comprised the vertebrae were primarily made of compact bone (Reid 1996). The specific gravity (SG) of compact bone is 1.8–2.0 in most tetrapods (Spector 1956), so an element with an ASP of 0.60 (and therefore a compact bone proportion of 0.40) would have an in-vivo SG of 0.7–0.8. Some sauropod vertebrae were much lighter. For example, *Sauroposeidon* has ASP values up to 0.89 and therefore SG as low as 0.2 in some parts of its vertebrae. On the other hand, many basal sauropods had ASPs of 0.30–0.40 and therefore SG of 1.1–1.4.

An important effect of postcranial pneumaticity is to broaden the range of available densities in skeletal construction. Animals without postcranial pneumaticity, including mammals and ornithischian dinosaurs, are constrained to build their skeletons out of bone tissue (SG = 1.8– 2.0) and marrow (SG = 0.93; Currey and Alexander 1985, p. 455). Therefore, the whole-element densities of their postcranial bones will always be between 1.0 and 2.0; they cannot be more dense than bone tissue, nor can they be constructed entirely out of marrow. The pneumatic bones of pterosaurs and saurischian dinosaurs are made of bone tissue (SG = 1.8–2.0) and air space (SG = 0), which allows them to have whole-element densities that are much lower. The lightest postcranial bones for which data are available are those of *Sauroposeidon* and some pterosaurs, which had SG as low as 0.2 (calculated from data in Currey and Alexander 1985). The cranial bones of some birds are even lighter. Seki et al. (2005) reported an SG of 0.05 for the "bone foam" inside the beak of the toucan (*Rhamphastos toco*), and an SG of 0.1 for the entire beak. To

date, this is the lightest form of bone known in any vertebrate.

While the impact of soft-tissue diverticula is more difficult to assess, it is easy to imagine that the density of a typical neosauropod neck may have been less than 0.5 kg/dm^3. Although pneumaticity was undoubtedly an important adaptation for increasing the length of the neck without greatly increasing its mass, a longer neck remains more mechanically demanding than a shorter neck of the same mass, because that mass acts further from the fulcrum of the cervicodorsal joint, increasing the moment that must be counteracted by the epaxial tension members. Also, longer trachea and blood vessels cause physiological difficulties: weight support is only one of the problems imposed by a long neck.

While pneumaticity may be necessary for the development of a long neck, it is clearly not sufficient: while three groups of theropods, all pneumatic, evolved necks in the 2–2.5 m range, and pneumatic pterosaurs attained 3 m, these remain well short of even the less impressive sauropod necks.

Extent of Soft-Tissue relative to Size of Vertebrae

In most extant vertebrates including birds and crocodilians, the diameter of the neck is three or four times that of the cervical vertebrae that form its core. Even in long, thin-necked animals such as the ostrich, the muscular part of the neck is twice as wide and 2.3 times as tall as the enclosed vertebra (Fig. 4.1), and if the trachea and skin and included the soft-tissue is included the dorsoventral thickness of the neck is fully 3.3 times that of the vertebra alone (Dzemski and Christian 2007, figure 2). (In the caption to Wedel [2003, figure 2], from which Fig. 4.1 of the present paper is modified, the small airspace ventral to vertebra was misidentified as the trachea. In fact it is a complex of diverticula around the carotid arteries.)

If the necks of sauropods were as heavily muscled as those of ostriches, then they would have appeared in cross section as shown in Fig. 4.2. But life restorations of sauropods going back to the 1800 have been unanimous that this cannot have been the case in sauropods, as such over-muscled necks would have been too heavy to lift; and the various published reconstructions of sauropod neck cross sections (e.g., Paul 1997, figure 4; Schwarz et al. 2007, figure 7, pp. 8A, 9E) all agree in making the total diameter including soft-tissue only 105–125% that of the vertebrae alone.

This is a consequence of scaling, which makes it impossible for sauropod necks to be similar to those of ostriches. Consider an ostrich neck scaled up by a linear factor of L. The weight exerted by the neck is proportional to L^3 but the cross-sectional area of the bracing members is proportional to only L^2. Stress is force/area, which is proportional to $L^3/L^2 = L$, so the stress on the bracing members that support the neck varies linearly with L. (The weight of the neck acts at a distance proportional to L from the torso, and the bracing members acts at a distance proportional to L above the neck-torso articulation, so these factors cancel out of the balancing moment equation.) Since isometric similarity is precluded the necks of sauropods had to be re-engineered in order to attain such great sizes. Can that have been done by *reducing* the amount of muscle?

In fact, comparing the restored neck of a sauropod with that of an ostrich scaled to the same body size, it is apparent that the sauropod neck has not so much reduced the size of the neck

muscles as increased the size of the cervicals vertebrae themselves (Fig. 4.3): they are much larger compared to the torso than in the ostrich. Simply increasing the size of the vertebrae would not be a good strategy for neck support, because bone is the densest material in the body apart from tooth enamel and dentine. But as noted above, sauropod vertebrae were very pneumatic, typically consisting of 60% air. In effect, sauropods inflated their vertebrae within the muscular envelope of the neck, moving the bone, muscle and ligament away from the centre so that they acted with greater mechanical advantage: higher epaxial tension members, lower hypaxial compression members, and more laterally positioned paraxials.

Muscle Attachments

In extant animals, the mechanically significant soft tissues of the neck (muscles, tendons and ligaments) can be examined and their osteological correlates identified. In extinct animals, except in a very few cases of exceptional preservation, only the fossilized bones are available: but using extant animals as guides, osteological features can be interpreted as correlates of the absent soft tissue, so that the ligaments and musculature of the extinct animal can be tentatively reconstructed (Bryant and Russell 1992; Witmer 1995). In order to do this for sauropods, it is necessary first to examine their extant outgroups, the birds and crocodilians.

In all vertebrates, axial musculature is divided both into left and right sides and into epaxial and hypaxial (i.e., dorsal and ventral to the vertebral column) domains, yielding four quadrants. In birds, the largest and mechanically most important epaxial muscles (M. longus colli dorsalis and M. cervicalis ascendens) insert on the epipophyses of the cervical vertebrae – that is, distinct dorsally projecting tubercles above the postzygapophyses. The large hypaxial muscles (M. flexor colli lateralis, M. flexor colli medialis, and M. longus colli ventralis) insert on the cervical ribs (Fig. 5; Baumel et al. 1993; Tsuihiji 2004). The osteology of the cervical vertebrae makes mechanical sense; the major muscle insertions are prominent osteological features located at the four "corners" of the vertebrae (Fig. 6.1). Non-avian theropods resembled birds in this respect, having prominent epipophyses and sizable cervical ribs, which point in the four expected directions (Fig. 6.2).

The cervical architecture is rather different in crocodilians, and in non-archosaurian diapsids such as lizards, snakes, ichthyosaurs and plesiosaurs: there are no epipophyses, and the main epaxial neck muscles are the Mm. Interspinales, which attach to the neural spines rather than to epipophyses (Fig. 6.3). In most sauropods, the cervical vertebrae do have epipophyses, but the neural spines are as prominent or more so (Fig. 6.4). In this respect, sauropod osteology is intermediate between the conditions of crocodilians and birds – so the widely recognized similarity of sauropod cervicals to those of birds (e.g., Wedel and Sanders 2002; Tsuihiji 2004), while significant, should not be accepted unreservedly. Since the prominent neural spine serves as the primary attachment site for epaxial muscles in most theropod outgroups, the condition in birds and other theropods is derived; that of sauropods retains aspects of the primitive condition.

Although sauropods shared a common bauplan, their morphological disparity was much greater than has usually been assumed (Taylor and Naish 2007, pp. 1560–1561). This disparity is particularly evident in the cervical vertebrae (Fig. 7). Those of *Apatosaurus* Marsh 1877, for example, are anteroposteriorly short and dorsoventrally tall, and have short, robust cervical ribs mounted far ventral to the centra; the cervical centra of *Isisaurus colberti* Jain and

Bandyopadhyay 1997 are even shorter anteroposteriorly, but have more dorsally located cervical ribs; by contrast, the cervical vertebrae of *Erketu ellisoni* Ksepka and Norell 2006 are relatively much longer and lower, and have long, thin cervical ribs mounted only slightly ventral to the centra, which are sigmoid rather than cylindrical. Towards the middle ground of these extremes fall the cervical vertebrae of *Giraffatitan* which are anteroposteriorly longer and dorsoventrally shorter than those of *Apatosaurus*, but not as anteroposteriorly long or as dorsoventrally short as those of *Erketu*. In light of the demanding mechanical constraints that were imposed on sauropods, it is surprising that their necks vary so much morphologically, with different lineages having evolved dramatically different solutions to the problem of neck elongation and elevation.

Interpretation of sauropods as living animals is made especially difficult by the lack of good extant analogues. Among animals with long necks, giraffes, camels, and other artiodactyls have very different cervical osteology and (we assume) myology, and even the longest of their necks, at about 2.4 m, only one sixth the length attained by some sauropods. Birds are phylogenetically closer to sauropods, and some birds (e.g., swans and ostriches) have proportionally very long necks. Furthermore, the presence in most sauropods of epipophyses similar to those of birds suggests that sauropods were myologically similar to birds. However, the small absolute size of birds means that the forces acting on their necks are so different that we can't assume that sauropod necks functioned in the same ways – just as the problems involved in flight through air for high-Reynolds number fliers such as birds are very different than than they are for low-Reynolds number fliers such as fruit-flies, whose aerodynamics are dominated by friction drag rather than form drag.

Because sauropods were so much bigger than their relatives, and their necks so much longer, mechanical considerations in the construction of their necks were significantly more important than in their outgroups. Furthermore, the great size and shape disparity between sauropods and their outgroups means that interpretations of cervical soft-tissue anatomy in sauropods cannot be based purely on the extant phylogenetic bracket method: this alone would be no more informative than trying to determine the anatomy of elephants from that of manatees and hyraxes.

With all these caveats in mind, the best extant analogues for sauropod necks nevertheless remain those of birds: they are the only extant animals that share with sauropods epipophyses above their postzygapophyses, pronounced cervical ribs, and pneumatic foramina (Fig. 6.1, 6.4). The first two of these features were inherited from a common saurischian ancestor. The foramina seem to have been independently derived in birds, but this was possible because air sacs and soft-tissue pneumatic diverticula were likely present in the common saurischian ancestor (Wedel 2006b, 2007b). These observations enable us to draw conclusions about sauropod neck soft tissue beyond what the extant phylogenetic bracket would allow. Specifically, the epipophyses are osteological correlates of the M. longus colli dorsalis and M. cervicalis ascendens epaxial muscles, which must therefore have been present in sauropods, although we can not conclude from this that they were necessarily the dominant epaxial muscles as they are in birds.

