ORYCTOS, Vol. 1 : 113-120, Octobre 1998

NOT CRANES OR MASTS, BUT BEAMS : THE BIOMECHANICS OF SAUROPOD NECKS

John MARTIN[1], Valérie MARTIN-ROLLAND[2] and Eberhard (Dino) FREY[3]

[1]Leicester City Museum, New Walk, Leicester LEI 7EA, and Department of Geology, Leicester University, Leicester LE1 7RH; U. K.

[2]Musée des Dinosaures, 11260 Espéraza, France.

[3]Museum für Natürkunde Karlsruhe, Postfach 6209, D-76042, Germany.

Abstract : The mechanics of sauropod necks are still poorly understood, judging from many recent life reconstructions. Only seven or eight sauropod taxa have necks well-enough known for their mobility and posture to be reconstructed fully and reliably. In these animals, the limits of mobility imposed by the zygapophyseal and central articulation structures may be calculated. Simple biomechanics shows that sauropod necks were segmented beams, and that the way in which segmented beams must be braced adds further limits to mobility. The bracing systems implied by the vertebral anatomy can be reconstructed, based partly on an appreciation, from extant animals, of what soft-tissue structures were possible given a particular set of bone geometries. Sauropod necks were dorsally-braced, ventrally-braced or a combination of the two: each system was associated with a distinctive, exclusive, group of vertebral features - high, low or divided neural spines, large or small transverse processes and short or elongated cervical ribs. The two sets of mobility-controlling systems (joint morphology and bracing) made the necks of all "popular" sauropods relatively, or very, rigid structures, and also show that they were habitually carried with the ventral aspect "down" with respect to gravity - in other words as beams, not masts.

Key words : Dinosaur, sauropod, biomechanics, necks, life reconstructions.

Ni grues ni mâts, mais timons - Biomécanique des cous de sauropodes

Résumé : D'après de nombreuses reconstitutions récentes, la mécanique du cou des sauropodes demeure méconnue. Au sein des sauropodes, seuls sept ou huit ont le cou suffisamment connu pour permettre une reconstitution complète et fiable de sa position et de sa mobilité. Chez ces animaux, les limites de la mobilité (imposées par les zygapophyses et l'articulation du centrum) peuvent être calculées. Des principes simples de biomécanique montrent que le cou peut être assimilé à une poutre segmentée. La manière dont ces segments doivent être soutenus ajoute des limites supplémentaires aux possibilités de mobilité. Le système de soutien imposé par l'anatomie vertébrale peut être reconstitué, partiellement fondé sur une appréciation (à partir d'animaux actuels) des dispositions particulières des structures osseuses qui permettent de définir le type de parties molles correspondantes. Le cou des sauropodes était soutenu dorsalement, ventralement ou par une combinaison des deux, chaque système étant associé à un groupe unique et distinct de caractères vertébraux (épine neurale haute, basse ou divisée, grands ou petits processus transverses, et côtes cervicales courtes ou allongées). Les deux systèmes possibles du contrôle de la mobilité (morphologie articulaire et type de soutien) font du cou de tous les sauropodes « populaires » une structure assez ou très rigide et montre également que le cou était habituellement porté horizontalement, en d'autres termes comme un timon et non comme un mât.

Mots clés : Dinosaure, sauropode, biomécanique, cou, reconstitutions.

INTRODUCTION

Popular life reconstructions regularly show sauropods with the neck held almost vertically, or in an artistically flexed 's' curve, suggesting that the animals could browse high in the trees or fight by "necking" (e.g. Bakker, 1986; Paul, 1987). On the other hand, some studies (e.g. Coombs, 1975 ; Martin, 1987 ; Dodson, 1990) have argued that there were rather severe mechanical limits to the flexibility of sauropods' necks as a result of their complex intervertebral articulation systems. The limits imposed by the zygapophyseal and centrapophyseal morphology of sauropod necks may be calculated quite accurately in the few taxa that are well-enough known (Martin, 1987 ; Stevens & Parrish, 1996).

