

Mechanics of posture and gait of some large dinosaurs

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Dimensions of dinosaur bones and of models of dinosaurs have been used as the basis for calculations designed to throw light on the posture and gaits of dinosaurs.

Estimates of the masses of some dinosaurs, obtained from the volumes of models, are compared with previous estimates. The positions of dinosaurs' centres of mass, derived from models, show that some large quadrupedal dinosaurs supported most of their weight on their hind legs and were probably capable of rearing up on their hind legs.

Distributions of bending moments along the backs of large dinosaurs are derived from measurements on models. The tensions required in epaxial muscles to enable *Diplodocus* to stand are calculated. It is likely that the long neck of this dinosaur was supported by some structure running through the notches in the neural spines of its cervical and dorsal vertebrae. The nature of this hypothetical structure is discussed.

An attempt is made to reconstruct the walking gait of sauropod dinosaurs, from the pattern of footprints in fossil tracks.

The dimensions of dinosaur leg bones are compared to predictions for mammals of equal body mass, obtained by extrapolation of allometric equations. Their dimensions are also used to calculate a quantity which is used as an indicator of strength in bending. Comparisons with values for modern animals lead to speculations about the athletic performance of dinosaurs.

Estimates of pressures exerted on the ground by the feet of dinosaurs are used in a discussion of the ability of dinosaurs to walk over soft ground.

KEY WORDS:—Dinosaur – Saurischia – Ornithischia – posture – gait – locomotion.

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INTRODUCTION

The largest dinosaurs are particularly interesting, because they were much larger than any modern terrestrial animal. It would be more difficult for a large

animal, than for a geometrically similar small one, to support the weight of its body. This is because body weight would be proportional to the cube of linear dimensions, but the cross-sectional areas (and therefore the strengths) of the muscles and bones would be proportional only to the square of linear dimensions. What postures and movements were possible for the large dinosaurs, and how did they stand and move? Many attempts have been made to answer these questions (for example Bird, 1944; Bakker, 1968, 1971, 1978; Galton, 1970; Coombs, 1975; Alexander, 1976; Thulborn, 1982). This paper tries again, using only quantitative arguments.

Bakker (1978) suggested that some of the large quadrupedal dinosaurs habitually stood on their hind legs to browse from trees. This paper assesses the possibility by locating the centres of mass of models, estimating the positions of the centres of mass of actual dinosaurs and considering whether the hind feet could be brought directly under the centre of mass (as they would have to be, to enable the animal to stand bipedally). Thompson (1917) made a qualitative comparison between dinosaurs and bridges, and drew schematic diagrams of the distribution of bending moments along dinosaurs. In this paper the bending moments are calculated, for several dinosaurs, and used to calculate forces and stresses that must have acted in intervertebral discs and back muscles. Bird (1944) used fossil footprints as evidence that large sauropod dinosaurs could walk on land and Alexander (1971) argued (from bone dimensions) that their leg bones were strong enough to support them. In this paper, the dimensions of the leg bones of some of the largest dinosaurs are compared with estimates for mammals of equal mass, obtained by extrapolation from actual mammals. Alexander (1976) argued that known footprints of large dinosaurs record walking, though some footprints of smaller dinosaurs record running. A case of a large bipedal dinosaur apparently running fast was subsequently discredited (Thulborn, 1981). Surviving footprints cannot, however, eliminate the possibility that very large dinosaurs sometimes ran. In this paper, the feasibility of their running is assessed by considering the strengths of their leg bones. Bakker (1971) suggested that sauropod dinosaurs would have been in severe danger of getting bogged down, if they ventured onto soft ground. In this paper, that possibility is examined by estimating the pressures that the feet of dinosaurs imposed on the ground.

MATERIALS AND METHODS

Bone dimensions used in this paper are those of the following dinosaurs and have been taken from the papers which are referred to.

Order Saurischia, suborder Theropoda

Antrodemus valens U.S. National Museum 4734 (Gilmore, 1920)

Tyrannosaurus rex American Museum of Natural History 5027 and 973 (Osborn 1906, 1916)

Order Saurischia, suborder Sauropodomorpha

Apatosaurus louisae Carnegie Museum 3018 (Gilmore, 1936)

Brachiosaurus brancai Berlin Museum SII (Janensch, 1950)

Diplodocus carnegiei Carnegie Museum 84 (Hatcher, 1901; Holland, 1906)

Order Ornithischia, suborder Ornithopoda

Iguanodon bernissartensis IRSNB Brussels 1534 (Norman, 1980)

Order Ornithischia, suborder Stegosauria

Stegosaurus unguatus U.S. National Museum 6646 (Gilmore, 1914)

Order Ornithischia, suborder Ceratopsia

Triceratops "prorsus" U.S. National Museum 4842 (Hatcher, 1907. See Lull, 1933, on the specific name).