Neural Spines

The neural spines and epipophyses of sauropods both anchored epaxial muscles, but as they were differently developed in different taxa, they were probably of varying mechanical importance in different taxa. For example, based on their relative heights, epipophyses probably

dominated neural spines in *Apatosaurus* (Fig. 7.1) but neural spines may have dominated in *Isisaurus* Wilson and Upchurch 2003 and *Giraffatitan* (Fig. 7.3, 7.4). In some sauropods, including *Erketu* and *Mamenchisaurus*, which were proportionally long-necked even by sauropod standards, the neural spines are strikingly low, and the epipophyses no higher – a surprising arrangement, as low spines would have reduced the lever arm with which the epaxial tension members worked. Among these sauropods with low neural spines, some have rugose neurapophyses with spurs directed anteriorly and posteriorly from the tip of the spine (Fig. 8). These appear either to have anchored discontinuous interspinous ligaments, as found in all birds (see Wedel et al. 2000b, figure 20), or to have been embedded in a continuous supraspinous ligament, as found in the ostrich (Dzemski and Christian 2007, pp. 701–702).

In some sauropods, the cervical neural spines are bifid (i.e., having separate left and right metapophyses and a trough between them). This morphology appears to have evolved at least five times (in *Mamenchisaurus*, flagellicaudatans, *Camarasaurus* Cope 1877, *Erketu* and *Opisthocoelicaudia* Borsuk-Bialynicka 1977) with no apparent reversals (Wedel and Taylor, in review). This morphology, then, seems to have been easy for sauropods to gain, but difficult or perhaps impossible to lose. Bifid cervical vertebrae are extremely uncommon in other taxa, and among extant animals they are found only in ratite birds, e.g., *Rhea americana* Linnaeus 1758 (Tsuihiji 2004, figure 2B), *Casuarius casuarius* Brisson 1760 (Schwarz et al. 2007, figure 5B) and *Dromaius novaehollandiae* Latham 1790 (Osborn 1898, figure 1). It has often been assumed that in sauropods with bifid cervical spines, the intermetapophyseal trough housed a large ligament analogous to the nuchal ligament of artiodactyl mammals (e.g., Janensch 1929, plate 4; Alexander 1985, pp. 13–14; Wilson and Sereno 1998, p. 60). Such an arrangement seems unlikely, as lowering the ligament into the trough would reduce its mechanical advantage; however, this is similar to the arrangement seen in *Rhea americana*, in which branches of the "nuchal ligament" attach to the base of the trough (Tsuihiji 2004, figure 3). More direct evidence is found in ligament scars in the troughs of some diplodocids: these can be prominent, as in the doorknob-sized attachment site in the *Apatosaurus* sp. cervical OMNH 01341 (Fig. 9.1).

However, ligament cannot have filled the trough as envisaged by Alexander (1985, figure 4C), because pneumatic foramina are often found in the base of the troughs of presacral vertebrae, for example in the cervicals of *Apatosaurus* (Fig. 9.1) and the dorsal vertebrae of *Camarasaurus* sp. CM 584 (Fig. 9.2). In some specimens, a ligament scar and pneumatic foramen occur together in the intermetapophyseal trough (Fig. 9.1; Schwarz et al. 2007, figure 6E). Pneumatic diverticula are sometimes found between the centropostzygapophyseal laminae even in sauropods with non-bifid spines, as shown by the isolated brachiosaurid cervical MIWG 7306 from the Isle of Wight (Naish 2008), so the presence of soft-tissue diverticula in this location is probably primitive for Neosauropoda at least.

One possible advantage of bifid spines would be to increase the lateral leverage of the ligaments and muscles that attach to the metapophyses, enabling them to contribute to lateral stabilisation and motion as well as vertical. A cantilevered beam, which is what a sauropod neck is in mechanical terms, requires only a single dorsal tension member to stabilize it vertically, but two (one on each side) to stabilize it horizontally. A sauropod neck that was supported from above only by a single midline tension member would need additional horizontal stabilization from muscles and ligaments not directly involved in support.

Whatever the advantages of bifid spines, they were clearly not indispensable, as some sauropod lineages evolved very long necks with unsplit spines (e.g., brachiosaurids, culminating in *Sauroposeidon*, and most titanosaurs, including the very long-necked *Puertasaurus*). Even in taxa that do have bifid spines, they are rarely split through the whole series: for example, the first eight cervicals of *Barosaurus* do not have bifid spines (McIntosh 2005; MJW, pers. obs). Even in *Camarasaurus lewisi* BYU 9047, in which every postaxial cervical vertebra is at least partially bifid (McIntosh et al. 1996b), the bifurcation is very slight in the anterior cervicals and probably of little mechanical consequence. If bifid spines conferred a great advantage, they would presumably be found throughout the neck – although the importance of stability, and the difficulty of attaining it, is greater in the posterior part of the neck, which bears greater forces than the anterior part. Since bifid spines always occur together with unsplit spines, it seems likely that however they were used mechanically, it was probably not radically different from neural spine function in vertebrae with unsplit spines.

Epipophyses

As noted above, the epipophyses are the insertion points of the largest and longest epaxial muscles in birds, whereas in crocodilians the epipophyses are non-existent, and no major muscles insert above the postzygapophyses (Tsuihiji 2004). Epipophyses are found in most, though not all, sauropods and theropods. For example, they are absent in the titanosaurs *Malawisaurus* (pers. obs., MJW; Gomani 2005, figure 8) and *Isisaurus*, (Fig. 7.3); but their presence in other titanosaurs such as *Rapetosaurus* Curry Rogers and Forster 2001 (Curry Rogers and Forster 2001, figure 3A) and *Saltasaurus* Bonaparte and Powell 1980 (Powell 1992, figure 5) and in outgroups such as *Giraffatitan* (Fig. 7.4) and *Camarasaurus* (Osborn and Mook 1921, plate LXVII, figure 9; McIntosh et al. 1996a, figure 29) indicates that their absences in *Malawisaurus* and *Isisaurus*, if not due to damage to the material, represent secondary losses.

The existence of epipophyses on the cervical vertebrae of most sauropods, together with those in theropods and birds, suggests that epaxial muscles were inserting above the postzygapophyses at least by the origin of Saurischia. Epipophyses are also known in basal ornithischians, e.g., *Lesothosaurus* Galton 1978 (Sereno 1991, figure 8A) and *Heterodontosaurus* Crompton and Charig 1962 (Santa Luca 1980, figure 5A), and also in the basal pterosaur *Rhamphorhynchus* Meyer 1846 (Bonde and Christiansen 2003, figures 6–9), suggesting that these insertion points were in use at the base of Dinosauria and possibly Ornithodira.

In sauropods, the size and location of the epipophyses is variable: in C8 of *Giraffatitan*, the epipophyses are approximately half as high above the centrum as the neurapophysis (Fig. 7.4); in anterior cervicals of *Erketu*, the epipophyses are equally as high as the tips of the neural spines (Fig. 7.5), although the spines are higher in posterior cervicals. It is possible that in the posterior cervicals of some *Apatosaurus ajax* Marsh 1877 specimens, the epipophyses are higher than the metapophyses (Fig. 7.1), but it is difficult to be sure as the vertebrae that seem to most closely approach this condition are at least partly reconstructed in plaster (Barbour 1890, figure 1). In any event, it is clear from preserved sequences of *Apatosaurus* cervicals (Gilmore 1936, plate XXIV; Upchurch et al. 2005, plate 1) that in this genus the neural spines are proportionally higher relative to the epipophyses in the anterior cervicals than in the posterior. The trend is opposite in *Erketu*, in which the epipophyses increasingly dominate neural spines anteriorly. This further

demonstrates the variety of different mechanical strategies used by different sauropods to support their long necks. In those sauropods without ostensible epipophyses, it can not necessarily be concluded that muscles did not insert above the postzygapophyses: phylogenetic bracketing suggests that they did, but the insertions are not marked by obvious scars or processes and these muscles were probably less important than those attached to the spine.

Cervical Ribs

In extant birds, cervical ribs are the insertion points for the M flexor colli lateralis, M flexor colli medialis and M longus colli ventralis hypaxial muscles (Zweers et al. 1987; Baumel et al. 1993; see also Fig. 5). No bird has cervical ribs long enough to overlap, but the tendons that insert on the cervical ribs do overlap and are free to slide past each other longitudinally. In less derived saurischians, including sauropods, the ventral tendons are ossified into long, overlapping cervical ribs which are secondarily shortened in Diplodocoidea and in Maniraptoriformes, including birds. The null hypothesis is that the long cervical ribs of theropods and sauropods functioned similarly to the short cervical ribs and long tendons of birds, as the insertions of long hypaxial muscles. However, some aspects of muscle insertion in sauropod necks are mysterious and may be illuminated by closer comparisons to their extant relatives.

In birds, ossification (or at least mineralization) of tendon has many functional effects: it (1) restricts tendon deformation; (2) reduces tendon strain at a given stress; (3) accommodates higher load bearing (to a point; see below); and (4) reduces damage to the tendon (Landis and Silver 2002, p. 1153). In general, proportionally longer and thinner tendons are more extensible and allow more elastic recoil, and shorter, thicker tendons are less extensible and provide less elastic recoil (Biewener 2008, pp. 272–274). Mineralization or ossification reduces the extensibility of a tendon, and can allow a long, thin tendon to behave more like a short, thick one. Ossified tendons in the lower limbs of birds are typically found distal to the knee (Hutchinson 2002, p. 1071), where the tendons are constrained to be long and thin by the overall construction of the limb; ossification may be the only viable way for birds to advantageously shift the mechanical properties of these tendons.

The long hypaxial tendons in the necks of sauropod dinosaurs may have been similarly constrained. Ossification of the hypaxial tendons into long cervical ribs may have provided several benefits for sauropods:

- Long tendons move the bulk of the hypaxial neck muscles closer to the base of the neck, which reduces the lever arm of the neck mass. Tendon has a much lower Young's modulus than bone, and reducing the elastic recoil of the hypaxial tendons would have allowed the hypaxial muscles of sauropods to more directly affect the vertebrae to which they were attached. Reduced tendon elasticity is known to improve position control of the involved muscles (Alexander 2002, p. 1009).

- It has been suggested (Wedel et al. 2000b, p. 380) that elongate cervical ribs may have played a role in ventrally stabilizing the neck, i.e., preventing involuntary dorsal extension by contracting antagonistically against the stronger epaxial tension members (which had to counteract gravity in addition to shifting the mass of the neck).