This paper applies the principles of biomechanics to sauropods' necks to help resolve the dilemma. An important limitation of the project is that there are very few reliable specimens on which to base our conclusions.

LIMITS OF KNOWLEDGE -SAUROPOD NECKS

Only one or two prosauropod and perhaps eight sauropod taxa are well-enough known for a near-complete, accurate reconstruction of the neck skeleton to be made. In most cases, too (exceptions being *Plateosaurus* and, perhaps, *Shunosaurus* in which several or many individuals belonging to one species are known) there is only one individual animal known. Does this animal represent the constructional situation in a species, genus or higher taxon?

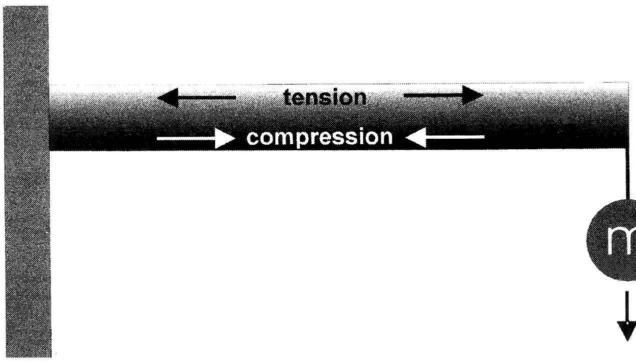
TAXON	AGE	NECK known...	SITUATION
PROSAUROPODA			
Thecodontosaurus	Norian-Carnian	incompletely	?
Anchisaurus	Pliensbachian or Toarcian	incompletely ?	?
Massospondylus	Hettangian-Pliensbachian	nearly completely.	?10 low, undivided neural spines; "long ribs"
Yunannosaurus	Hettangian-Pliensbachian	incompletely.	?
Mussaurus	Norian	? completely	?
Ammosaurus	Pliensbachian or Toarcian	incompletely	?
Plateosaurus	Norian	many, completely	10 low, undivided neural spines; ribs 2-3 segments
Sellosaurus	Norian	incompletely	?
Euskelosaurus	Carnian or Norian	incompletely	?
Lufengosaurus	Hettangian-Pliensbachian	incompletely.	?
Melanorosaurus	Carnian or Norian	incompletely.	?
Riojasaurus	Norian	completely ?	?
SAUROPODA			
Vulcanodon	? Hettangian	?	?
Barapasaurus	? "early Jurassic"	?	?
Cetiosaurus	Bajocian-Bathonian	nearly completely	14 medium, undivided neural spines; ribs 1-2 segments
Haplocanthosaurus	Kimmeridgian-Tithonian	nearly completely	14 medium, undivided neural spines; ribs 1-2 segments
Patagosaurus	Callovian	? partially	?
*Shunosaurus*v	Bathonian-Callovian	? completely	?15 medium, undivided neural spines; ribs ?
Omeisaurus	Bathonian-Callovian	?partially	?
Mamenchisaurus	late Jurassic	incompletely	8 low, undivided + ?14 medium, undivided neural spines; ribs 2-3 segments
Phuwiangosaurus	?	?	?
Euhelopus	? Kimmeridgian	Nearly completely	?12 low-medium, undivided + 3 medium-high divided neural spines; ribs 2-3 segments
Diplodocus	Kimmeridgian-Tithonian	? completely	7 medium, undivided + 8 medium, divided neural spines; ribs 1-2 segments
Barosaurus	Kimmeridgian-Tithonian	nearly completely	?15 medium, undivided + ?2 medium, divided neural spines; ribs 1-2 segments
Apatosaurus	Kimmeridgian-Tithonian	nearly completely	7 low, wide but undivided + 8 low, widely divided neural spines; ribs <1 segment
Dicraeosaurus	Kimmeridgian	?nearly completely	?4 high, undivided + ?7 high, divided neural spines; ribs 1 segment
Brachiosaurus	Kimmeridgian-Tithonian	?nearly completely	?13 low, undivided neural spines; ribs 1-2 segments

