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15 March 1998; accepted 9 April 1999

Neck Posture and Feeding Habits of Two Jurassic Sauropod Dinosaurs

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Articulated digital reconstructions of two diplodocid sauropods revealed cervical poses and feeding envelopes. The necks of *Diplodocus* and *Apatosaurus* were nearly straight but gently declined such that the heads, which were themselves angled downward relative to the neck, were close to ground level in their neutral, undeflected posture. Both necks were less flexible than conventionally depicted, and *Diplodocus* was less capable of lateral and dorsal curvature than *Apatosaurus*. The results suggest that these sauropods were adapted to ground feeding or low browsing, contrary to the view that diplodocid sauropods were high browsers.

The fauna of the Late Jurassic Morrison Formation was dominated by huge, long-necked sauropod dinosaurs. At least six genera occur in the Morrison and five genera occur, apparently sympatrically, in the main quarry at Dinosaur National Monument (*1, 2*). The abundance, size, and diversity of sauropods suggest that they played a central role in the Morrison and other continental ecosystems of the Jurassic and Cretaceous.

The key to understanding the feeding strategies of sauropods lies in the biomechanics of their elongate necks. When first described (*3, 4*), *Diplodocus* was depicted with a neck that was nearly horizontal, or sloping down with a gentle dorsal arch (*5, 6*). Recently, *Diplodocus* and other sauropods have been restored (*7–9*) with their heads far above ground level, with a sharp, swanlike dorsiflexion in the neck. Additionally, several taxa were depicted in a tripodal (hind limbs plus tail) pose (*7, 9*). These inferences of near-vertical necks in sauropods have sparked a lively debate (*10–12*) about how the sauropod circulatory system pumped blood to the elevated head; this has yielded such creative suggestions as the presence of multiple hearts in the diplodocid *Barosaurus* (*12*).

It is difficult to evaluate these alternative hypotheses by direct manipulation (*13*) of the original specimens because their fossil remains are too awkward, heavy, and fragile to move in articulation manually. In addition, postdepositional distortion often prevents proper articulation. As an alternative, we chose to manipulate detailed digital models of sauropod skeletons with an interactive graphics software package (*14*) for constructing and articulating three-dimensional (3D) models of dinosaur skeletons. The entire axial skeleton and the major elements of the appendicular skeleton are rendered with dimensional accuracy. Because the study concerns neck biomechanics, the geometry governing the mobility between each pair of cervical vertebrae was modeled in detail, with zygapophyseal facets reconstructed as complex 3D surfaces (*15*) that were precisely positioned and oriented with respect to their associated centra by 24 adjustable parameters for each vertebra. This degree of modeling permitted reconstruction of the limits of deflection attainable by each neck vertebra. The posture for the trunk and limbs was based on previous reconstructions and is not addressed here.

We modeled two well-known Late Jurassic sauropod taxa, *Apatosaurus* and *Diplodocus*. These genera were selected because they were close relatives (*16–19*) and were sympatric during the Late Jurassic (*1, 2*). Both genera are known from nearly complete skeletons [mounted Carnegie Museum of Natural History (CM) specimens CM 3018 (*Apatosaurus louisae*) and CM 84 (*Diplodocus carnegii*)]. These specimens share the same number of neck vertebrae and have shorter forelimbs than hindlimbs, yet differ from one another in build and vertebral form.

The neutral pose and flexibility among cervical vertebrae was constrained by the placement, size, and 3D shape of their pre- and postzygapophyses. The movement of adjacent vertebrae, relative to the ball-and-socket articulations of the centra, induces rotation and translation of the articulated pre- and postzygapophyses. This movement places tension on the synovial capsule surrounding each zygapophyseal pair. Our manipulation of muscle and ligament preparations of extant bird necks indicated that synovial capsules constrain movement such that paired pre- and postzygapophyses could only be displaced to the point where the margin of one facet reaches roughly the midpoint of the other facet, at which point the capsule is stretched taut (*20*). In other words, one facet could slip upon the other until their overlap was reduced to about 50%. In vivo, muscles, ligaments, and fascia may have further limited movement (*20*); thus, the digital manipulations reported here represent a "best case" scenario for neck mobility.