- Stiff cervical ribs would have helped provide lateral stabilization for the neck, which would

have been especially important in taxa with epaxial tension members concentrated on the midline (i.e., those with non-bifid spines) as discussed above.

(It has also been suggested by Martin et al. [1998] that the cervical ribs of at least some sauropods functioned as incompressible ventral bracing members. But this hypothesis is badly flawed – see Wedel et al. 2000b, p. 379–380 and Wedel et al., in prep.)

If either of the first two hypotheses is accurate, it is difficult to understand why diplodocids evolved apomorphically short cervical ribs, especially long-necked forms such as *Barosaurus* and *Supersaurus.* If the primary role of long cervical ribs was in providing lateral stabilization for taxa with midline epaxial tension members, then the need for this stabilization would be reduced in forms with bifid spines, such as diplodocids, which shifted their epaxial tension members laterally as they were attached to the metapophyses. This, however, would raise the question of why other taxa with bifid spines (e.g., *Camarasaurus*) also retained elongate cervical ribs, and in the case of *Mamenchisaurus* apparently evolved apomorphically long cervical ribs (Russell and Zheng 1993, pp. 2089–2090). It may be that these taxa retained their epaxial tension members primarily on the midline, in the intermetapophyseal trough, while diplodocids shifted theirs laterally; but we know from osteological evidence (see above) that at least some diplodocids did have ligaments or muscles anchored within the trough.

Apatosaurus presents a final riddle regarding cervical ribs. Even among diplodocids, it had extraordinary cervical ribs: very short, very robust, and positioned very low, far below the centra on extremely long parapophyses (Fig. 7.1, 7.2), so that the neck of *Apatosaurus* must have been. triangular in cross-section. What function can the ribs have evolved to perform? They were much too short to have functioned efficiently in horizontal or vertical stabilization, and in any case seem over-engineered for these functions. It is tempting to infer that the autapomorphies of the neck in *Apatosaurus* are adaptations for some unique aspect of its lifestyle, perhaps violent intraspecific combat similar to the "necking" of giraffes. Even if this were so, however, it is difficult to see the benefit in *Apatosaurus excelsus* (Marsh 1879a) of cervical ribs held so far below the centrum – an arrangement that seems to make little sense from any mechanical perspective, and may have to be written off as an inexplicable consequence of sexual selection or species recognition.

Asymmetric Elongation of Cervical Ribs and Epipophyses

A central paradox of sauropod cervical morphology is that in the elongation of the cervical ribs, the vertebrae appear better adapted for anchoring hypaxial than epaxial musculature – even though holding the neck up was important and, due to gravity, much more difficult than drawing it down. First, the cervical ribs present a greater area for muscle attachment than the epipophyses do; and second, the much greater length of the cervical ribs in most sauropods enabled the hypaxial musculature to be shifted backwards much further than the epaxial musculature, as the epipophyses are not elongate in any known sauropod. We know that posterior elongation of the epipophyses is developmentally possible in saurischians, because those in the tail of *Deinonychus* Ostrom 1969a are extended to the length of a centrum (Ostrom 1969b, figure 37). Fig. 10 shows the cervical skeleton of *Euhelopus* as it actually is, and reconstructed with speculative muscle attachments that would have been more mechanically efficient: why did sauropod necks not evolve this way? In fact, there are several reasons.

- First, positioning and moving the neck for feeding would have required fine control, and precise movements requires short levers.

- Second, although bone is much stiffer than tendon, it is actually not as strong in tension, so that an ossified tendon is more likely to break under load.

- Third, muscles expand transversely when contracted lengthways. For epaxial muscles in sauropods necks, this expansion would strongly bend ossified epipophyseal tendons, subjecting them to greater stress than simple longitudinal tension. (The same effect would also have caused some bending of cervical ribs, but the lower stresses in ventral musculature would have reduced the effect.)

Short Neural Spines in Long Necks

In many cases, the sauropods with the proportionally longest necks are also those whose necks superficially make the least mechanical sense. It is particularly notable that mamenchisaurids (*Mamenchisaurus* and *Omeisaurus*) have very low neural spines, as does *Erketu* in the preserved, anterior, cervicals. Since excessively long neural spines would impede neck extension by overlapping with each other, as in dicraeosaurids, shorter spines would be advantageous for improving neck flexibility. But these low spines would have reduced the lever arm with which epaxial tension members acted.

A speculative explanation, at least, can be offered. Counter-intuitively, the height above the centrum at which a muscle of given size acts has no effect at all on its ability to move the vertebra through a given arc. Although muscles attached to a short spine need to exert greater force to allow for the shorter lever arm, they correspondingly need contract a shorter distance in order to raise the neck by the same amount. Low neural spines, then, may have been connected by strongly pennate muscles, able to contract very forcefully but only over a short distance.

In an animal adopting this low-spine strategy to neck elongation, the difficulty is simply one of fitting the muscle into the space available. A lower limit to neural spine length is imposed by the volume of muscle needed to produce the range of motion. (Raising the neck is work, and while the force exerted by a muscle is proportional to its cross-sectional area, the work it can do varies with volume, so shorter muscles need a correspondingly larger cross-sectional area.)

Another possibility is that taxa with short spines had shifted almost all of their epaxial muscle attachments to the epipophyses, as with the long dorsal muscles of birds. In birds, the long multisegment epaxial muscles are free to "bowstring" across the dorsal curvature at the base of the neck (van der Leeuw et al. 2001, figure 5). Short neural spines do not indicate poor mechanical advantage for these muscles, because they act at high angles of inclination to the long axis of each vertebra. Tall neural spines increase mechanical advantage of muscles when the vertebrae are held horizontally, but this is unlikely to have been a common posture for sauropods (Taylor et al. 2009).

Homology and Analogy of Vertebral Features

Bony attachment sites for the large cervical muscles have varied along the evolutionary line from basal amniotes to birds (Fig. 11). In extant lizards and crocodilians, as in basal archosaurs (Fig. 11.1), the neural spine is very large and anchors essentially all of the large multisegment

epaxial muscles (Tsuihiji 2005, figure 2), and there are no epipophyses at all. However, in extant birds, as in non-avian theropods (Figs. 11.4, 11.5), the epipophyses are more prominent and significant than the neural spines and serve as insertion points for all of the multisegment dorsal muscles. The very short neural spines serve as the origins of long dorsal muscles running anteriorly from each vertebra, but the only muscles that insert on the spines and adjacent bony ridges are the small and short Mm. interspinales and Mm. intercristales.

In intermediate forms such as sauropods the situation is more complex, as both the neural spines and epipophyses are prominent – to varying degrees in different species. In sauropods with unsplit neural spines, such as *Giraffatitan* (Fig. 11.2), the muscles of the neural spine were presumably significant, and would have acted primarily along the midline of the neck. The muscles of the epipophyses were also present, but because their insertions are positioned laterally, the action of these muscles would have functioned both in support and in lateral movement. In sauropods with bifid neural spines, such as *Camarasaurus* (Fig. 11.3), the muscles inserting on the neural spine were also laterally displaced, so that they as well as the Mm. longus colli dorsalis would have had the dual function of support and lateral motion. In sauropods with bifid spines, then, the one- or two-segment Mm. intercristales and Mm. interspinales shared the function of lateral stabilization and movement with the multisegment Mm. longus colli dorsalis.

It is tempting to imagine an evolutionary pathway in which bifurcation of neural spines was an intermediate step in the evolutionary shift of the insertions of the large multisegment epaxial muscles from the neural spine to the epipophyses. However, this explanation cannot be correct, as bifid spines are not known in taxa along the line to birds – only in sauropods and a few modern birds. This is particularly clear in Fig. 11.4, where a small neural spine remains in the cervical of *Majungasaurus*, but is dominated by epipophyses. The sequence instead seems simply have been one of progressive reduction of the neural spine and enlargement of the epipophyses. The outcome of this evolutionary sequence, as shown in Fig. 11.5, is that from a myological perspective, modern birds have functionally bifid neural spines: that is, their vertebrae have evolved in a way that is analogous with the true bifid spines of sauropods even though it is not homologous.

CONCLUSIONS: WHY GIRAFFES HAVE SUCH SHORT NECKS

Reviewing the characters that facilitate the evolution of long necks, it is apparent that only sauropods have them all (Table 3). Although the necks of giraffes are the longest of any extant animals, they are shorter by a factor of six than those of the longest sauropods, because they have relatively small torsos, relatively large, heavy heads, only seven cervical vertebrae, no air-sac system and no vertebral pneumaticity. Absence of elongated cervical ribs may also impede neck elongation. In defence of giraffes, they are relative latecomers in evolutionary terms: given a few tens of millions more years, it is conceivable that they might overcome some of these disadvantages to evolve longer necks. But in some respects they seem locked into a mammalian pattern that will always prevent them from matching the necks of sauropods: extensive oral processing of food requires a large head with heavy teeth; almost no mammal has evolved more than seven cervical vertebrae; and the mammalian lung has attained a local maximum of efficiency that makes it unlikely ever to evolve into something analogous to the avian flow-through lung, so both and air-sac system and vertebral pneumaticity are precluded.

Similarly, ostriches seem unlikely ever to evolve really long necks, despite the prerequisite small heads and avian lung, simply because they are small bipeds. Birds seem unable to attain sizes exceeding the 500 kg of the "elephant bird" *Aepyornis maximus*, probably because of the tight correlation between adult body size and egg size, and the strong mechanical constraints on the latter: as body size increases, the eggs approach a point at which the shell cannot simultaneously be thick enough to support the egg and thin enough for the hatchling to break out of (Murray and Vickers-Rich 2004, p. 212, Birchard and Deeming 2009).

Some of the other long-necked taxa listed in Table 3 seem to have been better equipped to evolve longer necks. It is impressive the azhdarchid pterosaurs seem likely to have achieved 3m while retaining flight: no doubt their pneumaticity was a key feature in making this possible in spite of their large heads. Nevertheless, the absolute size constraints imposed by flight make it unlikely that pterosaurs would have greatly exceeded this mark even had they survived the end-Cretaceous extinction.

The three theropod clades mentioned above (ornithomimosaurs, therizinosaurs and to a lesser extent oviraptorosaurs) appear to have had small heads, proportionally similar in size to those of sauropods, as well pneumatic systems that invaded their vertebrae. Why did they not evolve necks as long as those of sauropods? Possible reasons include the following:

- All theropods were bipedal, and the demands of bipedal locomotion may have prevented them from evolving the giant body sizes that are required for very long necks.