TABLE 1. Completeness of well-known sauropodomorph dinosaurs'necks

BIOMECHANICS - SAUROPOD NECKS WERE BRACED BEAMS

A simple beam supported at just one end, like a crane jib, has its upper part stressed by tension while its lower part is under compression (fig. 1). Most engineering beams are braced, either by their cross-sectional design, by internal struts or by external braces, to distribute and reduce these stresses. The Forth Bridge, near Edinburgh, Scotland, shows how this works. It is a cantilever bridge; each half-section is a beam braced above and below and supported at one end by a leg. Civil engineering does not make segmented, mobile-jointed beams (except for those wooden toy snakes), but long-necked animals (like sauropods) have them. A segmented, flexible beam cannot be unbraced. Because each segment needs to be free to move against its neighbours, the tensile and compressive stresses must be redistributed away from the intersegmental articulations by bracing systems running the whole length of the structure.

FIGURE 1 - A simple, unbraced beam supported at one end. The effect of gravity on the unsupported structure is to place the upper part under tension while compressing the lower part.



Just like the Forth Bridge, a horizontal beam has to be braced above and below; in living structures this means dorsal and ventral bracing systems. If the beam is tilted, the detailed geometry (including the orientation of the bracing members) changes, but the principle remains the same. For stability in all orientations, the beam has a minimum of three bracing members - at least one dorsal and two ventral. The dorsal braces are tension members while the ventral set work in compression (again, like the Forth Bridge) and, in living constructions, the distinction is reflected in the morphology of the bracing members and the materials of which they are made. In sauropods, the dorsal, tensile bracing elements were almost certainly unmineralised connective tissues, mainly ligaments but also tendons and muscles, while the ventral, incompressible elements were rigid or elastic tissues, like bone or cartilage. Muscles, in addition to applying power, provided hydraulic stabilisation for the other structures, but they would not have been important in maintaining the neck in its "normal", rest position (otherwise sauropods would have constantly felt like you do trying to hold your arm out straight for more than two minutes). This, if nothing else, shows why bracing structures and bone articulation locks were so important to sauropods - just as they are to us in, for example, our ability to lock our knees so that we can stand for long periods without tiring.

Sauropod neck ligament systems have been described before, particularly in discussions of the function of divided neural spines (e.g. Alexander, 1985, and references therein), as "cables" supporting a "crane jib". Recognition of a ventral system, and of its function in combination with the dorsal structures as bracing for the neck, is new in this paper. In sauropods the long, forward and backward directed processes of the cervical ribs, together with associated soft tissue structures, provided the ventral bracing system. By recognising this, we can begin to understand the engineering of sauropod necks.

Biological structures, presumably because of the way evolution "works" (e.g. Dawkins, 1986, etc.), tend to be compromises in any case. But the stresses produced by gravity, by the inertia of a long, swinging structure and by muscle-to-bone reactions on a dynamic, flexible beam (which may be twisted, raised and turned all at the same time by its owner's behaviour) are extremely complex, and mean that the construction has to be versatile.

For this reason, the observed situation is that dorsal and ventral bracing systems were more or less combined in sauropod necks: mainly dorsally braced, mainly ventrally braced, or combined systems are known.

Each bracing style produces a distinctive neck structure with a predictable range of movements. Of particular importance in view of interest in the range of movements, and thus behaviour, available to sauropods, is that analysis of intersegmental joint structures and of bracing and motive systems shows that sauropod necks were relatively inflexible, more or less horizontal, structures.

Moreover, "down" (the direction of gravitational force on the construction) was always anatomically ventral and is indicated by the incompressible bracing system. The bracing systems seen in sauropod necks are not those of engineering masts, which must have at least three, symmetrically disposed, members of similar sense (all tensile or all compressional); sauropod necks are structures with a "normal" orientation substantially less than 90° above (or below) horizontal. Not even in *Brachiosaurus* was the neck held straight up under normal conditions : there is no biomechanical evidence in the fossil record for swan-necked sauropods.

