

**NECK POSTURE, DENTITION, AND FEEDING STRATEGIES
IN JURASSIC SAUROPOD DINOSAURS**

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INTRODUCTION

Sauropod dinosaurs represent the extremes of both gigantism and neck elongation in the history of terrestrial vertebrates. Neck lengths were extreme in both absolute and relative measure. The necks of the Jurassic sauropods Barosaurus and Brachiosaurus were about 9m long, well over twice the length of their dorsal columns. Even the relatively short-necked Camarasaurus, with a cervical column about 3.5 m long, had a neck substantially longer than its trunk. Because of their elongate necks, massive bulk, abundance, and diversity, the feeding habits of the sauropod dinosaurs of the Jurassic period has been a subject of inquiry and dispute since relatively complete fossils of this clade were first discovered over 100 years ago. Analysis of the functional morphology and paleoecology of sauropods has led to a diversity of interpretations of their feeding habits. Sauropods have been interpreted as high browsers, low browsers, aquatic, terrestrial, bipedal, tripodal, and have even been restored with elephant-style probosces. Furthermore, differences in neck length, body shape, cranial anatomy, and dental morphology. Here we will review various lines of evidence relating to feeding in sauropods and reconsider them in light of our own studies on neck pose, mobility, and inferred feeding envelopes in Jurassic sauropods.

Sauropods varied considerably in body plan and size, resulting in a range of head heights across the different taxa, when feeding in a neutral, quadrupedal stance. Reconstructions have often differed in the depiction of a sauropod taxon in neutral pose, both in the placement of the elements of the appendicular skeleton and the curvature of the axial skeleton. More precise determination of neutral feeding height would permit sorting sauropod taxa into a vertical range of feeding niches, followed with an analysis of extremes of neck mobility and postural repertoire for more specialized forms of feeding. Dentition morphology and microwear provide additional indirect evidence of feeding preferences (e.g., Barrett and Upchurch, 1994, 2000; Calvo, 1994; Fiorillo, 1995, 1998). Evidence regarding the vegetation consumed by different sauropod taxa can then be correlated with their specific range of feeding heights.

Postural Reconstructions

The basic quadruped body plan can be considered architecturally as an axial skeleton suspended between the pectoral and pelvic girdles and appendicular skeleton. In reconstructing the overall body plan of a given taxon, some portions of the skeleton can be regarded as independent assemblies amenable to modeling in isolation from the rest of the skeleton. For instance, the intrinsic curvature of the axial skeleton can be determined by carefully placing successive vertebrae in articulation in a state of neutral deflection (see below). Whereas the vertebral column may be differentiated into cervical, dorsal, sacral, and caudal series, these individual segments form a smoothly varying curve when assembled into a continuous column. The fore- and hindlimbs can also be studied initially in isolation, relying primarily on the morphology of the component elements and modern analogues to guide the reconstruction. The articulation with least certainty is the attachment of the pectoral girdle to the axial skeleton, as there is no bony articulation between these units, and thus the nature of the attachment must be inferred more indirectly (Parrish and Stevens, 2002; Parrish et al., in prep). An initial analysis of the skeleton as a set of subassemblies disregards factors such as the droop in a cantilevered tail or neck due to gravity, or the splay to the metatarsals and digits in the pes in reaction to the compressive forces and moments applied to a foot when standing in static equilibrium. Although not insignificant, they are beyond the scope of a reconstruction focusing on feeding.

For purposes of this study, the most important information derived from such a structural analysis are: 1) the height and slope of the axial skeleton at base of the neck, 2) the length and curvature of the neck, and 3) the resultant position of the head when the animal is in a neutral standing posture. Once the neutral pose is established, biomechanical analysis of the range of motion within the neck would give some indication of the animal's feeding height.

Neutral Pose and Intrinsic Curvature along the Axial Skeleton

Careful analysis of the undeflected state of sauropod necks is of central importance to

understanding their feeding habits. Of all aspects of sauropod biology, perhaps the greatest divergence of opinion has concerned the curvature of the neck. The early reconstructions of most sauropods depicted the necks as cantilevered ahead of the animal and generally descending at the base due to the arch of the back, and often gently upcurved cranially (e.g., Holland, 1906; Gilmore, 1925, 1936; Hatcher, 1901; Osborn and Mook, 1921). Only a few sauropod taxa were initially reconstructed as having giraffe-like necks, with sharp upwards curvature at the base (Wiman, 1929, fig. 3; Janensch, 1950b, Taf. VI-VIII). Over the decades since their initial descriptions, however there has been a general trend towards depicting sauropods as having ascending necks, some with necks much more steeply curved than originally depicted. A swan neck is often assumed by default, for instance, in an illustration of *Opisthocoelicaudia*, a taxon for which the neck is unknown (Paul, 2000, p. 406) contrary to the original description which concluded the neck would have been horizontal or downward curving (Borsuk-Bialynicka, 1977, fig. 19). Paul (2000, p. 92) suggests that some sauropod necks had thick intervertebral discs, effectively wedges between successive centra, that induced upward curve at their base.

Sauropod necks, however, were strongly opisthocoelous, with central articulations that closely resemble the mammalian opisthocoelous biomechanical design, consisting of condyles that insert deeply in cotyles of matching curvature, leaving little room for cartilage. In modern quadrupeds with opisthocoelous cervicals, such as the horse, giraffe, and rhino, the central condyle and cotyle are separated by only a few millimeters. In avians, heterocoely is similarly associated with very precisely matching articular facets and tight intervertebral separations. Across a large range of extant vertebrates, substantial intervertebral separations are associated with platycoelous vertebrae while vertebrae with nonplanar central articular geometry generally have little intervening cartilage, and thus little room for conjecture regarding their undeflected state.

Neutral Deflection -- The neutral state of deflection between successive vertebrae is defined geometrically by the alignment of the zygapophyses and nulling the deflection at the central articulation (Stevens and Parrish, 1999). The pre- and postzygapophyses, if present, are generally centered within their range of dorsoventral travel when the two vertebrae are in the undeflected state. Simultaneously, the central facets will be in a neutral or undeflected state. For

platycoelous vertebrae, the two planar articular surfaces are parallel when undeflected, a state particularly easy to verify in lateral view. Determining the neutral position for opisthocoelous vertebrae requires closer scrutiny of the margins of the central articulation. The synovial capsule surrounding the condyle-cotyle pair at the centrum generally exhibits circumferential attachment scars surrounding the condyle and cotyle. These ridges are parallel when the joint is undeflected, and especially apparent when viewing osteological mounts of extant vertebrates in lateral aspect. Note that the gap across these margins at the centrum is necessarily wider than the actual intervertebral separation deep within the ball and socket to accommodate the displacement of the cotyle during mediolateral and dorsoventral deflection.