- The long-necked theropods may not have been under the same selection pressure to evolve long necks as were sauropods. If they were omnivorous, for example, then their use of more nutritious food may have mitigated the need for increased feeding envelopes. Among extant theropods, the ostrich is proportionally long-necked but feeds mostly from the ground (Dzemski and Christian 2007), and so has no selective pressure to evolve a yet longer neck.

- All of the largest long-necked theropods lived in the Late Cretaceous, two of them in the Campanian–Maastrichtian. Had they not died out at the end of the Cretaceous, they might have gone on to attain larger size. On the other hand, sauropods attained large size very quickly in evolutionary terms, with a 104 cm humerus from the late Norian or Rhaetian indicating a *Camarasaurus*-sized sauropod only about ten million years after the first known dinosaurs (Buffetaut et al. 2002b). If theropods did not evolve larger body size in the 150 million years available to them, it seems likely that they did not have the potential to do so.

- Finally, it should be noted that all three of the long-necked theropods discussed above are known from incomplete remains that do not include any informative cervical material. It is possible that neck length was positively allometric in these clades, as in sauropods, and they may have had necks somewhat longer than isometric scaling suggests.

In summary, no other clade has all of the suggested adaptations for long necks that are found in sauropods. Were it not for the end-Cretaceous extinction, non-avian theropods would have been the best candidates for evolving sauropod-like neck lengths, due to the combination of pneumaticity, small heads in some clades. and potential for large body size.

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Neck statistics of some sauropods, chosen because of unusually long, short or complete necks.

Table 1. Neck statistics of some sauropods, chosen because of unusually long, short or complete necks.

Taxon	Neck length (m)	Cervical count	Longest centrum (cm)	Longest cervical rib (cm)	Maximum elongation index			
Mamenchisaurus hochuanensis	9.5	19	73	C11	210	C14	2.9	C6
Mamenchisaurus sinocanadorum	12 est.	19?			≥ 410			
Brachytrachelopan mesai	1.1 est.	12?	10		≤ centrum		≤ 1	
Apatosaurus louisae	5.9	15	55	C11	39	C11	3.7	C4
Diplodocus carnegii	6.5	15	64	C14	48	C11	4.9	C7
Barosaurus lentus	8.5 est.	16?	87	C14	< centrum		5.4	C8
Supersaurus vivianae	15.0 est.	15?	≥ 138		≤ centrum			
Giraffatitan brancai	8.5	13	100	C10	290	C7	5.4	C5
Sauroposeidon proteles	11.5 est.	13?	125	C8	342	C6	6.1	C6
Euhelopus zdanskyi	4.0	17	28	C11	72	C14	4.0	C4

Air Space Proportion (ASP) of sections through sauropod vertebrae.

Air Space Proportion (ASP) of sections through sauropod vertebrae. Measurements are taken from CT sections, photographs, and published images. Sections are transverse unless otherwise noted. Although this dataset is almost three times as large as that reported by Wedel (2005), the mean is the about same, 0.61 compared to 0.60. Abbreviations: C, cervical; Cd, caudal; D, dorsal; P, presacral.

Table 2. Air Space Proportion (ASP) of sections through sauropod vertebrae. Measurements are taken from CT sections, photographs, and published images. Sections are transverse unless otherwise noted. Although this dataset is almost three times as large as that reported by Wedel (2005), the mean is the about same, 0.61 compared to 0.60. Abbreviations: C, cervical; Cd, caudal; D, dorsal; P, presacral.

Taxon	Region		ASP	Source
Apatosaurus	C	condyle	0.69	OMNH 01094
		mid-centrum	0.52	"
		posterior centrum	0.73	"
		cotyle	0.32	"
	C	condyle	0.63	OMNH 01340
		mid-centrum	0.69	"
		cotyle	0.49	"
	C	condyle	0.52	CM 555 C6
		mid-centrum	0.75	"
		posterior centrum	0.59	"
		cotyle	0.34	"
	C	parapophysis	0.6	BYU 11998
	C	cotyle	0.7	BYU 11889
Brachiosaurus	C	condyle	0.55	BYU 12866
		mid-centrum	0.67	"
		posterior centrum	0.81	"
Brachiosauridae	C	mid-centrum	0.89	MIWG 7306
	P		0.65	Naish and Martill (2001, plate 32)
	P		0.85	Naish and Martill (2001, plate 33)
	P		0.85	MIWG uncatalogued
Camarasaurus	C	condyle	0.51	OMNH 01109
		mid-centrum	0.68	"
		cotyle	0.54	"
	C	condyle	0.49	OMNH 01313
		mid-centrum	0.52	"
		cotyle	0.5	"
	D	mid-centrum	0.58	Ostrom and McIntosh (1966, plate 23)
	D	mid-centrum	0.63	Ostrom and McIntosh (1966, plate 23)
	D	mid-centrum	0.71	Ostrom and McIntosh (1966, plate 23)
Chondrosteosaurus	P	centrum (horiz.)	0.7	Naish and Martill (2001, figure 8.5)
Diplodocus	C	condyle	0.56	BYU 12613
		mid-centrum	0.54	"
		posterior centrum	0.66	"
Giraffatitan	C	condyle	0.73	Janensch (1950, figure 70)
	C	condyle (sagittal)	0.57	Janensch (1947, figure 4)
	D	mid-centrum	0.59	Janensch (1947, figure 2)
Haplocanthosauru	C	condyle	0.39	CM 879-7

s

		mid-centrum	0.56	"
		posterior centrum	0.42	"
		cotyle	0.28	"
	D	mid-centrum	0.36	CM 572
Malawisaurus	C	condyle	0.56	MAL-280-1
		mid-centrum	0.62	"
	C	condyle	0.57	MAL-280-4
		mid-centrum	0.56	"
Phuwiangosaurus	C	mid-centrum	0.55	Martin (1994, figure 2)
Pleurocoelus	C	mid-centrum	0.55	Lull (1911, plate 15)
Saltasaurus	D	centrum (horiz.)	0.62	Powell (1992, figure 16)
		mid-centrum	0.55	"
		neural spine (horiz.)	0.82	"
	D	prezygapophysis	0.78	Powell (1992, figure 16)
Sauroposeidon	C	prezyg. ramus	0.89	OMNH 53062
		postzygapophysis	0.74	"
		anterior centrum	0.75	"
Supersaurus	C	mid-centrum	0.64	WDC-DMJ021
Tornieria	C	mid-centrum	0.56	Janensch (1947, figure 8)
	C	posterior centrum	0.77	Janensch (1947, figure 3)
	D	condyle (sagittal)	0.78	Janensch (1947, figure 9)
	Cd	mid-centrum	0.47	Janensch (1947, figure 7)
Sauropoda indet.	C	mid-centrum	0.54	OMNH 01866
	C	posterior centrum	0.46	OMNH 01867
	C	mid-centrum	0.55	OMNH 01882
	MEAN		0.61	

Neck-elongation features by taxon.

Table 3. Neck-elongation features by taxon.

	Absolutely large body size	Quadrupedal stance	Small head	Numerous cervical vertebrae	Elongate cervical vertebrae	Air-sac system	Vertebral pneumaticity
Human							
Giraffe		✔			✔		
Ostrich			✔	✔	✔	✔	✔
Paraceratherium	✔	✔					
Therizinosaurus	✔		✔			✔	✔
Deinocheirus	✔		✔			✔	✔
Gigantoraptor	✔		✔			✔	✔
Arambourgiania					✔	✔	✔
Sauropods	✔	✔	✔	✔	✔	✔	✔

Figure 1

Necks of long-necked non-sauropods, to the same scale.

Necks of long-necked non-sauropods, to the same scale. The giraffe and *Paraceratherium* are the longest necked mammals; the ostrich is the longest necked extant bird; *Therizinosaurus*, *Deinocheirus* and *Gigantoraptor* are the longest necked representatives of the three long-necked theropod clades and *Arambourgiania* is the longest necked pterosaur. *Arambourgiania* scaled from *Zhejiangopterus* modified from Witton and Naish (2008, figure 1). Other image sources as for Fig. 2. Alternating pink and blue bars are one meter in height.
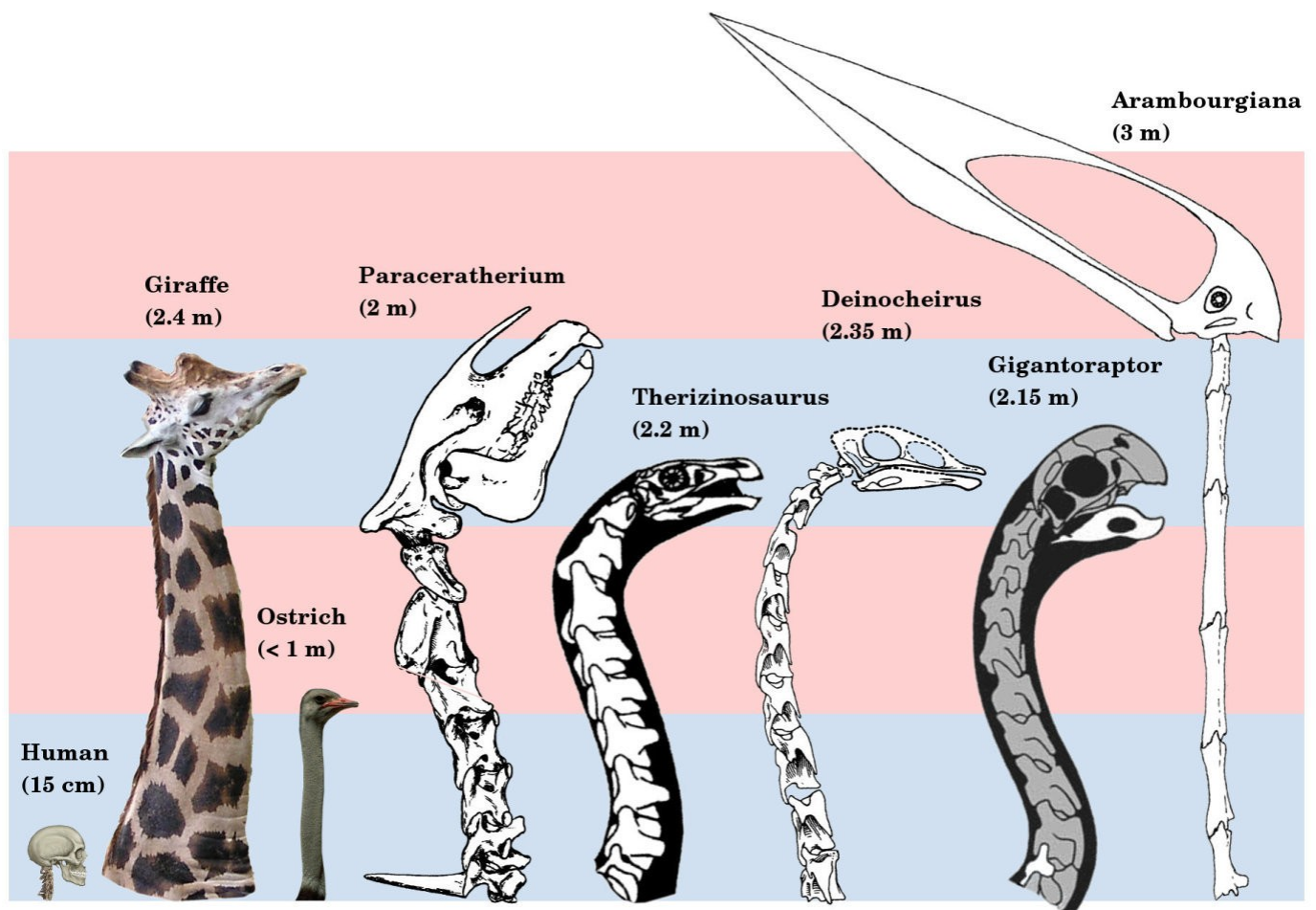
Figure 2

Full skeletal reconstructions of selected long-necked non-sauropods, to the same scale.