LIVING ANIMALS

No extant animal provides a perfect anatomical or mechanical analogue for the extremely elongated neck of sauropods. Study of living long-necked animals can be instructive, however.

In birds, several genera have very elongated but flexible necks. The largest bird, the ostrich *Struthio*, might be expected to provide a good model for sauropod neck construction, but both the vertebral anatomy and arrangement of muscle insertions in birds are completely different. The great flexibility of bird necks is provided by the increased number of vertebrae (eighteen in *Struthio*, fourteen in the flamingo *Phoenicopterus* and 25 in swans *Cygnus*), their mode of inter-central articulation (with saddle-shaped surfaces), and the absence of cervical ribs.

Among mammals the giraffe *Giraffa* is often compared with sauropods. Differences in vertebral number (seven) and anatomy and in the absence of developed cervical ribs again prevent exact comparison. However, the very strong and inextensible *ligamentum nuchae* of giraffes and other mammals has been used as a model for the situation in some sauropods. The ligament connects the tips of all the neural spines along the neck and connects them mechanically to the vertebrae of the back (as far as the fourth thoracic vertebra in horses, for example). It plays an important role in supporting the head, maintaining the neck in "neutral" position without muscular action. The ligament is also known to be important in mammal locomotion, in Equidae and large ruminants for example.

Unfortunately, no living reptile has a long neck. Snakes could be thought of as long-necked, but their vertebral anatomy and cervical ribs differ from those in sauropods. Although not long-necked, some crocodiles do have a strikingly informative, and perhaps analogous, neck anatomy. Dissection of the neck of a specimen of *Palaeosuchus trigonatus* clearly shows the elongated cervical ribs to overlap one another and to be tightly connected by ligaments. The powerful ligaments and associated short muscle masses bind the ribs together in a bundle, so that the anterior neck vertebrae and ribs form an almost immobile unit. The importance of the rib system to the whole structure is demonstrated by cutting the costal ligaments: the neck immediately becomes flexible without their contribution. In the crocodile, the cervical ribs and connective tissues provide two ventrolateral bracing structures working against the compressive load and counteracting the system provided by the dorsal muscles and dermal scutes, thus stabilising the neck. The structure is a model applicable in part to the situation in sauropod necks.

In general, observation of neck mobility and study of anatomy in living animals, and comparison of the results with the possible range of mobility in skeletal preparations of the same species, remains a useful tool for testing the likely mobility limits of fossil skeletons.

THREE CLASSES OF SAUROPOD NECK

1. Dorsally braced

A segmented beam braced dorsally by flexible tensile elements (figure 2) has enhanced mobility but sacrifices stability. In effect, the vertebral segments are simply "slung" beneath a bracing "cable" and there is a risk of loss of control should the beam be twisted so that the centre of mass approaches the level of the bracing member.

To reduce this risk, the bracing system must be powerful and positioned high above the centre of mass. Complex intervertebral joint locks are also necessary, while massive dorso-lateral tensional systems provide power and secondary bracing by taking over from the main bracing members when the beam is twisted; they too are rendered more effective by being as far from the axis of the beam as possible.

Dorsally-braced neck constructions seem to have been least common among the known sauropods. The bracing system was distanced from the main body of the vertebral column by high neural spines. These were typically divided (forked) to increase the volume of the suspension ligaments, which (especially in the "nuchal" region where leverage was greatest) must have been massive and long enough to bridge several segments.

The dorso-lateral systems were powerful tendino-muscular structures; long lever arms for the muscles and enhanced control of yawing were provided by long and strong transverse processes. All these structures imply large mass, which restricted the number of segments in, and absolute length of, the neck.

