Neck Posture of Sauropod Dinosaurs

Stevens and Parrish's report (*1*) represents a major advance in our understanding of neck posture in sauropod dinosaurs, but there are certain aspects of their work that require clarification. Stevens and Parrish determined the feeding envelopes (the maximum vertical and horizontal extent of head movements) of *Apatosaurus* and *Diplodocus* using three-dimensional digital modeling of the neck vertebrae. The size and shape of these envelopes were calculated based on the assumption that the base of the neck is essentially a fixed reference point, and that therefore the trunk and shoulder regions only contribute information on the static position of the base of the neck. In diplodocid sauropods, however, the three to four most anterior trunk vertebrae possess prominent ball-and-socket joints between elongated vertebral centra, and have transversely broadened zygapophysial articular facets that are situated far from the midline (*2, 3*). These features are also present in posterior cervicals, suggesting that the anterior trunk region could modify head position by providing additional dorsiflexion. Even mild flexure at the shoulder region, when magnified by the length of the neck, would have an important impact on ultimate head position. Thus, future studies should incorporate detailed models of anterior trunk vertebrae as a means of more precisely estimating the feeding envelope size and shape.

A second difficulty with Stevens and Parrish's analysis is that their data for *Apatosaurus* was derived from a single specimen in the Carnegie Museum (CM 3018). This generally well preserved specimen has suffered severe damage at the base of the neck, and the three most posterior cervicals are thus represented by plaster models that cannot provide reliable anatomical data (*2, 3*). Although Stevens and Parrish acknowledge that the morphology of the posterior cervicals is particularly influential in determining the nature of the feeding envelope, they do not mention this problem, and it is not clear how this gap in the data was addressed in their analyses. This deficit could have had a profound impact on Stevens and Parrish's conclusions, and until this problem is resolved, it will be difficult to evaluate accurately their hypothesized differences in neck posture and browse height for *Diplodocus* and *Apatosaurus*.

Even so, although the problems outlined above cast some doubt on the details of Stevens and Parrish's interpretations, the general proposal that diplodocids were low-level browsers is well supported by their work and several previous studies (*4–6*). For

example, dicraeosaurids (close relatives of the diplodocids) possess tall neural spines in the cervical region that would make dorsiflexion of the neck almost impossible (*5*). Furthermore, studies of jaw mechanics and tooth macro- and micro-wear have independently concluded that *Diplodocus* browsed at lower levels than did most other sauropods (*4–6*).

The use of three-dimensional digital modeling in dinosaurian biomechanics represents an exciting and important advance, but future studies of sauropod neck posture should include more specimen samples and take into account relevant anatomy from the anterior trunk region.

Paul Upchurch
Department of Earth Sciences
University of Cambridge
Downing Street
Cambridge, CB2 3EQ, United Kingdom
E-mail: pupc98@esc.cam.ac.uk

References and Notes
1. K. A. Stevens and J. M. Parrish, *Science* **284**, 798 (1999).
2. C. W. Gilmore, *Mem. Carnegie Mus. Nat. Hist.* **11** (no. 4) (1936).
3. Personal observation of diplodocid material at the Carnegie Museum, Pittsburgh.
4. P. M. Barrett and P. Upchurch, *Gaia* **10**, 195 (1994).
5. ———, in *Sixth Symp. Mesozoic Terr. Ecosyst.*, A. Sun and Y. Wang, Eds. (China Ocean Press, Beijing, 1995), pp. 107–110.
6. P. Upchurch and P. M. Barrett, in *The Evolution of Terrestrial Herbivory*, H.-D. Sues, Ed. (Cambridge Univ. Press, Cambridge, in press).

Response: Upchurch observes that our diplodocid feeding-envelope computations are relative to a fixed point at the base of the neck and do not include the effects of bending at the trunk. We agree that the anterior dorsal vertebrae exhibit articular facets suggestive of considerable flexibility, and that even slight lateral bending of the trunk would assuredly have increased the deflection of the distal head. For that matter, even greater lateral reach would have been achieved, with the advantage of maintaining balance, if the diplodocid were to take a step laterally with its forelimbs, essentially pivoting about its hind limbs (an economical movement, given the proximity of the center of mass to the hind limbs). Holding the head artificially fixed for this study, however, permits one to isolate and compare neck flexibilities. The published deflection figures do not represent their maximum feeding envelopes, for in life it would be natural to recruit body move-

ments to increase lateral travel as the neck approached its limit of flexion.

