Historical Biology, 1990, Vol. 3, pp. 313–318 Reprints available directly from the publisher Photocopying permitted by license only © 1990 Harwood Academic Publishers, GmbH Printed in the United Kingdom

BOOK REVIEWS

DYNAMICS OF DINOSAURS AND OTHER EXTINCT GIANTS by R. McNeill Alexander. 1989. Columbia University Press, New York, 167 pp.

R. McNeill Alexander has made important contributions to the study of the biomechanics of dinosaurs and other beasts past and present in a series of papers. The results form the core of his new and novel book, *Dynamics of Dinosaurs and other Extinct Giants*. A melding of physics and biology, it is much needed in a century where the two sciences have often neglected one another. Also, a quantitative structural examination of dinosaurs is vital to understanding their function and performance. Alexander is better able than most paleontologists to carry out this kind of work, although it would not hurt if he had more of a paleontologist's familiarity with his fossil subjects.

The opening chapter of this slim volume starts out with a brief look at dinosaurs that, although reasonably accurate, is not a particularly inspired outline of this ongoing age of astounding discoveries. Things become more interesting in Chapter II, in which the mass of various dinosaurs is estimated. Here appear some of the problems that hinder Alexander's work. The worst of these is his use of the BMNH dinosaur models for volume estimates. These toys are obsolete, and are simply not accurate enough to belong in and form the basis for serious scientific investigations. The basic proportions of the models are in error (Fig. 1). While the mounted skeletons of Brachiosaurus brancai and Mamenchisaurus hochuanensis share necks of nearly the same length, in the BMNH models they differ by a third. The ribcages of all the sauropods are too bulky, either because of misproportioning or the misarticulation of the anterior ribs that is common on mounted skeletons. Tyrannosaurus rex is too small headed and chested, and too long tailed, the *Iquanodon bernissartensis* model is excessively fat bellied, and has a tail that is too long and thick. The surface topography of the models does not closely follow the superficial contours and cross sectional profiles indicated by the bone structure and probable musculature of the subjects-the form of the sauropods' necks being especially unsatisfactory-and the continuous molding of the upper limbs with the body tends to artificially increase the models' volumes. Because animals do float, the specific gravity of 1.0 used in the book seems too high. 0.95 is probably the most satisfactory value for most animals, but pneumatic dorsals suggest that sauropod trunks were a less dense 0.9 or so. Nor does Alexander take into account the intense pneumatic nature of sauropod necks, which must have driven their density to 0.6 or less. For these reasons Alexander's mass estimates for *Diplodocus* carnegii, B. brancai, I. bernissartensis and, to a lesser degree, T. rex are too high, even if heavy seasonal fat deposits are included.

Alexander was the first to examine the speed implications of dinosaur trackways. At first these seemed to imply that dinosaurs may have been rather slow, but in Chapter III he notes that these trackways merely measure ordinary walking paces, not top speeds. An increasing number of trackways show running speeds, those of some half tonne theropods being the most notable (Alexander seems unaware of a 314

BOOK REVIEWS

Stor (Derival service) from extension of the residuced service table in service interspectively derived in the service service interspective services of the residuced service in the service of the beam intersection of the service service service in the beam intersection of the service service service in the beam intersection of the service service service in the exception of the service service service service in the service of the service service service service service in the service service service service service service service service service in the service service service service service service service service services and service serv

3. And S. Har Wood, Manual Mark, and Andread Mark and Santa S Santa S



Figure 1 An outline of *Brachiosaurus brancai* based on a high fidelity skeletal restoration of HMN SII (solid line), compared to the outline of the obsolete 1/40 scale BMNH model of the same specimen (dashed line). Drawn to the same scale, bar equals 2 m.

Kayenta trackway that seems to show a small bipedal dinosaur running at racetrack speeds). A very intriguing observation of Alexander's notes that thoroughbreds and greyhounds, bred wholly for speed, may be the world's fastest animals at some 60 km/h. His pursuits of ungulates and ostriches could not get them to go much over 50 km/h, and a galloping white rhino made only 30 km/h. There are some citations for higher speeds measured from films in the literature, but Alexander may be right that wild animals are not quite the speedsters they seem to be, and that these speeds are similar to those of the faster dinosaurs.

