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Review

Dinosaur biomechanics

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Biomechanics has made large contributions to dinosaur biology. It has enabled us to estimate both the speeds at which dinosaurs generally moved and the maximum speeds of which they may have been capable. It has told us about the range of postures they could have adopted, for locomotion and for feeding, and about the problems of blood circulation in sauropods with very long necks. It has made it possible to calculate the bite forces of predators such as *Tyrannosaurus*, and the stresses they imposed on its skull; and to work out the remarkable chewing mechanism of hadrosaurs. It has shown us how some dinosaurs may have produced sounds. It has enabled us to estimate the effectiveness of weapons such as the tail spines of *Stegosaurus*. In recent years, techniques such as computational tomography and finite element analysis, and advances in computer modelling, have brought new opportunities. Biomechanists should, however, be especially cautious in their work on animals known only as fossils. The lack of living specimens and even soft tissues oblige us to make many assumptions. It is important to be aware of the often wide ranges of uncertainty that result.

Keywords: dinosaur; biomechanics; locomotion; jaws; behaviour

1. INTRODUCTION

Were large dinosaurs lumbering monsters, barely able to support their huge weight, or could they have moved with reasonable speed and agility? How could the long, horizontal necks of some sauropods have been supported and how could blood have been pumped to the brains of others that apparently carried their heads 8 m above their hearts? How strong a bite could be inflicted by the huge jaws of tyrannosaurs and what was the chewing action of herbivores such as the hadrosaurs? Can we reconstruct the sounds that some dinosaurs may have made and the possible fighting behaviour of others? Light has been shed on all these questions by application of the principles of mechanics, as this review will show.

This is not a general review of dinosaur locomotion, jaw action, sound production, etc. Many valuable contributions to functional morphology are omitted because they do not make explicit use of physical mechanics. Topics such as heat balance, which depend mainly on aspects of physics other than mechanics, have no place in this review. The possibility of flight by feathered dinosaurs is also omitted, although it raises interesting aerodynamic questions.

2. BODY MASS AND CENTRE OF MASS

Many problems of dinosaur biomechanics require estimates of the mass of the whole or of some part of the body and of the position of the centre of mass. The traditional method of estimating mass has been to measure the volume of a reconstruction of the intact animal and multiply by an estimate of the body density. Colbert (1962) and Alexander (1985), among others, used scale models of dinosaurs. Colbert measured their volumes by displacement of sand. Alexander weighed models in air and in water and applied Archimedes' Principle. More recent papers have based estimates of the volumes of Mesozoic reptiles on reconstructed lateral and dorsal views (Motani 2001; Seebacher 2001) or on three-dimensional computer reconstructions (Henderson 1999). The animal's body has been represented as a series of slices and its volume determined by numerical integration.

Tissues vary in density. Muscles have densities of around 1050 kg m^{-3}, fat around 900 kg m^{-3}, bone around 2000 kg m^{-3} and the air in the lungs 1 kg m^{-3} (see, for example, Alexander 1983*a*). Dinosaur masses might be calculated from these densities, using estimates of the volume of each tissue. Instead, most authors have used estimates of the overall density of the body, usually 1000 kg m^{-3}. This is the density of a crocodile floating in fresh water with only the tips of its nostrils above the surface or of a human with moderately inflated lungs. Vertebrates with air sacs may, however, be considerably less dense. For example, Alexander (1983*b*) found that a plucked goose carcase had a density of only 937 kg m^{-3}. O'Connor & Claessens (2005) presented evidence that non-avian theropods had bird-like air sacs. Incorrect assumptions about air sacs are unlikely to result in errors greater than 10%, in estimated dinosaur masses.

Estimates of body mass derived from reconstructions, even from reconstructions based on the same individual fossil, may differ by factors up to at least 1.5, depending on whether the restorer favoured a skinny physique or a stout one (see the comparisons in Alexander (1989), Henderson (1999) and Seebacher (2001)). Great care may be taken in the reconstruction, building it up on the skeleton muscle by muscle (Paul 1987), but the restorer must depend either on subjective judgement or on doubtful assumptions, based on modern animals, about the relative volumes of skeleton and soft tissue.

