

Tipsy punters: sauropod dinosaur pneumaticity, buoyancy and aquatic habits

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Recd 14.10.03; Accptd 04.11.03; Published online 12.12.03

Sauropod dinosaurs were the largest terrestrial animals to have ever existed, and are difficult to interpret as living animals owing to their lack of living descendants. With computer models that employ the basic physics of buoyancy and equilibrium, it is possible to investigate how the bodies of these animals would have reacted when immersed in water. Multi-tonne sauropods are found to be extremely buoyant and unstable in water when aspects of their probable respiratory anatomy are considered, which obviates the old problem of them being unable to breathe when fully immersed. Interpretations of 'manus-only' trackways made by floating sauropods will depend on the details of buoyancy as not all sauropods float in the same manner.

Keywords: sauropods; biomechanics; buoyancy; stability; trackways

1. INTRODUCTION

Studies of the biomechanics of sauropod dinosaurs are important for elucidating what the vertebrate body is capable of at extremely large size. However, sauropods are among the most peculiar of extinct vertebrates, and their unique mix of characters, coupled with their extreme body size, makes them interesting but difficult to interpret in functional terms (Coombs 1975; Dodson 1990). Given their body size similarity with extant whales, a fundamental question following the initial discoveries of sauropods in the early 1800s (McIntosh *et al.* 1997) was whether these animals were aquatic, terrestrial or something in between (Coombs 1975). With rare exceptions (Riggs 1904), sauropods were initially thought to have been too heavy to have supported their mass on land, and to have been principally water dwellers. The modern consensus is that sauropods were fully terrestrial based on a range of biomechanical, ecological and sedimentological evidence (Bakker 1971; Coombs 1975; Alexander 1985).

A perceived fatal blow to the idea of aquatic sauropods was the observation that the water pressure acting on the body of a sauropod submerged under several metres of water would have collapsed the lungs and airways, with fatal results (Kermack 1951). However, this prediction rests on the assumption that sauropods would have been dense enough to sink to the bottom of a body of water. Despite evidence from the mid-nineteenth century that sauropods possessed pneumatized axial skeletons (Seeley

1870) and interpretations of this pneumaticity as an adaptation for weight reduction (Marsh 1877) or as 'floats' (Cope 1878), the effects of these lightened skeletons on the animal's ability to sink or float were generally neglected. Illustrations of sauropods as living animals, beginning in the 1890s (Ballou 1897) and continuing through the first three-quarters of the twentieth century, regularly showed sauropods fully immersed in lakes (Augusta 1957). It was not until the 1970s and early 1980s that the possible effects of the pneumatized skeletons of sauropods on their buoyancy were truly appreciated (Coombs 1975; Paul 1988).

Using modern restorations and recent insights into sauropod anatomy and physiology, this paper presents the results of using a mathematical/computational model (Henderson 2003) to investigate what would happen if sauropods, with their highly pneumatized skeletons, were put in water of sufficient depth to enable them either to float freely or to sink.

2. MATERIAL AND METHODS

Four sauropod models were generated: *Apatosaurus*, *Brachiosaurus*, *Camarasaurus* and *Diplodocus* (Paul 1997). Derived sauropod dinosaurs exhibit extensive development of lateral and internal excavations of their dorsal and cervical vertebrae, and comparative studies of the development of skeletal pneumaticity in living birds and sauropods strongly suggest that the latter had a system of air sacs similar to that of the former (Wedel 2003a,b). Additional support for the existence of a bird-like lung and air-sac configuration comes from a theoretical analysis of the physical limits and probable respiratory efficiency in sauropods, given their long necks (Daniels & Pratt 1992). The basic tissue density for axial body was set to that of water (1000 g l^{-1}), while the limbs were set to 1050 g l^{-1} due to their higher proportion of bone. Because the thoracic and abdominal air sacs of birds occupy ca. 15% of the trunk volume (Proctor & Lynch 1993), the density of the trunk region was reduced to 850 g l^{-1} . The lung volume of living mammals ranges between 8% and 10% of the axial body volume (Schmidt-Nielsen 1984), and in light of the more efficient avian type of lung (Proctor & Lynch 1993), the lung volume of a sauropod was estimated to be no more than 8% of the axial body volume. Inclusion of the lung space will further reduce the anterior trunk density. Computer-aided tomography scans of the cervical vertebrae of sauropods show that there is more empty space than bone (Wedel 2003b). These internal cavities and the deep lateral excavations of the vertebrae were represented by paired ellipsoidal cavities along the ventro-lateral edges of the neck centred at positions between the cervical ribs. When combined with the volume occupied by the trachea (Daniels & Pratt 1992) and oesophagus (Proctor & Lynch 1993), this set of cavities resulted in a neck density of 600 g l^{-1} . This neck density may seem low, but a density of 300 g l^{-1} has been determined for a goose (Bramwell & Whitfield 1974). Systems of paired air sacs were also placed in the proximal caudal, sacral and dorsal vertebrae, which reduced local body densities by ca. 2–3%. The three-dimensional positions of all of the air sacs and the lungs are used in determining the final position of the centre of mass (CM). See electronic Appendix A (available on The Royal Society's Publications Web site) for a proposed configuration of the low-density components within the body of a *Brachiosaurus*. Masses and geometric properties of all of the models are summarized in table 1.