Chapter IV is perhaps the most important in the volume. In it Alexander calculates the loading versus the strength of dinosaur limbs, compares them to those of mammals and birds, and arrives at conclusions regarding the "athletic" abilities of various dinosaurs. Those who have characterized the notion of galloping *Triceratops* and so on as "preposterous" or "impossible" might find it less so in view of Alexander's calculation that it was much stronger limbed than an elephant, and as well stressed for running as a Cape buffalo. This is in accord with the work of other biomechanists such as Thomas MacMahon and Richard Taylor that big size and speed need not always contradict one another—conservative paleontologists

1 - KI . V 16.

BOOK REVIEWS

take note! Alexander is himself less comfortable with his estimate that *Tyrannosaurus rex* was weaker limbed than a human. As I have shown elsewhere, even the biggest tyrannosaurs shared essentially the same limb design with the undoubtedly swift ostrich-mimics, and a basic principle of engineering is that machines that are built the same way will work and perform much the same way too. By the same token, animals do not become slower just because they have grown up, so adult tyrannosaurs should have been as fast as the gracile but otherwise identical little beasts they began life as. These observations suggest that *T. rex* was much more athletic than a human. A problem with Alexander's procedure is one that often marks work in his field, that adequate tests were not performed. The stresses incurred by the legs of small and medium sized theropods as they made running trackways should have been calculated, seen if they matched favorably with the calculated strength of their bones, and then these well founded, hard data used to better examine the biggest tyrannosaur.

In general, the overestimate of masses common to Alexander's dinosaurs may have caused him to underestimate the relative strength of their limbs, especially lightweight *Diplodocus* which probably was not weaker boned than an elephant. The inaccuracy of the models used also makes his calculations of mass distribution and relative limb loading of little use—indeed, one can doubt whether it will ever be possible to reliably model the complex distribution of mass in extinct vertebrates that have no close living relatives. We may have to live with using limb bone cross sectional areas to arrive at a rough estimate of limb loading, despite the problems of circularity noted by Alexander. A related subject badly in need of a biomechanical stress analysis is the thick cartilage that covers most dinosaur limb joints. A small point of confusion arises from Alexander's use of the word "run" to describe the fastest gait of the elephant, it may be better to restrict this term to only those gaits that include a phase in which no feet contact the ground.

Necks and tails are the subject of Chapter V, and Alexander makes the simple yet perceptive point that since diplodocid sauropods already bore most of their mass on their hindlegs, they should have had little trouble in rearing up to increase their browsing reach. This is even more true in view of the ability of front-heavy elephants to stand two-legged—another "radical" idea receives support from the engineering viewpoint.

Alexander then calculates the thickness of the dorsal ligaments that supported the neck of *Diplodocus*, but he overestimates the mass of the neck of *Diplodocus* by some two thirds because he ignores the pneumatic spaces. This implies that the dorsal ligaments were thinner than Alexander shows, and when combined with the probability that many of the ligaments ran between and lateral to the neural spines, it is likely that the center-most ligaments did not completely fill the space between the V-spines. Like others, the author has not seen the films showing that femoral action in fast running ostriches approaches that of mammals. Alexander speculates on the possibility that the whip tails found in many sauropods could have produced a supersonic crack, and I hope he does a more in depth investigation of this fascinating question. The differing biomechanics behind the action of the tail clubs of ankylosaurids, which vary tremendously in size between species of similar body mass, are another fertile ground for this kind of research. Although recent suggestions that these clubs were exclusively thermoregulatory organs need not be taken seriously, one wonders if they really could crack tyrannosaur metatarsals, or smash their ribcages. Similar questions apply to the new Chinese sauropod tail clubs, which are small objects at the end of longer, more supple tails. Then there are stegosaur tails and their spikes, the latter which vary from the very long, slender spines of *Stegosaurus longispinus* to the remarkably stout anterior pair in big, old *S. stenops* individuals (these are not shoulder spines, as has been suggested by Robert Bakker).