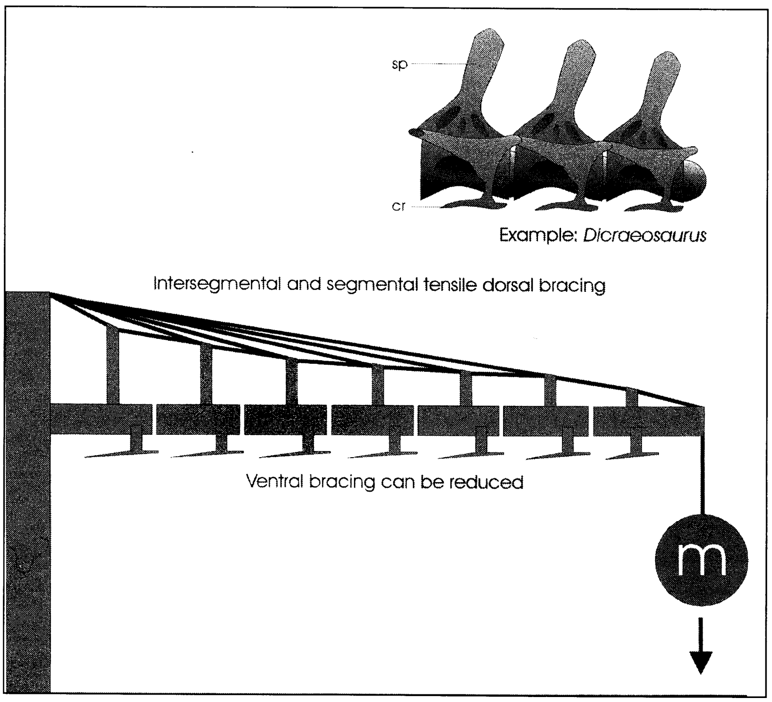


FIGURE 2 - A segmented, flexible beam with mainly dorsal bracing and, above, three schematic neck vertebrae of *Dicraeosaurus*, with very high neural spines and short cervical ribs.

2. Ventrally braced

In contrast (figure 3), a segmented beam braced ventrally by incompressible structures is inherently stable but inflexible, relatively speaking. There must be at least two ventro-lateral braces to take care of the effects of twisting the beam, while the bracing system can only transmit the compressive load if it is structurally continuous and thus so constructed that it overlaps several or many segments. Otherwise the engineering problems are simplified in comparison with a dorsally braced beam, and the mass of stabilising "superstructure" can be reduced: in fact it is advantageous to keep any other control and motive systems close to the centre of mass and within an envelope above the ventral braces.

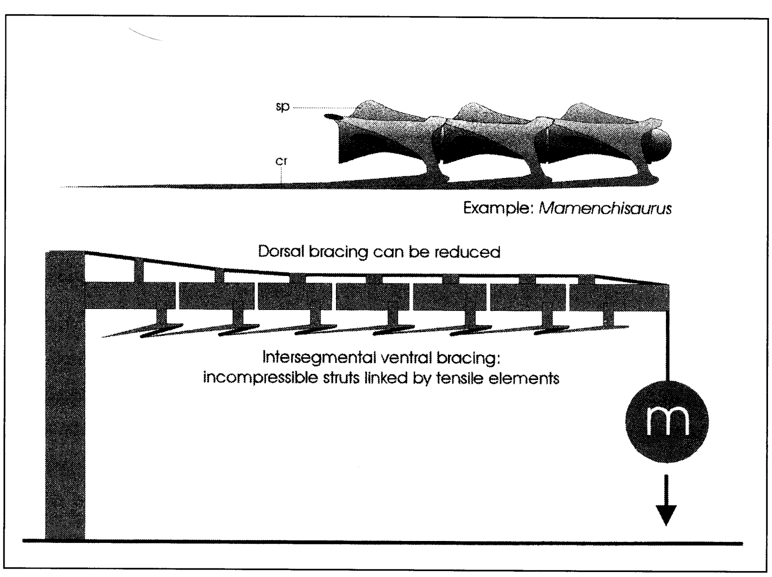


FIGURE 3 - A segmented, flexible beam with mainly ventral bracing and, above, three schematic neck vertebrae of *Mamenchisaurus*, with low neural spines and bundles of elongated cervical ribs.