3. RESULTS

The modelling process was tested with the body forms of two living animals that are known to be either semi-aquatic (American alligator, *Alligator mississippiensis*) or capable of swimming when required (Asian elephant, *Elephas maximus*). From observations of the depths of immersion and body orientations of floating crocodilians (Smith 1979) and elephants (Chadwick 1991), it is clear that the models can reproduce the equilibrium buoyant states of these animals (table 1; figure 1).

All four sauropod models attained rotational and translational equilibrium at the water surface (figure 2a), with an important buoyant effect arising from the low-density

Table 1. Basic properties of the models of the living and extinct animals in this study.

(The lung volume is expressed as a percentage of axial volume. Body length is measured from the tip of the tail to the tip of the snout, except for the elephant (*Elephas*) where it was measured from the base of the tail to the base of the trunk.)

	total mass (kg)	axial mass (kg)	leg mass (kg)	arm mass (kg)	lung volume (%)	mean density (g l^{-1})	body length (m)
<i>Alligator</i>	131	118	5.07	1.67	9.15	953	3.06
<i>Elephas</i>	1599	1162	105	113	8.44	953	2.35
<i>Apatosaurus</i>	17273	13900	1367	319	7.8	818	21.8
<i>Diplodocus</i>	12099	10002	880	169	7.9	814	24.5
<i>Brachiosaurus</i>	25789	20305	1753	989	7.6	796	23.9
<i>Camarasaurus</i>	12177	10062	788	271	7.7	791	15.5

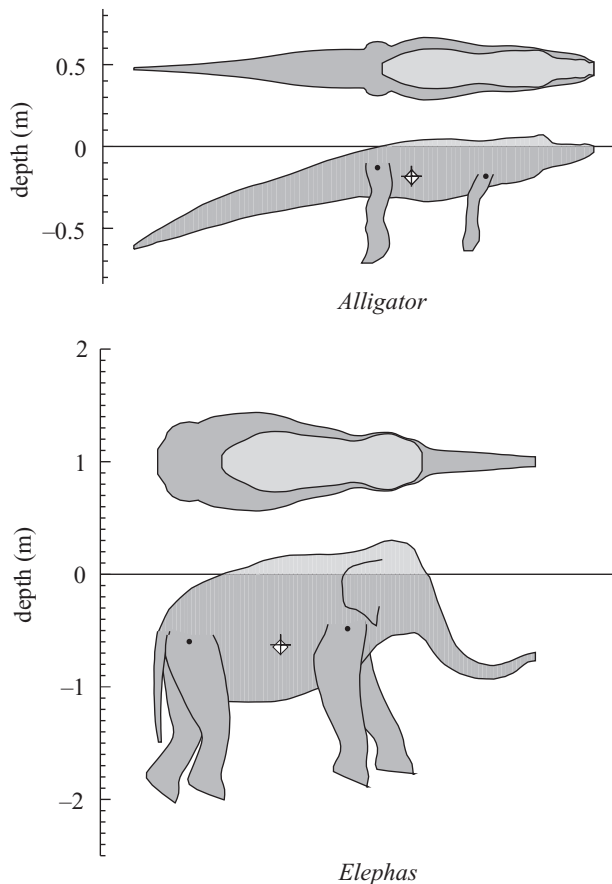


Figure 1. Demonstration of the modelling software replicating the states of immersion and inclination seen in living, freely floating, long-tailed and large animals: American alligator (*Alligator mississippiensis*) and Indian elephant (*Elephas maximus*). See table 1 for summary data. Open diamonds mark the centre of buoyancy. Black plus symbols mark the centre of mass. Black dots mark the limb sockets.