The intrinsic curvature of the vertebral column for a given taxon can be determined by placing successive elements in neutral deflection. This procedure can be performed graphically based on lateral view depictions such as photographs and engravings of verified dimensional accuracy of specimens (see below). Whereas two-dimensional analysis is sufficient to establish the neutral pose along a vertebral column, a three-dimensional reconstruction is required to estimate the range of motion and curvature achievable (Stevens and Parrish, 1999; Stevens 2002; Stevens & Parrish, in press; Stevens, in prep).

The neutral pose within the presacral vertebral column is defined geometrically by nulling the angular deflection at each joint, and would presumably correspond to a rest state at each joint along the column. There is consistency between the geometrically-defined neutral posture and the pose habitually held by the behaving animal, determined by direct manipulation of the cervical vertebral columns of a variety of extant vertebrates. For example, the neutral pose reveals the sigmoid curvature characteristic of avian and equine necks, the catenary shape of the camel's neck, and the sharp upturn at the base of the otherwise straight giraffe neck. The giraffe neck is particularly relevant to the reconstruction of sauropod necks, owing to the historical and persisting interpretation of some sauropods as giraffe analogues, especially as regards the presumed upturn at the base of the neck. The adult giraffe neck is sharply angled at its base while held in the undeflected, neutral position (Stevens and Parrish, in press). This angulation arises not from deflection at the intervertebral joints, but from keystone-shaped cervicothoracic

vertebrae, the most wedge-shaped being C7. 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, in the undeflected state, reflecting the morphology of the vertebrae.

Neutral Posture of the Presacral Axial Skeleton

For a number of well preserved sauropods, the original lateral view illustrations of individual vertebrae, based on photographs taken of the prepared vertebrae prior to mounting, provide a valuable resource for reconstructing the neutral posture of their axial skeletons. The presacral vertebrae of Apatosaurus, Brachiosaurus, Cetiosaurus, Diplodocus, Dicraeosaurus, and Euhelopus will be reviewed here (see Stevens, in prep.). In Fig. 1, digital scans of the individual steel engravings of the presacrals of Apatosaurus louisae from Gilmore (1936, plates XXIV-XXV) were adjusted for scale and composited using Photoshop[®], placing each successive pair of vertebrae into neutral deflection. With the exception of the incomplete preservation of cervical 5, the reconstruction of the last cervical, and some distortion to a few neural arches in the anterior dorsals, the entire presacral series reconstructed into a very gentle arch, with remarkably little curvature to the dorsals. The composite image shows the vertebrae as transparent, revealing the insertion of the central condyle within cotyle, and the centering and superposition of the zygapophyses.

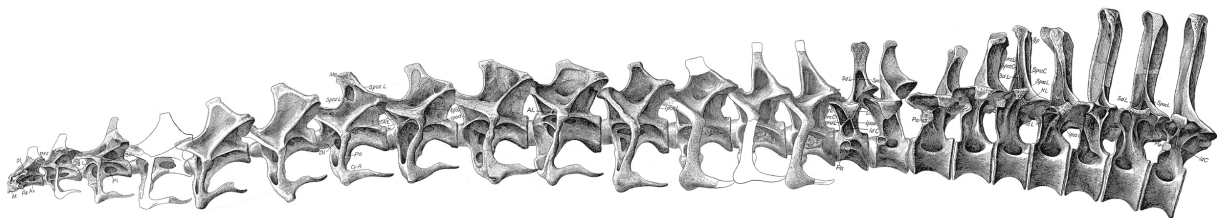


Figure 1. Apatosaurus louisae presacral vertebral column reconstruction in neutral position.

Fig. 2 shows a composite of the individual dorsal vertebrae D1-D10 and cervicals C10-C15 from the companion mount, Diplodocus carnegii (Hatcher, 1901, plates IV, VII). Note that the midcervicals in this specimen (CM 84) are significantly distorted, and are thus not included in this neutral-pose composite.

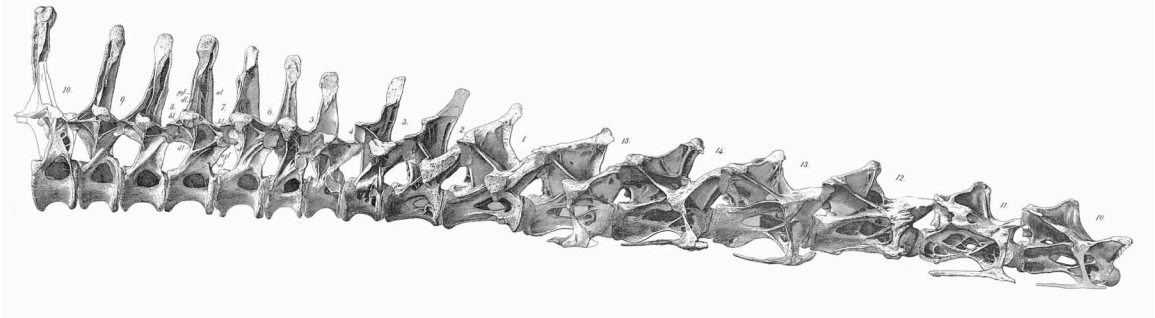


Figure 2. Diplodocus longus vertebrae C10-D10 in neutral pose.

Fig. 3 shows the composited presacrals of Dicraeosaurus hansemanni, from (Janensch, 1929a, Taf. I). The dorsal column is more distinctly arched, but again the cervicodorsal transition is straight, as in the other diplodocids.

