Head and Neck Posture in Sauropod Dinosaurs Inferred from Extant Animals

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The neck posture of sauropod dinosaurs has long been controversial. Recent reconstructions position the cervical vertebrae and skull in an "osteological neutral pose" (ONP), the best fit arrived at by articulating the vertebrae with the zygapophyses in maximum contact. This approach in isolation suggests that most or all sauropods held their necks horizontally. However, a substantial literature on extant amniotes (mammals, turtles, squamates, crocodilians and birds) shows that living animals do not habitually maintain their necks in ONP. Instead, the neck is maximally extended and the head is maximally flexed, so that the mid-cervical region is near vertical. Unless sauropods behaved differently from all extant amniote groups, they must have habitually held their necks extended and their heads flexed. The life orientation of the heads of sauropods has been inferred from the inclination of the semi-circular canals. However, extant animals show wide variation in inclination of the "horizontal" semi-circular canal: the orientation of this structure is not tightly constrained and can give only a general idea of the life posture of extinct animals' heads.

Key words: Dinosauria, Sauropoda, extant amniotes, posture, neck, head, semi-circular canals.

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Introduction

The neck posture of sauropod dinosaurs has been controversial for as long as their body-plan has been understood, and it remains so today. Some workers have reconstructed upward-sloping necks maintained in S-curves (e.g., Osborn and Mook 1921: pl. 84; Janensch 1950: pl. 8; Paul 1988: fig. 1; Christian and Dzemski 2007), and others have reconstructed straight, horizontal or slightly downward-sloping necks (e.g., Marsh 1883; Hatcher 1901: pl. 13; Martin 1987; Stevens and Parrish 1999). At one extreme, Paul (1988, 1997, 1998) has consistently reconstructed sauropods with near-erect necks that make an angle of 45° to 90° with the torso.

By physically manipulating vertebrae (e.g., Martin 1987), or by reconstructing an articulated cervical series from drawings (e.g., Stevens and Parrish 2005a), several authors have aligned the cervical vertebrae of sauropods into articulated series with maximum overlap between zygapophyses. The resulting pose has been termed the osteological neutral pose (ONP). Stevens and Parrish's (1999) report on their DinoMorph project, using digital modelling of zygapophyseal articulations to determine ONP and range of motion, argued that *Diplodocus* and *Apatosaurus* habitually held their necks at or below horizontal, and could not raise their necks far above the horizontal. Stevens and Parrish (2005a: 218) subsequently stated that the ONP for all studied sauropods, as determined from horizontal cervico-dorsal transitions and the absence of keystoned centra at the neck base, indicate a near-horizontal neck that curves gently downwards. They further asserted (2005a: 215) that the habitual pose of animals in life corresponds to the ONP, claiming that "with no known exception, the curvature characteristic of the axial skeleton of a given vertebrate arises, not from chronic flexion out of the neutral position, but from the morphology of the vertebrae in the undeflected state". Likewise, Stevens and Parrish (2005b: 182) stated that "when the vertebrae of extant mammals are placed in neutral pose, they replicate their habitual, characteristic posture". In the same study (p. 185), they equated ONP with mean feeding height, although supporting data from animals in the wild is lacking. Since the publication of Stevens and Parrish (1999), subhorizontal neck-posture for sauropods has been largely unchallenged: apart from conference abstracts, the only responses have been offered by Upchurch (2000) and Christian and Dzemski (2007). Horizontal necks seem to have been accepted as the new orthodoxy, not through independent replication of Stevens and Parrish's (2005a, b) results, nor through their hypothesis having survived attempted rebuttals, but simply through lack of published counter-arguments.

The orientation of sauropod skulls has also been the subject of speculation. Witmer et al. (2003: 951) and Chatterjee and Templin (2004: 54) claimed that the horizontal semi-circular canals (HSCCs) of tetrapod skulls are habitually held

horizontally, and hence that HSCC orientation provides a reliable guide to skull orientation in life. Sereno et al. (2007: fig. 1G) illustrated HSCC orientation relative to total skull morphology for four sauropodomorphs: with the HSCCs held horizontal, the long axis of the skull of the basal sauropodomorph *Massospondylus* is angled 15° upward, and those of the sauropods *Camarasaurus*, *Diplodocus*, and *Nigersaurus* 15°, 30°, and 67° downward. On the basis of the sharply inclined skull of *Nigersaurus*, and the assumption that the animal fed on low-growing vegetation, Sereno et al. (2007: fig. 3) reconstructed a downward-sloping neck for this taxon.