Full skeletal reconstructions of selected long-necked non-sauropods, to the same scale. 1, *Paraceratherium,* modified from Granger and Gregory (1936, figure 47). 2, *Therizinosaurus,* scaled from *Nanshiungosaurus* modified from Paul (1997, p. 145). 3, *Deinocheirus,* scaled from *Struthiomimus* modified from Osborn (1916, plate XXVI). 4, *Gigantoraptor*, modified from Xu el al. (2007, figure 1). 5. *Elasmosaurus,* modified from Cope (1870, plate II, figure 1). Scale bar = 2 m.
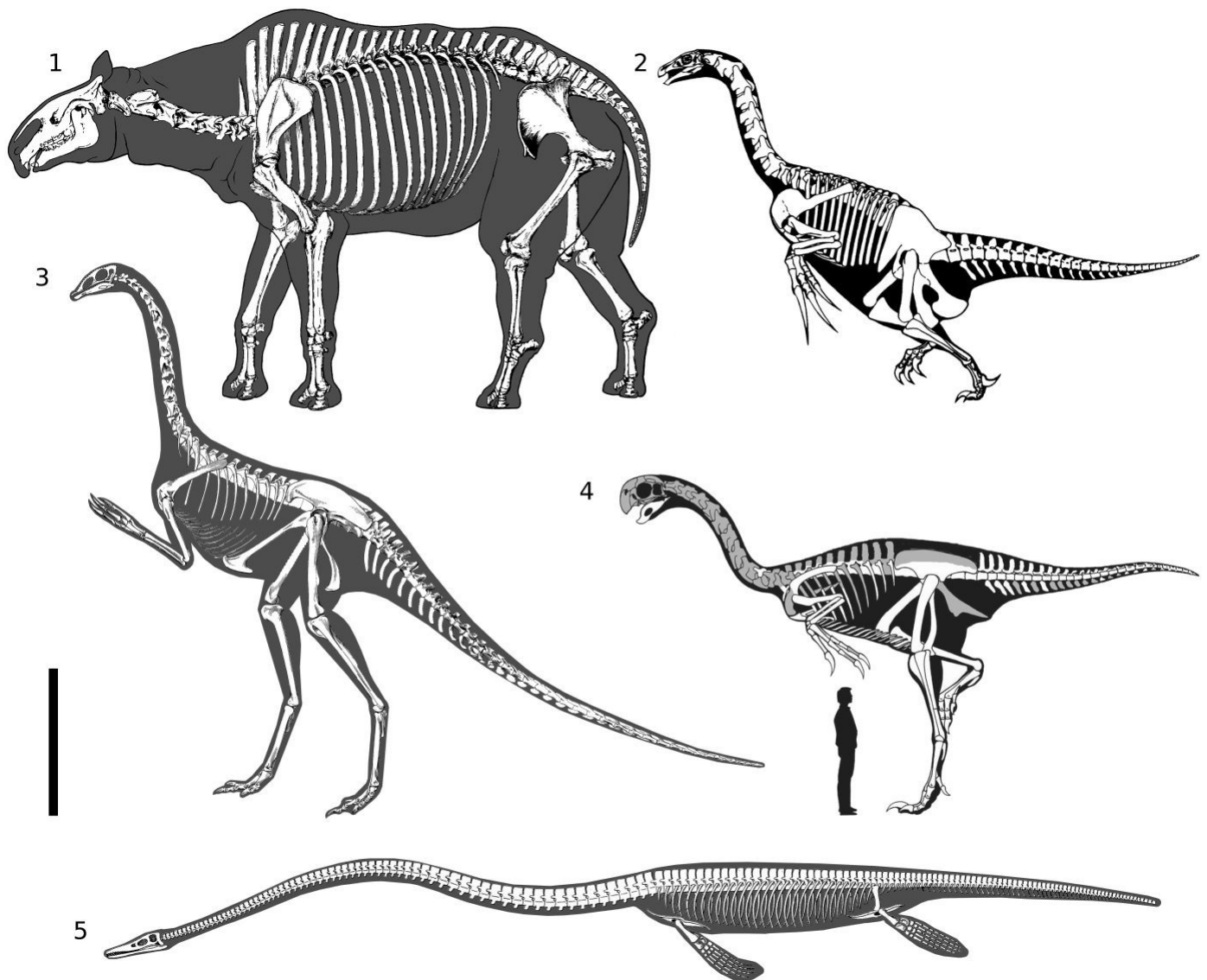
Figure 3

Necks of long-necked sauropods, to the same scale.

Necks of long-necked sauropods, to the same scale. *Diplodocus*, modified from elements in Hatcher (1901, plate 3), represents a "typical" long-necked sauropod, familiar from many mounted skeletons in museums. *Puertasaurus* modified from Wedel (2007a, figure 4-1). *Sauroposeidon* scaled from *Brachiosaurus* artwork by Dmitry Bogdanov, via commons.wikimedia.org (CC-BY-SA). *Mamenchisaurus* modified from Young and Zhao (1972, figure 4). *Supersaurus* scaled from *Diplodocus*, as above. Alternating pink and blue bars are one meter in width. Inset shows Fig. 1 to the same scale.
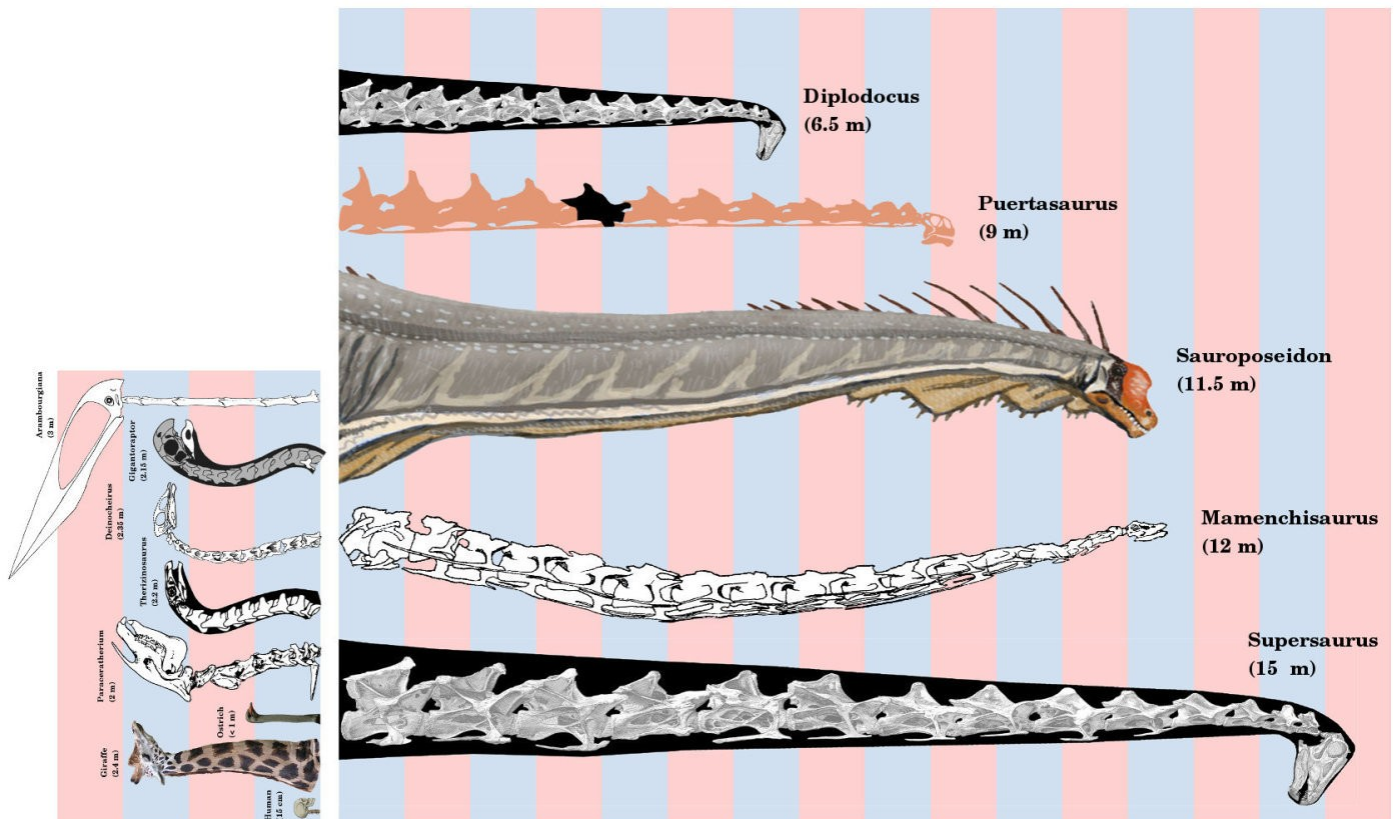
Figure 4

Extent of soft tissue on ostrich and sauropod necks.