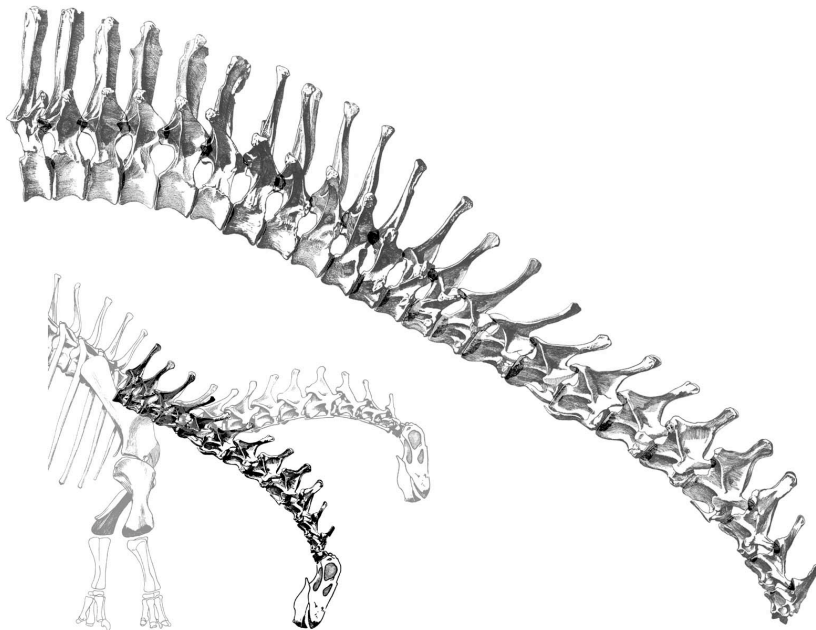


Figure 3. Dicraeosaurus hansemanni presacral vertebral column reconstruction in neutral position, a composite of the presacral vertebrae individually figured in Janensch (1929a, Taf. I). Inset: superposition of composite onto reconstruction in Janensch (1929a, Taf. XVI).

Since its initial description, Euhelopus zdanskyi (Wiman, 1929, Taf. III) has been given giraffe-like interpretations of increasing slope (from about 38 to 65 degrees, c.f. Wiman, 1929, fig. 3; McIntosh et al., 1997, fig. 20.9; Paul, 2000, appendix A). The neck in neutral position, however, is remarkable in its linearity from C1 to at least D2, when the postmortem dorsiflexion “death pose” is removed posterior to C17, as shown in Fig. 4 (Stevens and Parrish, in press; Stevens, in prep.).

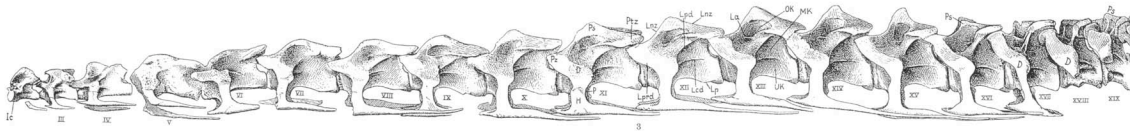


Figure 4. Euhelopus zdanskyi (from Wiman, 1929, Taf. III), with C17 and D1 rotated digitally to remove the postmortem “death pose” dorsiflexion.

Death pose dorsiflexion was also responsible for the swan-neck pose of the juvenile Camarasaurus lentus (Gilmore, 1925, fig. XIV). The postzygapophyses are in fact displaced posteriorly far from neutral position, many completely out of articulation (Parrish and Stevens, 1998). The posterior cervicals and anterior dorsals show no evidence of the wedge shape needed to induce curvature (Osborn & Mook, 1921, plate LXVIII, DNM 28; CMNH 11338; CMNH 11069). Despite the popular depiction of Camarasaurus with a sharply upturned neck, the initial reconstruction (Fig. 5) showing the cervicodorsals as approximately horizontal is born out by the mounting of actual fossil material in this region of the axial skeleton (see mount at Wyoming Dinosaur Center and “Annabelle” at the Natural History Museum, University of Kansas).



Figure 5. Original Camarasaurus reconstruction from (Osborn and Mook, 1921, fig. 28) showing an essentially horizontal cervicodorsal transition.

Brachiosaurus brancai was originally drawn (and mounted) with a giraffe-like ascending neck (Janensch, 1950, Taf. VIII), by providing the last few cervical vertebrae and the first dorsal vertebra with distinctly wedge-shaped centra. In some subsequent reconstructions and analyses (McIntosh, et al., 1997, fig. 20-16; Paul, 1988, 2000, appendix A; Christian and Heinrich, 1998) the neck is depicted as reaching or exceeding the vertical while in a state of neutral deflection (but c.f. [Czerkas and Czerkas 1991, p. 132; Martin et al. 1998]). The neck is reconstructed in Fig. 6 (Stevens, 2002, text fig. 2-3) by compositing the original steel engravings from Janensch (1950, abb. 17-50) in neutral pose. The result is a very gentle downward curving neck extending from a straight cervicodorsal series; the centra at the base of the neck show no evidence to suggest providing this sauropod with a giraffe-like elevated neck. In particular, the centra of the cervicodorsals from C10 to D2, which were found articulated within a single block, are spool-shaped, not wedge-shaped, and their resulting neutral pose is straight, not ascending.

The anterior cervicals of Brachiosaurus (both specimens SI and SII, see Fig. 6b) curve downward in neutral position, a configuration apparent in other sauropods such as Cetiosaurus (Fig. 7) and the diplodocids. This droop is likely important in orienting the head ventrally in support of downward feeding (see below).

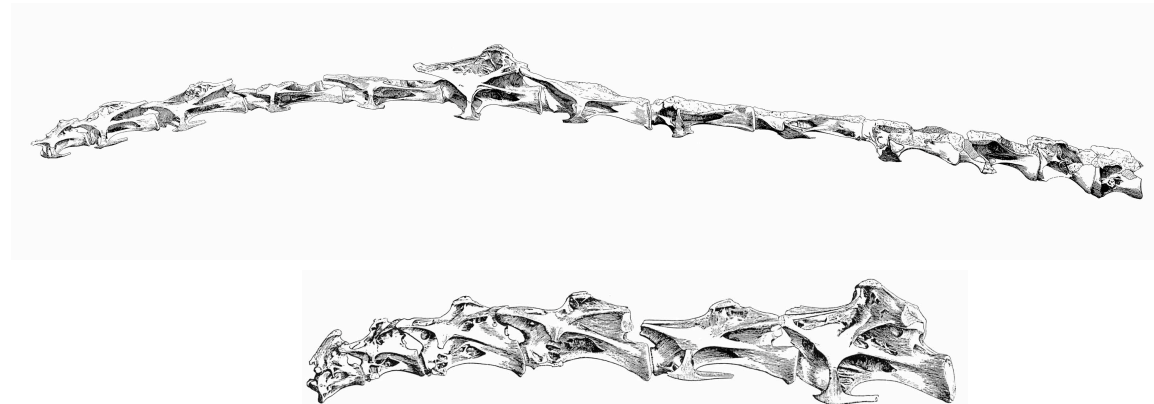


Figure 6. In a, Brachiosaurus brancai specimen SII neutral pose composite of C3-D2. In b, specimen SI neural pose composite from C2-C7. Both exhibit gentle droop cranially also observed in neutral pose reconstructions of some other sauropod necks. From Janensch (1950b).