Stevens and Parrish (2005a: 225) defined "neutral position" of the head with respect to the neck as "the situation where the long axis of the brainstem cavity and the neural canal of the atlas/axis are horizontal" (presumably meaning parallel).

Here, we use data from the neck postures and HSCC orientation of extant tetrapods to re-evaluate sauropod head and neck posture.

Institutional abbreviations.—BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; CM, Carnegie Museum of Natural History, Pittsburgh, USA; DMNH, Denver Museum of Natural History, Denver, USA; RAM, Raymond M. Alf Museum of Paleontology, The Webb Schools, Claremont, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

Other abbreviations.—HSCC, horizontal semi-circular canal; ONP, osteological neutral pose.

Posture in extant amniotes

Neck posture.—Live animals do not maintain their necks and heads in ONP. In X-ray studies of live primates, cats, rabbits, rodents, and birds, Vidal et al. (1986) and Graf et al. (1992, 1995) showed that in all these animals, (i) the cervical column is elevated nearly to the vertical during normal functioning; (ii) the middle part of the neck is habitually held relatively rigid; (iii) the neck is maximally extended at the cervico-dorsal junction and maximally flexed at the cranio-cervical junction; and (iv) it is the cranio-cervical and

Fig. 1. Recent Cape hare *Lepus capensis* Linnaeus, 1758 RAM R2 in right lateral view, illustrating maximally extended pose (**A**) and ONP (**B**): skull, cervical vertebrae 1–7 and dorsal vertebrae 1–2. Note the very weak dorsal deflection of the base of the neck in ONP, contrasting with the much stronger deflection illustrated in a live rabbit by Vidal et al. (1986: fig. 4).