neck which acts to rotate the body counterclockwise (when viewed from the right). The original problem of sauropods being unable to breathe while walking along the bottom of a lake can now be seen as irrelevant. The positive buoyancy of these animals, resulting from a mean density of *ca.* 80% that of water, would have made it impossible for them to walk along the bottom of a lake or river while fully immersed. In all four models their centres of buoyancy (CBs) lie below their CMs, which describes

a situation of unstable equilibrium (Halliday *et al.* 1993). When floating clear of the lake or river bed, these animals would probably roll onto their sides and be in serious difficulty, although the buoyant neck would prevent them from completely capsizing. Unlike crocodilians with their relatively broad trunks, the transversely narrow and deep bodies of sauropods (Bakker 1971) would be unable to provide the passive buoyant force necessary to restore equilibrium (Brown 1997), and this reinforces the idea that sauropods were primarily terrestrial animals. The largest neck of any model is that of *Brachiosaurus*, which represents only 8% of the total body mass. Altering the positions of the head and neck of the models would have only minor effects on the resulting equilibrium orientations of the models.

4. DISCUSSION

The question arises as to what was the maximum water depth into which these animals could have waded before they would have become detached from the substrate. This was determined by setting each model in a standing position with all four feet on the substrate, and then simulating a rising water level while simultaneously computing the upwards buoyant force (figure 2b). The non-uniform density of the sauropod models results in the CM not being coincident with the CB. This has the effect that the buoyant force will not be equal on the fore and hind feet, just as the downward weight force acting on them is not equal. The critical depth limit was deemed to have been attained as soon as the buoyant force equalled or exceeded the smaller of the downward weight force components associated with the fore and hind limbs. For the macronarians *Brachiosaurus* and *Camarasaurus*, with their posteriorly positioned CBs, the hindlimbs would begin to lift up first. By contrast, *Diplodocus* has its CM very close to its hips, and would have experienced its forelimbs lifting up well in advance of its hind limbs. This susceptibility to forelimb floating is reflected in the relatively shallow maximum immersion depth for *Diplodocus* of just 2.4 m. This shallow critical depth is partly a function of the low mass of *Diplodocus*, but the relative position of the CM is also a factor. *Camarasaurus* has an almost identical weight to *Diplodocus*, but has a critical depth of immersion that is 33% deeper. It is the more centrally positioned CM of *Camarasaurus*, and less disparate loading of its hind and fore feet, which increases its limiting depth to 3.2 m.