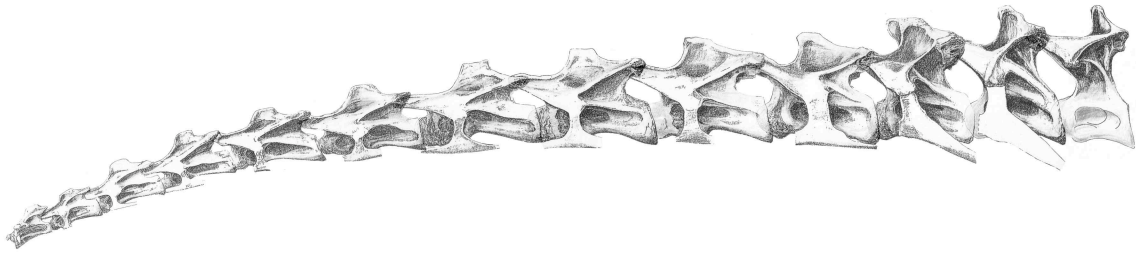


Figure 7. Cetiosaurus (LCM G468.1968) neural pose composite based on individual vertebrae drawn by John Martin.

Skeletal Reconstructions

The acetabulum can be regarded as the fulcrum about which the axial skeleton would pivot, according to differing estimations of glenoid and acetabular height and the placement of the pectoral girdles upon the ribcage. Amongst sauropod taxa little variation is apparent in the basic design of the hindlimbs, and reconstructions for a standing posture differ only marginally. For a sauropod in a standing pose, there is some room for interpretation regarding the degree of flexion of the hindlimbs at the knee, the thickness of cartilage at the knee and tarsus, and the specific angulation at the tarsus and pes, which all have some consequence on acetabular height. Sauropod forelimbs show much more variability across reconstructions, with variations in the articulation of the digitigrade manus, the degrees of pronation and elbow flexion (Christian et al, 1999), and the orientation of insertion of the humerus into the glenoid fossa.

The two factors having the greatest effect on head height are the degree of arch to the back and pectoral girdle placement, for a given reconstruction of the neck. A digital model of Apatosaurus louisae, created using DinoMorph[®], will illustrate. The neck will be held constant in neutral deflection based on the composite in Fig. 1 (see Fig. 9), along with the tail and limbs; only the arch to the back and placement of the pectoral girdles is varied.

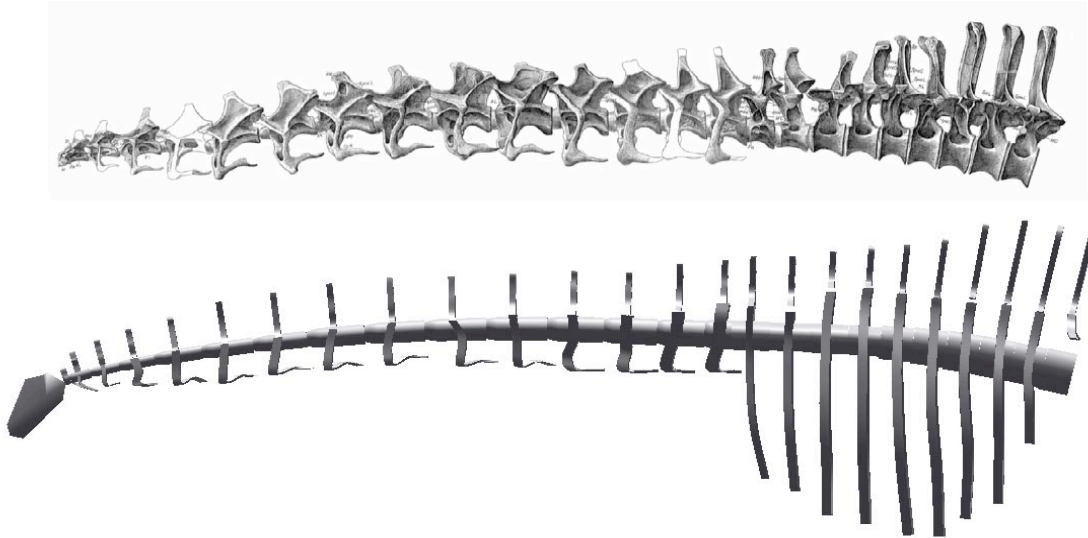


Figure 9. DinoMorph® model of the presacral axial skeleton of Apatosaurus louisae articulated in neutral pose, based on digital composite of individual vertebrae from Gilmore (1936).

The dorsal vertebrae in Fig. 9 form a very shallow arch, consistent with (Gilmore, 1936, plate XXXIV) and (Wilson and Sereno, 1998, foldout 1). In Fig. 10 the appendicular skeleton is added, and, for comparison, the dorsals are given a much more pronounced arch (McIntosh et al. 1997, fig. 20.12; Paul, 2000, appendix A).

Head height is substantially affected by the arch given to the dorsals. The more steeply arched, the greater the downslope of the base of the neck. Head height is also affected by pectoral girdle placement upon the ribcage: the head is raised or lowered proportionally to the ratio of the distance from head to acetabulum over the distance from the glenoid to acetabulum (about 2.5 for Apatosaurus) as the presacral column pivots about the acetabulum. Lowering the scapulae by 0.5 m relative to the ribcage (i.e. raising the ribcage with respect to the ground level), will result in raising the head by about 1.25 meter, for example. The corresponding multiplier is about 3 for Brachiosaurus, due to its relatively longer neck.