In this type of sauropod neck the bracing system was formed by the elongated cervical ribs and their associated soft structures. The overlapping rib processes were bound together by connective tissues and bundles of short-fibred muscles, a construction also seen in crocodilians' necks (Frey, 1988) including *Palaeosuchus*, as noted above. The longer the cervical ribs in sauropods were, the more segments combined as structurally functional units and the more rigid the neck became. To keep the mass of other structures close to the vertebral centra, the neural spines were low and the transverse processes relatively short. The smaller mass associated with this style of bracing permitted an increase in the length and number of segments, and consequently of the whole neck.

3. Dual systems

In most sauropods whose neck anatomy is well known the situation was a combination of the two extremes described here. The structures associated with dorsal bracing - neural spines and, to a lesser degree, transverse processes, were present and of moderate size. Ventral bracing was provided by moderately overlapping cervical ribs.

ASSIGNMENT OF WELL-KNOWN SAUROPODOMORPHS TO THESE CLASSES

Examples of dorsally braced systems are seen in *Dicraeosaurus* and *Apatosaurus*. Both had neural spines at least three times the height of the vertebral centrum. In *Dicraeosaurus* they were deeply forked, providing space for a greatly increased volume of suspension ligaments, which presumably ran between the pairs of spines from the shoulders (in fact from the hips - the dorsal vertebrae were also divided) to the back of the skull. In the neck they formed a powerful nuchal ligament (strictly speaking the analogue of this mammalian structure) with additional lateral branches inserting on the outer faces of the spines. As far as we know, the cervical ribs did not extend far into adjacent vertebral segments and so, because ventral bracing was reduced, flexibility was enhanced in the neck of this genus. The mounted skeletal reconstruction seen in the Humboldt-Museum, Berlin is a composite based on incomplete fossil material. It has unequally spaced and erratically oriented neural spines that may indicate an unusually sharp bend in the neck of *Dicraeosaurus,* or may simply be an error of reconstruction.

Apatosaurus was a special case of dorsal bracing. Its neural spines were little taller than the vertebral centrum, but they were very widely divided to accommodate a massive "nuchal ligament". The very large, wide transverse processes provided long lever arms for huge dorso-lateral muscles while the stout but short cervical ribs, which did not extend into adjacent segments, probably enhanced the leverage of a ventro-lateral muscle system. Together, these structures seem to have stabilised and powered an otherwise weakly braced construction, giving *Apatosaurus* a uniquely powerful but quite flexible neck among all known sauropods.

Ventrally braced systems are characteristic of very long-necked sauropods, particularly the Chinese taxa *Mamenchisaurus, Omeisaurus* and *Euhelopus*.

DORSALLY BRACED	VENTRALLY BRACED	COMBINATION
		Massospondylus
		Plateosaurus
Dicraeosaurus	*Mamenchisaurus*	*Diplodocus*
Apatosaurus?	*Euhelopus*	*Barosaurus*
	Omeisaurus	*Cetiosaurus*
	Brachiosaurus?	*Haplocanthosaurus*
	Camarasaurus?	*Brachiosaurus?*

TABLE 2. Assignment of well-known sauropods to classes of neck bracing

They had cervical ribs that extended far beyond one segment - over two in *Euhelopus*, three in *Mamenchisaurus*. The overlapping rib processes formed elongated bundles of up to four in the mid part of the neck. Neural spines were low (less than the height of the vertebral centrum) and undivided and the centra themselves were low and long.

The neck of *Brachiosaurus* is not fully known (the crucial posterior cervical vertebrae are incomplete) but, with its long cervical ribs (perhaps two segments long) and undivided, low anterior neural spines it appears to be an unremarkable, primarily ventrally braced construction.

A special case in this category is seen in *Camarasaurus*. The neural spines of the first eleven (of twelve) cervical vertebrae were modest and undivided and the cervical rib processes were enormously elongated (up to three segments long), indicating ventral bracing, but the vertebrae themselves were wide and short, the neural arches were high and the zygapophyses widely separated. *Camarasaurus* had a very powerful but inflexible neck.