The potential for flexibility in the anterior dorsals mentioned by Upchurch raises an interesting question. Could diplodocids flex these vertebrae as much as the generous articular facets would suggest? Significant lateral motion would be resisted by the dorsal ribs attached to these vertebrae and the overlying scapulae. Reconstructions vary in the hypothesized placement and orientation of the scapulocorocoids with respect to the cervicodorsal region. A comprehensive, three-dimensional analysis of the pectoral girdle and its relation to the dorsal vertebrae and ribs would be needed to begin to quantify anterior trunk flexibility, be it for feeding or for turning around.

Upchurch's second comment relates to the use of a single specimen, CM 3018, for our modeling of *Apatosaurus*. He observes that the mounted skeletal reconstruction of this animal has plaster reproductions of cervicals 13 to 15, and that we did not make clear how we dealt with this "gap in the data." The parametric modeling of the cervical series of both diplodocids involved 24 dimensional and positional parameters for each of the 15 cervicals plus three-dimensional reconstruction of their pre- and postzygapophyses. For *Apatosaurus* the quantitative parameters were taken from the work of Gilmore (*1*) and from the original specimen. The outline shape of the zygapophyses of the mounted specimen were traced directly and used to delimit their three-dimensional counterparts in Dino-Morph. The surface curvature of these facets was first reconstructed from the Gilmore figures, then compared across other posterior cervical sequences of *Apatosaurus* at the Field, the Carnegie, and the American Museum of Natural History. Across the *Apatosaurus* specimens examined, the articular facets show considerable regularity of design and proportion. The zygapophyses of the caudal cervicals are broad, flat, and pie-shaped, in sharp contrast to the narrow, curved, counterparts observed across several specimens of *Diplodocus* [see figure 1 of (*2*)]. Confidence in the validity of our digital models derives, in part, from how well the pairs of zygapophyses align in the undeflected state and how well they articulate through a range of angular deflections. The cervicals were modeled individually and assembled into a series with a few-centimeter longitudinal gap between the ball-and-socket centra. The paired pre- and postzygapophyses matched up well, with a few-centimeter gap between their facets and longitudinal superposition when the centra were essentially collinear. The internal coherence in the digital models supports our conclusion that the diplodocid necks were held in an essentially straight pose in the undeflected state, and gives some insight into the close

separation of articular facets within their synovial capsules in life. Both diplodocids had a slight ventriflexion of the neck in the region of the first few cervicals and little curvature most caudally. In *Diplodocus*, in the mid-cervical region, a significant residual angulation was found between successive vertebrae when their zygapophyses were brought into alignment, creating the downcurve in the *Diplodocus* model visible in figure 2b of (*2*). Regarding the potential for error induced by the reconstruction of the most caudal cervicals of *Apatosaurus* specimen CM 3018, the essentially linear trends observed in the parametric representation of this specimen appear characteristic of the cervicodorsal region of diplodocid sauropods in general, that is, nothing interesting occurs in the transition between trunk and neck, which itself is interesting.

To compare the flexibility of these two diplodocids, the models were subject to the same criterion for limiting displacement at the paired zygapophyseal joints (the central ball-and-socket articulation turned out not to be limiting factors in either taxon). We are confident that the relative differences in neck flexibility that we reported are robust. Regarding their absolute measure, we reiterate that the extremes of deflection are not delimited by hard osteological stops, but by strain on the synovial capsules and cervical ligaments. Neck flexibility is meaningfully measured only approximately, even in extant animals, with substantial variation apparent at successive stages of dissection, especially when under active muscular control in the living animal. The residual uncertainty in our estimates due to reconstruction errors is likely of smaller magnitude. On the other hand, we share Upchurch's expectation that the anterior trunk region of these diplodocids contributed to their feeding movements, but to solve that requires study of their forelimbs.

K. A. Stevens
*Department of Computer and Information Science
Deschutes Hall
University of Oregon
Eugene, OR 97403, USA
E-mail: kent@cs.uoregon.edu*

J. M. Parrish
*Biological Sciences
Northern Illinois University
DeKalb, IL 60115, USA*

References
1. C. W. Gilmore, *Mem. Carnegie Mus. Nat. Hist.* **11** (no. 4) (1936).
2. K. A. Stevens and J. M. Parrish, *Science* **284**, 798 (1999).