A few measurements taken from other specimens have been adjusted to apply to those listed above. For example, the diameters of *Diplodocus* femur were taken from Hatcher's (1901) photograph of Carnegie Museum specimen 86, and multiplied by the ratio of femur lengths to obtain estimates of diameter for specimen 84.

Many of the measurements used in this paper could not be taken directly from skeletons, but required flesh reconstructions. These measurements were taken from solid plastic models, manufactured for and sold by the British Museum (Natural History). A leaflet issued by the museum's Publications Department describes these models as being made to a scale of 1/40, and this scale will be assumed in all calculations based on them. Their dimensions seem consistent with their being 1/40 scale models of the specimens listed above. The original models were made by the museum's chief modelmaker, Mr Arthur Heywood. Outlines of the models are included in Fig. 1.

Postures markedly different from those represented by the models have been suggested for *Tyrannosaurus* (Newman, 1970), *Iguanodon* (Norman, 1980) and the sauropods (Bakker, 1968, 1978). The model of *Diplodocus* was originally as shown in Fig. 1D but was altered for some of the experiments to the position shown in Fig. 1E, by heating and bending the neck.

The tail of the model *Tyrannosaurus* is shorter, relative to other parts of the body, than in Osborn's (1916) restoration but longer than in Newman's (1970).

The volumes of the models were determined by weighing in air and in water (see Alexander, 1983a). Accurate results are more easily obtained by this method than by displacement of sand (Colbert, 1962a) or of water (Charig, 1979). The volumes of the dinosaurs were calculated from those of the models by multiplying by 40³.

Calculation of the masses of the dinosaurs required an estimate of density. Colbert (1962a) assumed a density of 900 kg m⁻³, based on crude measurements of the densities of an *Alligator* and a *Heloderma*. In contrast, Cott (1961) obtained densities of 1080 kg m⁻³ for nine *Crocodilus* (masses up to 44 kg) by the more accurate method of weighing in air and in water. These measurements were made on dead specimens, but living reptiles can vary their density by inflating and deflating their lungs and also (to a small extent: see Cott's data) by taking in gastroliths. Living crocodiles sometimes rest motionless on the bottoms of rivers (Cott, 1961) and must then have densities greater than that of water. They also sometimes float with only their nostrils and the top of the head above the water, and must then have densities very slightly less than that of water. It will be assumed in this paper that dinosaurs had the same density as water, 1000 kg m⁻³.

The centres of mass of the dinosaur models were assumed to lie in the median plane. Their positions in that plane were found by suspension (Alexander, 1983a). The models were made of solid, homogeneous plastic (with a cavity occupying less than 0.5% of body volume near the centre of mass in some of