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Alexander (1985) located the centres of mass of solid plastic models of dinosaurs by the method of suspension (see Alexander 1983*a*). He applied a correction to take account of the air-filled volume of the lungs and assumed that bone was distributed uniformly in the body. Henderson (1999) used his computer models to locate centres of mass, again taking account of the air in the lungs.

Estimates of centre of mass position are subject to error, because the posture of the animal may be restored incorrectly. This is generally unlikely to introduce very large errors: see Alexander's (1985) discussion of the effect of neck posture on centre of mass position for *Diplodocus*.

Anderson *et al.* (1985) showed that the masses of quadrupedal mammals could be estimated reasonably accurately from the total of the circumferences of the humerus and the femur. They applied their mammal equation to quadrupedal dinosaurs, which are known from fossil footprints to have walked much as mammals do with their feet under the body. (Even 'wide-gauge' dinosaur trackways are much narrower, relative to leg length, than is usual in modern reptiles; Lockley *et al.* 2002.) Anderson and his colleagues had measured femur circumferences for birds and bipedal mammals, as well as for quadrupeds, but did not use them to calculate the masses of bipedal dinosaurs because 'the proportions of the posterior limb in bipedal dinosaurs resemble those in quadrupedal mammals more than those of birds and saltating mammals'. Instead, they modified their equation for quadrupedal mammals to calculate the masses of bipedal dinosaurs from the circumference of the femur alone. The method is very easy to use and needs only a humerus and a femur, not a complete skeleton. It has, however, two disadvantages. First, we cannot be certain that an equation derived from their sample of mammals will work well for dinosaurs. Carrano (2001) pointed out that most of the large mammals in their sample were ungulates, which differ from other mammals in the allometry of their limbs. He was also concerned that errors might result from dinosaurs having more robust femurs, relative to the humerus, than mammals. Second, the method of Anderson *et al.* is wholly inappropriate if the mass is required for calculation of stresses in leg bones: if you use a mass derived from leg bone dimensions for this purpose you are guilty of circular argument.

3. SPEED AND MANOEUVRABILITY

The faster an animal walks or runs, the longer in general are its strides. Alexander (1976) used this principle to estimate dinosaur speeds from the spacing of fossil footprints. Stride length depends on the size of the animal as well as the speed. Alexander's method of taking account of this depended on the concept of dynamic similarity. He predicted that similar animals running with equal Froude numbers ((speed)^2/(leg length$\times$gravitational acceleration)) would have equal relative stride lengths (stride length/leg length). Alexander & Jayes (1983) explained the theoretical basis for the prediction and showed that it is approximately true for bipedal and quadrupedal mammals. Alexander (1976) and later authors (see Thulborn 1990) used graphs of relative stride length against Froude number, derived from observations of mammals, to estimate speeds from dinosaur trackways.

The method cannot claim to be accurate. We cannot be certain that the relationship between relative stride length and Froude number was the same for dinosaurs as for mammals. The empirical points for mammals are widely scattered on either side of the regression line, showing that an observed stride length may be used at speeds that differ from the prediction of the graph by factors as large as 1.5. The method depends on doubtful estimates of leg length, usually based on footprint size, which may be misleading if erosion has removed the original surface of the substrate (Allen 1997) or if the substrate was very soft (Gatesy *et al.* 1999). Refinements to the method have been proposed, in attempts to make it more accurate (see Alexander 1991). Thulborn & Wade (1984) took account of differences between groups of dinosaurs in the ratio of foot length to leg length, and used a slightly different equation. In a careful kinematic analysis, Henderson (2003) evaluated alternative methods of estimating hip height from footprint length. Unfortunately, the other potential sources of error remain serious. Though it cannot predict precise speeds, the method is informative; there seems to be no likelihood of confusing a stroll with a sprint.