We measured the cervical vertebrae of CM

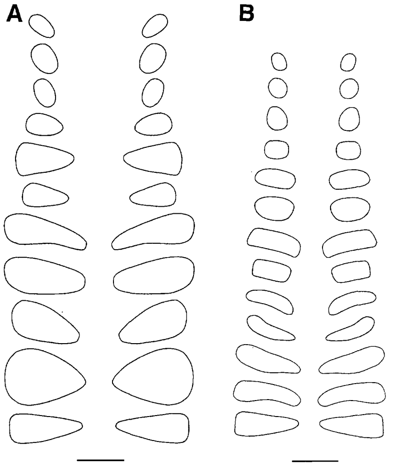

Fig. 1. Tracings of the articular facets of the prezygapophyses of (**A**) *Apatosaurus louisae* (specimen CM 3018) and (**B**) *Diplodocus carnegii* (specimen CM 84). Scale bars, 10 cm.

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84 and CM 3018. The dimensions of elements of the axial and appendicular skeletons were entered from tables in the monographic descriptions of these specimens (*3, 4*) and were verified by our photographs of the mounts. The 24 parameters for each of the 15 cervical vertebrae in each specimen were entered and graphed. The few outliers or discontinuities were examined for possible postmortem distortion and corrected by reference to the original material and by comparison with values taken from neighboring vertebrae. Finally, the margins of the articular facets of the zygapophyses, traced directly from the specimens (Fig. 1), were used to bound the 3D shapes of their digitally modeled counterparts.

We determined the neutral poses for each animal, wherein the paired articular facets of the postzygapophyses of each cervical vertebra were centered over the facets of the prezygapophyses of its caudally adjacent counterpart. In this position, the ligaments and musculature controlling the neck's movement were relaxed, and the stresses on the joint capsules connecting the paired zygapophyses were minimized. In the neutral pose, the necks of both diplodocid genera are remarkably straight, and the downward tilt of the spine at the shoulders brings the heads down to just above ground level (*21*). Diplodocids have V-shaped neural spines on their cervical vertebrae, which were probably attachment sites for parts of the nuchal ligament complex (*22*). Although living archosaurs do not have bifid spines, the presence of a compound nuchal ligament connecting the neural spines is common to birds and crocodilians (*23, 24*). At or near the neutral pose, such a nuchal ligament would be taut and would hold the neck in its horizontal, cantilevered position without much muscular exertion. In contrast, holding the neck in a raised position would have required continuous firing of the cervical dorsiflexors.

The posteroventral inclinations of the occipital condyles of *Apatosaurus* and *Diplodocus* (*25, 26*) indicate that the heads were bent downward in a near vertical orientation when in the neutral pose. The same condition is observed in extant ground-feeding ungulates. Moreover, the extreme dorsal placement of the orbits in both genera was accompanied by an arcuate narrowing of the frontals between the orbits that would have allowed effective anterior vision even when the head was angled steeply downward, and perhaps permitted a useful degree of binocular overlap ahead of the animal.

To determine the feeding envelope for each species, we brought the neck to maximum flexion laterally, then dorsally, ventrally, and subsequently in compound motion (*21*) (Fig. 2). In both lateral and vertical flexion, the most proximal cervicals created the greatest displacement from shoulder to head, producing in dorsal or lateral view an envelope of decreasing radius at the extremes