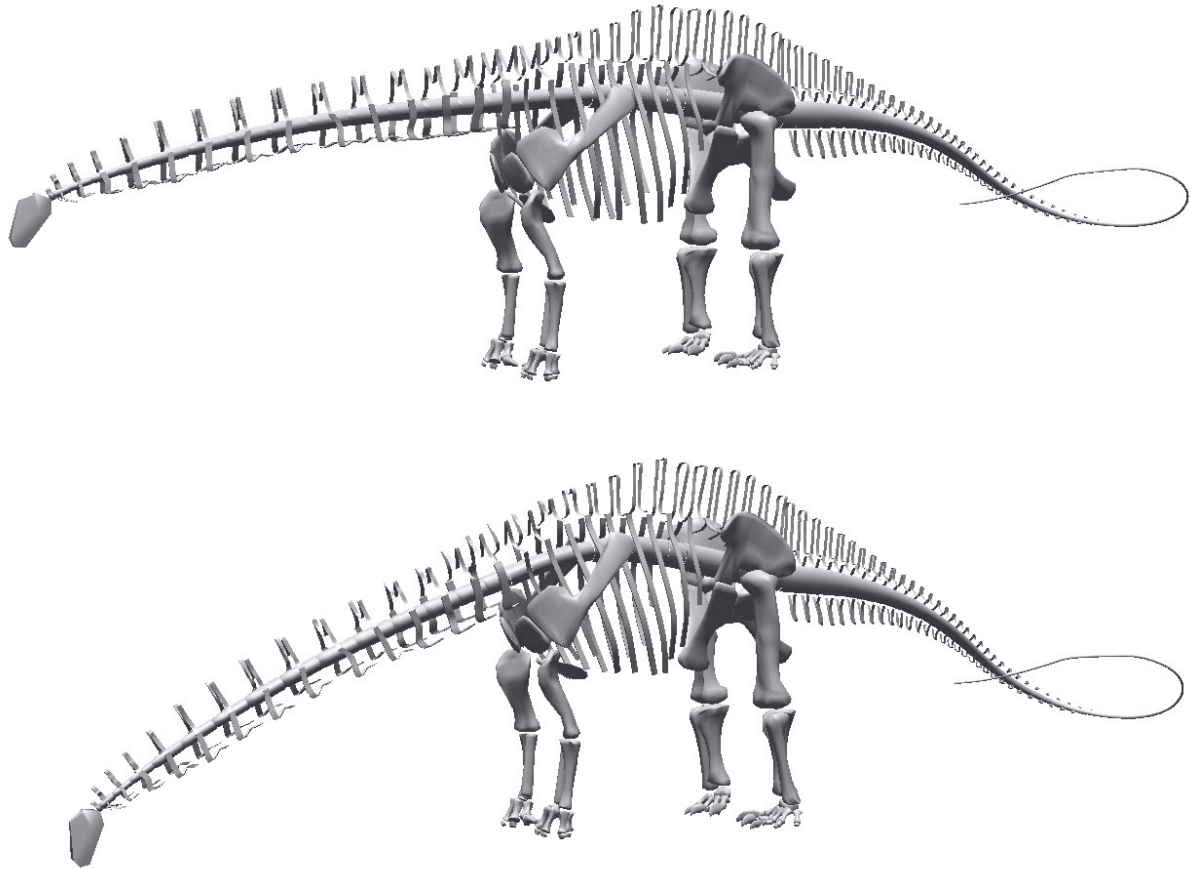


Figure 10. Two interpretations of the body plan of *Apatosaurus louisae* differing in pectoral girdle placement and the curvature given to the dorsal vertebral column.

Feeding Envelopes and Inferred Browsing Heights -- A “feeding envelope” is the range of head positions that can be reached by a tetrapod standing in one place and simply moving its neck relative to its body. Such an envelope might be estimated from the range of motion along the neck (Martin, 1987, fig. 3; Stevens and Parrish, 1999). The assumption of this approach is that the undeflected or neutral pose approximates the center of the feeding envelope for each taxon. The only ways a sauropod could deviate from such an envelope would be the following:

1) Rearing tripodally, as has been suggested by a variety of authors (but see Stevens and Parrish, in press, and Rothschild, this volume).

2) Flexion or extension of the dorsal vertebrae, such that the angulation and position of the anterior end of the dorsal series would increase or decrease in height, thereby varying the base height of the neck and, therefore, head height.

3) Splaying of the forelimbs to bring the neck closer to the ground, as in extant giraffes.

4) Hyperextension of the intervertebral ligaments in the cervical column beyond the observed limits to flexibility of such structures in extant archosaurs and mammals (Wedel and Saunders, 1999; Parrish and Stevens, 2001).

Martin (1987) estimated a curved feeding envelope for Cetiosaurus approximately 4.5 m wide by 3.5 m above ground level, based on a reconstruction in which the base of the neck slopes slightly downwards at the shoulder. In an earlier study of ours (Stevens and Parrish, 1999), the longer necks of Apatosaurus and Diplodocus were estimated to sweep through a lateral arc about 8 m wide, and surprisingly, to permit reaching downward below ground level, an adaptation perhaps related to aquatic feeding. The dorsal flexibility of Apatosaurus was somewhat greater than that of Diplodocus, 6 m versus 4 m, attributable primarily to the larger zygapophyses at the base of the neck of Apatosaurus. Fig. 11a shows the range of dorsoventral deflection for Apatosaurus, adapted from (Stevens and Parrish, 1999). Fig. 11b shows Brachiosaurus brancai (SII specimen) at the same scale, with the neutral neck pose based on the composite in Fig. 6. This DinoMorph™ skeletal reconstruction is based on Janensch (1929b, 1935-1936, 1950a, b). While the range of dorsoventral movements cannot be estimated due to the lack of preservation of the neutral arches. The head would reach over 9 m above ground level with a modest dorsiflexion of approximately 3 degrees/joint, and could reach ground level (without requiring a giraffe-like splay of the forelimbs to drink) by ventriflexion of slightly less than 8 degrees/joint proximally. It is not necessary to postulate osteological adaptations such as wedge-shaped centra for Brachiosaurus to have reached remarkable heights and achieve a huge feeding envelope, even if it had negligible ability to elevate the neck above its neutral pose (for muscular or cardiovascular reasons).