The rough estimates of speed obtained by this method have generally been less than 4 m s^{-1} for bipedal dinosaurs and 2 m s^{-1} for sauropods (Thulborn 1990). An exceptional trackway of a medium-sized (*ca* 500 kg) biped seems to show an 11 m s^{-1} sprint (Farlow 1981), and one made by a large theropod indicates a speed of 8 m s^{-1} (Day *et al.* 2002).

Running animals generally use their top speeds only rarely, so trackways made at maximum speed are unlikely to be found. Alexander (1985) tried to assess the athleticism of dinosaurs by considering the strengths of their leg bones. He used the dimensions of leg bones to estimate the strength indicator, a measure of the strength of the bone in bending in relation to the animal's weight. Animals with equal strength indicators have bones strong enough for dynamically similar running at the same maximum Froude number, irrespective of any difference in body size. An implied assumption here is that the animals are built with equal safety factors (strength/maximum expected stress). This approach led to the conclusion that *Apatosaurus* (a 35 ton sauropod) may have been about as athletic as an elephant and that *Tyrannosaurus* is unlikely to have run fast. Elephants can run at up to at least 6.8 m s^{-1} (Hutchinson *et al.* 2003), and an *Apatosaurus* at the same Froude number would have a speed of about 9 m s^{-1}.

Farlow *et al.* (1995) repeated the analysis for *Tyrannosaurus* using better material, and reached a similar conclusion: it is unlikely to have run faster than 10 m s^{-1}. They also presented a new argument for it being slow. Its vestigial fore limbs would have been useless to break its fall, if it had tripped. They made rough estimates of the forces that would have acted on its chest if it fell while running fast and concluded that they would probably have been fatal. Alexander (1996) used data from research on car crashes to confirm that the estimated forces should be expected to cause injury. Ostriches, however, run fast despite having no arms to break a fall and gibbons risk serious injury when they swing through trees. The conclusion that running would be risky does not necessarily imply that *Tyrannosaurus* did not run fast.

Bones of geometrically similar animals of equal density would have strength indicators proportional to (body mass)$^{-0.33}$, so small dinosaurs can be expected to have higher strength indicators than similar but larger dinosaurs. Given adequate muscles, this should have enabled them to run at higher Froude numbers (but not necessarily at higher speeds, because their legs were shorter). Christiansen (1998) estimated strength indicators for 25 individual theropods and found that they were generally larger for the smaller species. He used them to estimate maximum speeds (for example, 11 m s^{-1} for a 6 ton *Tyrannosaurus*), but noted that such estimates depend on many doubtful assumptions.

Speed estimates based on muscle dimensions incur additional uncertainty because no muscles are available for measurement. Hutchinson & Garcia (2002) and Hutchinson (2004) estimated the masses of muscle that would be needed to enable bipedal dinosaurs to run. For each dinosaur they estimated the position of the centre of mass of the body, the angles of the leg joints at mid stance and the moment arms and fascicle lengths of the leg extensor muscles. From these data, together with the measured lengths of the leg bones, they estimated the mass of leg extensor muscle required for running as a percentage of body mass. They acknowledged that there was scope for serious error in some of the parameters, but a sensitivity analysis added confidence to their conclusion that *Tyrannosaurus* may have been able to run, but is unlikely to have had enough muscle to run fast.