All other sauropods whose cervical vertebrae are well known had necks with ventral and dorsal bracing combined. A dorsal bracing system is indicated by neural spines about the same height as the vertebral centrum, often with deep pits for "nuchal ligaments"; the spines were sometimes divided in the posterior segments. At the same time, ventral bracing is indicated by long cervical ribs overlapping more than one segment. Combined constructions are seen in *Diplodocus, Cetiosaurus* and *Haplocanthosaurus*, and perhaps in *Brachiosaurus* (but see above), all of which had moderately long, relatively inflexible necks.

HOW THE SAUROPOD GOT ITS NECK : EVOLUTIONARY PATHWAYS

We hesitate to discuss the evolution and taxonomy of sauropods in the context of our analysis of the neck engineering of relatively so few specimens. There appear to be contradictions of recent taxonomies (e.g. Upchurch, 1995) in our grouping of, for example, *Apatosaurus* and *Dicraeosaurus* separately from other diplodocids, and of *Camarasaurus* closer to members of the Euhelopodidae (*sensu* Upchurch) than to brachiosaurids and other Neosauropoda. However, the "characters" we use to describe the bracing style and biomechanical construction of these animals' necks (neural spine and cervical rib morphology, proportional dimensions of the cervical centra) are not used by sauropod cladistic taxonomists, no doubt because these structures are so seldom well-preserved. Moreover, as we have studied only individual specimens, we should probably not generalise for higher taxonomic levels.

With these reservations, we can theorise that both exclusively ventrally braced and exclusively dorsally braced constructions, if they existed in nature, represented grades of evolution with no option for reversal. In both end-member ("highly-derived") constructions one of the two possible bracing systems has been completely dispensed with; reduction of one system could only have taken place if the other was originally also present and fully able to take over the load of the neck and head. In other words, all options are open for sauropod neck constructions with combined bracing systems, and therefore a dual bracing system, including the characteristic horizontal orientation and extension of the cervical ribs, has to be regarded as the theoretical "pre-construction" for sauropods.

This morphology of the cervical ribs is observed in the prosauropod *Plateosaurus*, and perhaps in *Massospondylus*. In *Plateosaurus* the cervical ribs overlap two or more vertebral segments. Ventral bracing of the construction was, clearly, mechanically possible, while dorsal bracing was provided by the structures associated with the neural spines and transverse processes. *Plateosaurus* had a combined bracing construction, which could have given rise to the constructional styles seen in all known sauropods. We draw no taxonomic conclusions !

SAUROPOD POSTURE IN POPULAR RECONSTRUCTIONS

Sauropods whose necks have been studied in detail have all been shown to have possessed relatively inflexible necks (with complex, limiting zygapophyseal articulations) that were, moreover, constructed as braced beams, not masts. They should be reconstructed in exhibits and artwork with the neck held more or less horizontal and only modestly flexed. Several recent and popular reconstructions of dinosaurs (*Barosaurus,* American Museum of Natural History exhibit, 1995; "Brontosaurus" (*Apatosaurus*) by Bakker, 1986, plate on p.14; *Brachiosaurus* by Paul, 1987, fig. 7 on p. 19) are artistically attractive but anatomically unlikely. Interestingly, the "giraffe-necked" epithet applied to the posture shown in such reconstructions is not entirely appropriate, given that female giraffe in the wild hold their necks horizontally, not vertically, for more than 50% of the time and that both sexes feed faster and more often with their necks low (Simmons & Scheepers, 1996).