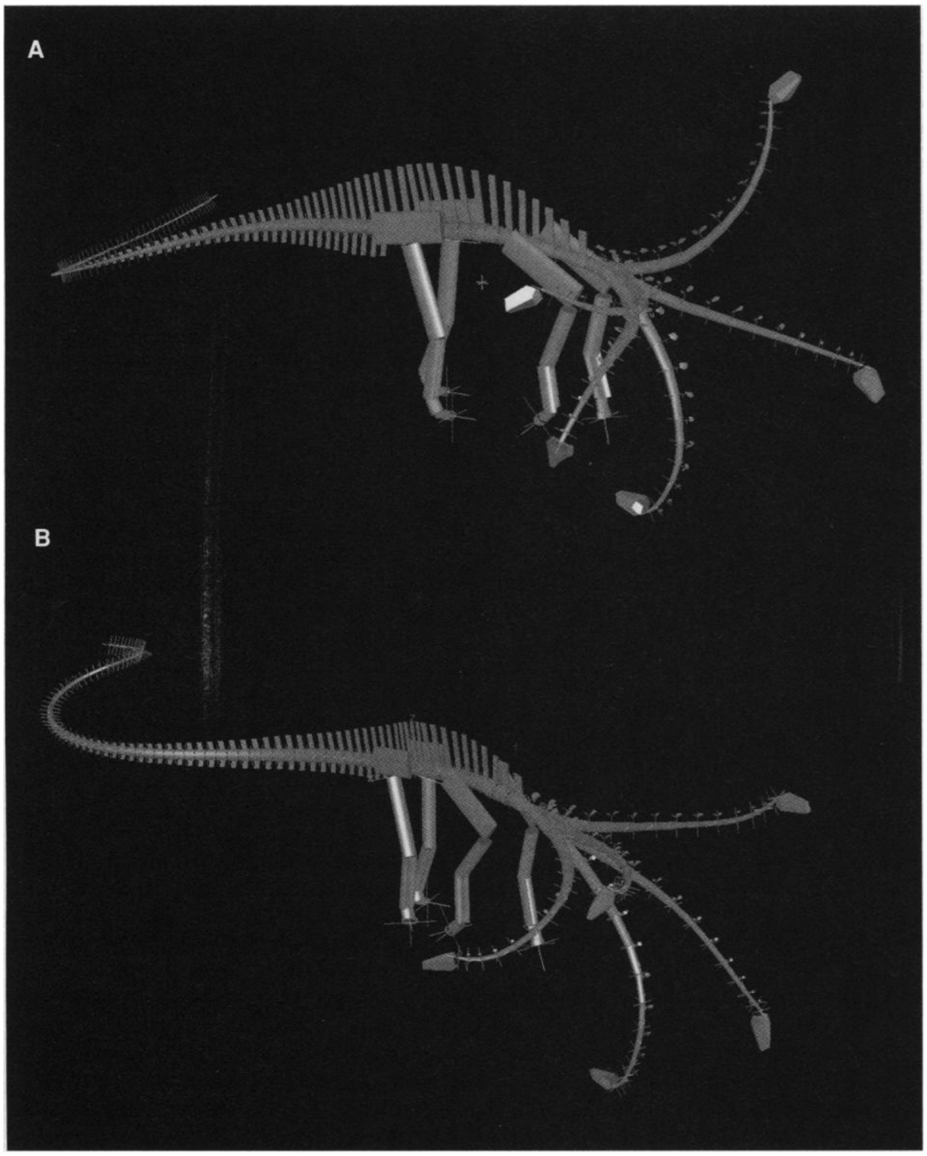

Fig. 2. Oblique views of (**A**) *Apatosaurus louisae* and (**B**) *Diplodocus carnegii* with superimposed images of extremes of dorsiflexion, ventriflexion, and low and high browsing to the right.

Table 1. Position of the atlantoccipital joint, relative to origin at ground level below the base of the neck, for *Apatosaurus louisae* (specimen CM 3018). Coordinates give the 3D position of the atlantoccipital joint (at the base of the cranium), where the origin of the coordinate system is at ground level directly below the base of the neck (below the C15/D1 joint) with the *x* axis positive to the right, *y* positive anteriorly, and *z* positive dorsally.

Coordinates (m)			Pose
x	*y*	*z*	
0	5.1	1.6	Neutral pose
0	3.7	5.9	Maximum dorsiflexion
0	1.1	1.5	Maximum ventriflexion
4.1	0.7	2.9	Maximum right extension
4.0	1.3	3.3	Maximum right, high position
0	4.8	4.6	High S-curve
0	0.9	10.5	Tripodal maximum height

Table 2. Position of the atlantoccipital joint, relative to origin at ground level below the base of the neck, for *Diplodocus carnegii* (specimen CM 84). Coordinates are given as in Table 1.

Coordinates (m)			Pose
x	*y*	*z*	
0	5.8	0.8	Neutral pose
0	5.9	4.3	Maximum dorsiflexion
0	2.5	1.6	Maximum ventriflexion
4.2	3.3	1.9	Maximum right extension
2.8	5.2	3.3	Maximum right, high browse
0	6.1	2.9	High S-curve
0	1.9	11.3	Tripodal maximum height

of flexion. In anterior view, the envelope had greatest height sagittally, and greatest width in pure lateral flexion (compare Tables 1 and 2). Laterally, *Apatosaurus* could curl its neck to form a tight U-curve, with its head extended laterally over 4 m, owing to the large, flat zygapophyses of the proximal cervicals. The zygapophyseal shape in *Diplodocus* permitted less angular deflection laterally, but the longer neck resulted in similar total lateral deflection of about 4 m.