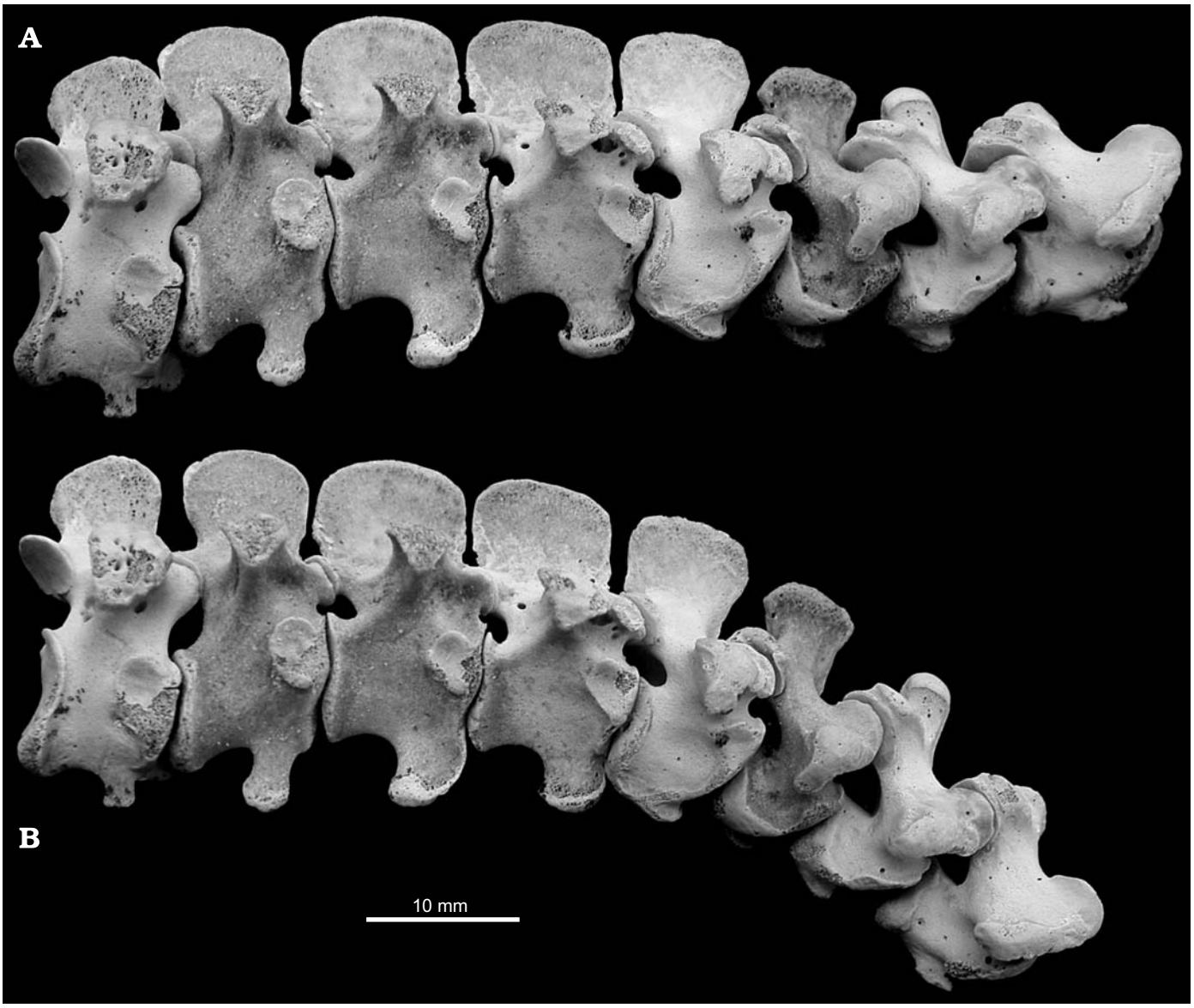

Fig. 2. Recent chicken *Gallus domesticus* Linnaeus, 1758 RAM R1 in right lateral view, illustrating maximally extended pose (**A**) and ONP (**B**): last four cervical and first four dorsal vertebrae. Note the strong ventral deflection of the base of the neck in ONP, contrasting with the very strong dorsal deflection illustrated in a live chicken by Vidal et al. (1986: fig. 7).

cervico-dorsal junctions that are primarily involved in raising and lowering the head and neck. (In life, these facts are obscured from view by soft tissue.) Articulating the cervical vertebrae of mammals (Fig. 1) and birds (Fig. 2) shows that the life postures illustrated by Vidal et al. (1986: figs. 4, 7) are not only far more elevated than ONP but extended more strongly than can be achieved with dry bones while keeping the centra articulated. It is apparent that the soft-tissue of the neck (e.g., intervertebral cartilage) enables greater flexibility in the neck than the bones alone suggest.

X-rays of other live animals show that birds and mammals are not unique in holding their necks extended relative to the dorsal series and their skulls flexed relative to the neck. These features are in fact widespread in non-avian reptiles and even occur in non-amniote tetrapods, strongly suggesting that extended necks and flexed heads are primitive for Amniota and even for crown-group Tetrapoda (Fig. 3). In salamanders, the short neck is slightly extended relative to the dorsal series, and the cranio-cervical junction is flexed (Simons et al. 2000: figs. 4, 5). A strongly extended neck and fully flexed head are present in turtles (Landberg et al. 2003: fig. 8). Vidal et al. (1986: fig. 8A) showed extension of 20° at the cervico-dorsal junction of a Savannah monitor lizard (*Varanus exanthematicus*), and other X-ray observations confirm this (Owerkowicz et al. 1999: fig. 2). In extant archosaurs, X-ray observations of crocodilians show that the neck is extended at c. 40° relative to the dorsal series (unpublished photographs), though examination of mounted skeletons shows that the base of the neck is undeflected when in ONP. In at least some extant reptiles, the cranio-cervical joint remains slightly flexed even when the