Carrier *et al.* (2001) discussed the manoeuvrability of running dinosaurs. Moments of inertia of geometrically similar bodies of equal density increase in proportion to (body mass)$^{1.67}$. If large dinosaurs ran, as they are generally believed to have done, with their bodies and tails horizontal (Galton 1970*a*; Newman 1970), their moments of inertia in yaw would have been very high. (Yaw is rotation about a vertical axis.) This would have made fast turning difficult, especially for bipeds. Carrier and his colleagues illustrated this point by experiments with human subjects whose moments of inertia were varied by attaching weights at different horizontal distances from the centre of mass. They suggested that carnosaurs may have reduced their moments of inertia by running with their trunks and tails sloping, forming the two arms of a V. They attempted to reconcile this suggestion with the evidence that is generally interpreted as showing that carnosaurs had stiff backs (for example, Newman 1970). Henderson & Snively (2004) found that dinosaurs' moments of inertia in yaw, with the back straight, scaled in proportion to (body mass)$^{1.55}$ for bipeds and (body mass)$^{1.62}$ for quadrupeds. In each case, the exponent is significantly less than for geometric similarity.

4. POSTURE

For a biped to balance, its foot should be under the centre of mass at mid stance. Typical birds, whose centres of mass are well anterior to the hip, achieve this by keeping the femur almost horizontal. Bipedal dinosaurs had long tails and, consequently, more posterior centres of mass. It is generally assumed that dinosaurs walked with their femurs more nearly vertical than birds. Jones *et al.* (2000) argued that *Caudipteryx*, which has a reduced tail, had a more anterior centre of mass than other bipedal dinosaurs and had bird-like leg proportions. They suggested that it must have walked like a typical bird. Christiansen & Bonde (2002), however, considered that their centre of mass position was incorrect, and Dyke & Norell (2005) pointed out that their argument depended on a doubtful estimate of trunk length.

Carrano & Biewener (1999) simulated the effect of a dinosaur tail by attaching weights posterior to the hips of chickens. They expected that the birds would run with their femurs more vertical, but instead they ran with their knees strongly bent, adopting a posture that would have imposed severe stresses on large dinosaurs' bones. Bending the knee moved the chickens' feet posteriorly because, unlike dinosaurs, their tibiotarsi were much longer than their femora (Carrano 1998).

Brachiosaurus is generally (and plausibly) restored with its neck sloping steeply up, in a giraffe-like posture. Other sauropods such as *Apatosaurus* and *Diplodocus* are usually shown with their long necks horizontal. Stevens & Parrish (1999) discussed the range of postures to which their necks could be bent. They built and manipulated three-dimensional computer models of the neck vertebrae. They assumed by analogy with bird necks that zygapophysial overlap would be reduced to 50% at the extremes of the range of movement. They concluded that both species could easily lower their heads to the ground and that they could raise them to 5.9 m (*Apatosaurus*) or 4.3 m (*Diplodocus*) above the ground. They also estimated the ranges of lateral movement.

Thompson (1942) made a qualitative comparison between a sauropod dinosaur and the Forth Bridge. The weight of the bridge causes bending moments that are balanced by tension members in the upper parts of the bridge and compression members in the lower parts. Similarly, bending moments in dinosaur necks were presumably balanced by tension in epaxial muscles or ligaments and compression in the vertebral centra. The cervical and anterior dorsal vertebrae of some sauropods have bifid neural spines. Alexander (1985) showed that the V-shaped spaces between them were large enough in *Diplodocus* to house either a pennate muscle or an elastic ligament, strong enough to provide most of the required support. Tsuihiji (2004) presented reconstructions of sauropod neck ligaments, based on comparisons with *Rhea*.

Bakker (1978) revived earlier suggestions that diplodocids may have browsed on high foliage by rising on their hind legs. Alexander (1985) discussed the feasibility of this. He had shown that the centre of mass of the body was only a little anterior to the hip joints. Thus *Diplodocus* could have moved its hind feet forward to a position vertically below the centre of mass. The animal would then be balanced on its hind feet and could easily raise its fore parts to the posture that Bakker had postulated. The manoeuvre would be much more difficult for *Brachiosaurus*, whose centre of mass was further anterior, but *Brachiosaurus* is believed to have browsed quadrupedally, in a giraffe-like posture.