Extent of soft tissue on ostrich and sauropod necks. 1, ostrich neck in cross section from Wedel (2003, figure 2). Bone is white, air-spaces are black, and soft tissue is grey. 2, hypothetical sauropod neck with similarly proportioned soft-tissue. (*Diplodocus* vertebra silhouette modified from Paul 1997, figure 4A). The extent of soft tissue depicted greatly exceeds that shown in any published life restoration of a sauropod, and is unrealistic. 3, More realistic sauropod neck. It is not that the soft-tissue is reduced but that the vertebra within is enlarged, and mass is reduced by extensive pneumaticity in both the bone and the soft-tissue.
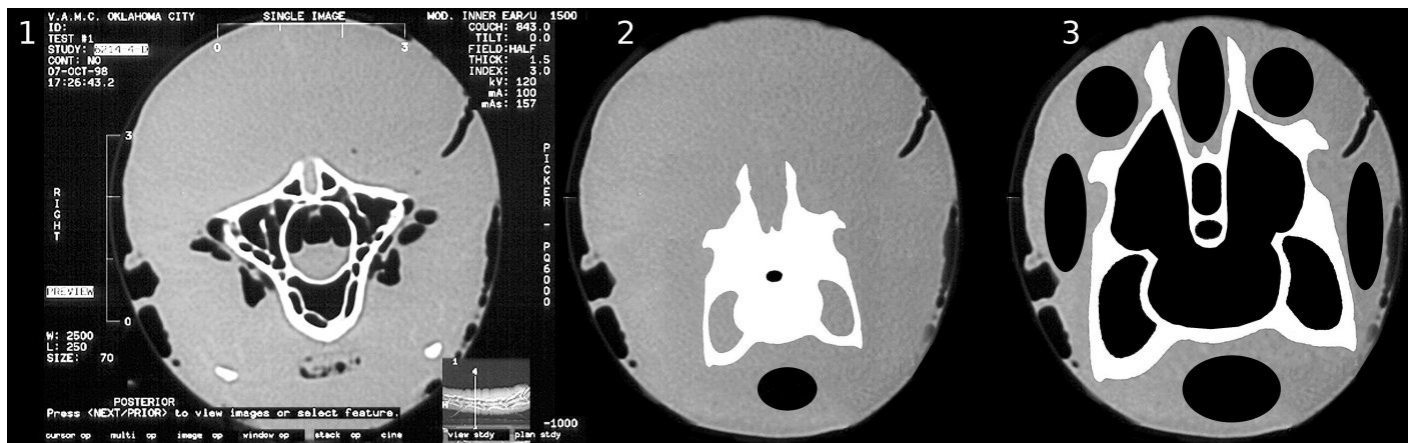
Figure 5

Simplified myology of that sauropod neck.

Simplified myology of that sauropod neck, in left lateral view, based primarily on homology with birds, modified from Wedel and Sanders (2002, figure 2). Dashed arrows indicate muscle passing medially behind bone. A, B. Muscles inserting on the epipophyses, shown in red. C, D, E. Muscles inserting on the cervical ribs, shown in green. F, G. Muscles inserting on the neural spine, shown in blue. H. Muscles inserting on the ansa costotransversaria ("cervical rib loop"), shown in brown. Specifically: A. M. longus colli dorsalis. B. M. cervicalis ascendens. C. M. flexor colli lateralis. D. M. flexor colli medialis. E. M. longus colli ventralis. In birds, this muscle originates from the processes carotici, which are absent in the vertebrae of sauropods. F. Mm. intercristales. G. Mm. interspinales. H. Mm. intertransversarii. Vertebrae modified from Gilmore (1936, plate 24).
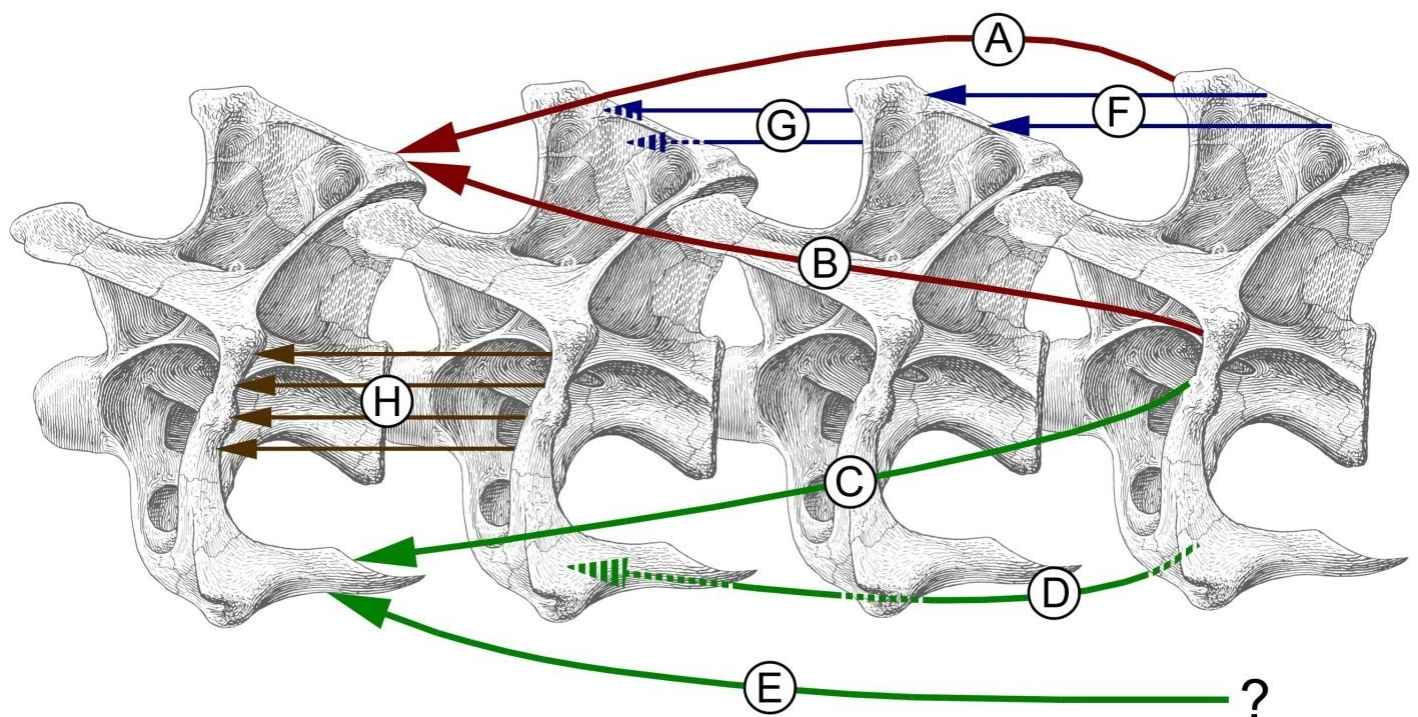
Figure 6

Basic cervical vertebral architecture in archosaurs.

Basic cervical vertebral architecture in archosaurs, in posterior and lateral views. 1, seventh cervical vertebra of a turkey, *Meleagris gallopavo* Linnaeus 1758, traced from photographs by MPT. 2, fifth cervical vertebra of the abelisaurid theropod *Majungasaurus crenatissimus* Depéret 1896, UA 8678, traced from O'Connor (2007, figures 8 and 20). In these taxa, the epipophyses and cervical ribs are aligned with the expected vectors of muscular forces. The epipophyses are both larger and taller than the neural spine, as expected based on their mechanical importance. The posterior surface of the neurapophysis is covered by a large rugosity, which is interpreted as an interspinous ligament scar like that of birds (O'Connor 2007). Because this scar covers the entire posterior surface of the neurapophysis, it leaves little room for muscle attachments to the spine. 3, fifth cervical vertebra of *Alligator mississippiensis* Daudin 1801, MCZ 81457, traced from 3D scans by Leon Claessens, courtesy of MCZ. Epipophyses are absent. 4, eighth cervical vertebra of *Giraffatitan brancai* (Janensch 1914) paralectotype HMN SII, traced from Janensch (1950, figures 43 and 46). Abbreviations: cr, cervical rib; e, epipophysis; ns, neural spine; poz, postzygapophysis.
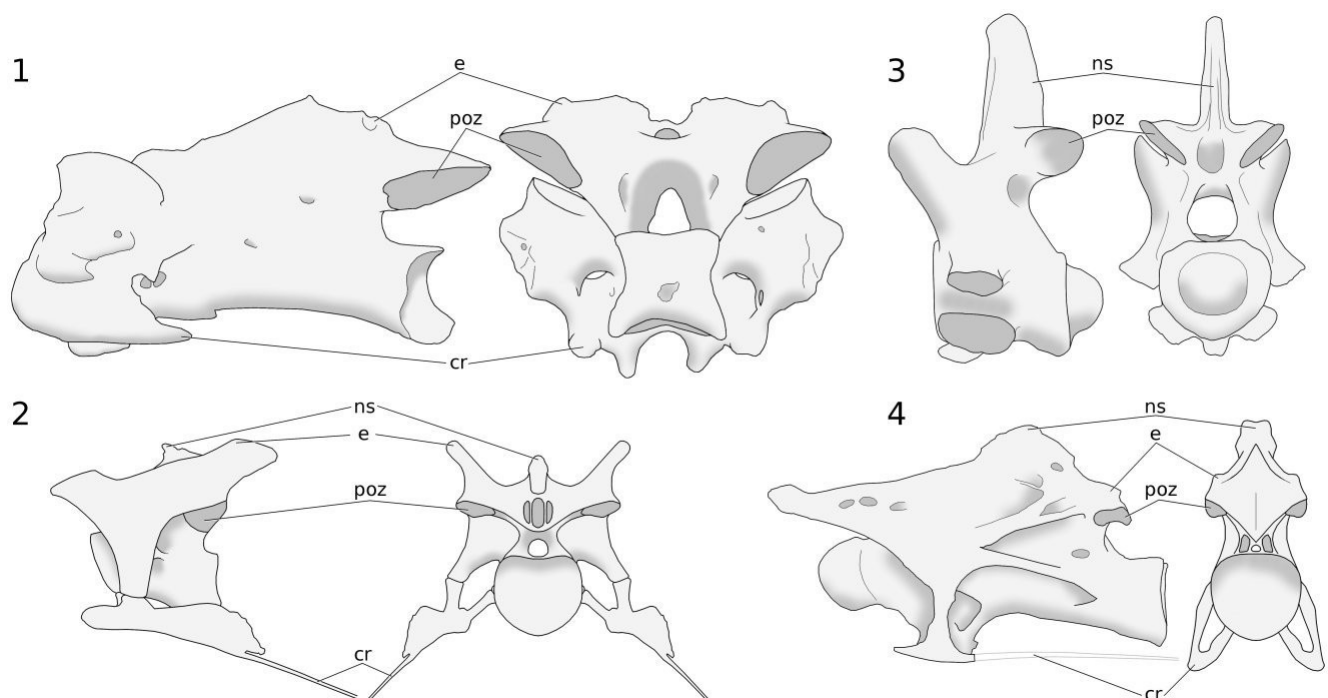
Figure 7

Disparity of sauropod cervical vertebrae.