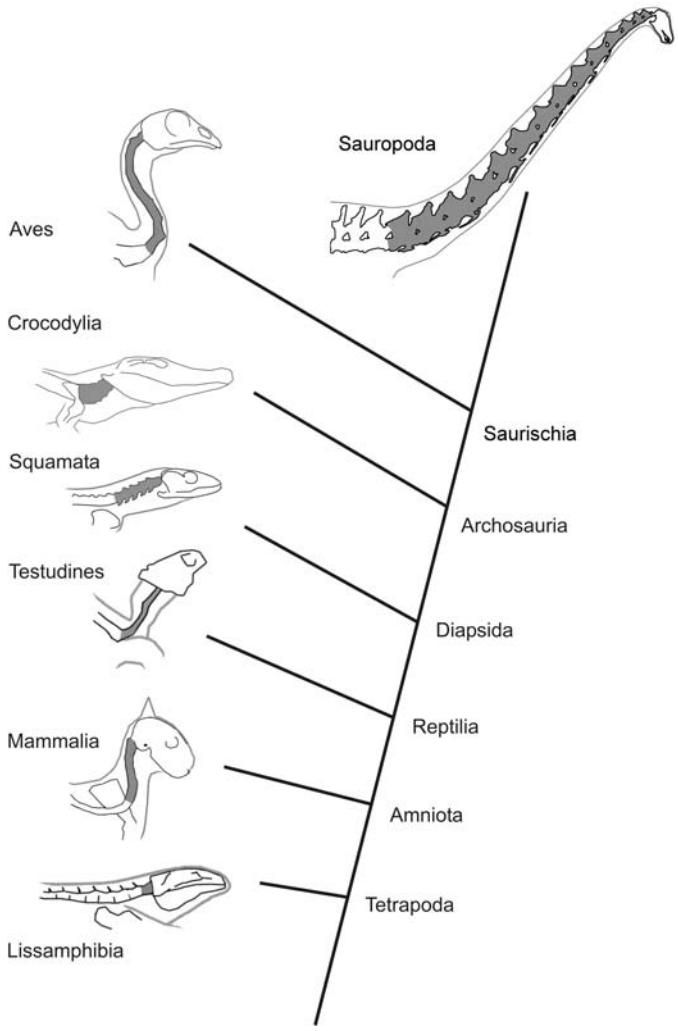

Fig. 3. Phylogeny indicating high-level relationships between tetrapod groups, habitual neck posture in extant groups, and inferred posture in sauropods. Cervical vertebrae shaded dark grey. Lissamphibia: *Ambystoma tigrinum*, after Simons et al. (2000: fig. 4); Mammalia: domestic cat *Felis catus* Linnaeus, 1758, after Vidal et al. (1986: fig. 3B); Testudines: box turtle *Terrapene carolina* (Linnaeus, 1758), after Landberg et al. (2003: fig. 8); Squamata: Savannah monitor *Varanus exanthematicus* (Bosc, 1792), after Owerkowicz et al. (1999: fig. 2A); Crocodylia: alligator *Alligator mississippiensis* (Daudin 1801), after unpublished photograph; Aves: chicken *Gallus gallus* (Linnaeus, 1758), after Vidal et al. (1986: fig. 7); Sauropoda: *Diplodocus carnegii*, modelled after vertebrae in Hatcher (1901: fig. 4, pl. 3).

rest of the cranio-cervical system is extended, i.e., when the animal is "reaching up" (Smith 1986: fig. 9; Druzisky and Brainerd 2001: figs. 1, 2; Landberg et al. 2003: fig. 8).

Head posture.—Although it has been claimed that HSCCs are habitually held horizontally, extant animals typically hold the skull such that the HSCCs are inclined anterodorsally: in rabbits, the HSCCs are tilted upwards by c. 16°, in guinea-pigs and domestic cats by c. 20°, in monkeys by 12°, and in humans by 22° (Graf et al. 1995, Spoor and Zonneveld 1998). These figures are significantly higher than the 5–10° above horizontal regarded as typical by Witmer et al. (2003: 951). Duijm (1951) figured HSCC orientation for 33 species of birds. The mean inclination was horizontal, but values ranged from 20° below horizontal to 30° above. Furthermore, habitual HSCC angles vary by more than 20° in humans (de Beer 1947; Spoor and Zonneveld 1998). Perhaps HSCC angles are inherently more variable in humans than in other tetrapods, but it is more likely that they are variable in all tetrapods and that this variability has only been discovered in humans because of the large sample. For all other species, the number of sampled individuals is very small, and sometimes only one.

Based on available data for birds and mammals, which are extremely limited compared to the diversity of both clades, the mean HSCC orientation across broad taxonomic groups is slightly inclined. However, the large range of values for individual taxa in both clades, and the large range of variation in the only well-sampled species, cast doubt on the hypothesis that semi-circular canal orientation provides a reliable guide for determining the normal posture of the head as assumed by Witmer et al. (2003) and Chatterjee and Templin (2004).