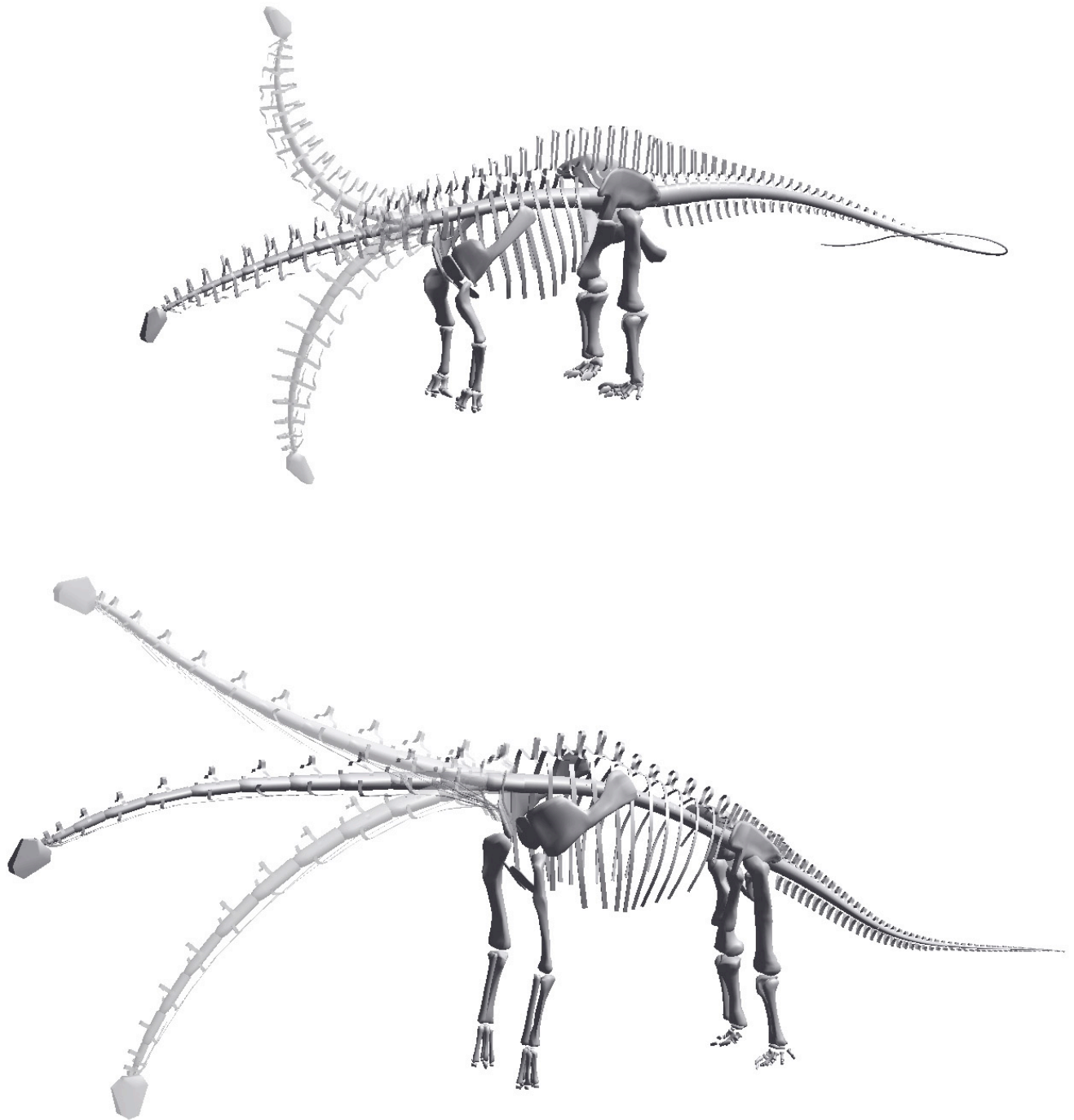


Figure 12. *Apatosaurus louisae* and *Brachiosaurus brancai*, to same scale, showing osteologically-determined neutral pose to presacral axial skeleton (see text).

Sauropod Dentition

The basal members of all dinosaur lineages for which an herbivorous diet is generally inferred (Sauropodomorpha and Ornithischia) share the same basic tooth form, consisting of a leaflike shape featuring an expanded crown and a serrated row of denticles occurring along the ridge dividing the labial and lingual surfaces of the tooth. In Sauropodomorpha, the leaf-shaped form predominates in prosauropods, particularly if one accepts Barrett's (1999, 2000) reassignment to the Sauropoda of the blunt teeth originally designated by Simmons (1965) as belonging to the prosauropod Yunnanosaurus. Yates and Kitching's recent (2003) analysis of Triassic sauropodomorphs has placed several taxa formerly considered part of a monophyletic Prosauropoda inside of the sauropod lineage, including Melanorosaurus and Anchisaurus.

The taxonomic reassessment of Anchisaurus, which is the most basal sauropod in Yates and Kitching's (2003) phylogeny, is significant because, unlike the other Triassic and Lower Jurassic sauropods, Anchisaurus is well represented by dental and cranial material. The teeth of Anchisaurus are leaf shaped, serrated, and recurved medially (Galton, 1976). Dentition among other basal sauropods is represented by isolated teeth of the Early Jurassic genera Barapasaurus and Kotasaurus (Yadigiri, 1988). Both possess coarse denticles and exhibit the expanded spoon shaped and lingually concave crown pattern that is characteristic of most non-diplodocid sauropods. Similar teeth are present in members of the Chinese sauropod clade Euhelopodidae, although some variation occurs in the size and distributions of denticles, which are absent altogether in Euhelopus. No sauropod teeth other than those of Barapasaurus, Kotasaurus, euhelopodids, and some unworn examples of the Tendaguru Brachiosaurus are serrated. The teeth of the Middle Jurassic sauropod Patagosaurus are similar in shape to those of Euhelopodidae (Bonaparte, 1986). Camarasaurus teeth are well known, and are similar in basic shape to those in Patagosaurus and euhelopodids, although the expansion of the crowns relative to the tooth base is less pronounced, as is the concavity of the lingual surface of the teeth (McIntosh and Berman, 1995).

The teeth of Brachiosaurus share the general spatulate configuration with Vulcanodon,

Euhelopodidae, and Camarasaurus (Janensch, 1935). Denticles are reported in some unworn Brachiosaurus teeth (Janensch, 1935) but are not visible in worn teeth. In contrast to those of Camarasaurus, the crowns of Brachiosaurus teeth exhibit minimal expansion relative to the base.

The teeth of Diplodocidae and Titanosauridae are both nearly circular in diameter, without any expansion of the crowns. In both families, the crowns taper gently to a point in the unworn condition, but form planar occlusal surfaces when worn (Holland, 1924; Barrett and Upchurch, 1994, Curry Rogers and Forster, 2001).

Dental Macrowear -- Wear facets are absent in the teeth of Anchisaurus, Barapasaurus and Kotasaurus, but a variety of wear facets are apparent in other sauropods for which dentition is known. In the euhelopodids Omeisaurus and Shunosaurus, step-shaped wear facets occur on the cranial and caudal margins of the teeth, which appear to be the result of significant tooth-tooth wear (Upchurch and Barrett, 2000), with the greatest amount of wear on the cranial facet. No such wear is apparent in the skull of Mamenchisaurus sinocanadorum (Russell and Zheng, 1993). Step-like tooth wear is also evident in Patagosaurus (Bonaparte, 1986). Significant concave wear facets are also visible on either side of the apices of the teeth in Camarasaurus (Madsen et al, 1995), although here the amount of wear is more symmetrical than in Patagosaurus and the euhelopodids.