Disparity of sauropod cervical vertebrae. 1, *Apatosaurus "laticollis"* Marsh 1879b holotype YPM 1861, cervical ?13, now referred to *Apatosaurus ajax* (see McIntosh 1995), in posterior and left lateral views, after Ostrom and McIntosh (1966, plate 15); the portion reconstructed in plaster (Barbour 1890, figure 1) is grayed out in posterior view; lateral view reconstructed after *Apatosaurus louisae* Gilmore 1936 (Gilmore 1936, plate XXIV). 2, *"Brontosaurus excelsus"* Marsh 1879a holotype YPM 1980, cervical 8, now referred to *Apatosaurus excelsus* (see Riggs 1903), in anterior and left lateral views, after Ostrom and McIntosh (1966, plate 12); lateral view reconstructed after *Apatosaurus louisae* (Gilmore 1936, plate XXIV). 3, *"Titanosaurus" colberti* Jain and Bandyopadhyay 1997 holotype ISIR 335/2, mid-cervical vertebra, now referred to *Isisaurus* (See Wilson and Upchurch 2003), in posterior and left lateral views, after Jain and Bandyopadhyay (1997, figure 4). 4, *"Brachiosaurus" brancai* paralectotype HMN SII, cervical 8, now referred to *Giraffatitan* (see Taylor 2009), in posterior and left lateral views, modified from Janensch (1950, figures 43–46). 5, *Erketu ellisoni* holotype IGM 100/1803, cervical 4 in anterior and left lateral views, modified from Ksepka and Norell (2006, figures 5a–d).
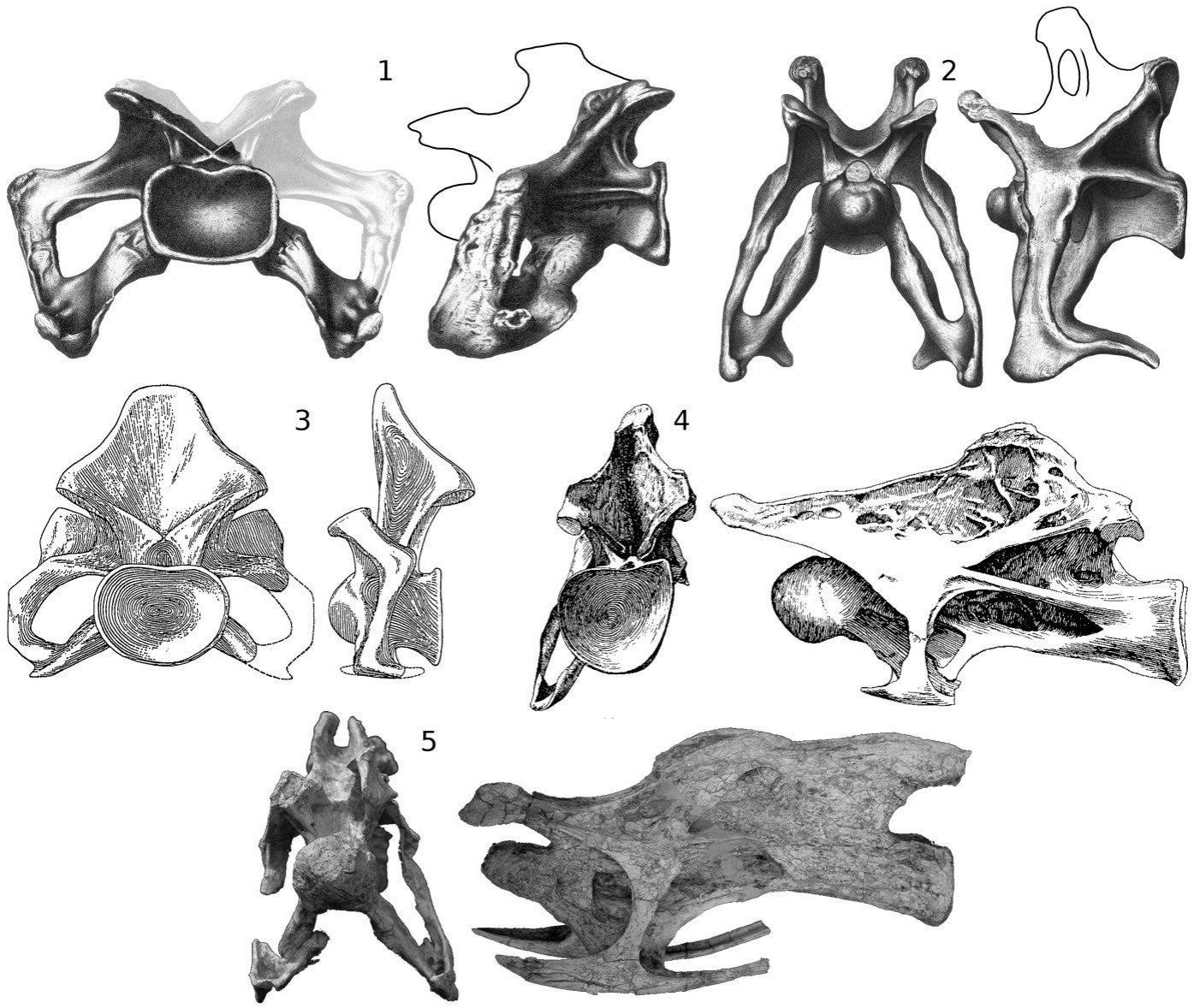
Figure 8

Sauropod cervical vertebrae showing anteriorly and posteriorly directed spurs projecting from neurapophyses.

Sauropod cervical vertebrae showing anteriorly and posteriorly directed spurs projecting from neurapophyses. 1, cervical 5 of *Sauroposeidon* holotype OMNH 53062 in right lateral view, photograph by MJW. 2, cervical 9 of *Mamenchisaurus hochuanensis* holotype CCG V 20401 in left lateral view, reversed, from photograph by MPT. 3, cervical 7 or 8 of *Omeisaurus junghsiensis* Young 1939 holotype in right lateral view, after Young (1939, figure 2). (No specimen number was assigned to this material, which has since been lost. D. W. E. Hone personal communication 2008.)
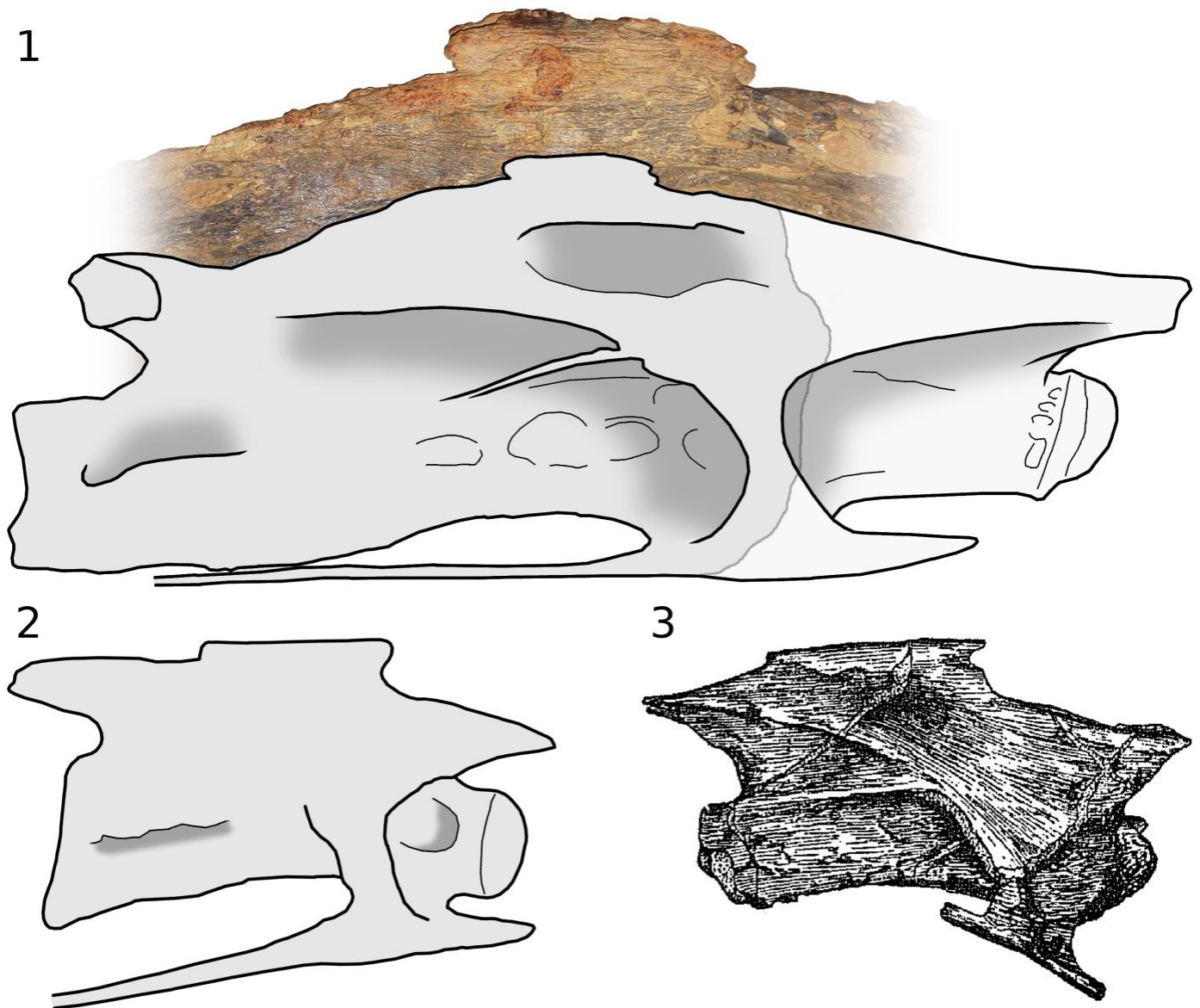
Figure 9

Ligament scars and pneumatic foramina in intermetapophyseal troughs.