Head and neck posture in sauropods

Problems with existing reconstructions.—While the work of Stevens and Parrish (1999) appears to constrain the possible poses of sauropod necks, their conclusions on neck inflexibility were dependent on the assumption that "one [zygapophyseal] facet could slip upon the other until their overlap was reduced to about 50%" (Stevens and Parrish 1999: 798), a figure based on unpublished manipulations of extant bird necks. The assumption is difficult to justify in the absence of published data, and seems to be contradicted by Stevens and Parrish themselves (2005b: 191), who observed that when giraffes bend their necks laterally there is almost no zygapophyseal overlap. Manipulation of vertebrae can lead to different conclusions regarding range of motion: whereas Stevens and Parrish's digital model indicated a straight, horizontal and inflexible neck in *Diplodocus carnegii*, physical manipulation of the mounted *Diplodocus* skeleton DMNH 1494, by Ken Carpenter, resulted in a mounted posture in which the neck is extended farther vertically and horizontally than is allowed by Stevens and Parrish's digital model (personal observation). Since the neck of this mount is a cast of the *Diplodocus carnegii* holotype CM 84, the very same individual used by Stevens and Parrish (1999), it is evident that the results of such computerised studies are not as objective as they may appear. Sauropod cervicals are large, fragile bones, and very rarely preserved complete and undistorted, so quantitative mechanical analyses based upon them are necessarily dependent on subjective interpretation just as qualitative analyses are. While the approach of Stevens and Parrish (1999) is a real and valuable contribution to rigour in the analysis of posture, it has not been widely recognised that, as with the phylogenies generated by cladistic analysis, the output of

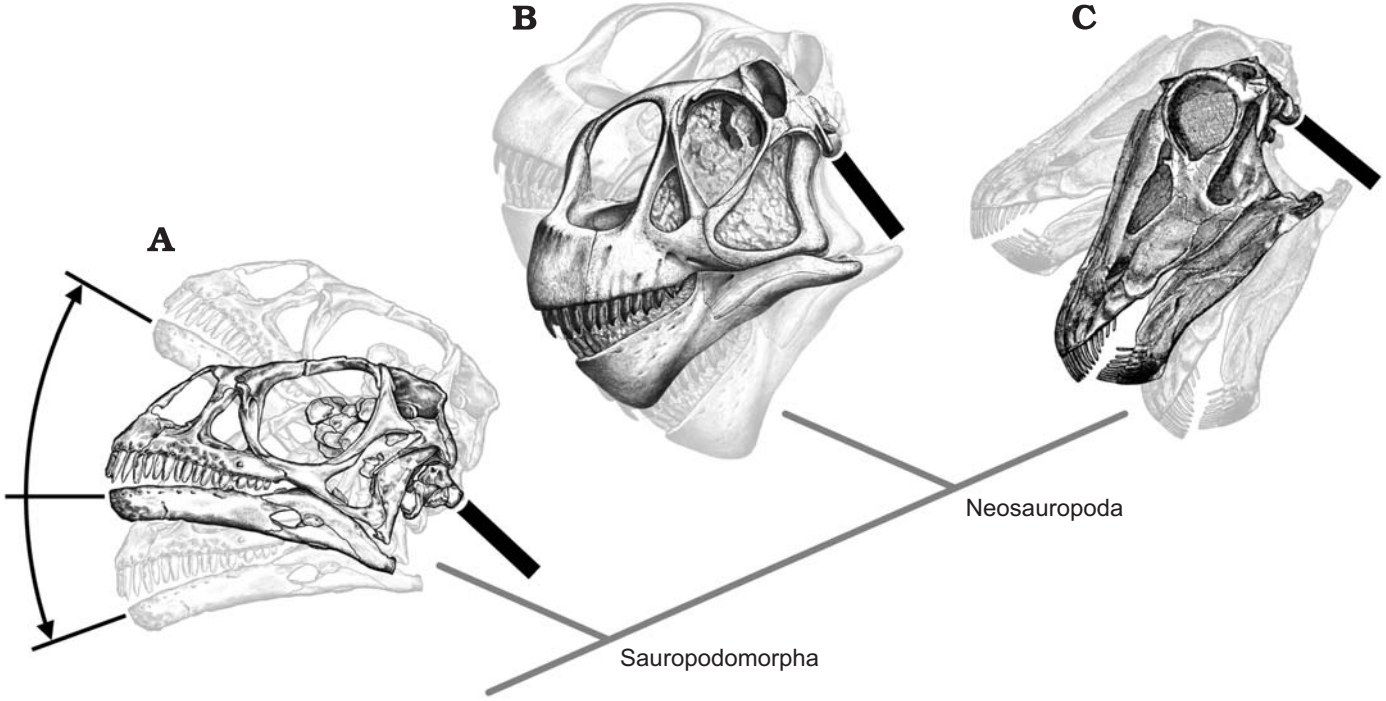

Fig. 4. Range of possible habitual head angles in the basal sauropodomorph *Massospondylus* (**A**) and the sauropods: *Camarasaurus* (**B**) and *Diplodocus* (**C**). Heads shown with HSSC oriented horizontally, and tilted 30° upwards and 20° downwards, the range of habitual orientations found for birds by Duijm (1951). Black bars indicate the angles of the anterior necks in neutral position relative to heads with HSCCs held horizontal. *Massospondylus* BP/1/4376 after Sues et al. (2004: fig. 1A), *Camarasaurus* CM 11338 after Gilmore (1925: pl. 16), *Diplodocus* USNM 2672 after Hatcher (1901: pl. 2).