Henderson (2004) discussed the buoyancy of sauropods, concluding that they were extremely buoyant and that their centres of buoyancy, when floating, would have been below their centres of mass, making them unstable. They would have been liable to roll over and float belly-up. The conclusion about buoyancy depends on his assumption that air sacs occupied 15% of the volume of the trunk,

and stability would depend on neck and tail postures. The evidence for air sacs in dinosaurs (O'Connor & Claessens 2005) does not tell us their size.

5. BLOOD FLOW IN LONG NECKS

The brains of *Brachiosaurus* and of *Barosaurus* (also believed to have stood in a giraffe-like posture) were about 8 m above their hearts. The hydrostatic pressure difference between the blood in the brain and in the heart would have been about 80 kPa. *Diplodocus* standing on its hind legs, as envisaged in the preceding section, would have had its brain about 6 m above its heart, with a hydrostatic pressure difference of 60 kPa. Modern reptiles generally have systolic pressures of only 5–10 kPa. These data raise questions about the supply of blood to the brain, which have been reviewed by Badeer & Hicks (1996).

The obvious conclusion from these data is that *Brachiosaurus* and *Barosaurus* must have had extraordinarily high systolic pressures of 85–90 kPa, 80 kPa to overcome the hydrostatic pressure difference and 5–10 kPa to overcome viscous resistance to blood flow. Choy & Altman (1992) suggested that *Barosaurus* may have had several hearts working in series, but there is no direct evidence for auxiliary hearts and so extraordinary a morphological novelty seems unlikely to have evolved. Badeer & Hicks (1996) argued that high systolic pressures were not required because the circulation to the head could operate as a siphon, with blood pressure in the head and upper parts of the neck well below ambient. Veins, however, generally have very flexible walls. They collapse, and flow in them is blocked, if the pressure of their contents falls below ambient (Seymour *et al.* 1993). Badeer & Hicks (1996) postulated exceptionally stiff-walled veins in *Barosaurus*' neck.

The problem of blood circulation to the brain arises for giraffes as well as for sauropods, albeit in less extreme form. Hargens *et al.* (1987) measured arterial pressures of 25 kPa at the bases of standing giraffes' necks and 15 kPa 1 m further up the neck. By extrapolation, systolic pressures in the heart must have exceeded 30 kPa. They found no subatmospheric pressures at any level in the jugular vein. The circulation to the head was plainly not functioning as a siphon. The possibility that *Barosaurus* had a single, very muscular heart, generating very high pressures, seems at least as likely as the alternatives of accessory hearts or stiff-walled veins. Seymour & Lillywhite (2000), however, thought it unlikely that large sauropods could have held their necks erect.

6. JAWS

Several authors have investigated the forces that could have been exerted by the formidable jaws of theropod dinosaurs. Erickson *et al.* (1996) described a *Triceratops* pelvis with deep bite marks apparently made by *Tyrannosaurus*. They estimated the force needed to make these marks by tests on bovine ilia, which are histologically similar to the *Triceratops* pelvis and were assumed to have similar mechanical properties. The force required was about 6.4 kN, which is not remarkably high for so large an animal. A 3.7 m *Alligator* exerted bite forces up to 9.5 kN (Erickson *et al.* 2003). Geometrically similar animals are expected to exert forces in proportion to the squares of their lengths, so a 10 m (*Tyrannosaurus*-sized) alligator could be expected to exert forces in the region of 70 kN.

Rayfield *et al.* (2001) estimated the bite forces that could be exerted by *Allosaurus*. They used clay to reconstruct the jaw muscles on a cast of an *Allosaurus* skull, then measured the cross-sectional areas of the clay 'muscles'. From these cross-sectional areas they calculated the force that could be exerted in a strong bite. Using an intermediate stress of 0.3 MPa, their calculations give a bite force of 1.6 kN. By scaling this estimate up, assuming geometric similarity, we can calculate that an *Allosaurus* of the size of *Tyrannosaurus* could be expected to exert about 5 kN.