The primary difference between these two genera was in dorsiflexion. The maximum feeding height was about 6 m for *Apatosaurus* compared to 4 m for *Diplodocus*. The shorter yet more flexible neck of *Apatosaurus* could have achieved a pose close to the high S-curve in which it is frequently depicted, whereas *Diplodocus* was barely able to elevate its head above the height of its back. The zygapophyseal design of *Apatosaurus* permitted greater decoupling between flexion in the horizontal plane and in the vertical plane. At the extremes of lateral flexion, *Apatosaurus* still had sufficient flexibility to feed from ground level up to more than 3 m, essentially squaring off the upper and lower corners of the feeding envelope. In contrast, lateral flexion of *Diplodocus* resulted in cumulative dorsiflexion distally, raising the head about 2 m above ground level in maximum lateral flexion, whereas the head of *Apatosaurus* could be at or near ground level with the same lateral flexion. Thus, the feeding envelope of *Apatosaurus*, in anterior view, was subrectangular (both high and low feeding at the lateral extremes), whereas that of *Diplodocus* was more diamond-shaped, with less vertical range permitted at the lateral extremes and less overall elevation. Surprisingly, the necks of both genera were capable of more ventriflexion than dorsiflexion, reaching at least 1.5 m below ground level.

The low browsing envelopes of *Diplodocus* and *Apatosaurus*, coupled with their similarities in skull shape and dentition (*27*), suggest that these two sympatric giants may have been feeding on the same kinds of vegetation. The abundance of both genera in Morrison deposits suggests either that both were generalized feeders or that the plants on which they fed were so abundant that competition between the two genera was not a factor. Despite the similarities in feeding envelopes and cranial morphology of the two diplodocids, *Diplodocus* had a longer neck (6.2 m versus 5.3 m) and was more gracile in body shape and vertebral design than *Apatosaurus*, which had roughly three times the mass.

The extreme ventral flexibility in diplodocids is beyond the mobility required for quadrupedal feeding. Their ability to ventriflex sharply would have allowed a diplodocid on the margin of a lake or river to extend its head outward and downward to graze on plants on or under the water. Alternatively, some workers (*7–9*) have advocated tripodality in diplodocids, and a tripodal *Diplodocus* could have fed from 6.3 to 11.6 m off the ground. However, the upper-canopy arborescent plants available for a high-feeding sauropod in the Late Jurassic consisted primarily of conifers and ginkgoes (*28–31*), neither of which would provide particularly nutritious forage for large herbivores like diplodocids (*32*). On the other hand, an abundance of soft, high-nutrition vegetation—in the form of ferns, cycadeoids, seed ferns, horsetails, and algae—was available to terrestrial sauropods feeding along the shores of perennial lakes and rivers (*33*), a scenario for which the great neck length and the ability to flex ventrally and traverse a broad lateral arc would have been advantageous. Moreover, the presence of a near horizontal neck in diplodocids renders moot the problem of supplying blood to an elevated sauropod brain. Rather than flexing their necks like dinosaurian counterparts of giraffes or swans, they appear to have fed more like giant, long-necked bovids.

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21 December 1998; accepted 18 March 1999

Morphological Clues from Multilegged Frogs: Are Retinoids to Blame?

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Morphological analysis was performed on multilegged deformed frogs representing five species from 12 different localities in California, Oregon, Arizona, and New York. The pattern of duplicated limbs was consistent with mechanical perturbation by trematode infestation but not with the effects of retinoids.

Reports of amphibians with supernumerary limbs from natural populations have been in the scientific literature for centuries, but the causes remain unclear (*1–3*). Recent reports of deformed frogs from Minnesota (*4*) and elsewhere have generated a resurgence of interest. Suggested causes include environmental pollution, ultraviolet irradiation (*3, 5*), genetic mutation, microbes, parasites, and some other disease (*2, 6*). Most reported malformations involve missing or extra hind limbs (*2–4*). Missing limbs are difficult to inter-