DinoMorph is a hypothesis to be tested by other lines of evidence rather than a firmly established fact.

In the ONP reconstructions of Stevens and Parrish (2005a: figs. 10.5–10.7), *Apatosaurus* and *Diplodocus* had downward-tending necks, and heads tilted downwards with their long axes about 35° below that of the anterior cervical vertebrae. Neither skull is in neutral position as reconstructed. The foramen magnum and occipital condyle are at a right angle relative to the long axis of the skull in both *Diplodocus* (McIntosh and Berman 1975: fig. 4; McIntosh 1981: fig. 6; Sereno et al. 2007: fig. 1g) and *Apatosaurus* (McIntosh 1981: fig. 11), and so according to Stevens and Parrish's own (2005a) definition of neutral position, the head must be reconstructed at a right angle to the neck. Such a head posture was figured for the dicraeosaurid *Amargasaurus* by Salgado (1999: fig. 9), but his reconstruction of the anterior part of the neck as ventrally inclined meant that the animal was depicted with its skull directed posteroventrally, a seemingly maladaptive pose that would not allow the animal to see in front of itself. In contrast, the right angle between the foramen magnum and skull axis led Fiorillo (1998: 9) to conclude that *Diplodocus* may have held its neck in an elevated, rather than horizontal, posture. To achieve the postures illustrated by Stevens and Parrish (2005a: figs. 10.5–10.7), the animals would have to hold their necks in ONP and their cranio-cervical joints extended by more than 50° rather than maximally flexed. A similar posture is illustrated for *Dicraeosaurus* by Wilson (2002: fig. 1). These postures are not supported by data from extant amniotes.

Inference from extant amniotes.—In extant amniotes, the neck is not habitually held in ONP when the animal is alert but is maximally extended, often more so than appears possible from the vertebrae alone, and the head maximally flexed. It is most parsimonious to assume elevated neck postures in sauropods (and other extinct reptiles), given that this is firmly indicated by the extant phylogenetic brackets at the levels of Saurischia, Archosauria, Diapsida, Reptilia and Amniota. Stevens and Parrish (2005b: 185) criticised Janensch's (1936: pl. 16) reconstruction of the diplodocoid *Dicraeosaurus hansemanni* (incorrectly cited as "Janensch 1929") because the neck was "abruptly dorsiflexed [i.e., extended] at the base and ... deflected downward cranially", whereas in fact this is exactly what would be expected. Among extant amniotes, it is notable that neck extension and skull flexion are strongest in those animals that walk on erect legs (mammals and birds) and weaker in those that sprawl (crocodilians, lizards, turtles, and lissamphibians). It may be that these two adaptations, erect legs and erect neck, are part of the same functional complex. If so, then dinosaurs, which, like mammals and birds, walked with erect legs, should also be expected to share strongly extended necks with these groups – in this respect resembling their closest extant relatives, Aves, more than their next, Crocodylia.

Stevens and Parrish (1999: 799) argued that little muscular effort is needed to hold a neck in ONP whereas holding it elevated requires continuous firing of the epaxial muscles. However, Graf et al. (1992: 132) pointed out that "the resting position of the head-neck ensemble, including the upright posture

of the cervical vertebral column, is almost exclusively the product of passive mechanical constraints [allowing] the maintenance of the resting head-neck posture with minimum energy expenditure". Also, the mass of a horizontal neck acts at a greater horizontal distance from the cervico-dorsal joint than a raised neck, requiring greater force at that joint to counteract gravity. For these reasons, an elevated neck posture, as seen in extant amniotes, is mechanically credible.

As discussed above, most birds and mammals hold their heads so that the HSCCs are not horizontal but somewhat inclined. However, since the range of interspecific variation is up to 50° in birds, the HSCC orientations shown by Sereno et al. (2007), while providing novel and valuable comparative data for sauropods, do not tightly constrain the habitual orientation of the skulls of these taxa in life (Fig. 4).