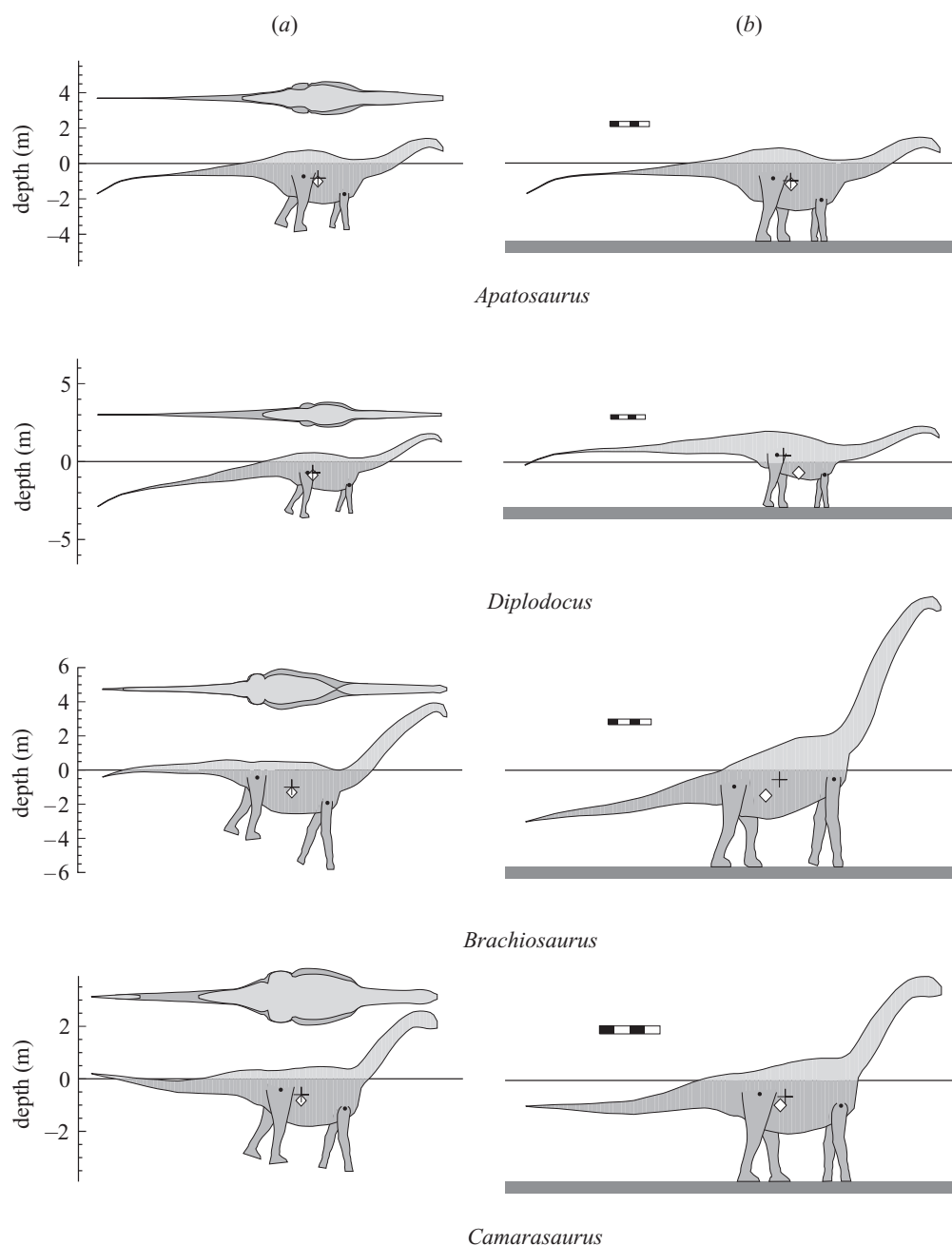


Figure 2. (a) Dorsal and lateral views of the equilibrium depths and orientations of freely floating sauropod dinosaurs. The combination of a highly pneumatized axial skeleton and a system of thoracic and abdominal air sacs in these dinosaurs reduces their density to *ca.* 80% that of water. The longer forelimbs of *Brachiosaurus* and *Camarasaurus* could have permitted them to propel themselves by poling along the bottom to produce manus-only trackways. (b) Graphical views of the critical water depths at which large sauropods would become buoyant. Critical depths: *Apatosaurus*, 3.7 m; *Brachiosaurus*, 4.3 m; *Camarasaurus*, 3.2 m; *Diplodocus*, 2.4 m. Scale bar in all figures is 2 m.

Starting in the 1940s (Bird 1944), there have been reports of sauropod trackways that consist predominantly of hand prints (reviewed in Lee & Huh 2002). It has been uncertain whether these trackways were made by floating sauropods, where only the forelimbs were in contact with the lake bed (Bird 1944; Lee & Huh 2002), or whether they represent undertracks (Lockley & Rice 1990). It is unlikely that the diplodocids could have been the makers of manus-only trackways, as their arms were clear of the substrate when immersed beyond their critical depth (figure 2a). However, floating *Brachiosaurus* and *Camarasaurus*, with their sub-horizontal trunks and their elevated hind feet, could have produced manus-only

trackways. *Brachiosaurus*, with its long forelimbs, would be an especially good candidate for this sort of activity, with the arms used to punt the animal along.

The preserved trackways of sauropods indicate that these animals frequently walked across marine, intertidal zones and along the muddy margins of lakes (Lockley 1991). Sedimentological evidence also indicates that the muds and sands of these areas were often under water, or just recently exposed, when the animals left their impressions (Pittman 1989; Lockley & Rice 1990). The fossil remains of sauropods are known from coastal settings (Weishampel 1996), and are often found near to, or mixed in with, fossils of marine organisms (Allen 1975;

Russell *et al.* 1980). These lines of evidence indicate that sauropods were not averse to moist conditions, and may have even preferred them (Dodson 1990). The interpretations presented here that sauropods could successfully walk in water that was at least as deep as their chest height are consistent with the association of sauropods and wet habitats.

Acknowledgements

I thank E. Snively and M. D. Thompson for comments on the manuscript, and M. F. Bonnan, D. B. Norman and M. J. Wedel for reviews. Funding was provided by a Natural Sciences and Engineering Research Council of Canada postdoctoral fellowship, the Jurassic Foundation and the University of Calgary.

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