It has been argued that *Brachiosaurus* had a more vertically disposed neck than other sauropods because its long forelimbs raised the shoulders and directed the neck upwards. Our biomechanical analysis suggests that *Brachiosaurus* had an unremarkable (primarily ventrally-braced) neck. There is no direct evidence that this animal had a neck posture different from other sauropods. The original descriptions of the skeletal anatomy of *Brachiosaurus brancai* (Janensch, 1914, 1929) are equivocal: of the two partially articulated specimens from Tendaguru, Janensch gave limb element lengths for only a few bones. The now "traditional" disparity of the fore- and hind-limb proportions (about 1.2:1) has been based on the 1937 mounted skeleton in the Humboldt-Museum, Berlin, which is a composite reconstruction of the most complete specimen, with replacement elements from other individuals and plaster modelling. Other taxa referred to *Brachiosaurus* (including *B. altithorax* Riggs, 1903 and *B. atalaiensis* Lapparent and Zbyszewski, 1957) appear, as far as the sparse evidence permits us to say, to have had front and hind limbs of roughly equal lengths. A careful new look at the fossil evidence is required to resolve this dilemma, but our provisional contention is that *Brachiosaurus* was a "four-square" sauropod; higher in front than most genera (those with limb proportions closer to 0.8:1), but not a dinosaurian giraffe.

REFERENCES

ALEXANDER, R. M. 1985. Mechanics of posture and gait of some large dinosaurs. *Zoological Journal of the Linnean Society, London,* **83** : 1-25.

BAKKER, R. T. 1986. *Dinosaur Heresies*. William Morrow, New York : 1-481.

COOMBS, W. 1975. Sauropod habits and habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **17** : 1-33.

DAWKINS, R. 1986. *The Blind Watchmaker.* Longman, London : 1-340.

DODSON, P. 1990. Sauropod paleoecology; pp. 402-407. *In* WEISHAMPEL, D. B. ; DODSON, P. & OSMÓLSKA, H. (eds.) *The Dinosauria.* University of California Press, Berkeley, Los Angeles and Oxford.

FREY, E. 1988. Das Tragsystem der Krokodile - eine biomechanische und phylogenetische Analyse. *Stuttgarter Beiträge zur Naturkunde,* **426** : 1-60.

JANENSCH, W. 1914. Ubersicht uber die Wirbeltierfauna der Tendaguru-Schichten...; *Archiv Für Biontologie*, **3** : 81-110

——————1929. Material und Formengehalt der Sauropoden in der ausbeute der Tendaguru-expediton. *Paleontographica,* Supp. 7, 1, 3, 1 : 1-25.

LAPPARENT, A. F. de & ZBYSZEWSKI, G. 1957. Les Dinosauriens du Portugal. *Mémoires des Services géologiques du Portugal,* **2** : 1-63.

MARTIN, J. 1987. Mobility and feeding of *Cetiosaurus* (Saurischia: Sauropoda) - why the long neck? pp. 154-159. *In* CURRIE, P.J. & KOSTER, E. H. (eds.) *4 th Symposium on Terrestrial Mesozoic Ecosystems, Short papers.* Tyrrell Museum of Paleontology, Drumheller, Alberta.

PAUL, G. S. 1987. The science and art of restoring the life appearance of dinosaurs and their relatives ; pp 5-49. *In* CZERKAS, S. J. and OLSON, E. C. (eds) *Dinosaurs Past and Present. Vol. II.* Natural History Museum of Los Angeles County, Los Angeles.

RIGGS, E. S. 1903. *Brachiosaurus altithorax,* the largest known dinosaur. *American Journal of Science*, (ser. 4) **15** : 299-306.

SIMMONS, R. E. & SCHEEPERS, L. 1996. Winning by a neck: sexual selection in the evolution of giraffe; *American Naturalist* **148** (5) : 771-786.

STEVENS, K. A. & PARRISH, J. M. 1996. Articulating three-dimensional computer models of sauropod cervical vertebrae. *Journal of Vertebrate Paleontology*, **16** (3) [abstracts].

UPCHURCH, P. 1995. The evolutionary history of sauropod dinosaurs; *Philosophical Transactions of the Royal Society, London*, B (1995), **349** : 365-390.

Note reçue le 01-12-1997
acceptée après révision le 28-02-1998