In all four sauropodomorphs figured by Sereno et al. (2007: fig. 1G), the occipital condyle is directed postero-ventrally when the HSCCs are horizontal. If the HSCCs were inclined upwards, as in most birds and mammals, the downward tilt of the occipital condyles would be even greater. Therefore, even if the cranio-cervical joints were held in ONP, the anterior part of the neck would be inclined in all four taxa. If the cranio-cervical joints were flexed as in extant terrestrial amniotes, the anterior portion of the neck would need to be even more steeply inclined in order to hold the HSSC horizontal, and would possibly have approached vertical in *Camarasaurus* and *Diplodocus* (Fig. 4B, C).

Paul (1997) reconstructed *Massospondylus*, *Camarasaurus*, and *Diplodocus* with elevated neck postures that agree with the data from extant amniotes. However, Paul (1997) reconstructed the skulls of all three taxa as horizontal. This puts the cranio-cervical joints near ONP, which is more correct than the extended positions shown by Stevens and Parrish (2005a) and Sereno et al. (2007), but falls short of the flexed postures documented for extant amniotes. Furthermore, in Paul's reconstructions of diplodocids most of the extension of the neck occurs in the middle of the series (e.g., Paul 1998: fig. 1(b)E), rather than at the cervico-dorsal junction. We therefore conclude that none of the recent hypotheses of sauropod head and neck posture are fully in accordance with the postures documented for terrestrial amniotes.

Finally, it is important to distinguish the normal alert posture of the head and neck from the feeding posture. Horses carry their heads angled sharply downward (de Beer 1947), and spend much of their time eating near the ground. However, they do not hold their noses just above ground level during locomotion, as diplodocoids have been reconstructed as doing (Stevens and Parrish 1999, 2005a, b; Sereno et al. 2007). In horses, feeding from the ground involves flexing the neck and extending the head, which is a reversal of the usual orientation of those joints in unrestrained alert poses or normal locomotion. We do not doubt that *Nigersaurus* was similarly capable of feeding in the posture shown by Sereno et al. (2007: fig. 3), but comparative data suggest that this was not the normal posture for *Nigersaurus* when it was not feeding.

Discussion

Equal dorsal and ventral flexibility.—In the absence of "osteological stops" (bony features that limit flexibility) a neck can extend as far dorsally of ONP as it can flex ventrally. This ability to extend the neck has benefits in increasing feeding range, improving predator detection and in dominance displays, so will often be exploited. Osteological stops are known for some extant animals: for example, Stevens and Parrish (2005b: fig. 6.13) show that the posteriormost cervical vertebra of the giraffe can rotate 30° ventrally from ONP with respect to the first thoracic vertebra, but only 9° dorsally. However, osteological stops are not apparent in any sauropod (Stevens and Parrish 2005b: 191), and so at each