Rayfield *et al.* (2001) also estimated the stresses that would act in the skull during strong biting. They used computational tomography scans of an *Allosaurus* skull as the basis for a remarkably detailed three-dimensional finite element model. They analysed this model and concluded that the skull was capable of withstanding forces on the tooth row up to 55 kN; it seemed over-engineered for bite forces generated by the jaw muscles. They suggested that the skull was adapted for slashing bites, in which the teeth struck the prey at high velocity, rather than static crushing bites. Frazzetta & Kardong (2002) challenged this interpretation. Rayfield (2005*a*) extended the study, focusing on the implications of suture morphology.

An investigation by Metzger *et al.* (2005) warns that the predictions of finite element models of skulls should be interpreted cautiously. They compared biting strains predicted by a three-dimensional finite element model of an alligator skull with strains measured *in vivo* by means of surgically implanted strain gauges. Predicted and observed principal strain magnitudes were not significantly correlated (it seems likely that the assumption of uniform bone properties throughout the model was false). Metzger *et al.* got better agreement for principal strain orientations.

Rayfield (2004, 2005*b*) performed two-dimensional finite element analyses of the skulls of *Tyrannosaurus* and *Coelophysis* skulls loaded by forces simulating biting. Restriction to two dimensions makes the problem much less complex, but inevitably reduces the reliability of the result.

Henderson (2002) had previously estimated the relative strengths of theropod skulls, treating them (unrealistically) as solid beams. This method can give only a very rough indication of the likely distribution of stresses (Metzger *et al.* 2005) because, far from being a solid beam, a skull is a three-dimensional framework of beams and plates of different thicknesses.

Weishampel (1984) investigated the jaw movements of ornithopod dinosaurs, treating them as three-dimensional problems in the kinematics of machines. He showed that the maxillary complex of hadrosaurs forms a hinge joint with the brain case. The grinding surfaces of the cheek teeth are angled in such a way that the upper jaws were forced apart as the lower jaw closed against them. Thus the teeth slid over each other, grinding rather than merely crushing the food.

7. DISPLAY AND FIGHTING

Two suggestions have been made that dinosaurs may have produced sounds that were important in display. First, the

crested lambeosaurine hadrosaurs have exceptionally long vocal tracts, due to the nasal cavity being extended by a loop in the crest. In a long-crested *Parasaurolophus* the vocal tract had a total length of 3.46 m. Weishampel (1981) noted that tubes of this length, open at both ends, have a resonant frequency of 48 Hz and suggested that the dinosaur used the resonance to generate sounds of this frequency. Longer-crested individuals would emit lower frequencies. Sexual selection by females could result in males evolving progressively longer crests.

This conclusion should perhaps be modified. The fundamental frequency of the voice, both of humans (Lieberman & Blumstein 1988) and of dogs (Riede & Fitch 1999), is not set by the resonant frequency of the vocal tract but by the vocal cords, and so can be varied. The vocal cords emit a fundamental frequency and a series of harmonics. The acoustic effect of the vocal tract is to modify the acoustic spectrum by enhancing harmonics that are close to the harmonics of its own resonance and suppressing intermediate harmonics. The enhanced frequencies are known as formants. A young boy and an adult man may sing the same note, but the different spacing of their formants, due to the different dimensions of their vocal tracts, make them sound quite different. Male *Parasaurolophus* may have emitted sounds whose fundamental frequencies were different from the resonant frequency of the vocal tract and females may have preferred the ones whose formants indicated a long vocal tract.

The second suggestion about sounds with a social function concerns sauropods such as *Diplodocus* and *Apatosaurus*, which have long tails that taper to a remarkably slender tip. Alexander (1989) suggested that they may have cracked their tails like whips. For example, rival males may have assessed each other in tail-cracking contests, analogous to the roaring contests of stags (Clutton-Brock 1982). Myhrvold & Currie (1997) made a quantitative analysis of the tail's efficacy as a whip. They concluded that a rapid transverse movement of the base of the tail would propagate waves towards the slender tip, which might well reach the supersonic speed needed for whip cracking.