In Brachiosaurus, small amounts of wear are observed, but generally on the lingual and labial sides of the crown rather than on the cranial and caudal margins. As in diplodocines and titanosaurs, this has been interpreted as evidence of tooth-to-tooth occlusion, rather than interdigitation of upper and lower teeth. In titanosaurs and diplodocines, this type of occlusion produces high-angle wear facets that resemble the point of a chisel (Fiorillo, 1998; Curry Rogers and Forster, 2001; Upchurch and Barrett, 2000).

Dental Microwear -- In studies of the teeth of mammals, and particularly those of fossil primates, dental microwear has been studied via scanning electron microscopy as a method of inferring diet in extinct vertebrates. The logic behind this approach is that different food types will create different, and distinctive, striations on the enamel of herbivore teeth that may be indicative of diet. This approach has been applied to sauropods by Fiorillo (1991, 1994, 1998),

Calvo (1994) and Barrett and Upchurch (1994, 1995), although studies to date have focused only on the teeth of Camarasaurus (Fiorillo, 1991, 1998), Diplodocus (Fiorillo 1991, 1998; Calvo, 1994; Upchurch and Barrett, 2000), and the titanosaurid Raptesaurus (Upchurch and Barrett, 2000).

All studies of diplodocid teeth showed labiolingual scratches across the wear facets, whereas the studies of Camarasaurus indicated both pits and scratches in adult teeth (Calvo, 1994; Fiorillo, 1998; Upchurch and Barrett, 2000). Fiorillo (1991) interpreted the absence of pits in juvenile Camarasaurus teeth as evidence for ontogenetic switching of diets. Upchurch and Barrett's (2000) study of one Rapetosaurus tooth indicated both coarse scratches and pitting on the wear surface.

Cranial Characters

Plesiomorphically, the skulls of sauropods resemble those of prosauropods like Plateosaurus (Huene, 1926; Galton, 1984). In the most basal sauropods for which relatively complete skulls are known (e.g., Anchisaurus, Shunosaurus, and Omeisaurus (the latter two of which are either basal Euhelopodidae [in Upchurch, 1998] or basal Sauropoda [Wilson, 2002] in the two most comprehensive recent phylogenetic analyses of sauropods), the skull is essentially convex in anterodorsal profile, with a modest snout.

Inclination of Skull -- Because of its presence in Euhelopodidae, Camarasaurus, Brachiosauridae and sauropod outgroups, the plesiomorphic pattern for sauropod cranial inclination appears to be one with the tooth row positioned horizontally relative to the long axis of the brain cavity running from the foramen magnum into the braincase. In Diplodocidae, Nemegtosauridae, and the Titanosauridae for which cranial material is known, the tooth row is inclined cranioventrally relative to this axis, such that the head would naturally tilt downwards in a neutral position (here defined as the situation where the long axis of the brainstem cavity and the neural canal of the atlas/axis are horizontal). Fiorillo (1998) noted these differences when comparing Camarasaurus with Diplodocus, interpreting the nearly 90 degree angulation of the

head relative to the neck in Diplodocus as an indication that it might have had a more erect vertical neck than that of Camarasaurus. However, the alternate interpretation, that the head was directed more ventrally in Diplodocus to facilitate low browsing, seems equally plausible. The diplodocids Apatosaurus and Diplodocus had sufficient neck ventral flexibility to reach far below ground level (Stevens and Parrish, 1999), a capability consistent with lacustrine feeding. Taken in conjunction with the presence of prognathous, peg-like cropping or sieving dentition, dorsally placed nostrils, and a ventrally trending neutral position for the cervical column, the downwards curvature of the head could have served as a means of grazing on or under the surface of the water while maintaining visual and olfactory vigilance. The absence of these features in Camarasaurus and Brachiosaurus would be consistent with a more generalized feeding envelope for these genera.

Configuration of Dentition and Inferred Jaw Mechanics -- The basal arrangement of dentition in Sauropoda is not dissimilar from the condition that is plesiomorphic for Sauropodomorpha and Dinosauria, consisting of an essentially isodont array of teeth that projected from most of the ventral surfaces of the maxillae and premaxillae without any diastema. The teeth are either mildly prognathous or essentially perpendicular to the long axis of the tooth row, and the plane defined by the bases of the teeth is parallel to that of the horizontal long axis of the braincase. The cranial end of the dentary is convex upwards in Anchisaurus (Galton, 1976), Plateosaurus (Galton, 1985), and Diplodocidae (Hatcher, 1901), so the possibility exists that the everted lower jaw is a plesiomorphic feature for Sauropoda and reversed in lineages such as the Euhelopodidae and Titanosauroida.

History of Inferences of the Use of Sauropod Necks in Feeding

The notion that sauropods used their necks to achieve significant lateral sweep can be traced back to Hay (1908). The concept of sauropods as low browsers has persisted for some taxa over the years. The idea of sauropods-as-molluscivores was first proposed by Holland (1924), who felt that the blunt, prognathous dentition of Diplodocus could have been utilized to

crack open unionid bivalves. Haas (1963), in his study of diplodocid jaw musculature, inferred Diplodocus was an aquatic filter feeder, specializing on floating crustaceans and/or mollusks. Both visualized the long neck as an adaptation for sweeping the head through a broad lateral arc without moving the body.

Alexander (1985) restored the neck of Diplodocus in an essentially lateral orientation, contending that the cervical musculature would have been insufficient to allow the neck to be raised significantly, and suggesting that a large nuchal ligament would have been instrumental in maintaining the neck in a horizontal orientation. Martin (1987) manually articulated the neck of the Leicester specimen of Cetiosaurus, and concluded that the neutral position for its neck was near-horizontal, with a slight downwards curvature (see also Fig. 7). Martin envisioned the neck of Cetiosaurus as primarily an adaptation facilitating lateral sweep of the head.

Dodson (1990) cited the broad vertical feeding ranges made possible by the elongate necks of sauropods, and suggested that neck length and mobility might facilitate niche partitioning of different genera.