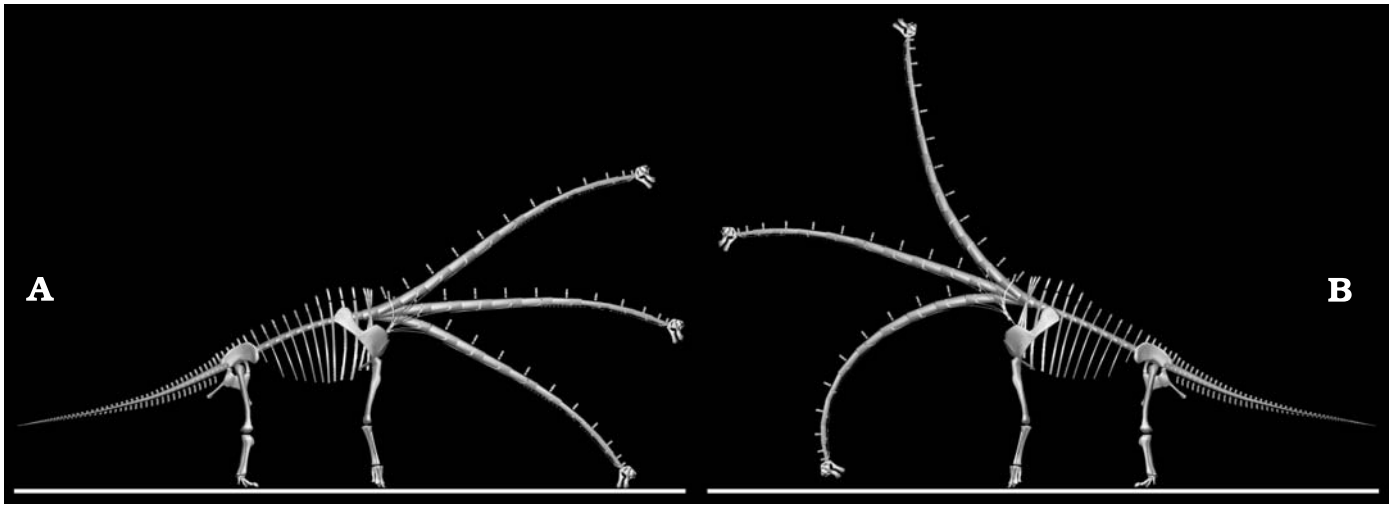

Fig. 5. Sauropod *Brachiosaurus brancai* reconstructions with low and high torso positions. Neck in ONP, in a drinking posture (**A**), and in a browsing posture (**B**) attained by deflecting the neck dorsally by the same amount as it is deflected ventrally to reach the ground. Torso, appendicular skeleton and ONP neck from Stevens and Parrish (2005b: fig. 6.8). Cervical joints deflected by 8° from ONP. See text for full details.

joint the achievable angles of flexion and extension, limited only by zygapophyseal displacement, are equal. Fig. 5 shows the consequences for *Brachiosaurus brancai* using Stevens and Parrish's (2005b: fig. 6.8) reconstructions of neutral posture. Here, we have used the versions of the torso in which the head is lowest (high pectoral girdle, arched back) and highest (low pectoral girdle, straight back), showing for each the ventral deflection from ONP required to reach the ground using Stevens and Parrish's (2005b: 194) estimate of 8° flexion at each proximal cervical joint, and the corresponding dorsal deflection achievable by 8° extension at each joint. In the low-head version, only the four most proximal joints (between C10 and D1) need be flexed to bring the head to ground level, and so only those four joints are extended to depict the corresponding browsing posture. In the high-head version, flexing all joints is necessary (and in fact not quite sufficient) to reach the ground, so the browsing posture also extends all joints. Based on data from extant animals, it seems likely that the base of the neck was actually more flexible than depicted here and the middle part of the neck less so, but since the neural arches of the cervico-dorsal transition are unknown in *Brachiosaurus brancai*, this cannot be determined.

It is unsurprising that ONP is not the habitual pose. Every animal must be able to lower its neck sufficiently to reach ground level in order to drink, and also has a maximally raised position: ONP is merely the midpoint between the postural extremes.

Were sauropods anomalous?—Can the habitual posture of extant amniotes be expected to apply to sauropods? Phylogenetic bracketing strongly supports this hypothesis as the neck posture described by Vidal et al. (1986) is found in both Aves and Crocodylia, the nearest extant outgroups of Sauropoda, as well as in the increasingly remote outgroups Squamata, Testudines and Lissamphibia.

However, some authors have postulated that the necks of sauropods, rather than representing an extreme development of mechanisms found in other vertebrates, were anomalous structures maintained using novel mechanisms. If this were so, then it would not be surprising if the habitual posture of sauropod necks was different from that of other vertebrates. For example, Martin et al. (1998) suggested that the necks of some sauropods were braced not only dorsally by ligaments, tendons and muscles acting as tension members, but also ventrally by cervical ribs acting as compression members; and Schwarz et al. (2007: 184) and Schwarz-Wings and Frey (2008) suggested that pressurised air-sacs in the necks of sauropods may have contributed to neck support. These and similar suggestions are unparsimonious, as they depend on anatomical novelties unknown in extant vertebrates and unsupported by evidence. Ventral bracing by cervical ribs would require a combination of length and robustness in the cervical ribs that is not seen in any sauropod: where the ribs are robust, as in *Apatosaurus*, they are too short to form a continuous incompressible brace; where long, as in *Brachiosaurus brancai*, they are too slender to support the neck. Bracing by inflation of the diverticula would require a radical re-plumbing of the respiratory system and the introduction of valves into the diverticula, something not seen in any extant bird. It is most parsimonious to assume that the necks of sauropods were supported by the same mechanisms as in their extant outgroups, and in similar postures.

Published speculation on the head and neck posture of sauropods has taken surprisingly little account of what is known of these subjects in extant amniotes. When considering the lifestyles of extinct animals, those of their extant relatives remain the best guide.

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