Bifid presacral vertebrae of sauropods showing ligament scars and pneumatic foramina in the intermetapophyseal trough. 1, *Apatosaurus* sp. cervical vertebra OMNH 01341 in right posterodorsolateral view, photograph by MJW. 2, *Camarasaurus* sp. dorsal vertebrae CM 584 in dorsal view, photograph by MJW. Abbreviations: las, ligament attachment site; pfa, pneumatic fossa; pfo, pneumatic foramen.
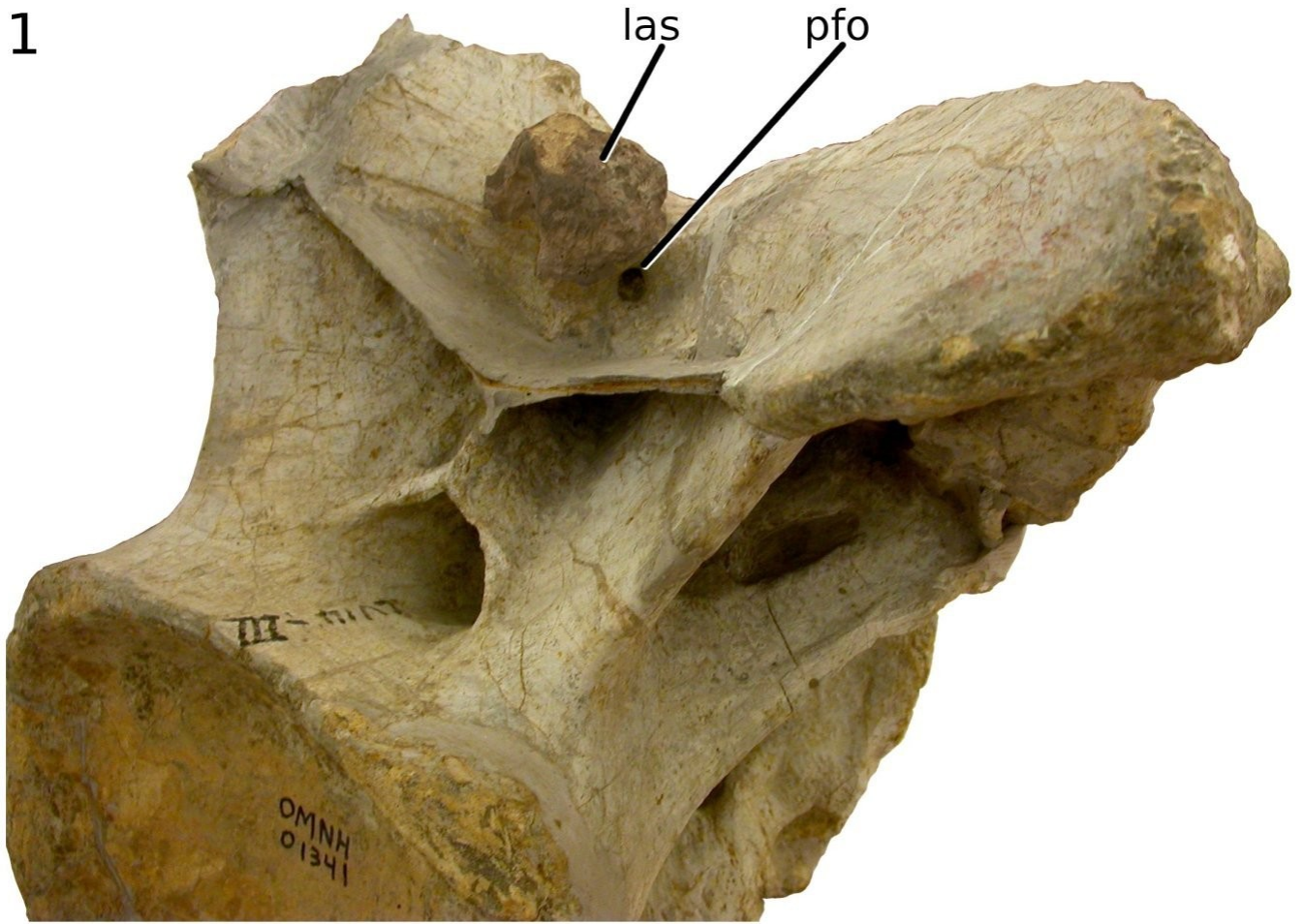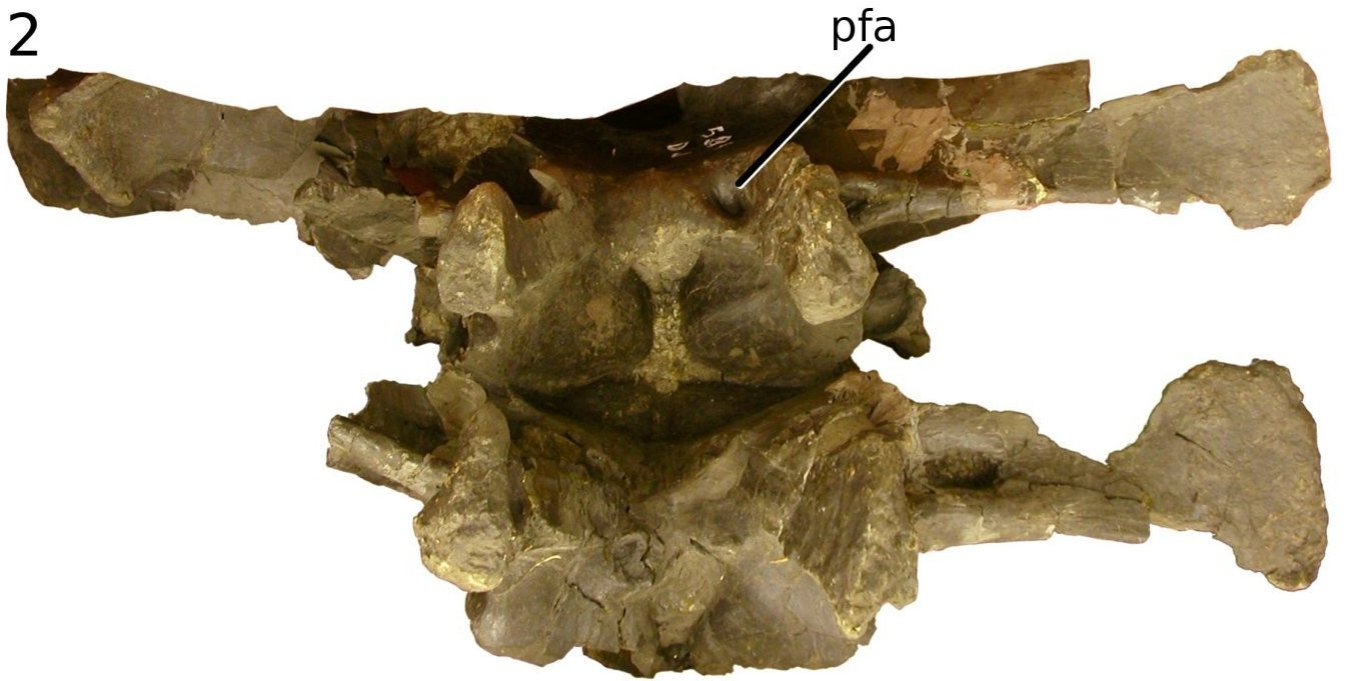
Figure 10

Real and speculative muscle attachments in sauropod cervical vertebrae.

Real and speculative muscle attachments in sauropod cervical vertebrae. 1, the second through seventeenth cervical vertebrae of *Euhelopus zdanskyi* Wiman 1929 cotype specimen PMU R233a- δ ("Exemplar a"). 2, cervical 14 as it actually exists, with prominent but very short epipophyses and long cervical ribs. 3, cervical 14 as it would appear with short cervical ribs. The long ventral neck muscles would have to attach close to the centrum. 4, speculative version of cervical 14 with the epipophyses extended posteriorly as long bony processes. Such processes would allow the bulk of both the dorsal and ventral neck muscles to be located more posteriorly in the neck, but they are not present in any known sauropod or other non-avian dinosaur. Modified from Wiman (1929, plate 3).
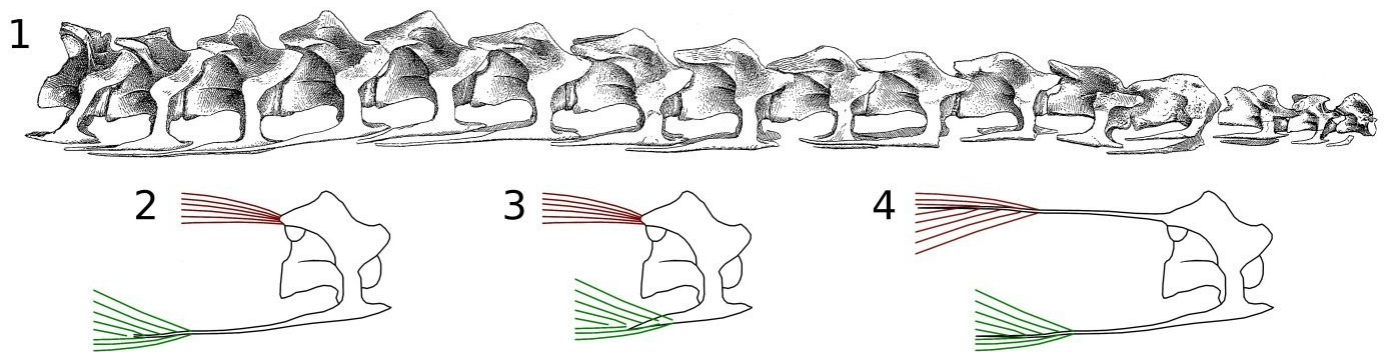
Figure 11

Archosaur cervical vertebrae in posterior view, Showing muscle attachment points in phylogenetic context.

Archosaur cervical vertebrae in posterior view, Showing muscle attachment points in phylogenetic context. Blue arrows indicate epaxial muscles attaching to neural spines, red arrows indicate epaxial muscles attaching to epipophyses, and green arrows indicate hypaxial muscles attaching to cervical ribs. While hypaxial musculature anchors consistently on the cervical ribs, the principle epaxial muscle migrate from the neural spine in crocodilians to the epipophyses in non-avial theropods and modern birds, with either or both sets of muscles being significant in sauropods. 1, fifth cervical vertebra of *Alligator mississippiensis*, MCZ 81457, traced from 3D scans by Leon Claessens, courtesy of MCZ. Epipophyses are absent. 2, eighth cervical vertebra of *Giraffatitan brancai* paralectotype HMN SII, traced from Janensch (1950, figures 43 and 46). 3, eleventh cervical vertebra of *Camarasaurus supremus*, reconstruction within AMNH 5761/X, "cervical series I", modified from Osborn and Mook (1921, plate LXVII). 4, fifth cervical vertebra of the abelisaurid theropod *Majungasaurus crenatissimus*, UA 8678, traced from O'Connor (2007, figures 8 and 20). 5, seventh cervical vertebra of a turkey, *Meleagris gallopavo*, traced from photographs by MPT.