Various dinosaurs have structures that seem likely to have served as weapons, either for contests between males or for defence against predators. The horns of ceratopsian dinosaurs could have been used in wrestling matches, like the contests between rival male antelopes and stags (Farlow & Dodson 1975). Farke (2004) showed that the horns of fighting *Triceratops* could have interlocked in ways consistent with observed injuries. Alexander (1989) had noted that *Triceratops* brow horns were more slender than predicted for antelopes of similar mass, but Farlow (1990) showed that they were stouter than antelope horns of equal length.

Carpenter *et al.* (2005) presented evidence that *Stegosaurus* used its tail spikes to defend itself. They showed that the size and orientation of a partially healed wound in an *Allosaurus* vertebra were consistent with its having been made by a *Stegosaurus* spike and they noted some *Stegosaurus* spikes that, on the evidence of remodelling, must have been broken in life. They calculated the stresses that might have acted in tail blows, using an estimate of the cross-sectional area of the tail muscles, and concluded that they could have caused the injuries to both species. They based their estimate of the force needed to pierce the *Allosaurus* vertebra on Erickson *et al.*'s (2003) tests on bovine ilia. They could have simplified their calculations and avoided some assumptions by adopting the approach that Alexander *et al.* (1999) applied to possible fights between male glyptodonts (large armoured mammals with tail clubs). These authors used the volume available for tail muscles to estimate the work that they could do, giving kinetic energy to the tail. They then considered whether this energy was sufficient to supply the work required to fracture a rival's carapace. Satisfactory application of this method to the *Allosaurus* injury would, however, have required measurement of the work required to drive a model of a *Stegosaurus* spike through an appropriate bone, such as a bovine ilium. The approach of Alexander *et al.* (1999) could be applied to ankylosaur tail clubs, which were presumably used for defence from predators and/or fights between rival males.

Galton (1970*b*) argued that the radial arrangement of trabeculae in the greatly thickened skull roofs ('domes') of pachycephalosaurs might be an adaptation for head-butting contests between males, like the fights between bighorn rams. Sues (1978) confirmed by photoelastic experiments on a model that compressive stresses in head-butting would be aligned with the trabeculae. Alexander (1989) pointed out that cancellous bone in the dome would have a cushioning effect in impacts between rival males. Goodwin & Horner (2004) showed that the largely cancellous structure of the dome was a juvenile feature; in adults it consisted almost entirely of compact bone. They argued that this was inconsistent with head-butting behaviour, but this claim is not convincing. Imagine a head-on collision between two 20 kg male *Stegoceras* running at $5\ \mathrm{m\,s^{-1}}$ (a speed measured by Kitchener (1988), from a film of fighting bighorn rams). Each would have a kinetic energy of 250 J, which would have to be dissipated in the impact. Only the kinetic energy of the head (perhaps 25 J) would have to be absorbed by the skull roof. The remainder could be absorbed by muscles in the neck and trunk, as seems to be the case in horned mammals (Kitchener 1988). Keratin has a strain energy capacity of $1500\ \mathrm{J\,kg^{-1}}$ (Vogel 2003), so allowing a factor of safety of 2, 30 g of keratin appropriately located on the dome could absorb 25 J, with no need for a contribution from cancellous bone.

8. CONCLUSIONS

Three conclusions may be drawn from this short review. First, application of (generally simple) mechanics has added substantially to our understanding of many aspects of dinosaur biology. Second, new techniques offer the hope of even better insights in the future. Computational tomography enables us to explore and measure hidden parts of fossils without damaging them. Finite element analysis makes it possible to calculate stresses in complex structures. Increasingly sophisticated computer software extends the feasible range of mathematical modelling. Finally, and less encouraging, the lack of living specimens or even well-preserved soft parts obliges biomechanists to depend on so many doubtful assumptions that their conclusions about dinosaurs (and especially their quantitative conclusions) must be interpreted very cautiously.

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