In Chapter VI, on fighting and vocalizing dinosaurs, Alexander apparently compared the diameter of just the bony core of a *Triceratops* horn to the horn sheaths that surround and strengthen the cores in ungulates. This mistake results in an understatement of the thickness and strength of the former's horns relative to the latter's. Nor is it certain that derived pachycephalosaurs really did bounce their spherical domeheads off one another—they did not interlock and would have rebounded billiard-ball fashion in dangerously irregular directions—but Alexander is certainly right in arguing that their presacral columns were curved in order to better absorb head butts. As for "singing" dinosaurs, I would like someone to carefully sculpt (from blown glass?) tubes to the exact shape and dimensions of the nasal passages of *Corythosaurus* and *Parasaurolophus*, so that we can hear higher fidelity reproductions of their voices.

In Chapter VII Alexander dismisses the usefulness of most methods of measuring dinosaur metabolism. In doing so he does not appear aware of the emerging consensus by Armand de Ricqlès, John Horner, R. Reid and others that dinosaur bone microstructure is indicative of rapid growth—although Alexander is not alone in this regard—and only endotherms are known to grow fast in the wild. Alexander admits that thermal flow patterns cannot determine dinosaur physiology by themselves, they are better used to explore how a dinosaur will work with a given physiology.

Chapter VIII shifts from dinosaurs to a fairly standard examination of big pterosaur aerodynamics—some of us dissidents are looking into their being heavier bodied, powered fliers rather than ultra light soarers. The discussion of marine reptile hydrodynamics in Chapter IX does not incorporate some of the most recent work on ichthyosaurs. This is unfortunate because Alexander may have some pertinent points about whether those ichthyosaurs that had the most sleek hydrodynamic shapes and big crescent tails were or were not dorsal finned, tail propelled racers in the mackeral shark- or tuna-like mold (Alexander incorrectly scales up a small ichthyosaur to giant dimensions in Fig. 9.1). The exploration of the extinction of Mesozoic reptiles and dinosaurs in Chapter X concentrates on the physical aspects and results of meteorite impacts and super eruptions. However, giant asteroids and comets were crashing into the Earth repeatedly in the Mesozoic without bringing the dinosaurs to grief, and trap formation was also a return engagement, so it remains unproven whether these were key agents in the extinction at the K/T boundary.

Chapters XI and XII respectively focus on the giant birds and mammals of the Cenozoic. Alexander misses citing Australian *Dromornis*, rather than *Aepyornis*, as the biggest known bird. The look at giant mammals is too short, and it is doubtful that *Indricotherium*, which is more gracile than proboscideans, massed 34 tonnes as suggested. The problem is further complicated by the fact that the American and Soviet skeletal restorations of this rhino differ greatly in neck length and ribcage depth, it will take a careful study to reveal this beast's true bulk—including whether a density of 0.95 or 0.9 is most appropriate for an ungulate with excavated vertebrae.

As an artist I am especially interested in illustrations, and I found this book's set to be adequate to explain the text. But they are too dull and simplistic for the modern renaissance in dinosaur art, especially in a book that examines their locomotory performance and the like. Perhaps the book's art is taking a

316

315

minimalist's view of the topic. The restorations based on the BMNH models have all the faults of the models themselves. Some of the other drawings are twenty years out of date. Most interesting is Fig. 4.7, which compares a running white rhino to a postulated galloping *Triceratops*. I very much hope that Alexander will publish detailed, full sequence motion figures based on the films of various running animals he has accumulated.

I think the book could have been longer, it is well written and Alexander does about as good a job as one can in incorporating formulas into the text. The greatest strength of this book is also its greatest weakness—that Alexander is not a full time student of vertebrate paleontology. The weakness is that it leads to errors that could have been avoided. The strength, and this is much more important, is that Alexander views dinosaurs from a different point of view, and examines them with methodologies not usually used by those inside the field. *Dynamics of Dinosaurs* is a good and useful start at using biophysical principles to better understand the form and function of dinosaurs and other extinct tetrapods.

> Gregory S. Paul 3109 N. Calvert St. Side Apt. Baltimore MD 21218 USA