Barrett and Upchurch (1994) proposed that Diplodocus might have served as both a high browser and a low browser, stripping vegetation in the high browse by pulling stems through its tooth comb. They cite the different types of wear observed on upper and lower teeth as evidence for these two types of feeding, and suggested that propalinal scratches on the teeth might be an artifact of branch stripping during high browsing. They held that the greatest amount of mobility in the cervical vertebral column of Diplodocus was in the most cranial vertebrae, and that this flexibility close to the head facilitated their branch stripping mechanism. In a subsequent (2000) review of sauropod feeding mechanisms, Upchurch and Barrett suggested that vulcanodontids, most euhelopodids, brachiosaurs, cetiosaurs, Camarasaurus, and Brachiosaurus were high browsers, whereas Shunosaurus and the Dicraeosauridae were low browsers.

Martin et al. (1998) proposed that sauropod necks were held essentially horizontally, and suggested that the cervical ribs served as a ventral compressive member that, along with the dorsal nuchal ligament, would have held the neck as a segmented, flexible horizontal beam. They identified Dicraeosaurus and Apatosaurus as taxa that were predominately dorsally braced,

and Euhelopodidae (sensu Upchurch), Brachiosaurus, and Camarasaurus as taxa that were braced more ventrally.

Jurassic Plant Communities and Implications for Sauropod Feeding

Globally, Jurassic floras are dominated by herbaceous plants and small trees, most significantly bennettitalean cycadeoids (tree ferns), true ferns, horsetails, cycads, and ginkgoes (Behrensmeyer et al., 1992; Coe et al., 1987). The Morrison Formation of the Western United States and the Tendaguru Formation of Tanzania represent the two major accumulations of Late Jurassic sauropod fossils. The Jurassic climates of both regions have been interpreted as strongly seasonal (Russell et al., 1980; Dodson et al., 1980; J.T. Parrish et al., in press). Paleoclimate modeling based on biome distributions (Rees et al., 1999) interpreted both regions as “winterwet”. The more thoroughly studied of the two formations, the Morrison, has most recently been interpreted as Savannah-like, dominated by herbaceous vegetation and traversed by large, everflowing rivers around which the greatest concentrations of trees would have occurred (J.T. Parrish et al., in press), although some other recent studies interpret the Morrison as a whole as more humid (e.g., Tidwell et al., 1998).

Inferred Sauropod Diets -- Because of the massive bulk of sauropods, most studies have assumed that their primary food source would be both highly nutritious and abundant (Weaver, 1983; Farlow, 1987). Weaver (1983) measured the caloric densities of extant members of plant groups that were abundant in the Late Jurassic, and reported a range of wet weights of 0.97-2.89 kcal/g for the various herbaceous and arborescent groups, with the highest values yielded for cycads and conifers, with somewhat lower values for ferns and ginkgoes, and the lowest values for horsetails. On the basis of her analysis, Weaver concluded that endothermy in Brachiosaurus was unlikely because the relatively low caloric content of Jurassic plants and the sauropod’s small mouth relative to body size would preclude sufficiently rapid intake to maintain an elevated endothermic metabolism.

Krassilov (1981) suggested a diet of ferns and horsetails for Diplodocids and cycads and

shrubs for camarasaurids, hypothesizing that the retraction of the nares in diplodocids was an adaptation for breathing while obtaining forage underwater. Dodson (1990), utilizing arguments of their abundance in Jurassic landscapes, cited ferns as the most likely candidate for a predominant sauropod food source, but also noted that these giant herbivores were not likely to have been specialists on particular plant types. Fiorillo (1998) suggested that microwear patterns favored an interpretation of Diplodocus specializing on cycads while Camarasaurus might have specialized on gingkoes.

Chin and Kirkland (1998) described what appear to be herbivorous dinosaur coprolites from the Mygatt-Moore quarry of the Morrison Formation. Although determination of the taxonomic identity of the dinosaurs producing the coprolites is problematic, they do include significant components (ranging from 8-52%) of organic matter, the identifiable components of which include woody tissue (5-14%), cuticle (0-8%) and seeds (0-6%). Taxa represented include cycadophytes, ferns, and conifers. J.T. Parrish et al. (in press) cite the presence of significant detrital matter in these coprolites as evidence for low browsing, although both the taxonomic uncertainty of the dinosaurs involved and the possibility of taphonomic disturbance of the coprolites makes direct inference of sauropod diets from these structures highly speculative.

Combining the current state of knowledge of the paleoecology of the Morrison Formation and Tendaguru with our reconstructions of the feeding envelopes of Late Jurassic sauropods leads to the following conclusions:

1. At least in the Morrison, the greatest abundance of trees were found along the riparian corridors, and herbaceous floras dominated elsewhere.
2. Feeding envelopes of the principal late Jurassic sauropods overlapped broadly, with diplodocids, euhelopodids, and dicraeosaurids clearly earmarked as low browsers with the potential for broad lateral sweep of their necks. Camarasaurus and Brachiosaurus both had straight necks that appear to have pointed slightly downwards in the neutral position, but the flexibility of the neck in Camarasaurus and the height of the base of the neck in Brachiosaurus indicate that these taxa would have been capable of high as well as low browsing.
3. Studies of cranial morphology, gross tooth shape, and dental microwear indicate that

the narrow-toothed sauropods (diplodocids, nemegtosaurs, at least some titanosaurs and euhelopodids) predominately fed by cropping relatively soft vegetation and/or by straining planktonic plants and animals. The broad toothed forms (Camarasaurus, Brachiosaurus, potentially vulcanodontids and cetiosaurs) apparently fed on more durable plant material, including cycads and perhaps conifers.

4. The vertical feeding envelopes of Jurassic sauropods overlapped broadly, suggesting that feeding height alone was not a predominant mode of niche partitioning among the abundant and speciose sauropods of the Morrison and Tendaguru.

Conclusions

Varying patterns of dental morphology, cranial anatomy, cervical design, and appendicular specialization indicate that sauropods similarly varied in their modes of feeding. Reconstructions of the neutral position of the vertebral column for six well-known Jurassic and Cretaceous sauropods (Apatosaurus, Brachiosaurus, Camarasaurus, Dicraeosaurus, Diplodocus, and Euhelopus) indicate that all of these taxa had necks inclined slightly downwards in the undeflected position. Morphological evidence for the near-vertical inclination of sauropod necks favored by some contemporary restorations of sauropods (such as trapezoidal-shaped cranial dorsals or caudal cervicals, indicators of thick intervertebral discs or other adaptations to create neck elevation) were not observed in any taxa analyzed for this study.

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