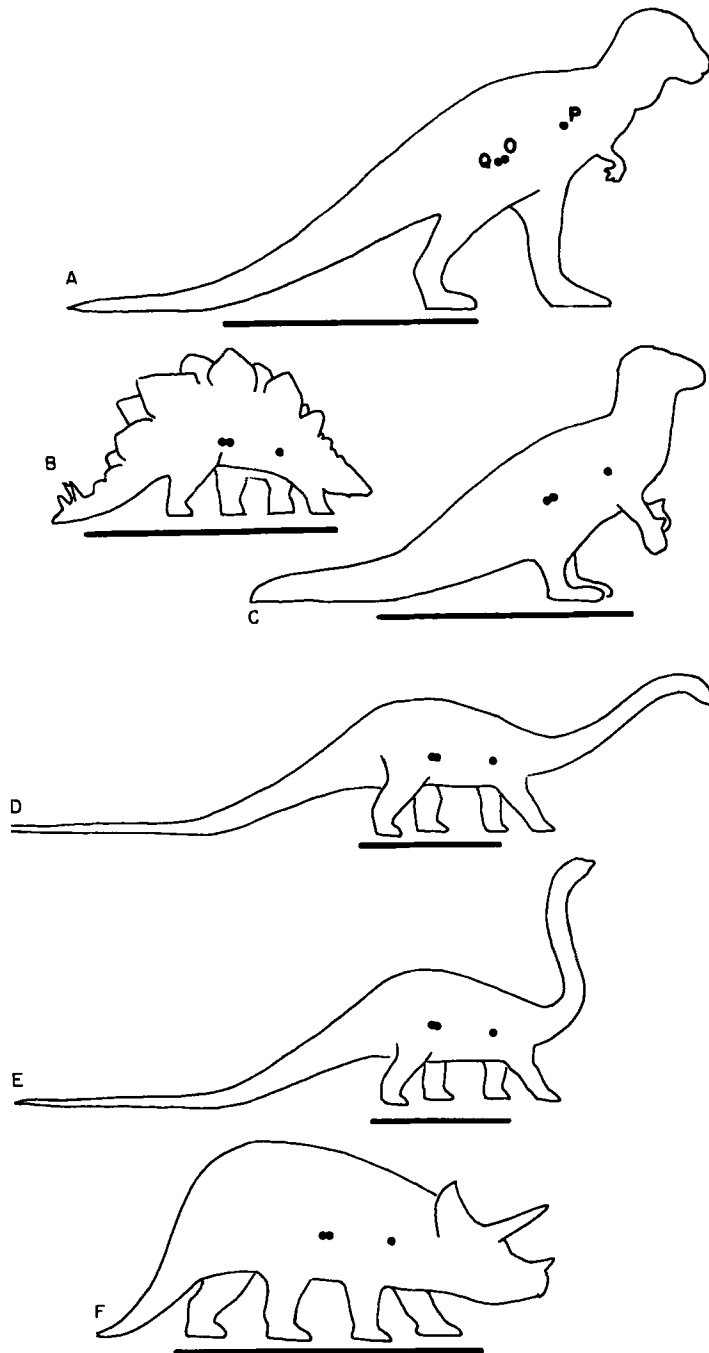


Figure 1. Outlines traced from photographs of the models. A, *Tyrannosaurus*; B, *Stegosaurus*; C, *Iguanodon*; D, E, *Diplodocus* in two positions; F, *Triceratops*. Scale bars = 0.1 m on the models or 4 m on the animals. The points (labelled in A only) are **O**, the centre of mass of the model; **P**, the assumed position of the centre of buoyancy of the lungs and **Q**, the calculated position of the centre of mass of the dinosaur. The order of the points (starting with the most anterior) is **P, O, Q** in every case.

them). If the dinosaurs similarly consisted of material of uniform density, their centres of mass would occupy positions corresponding to those of the models. However, dinosaurs presumably consisted of materials of densities ranging from about 1 kg m^{-3} (the gas in the lungs) to about 2000 kg m^{-3} (bone: see Spector, 1956). The bone was distributed widely in the body, and probably had little effect on the position of the centre of mass. The gas, however, was concentrated in the anterior part of the trunk and might be expected to affect the position of the centre of mass appreciably. Account was therefore taken of it.

Gans & Clark (1976) inflated the lungs of dead or anaesthetized *Caiman* and estimated that their tidal volumes were about 8.5% of body volume. Tenney & Tenney (1970) measured lung volumes for a wide variety of reptiles but dissected the lungs out before inflating them, so their values may not be realistic. Gehr *et al.* (1981) measured the volumes of the lungs of 32 species of mammal after inflating and fixing them *in situ*. They calculated a regression equation relating lung volume to body mass which predicts lungs of about 8% of body volume, for mammals with masses of a few tonnes. The calculations in this paper assume that the lungs of dinosaurs occupied 10% of body volume. This is a deliberately high estimate. It will be shown that the centres of mass calculated for dinosaurs with lungs of this size are close to those obtained directly from the models for dinosaurs of uniform density.

A dinosaur consisting of 10% by volume of lung gases of negligible density, and 90% by volume of tissues of density 1111 kg m^{-3} , would have an overall density of 1000 kg m^{-3} . A rough calculation indicates that a mean tissue density of 1111 kg m^{-3} is consistent with a bony skeleton making up about 14% of body mass (a percentage suggested by the allometric equation for mammals of Prange, Anderson & Rahn, 1979). Thus the assumptions of lungs occupying 10% of body volume, and of an overall density of 1000 kg m^{-3} , seem mutually consistent.

The method of locating the centre of mass, taking account of the lungs, is illustrated in Fig. 1A. **O** is the centre of mass of the model, located by suspension. **P** is the position in which the centre of buoyancy of the lungs was judged to lie after inspecting X-radiographs (in which the lungs appear as translucent regions) of a 1.1 m *Crocodilus niloticus* (Cott, 1961) and a 0.7 m *Varanus bengalensis*. **Q** is the estimated position of the centre of mass, taking account of the lungs. Since the lungs are assumed to occupy 10% of body volume, the distance **OQ** is 10% of **PQ**, or one ninth of **OP**. Also, **Q** lies on the straight line **OP**.

The fractions of body weight supported by the fore and hind feet were calculated for quadrupedal dinosaurs standing in the same positions as the models. It was assumed that the left and right feet of each pair exerted equal, vertical forces; that these forces acted midway between the anterior and posterior edges of the sole of each foot; and (initially) that the tail did not rest on the ground. The forces required on the feet, to balance their moments about the centre of mass, were calculated.

For calculations of bending moments in the neck, trunk and tail it was necessary to discover how the weight of each dinosaur was distributed along the length of the body. As a first step, the distribution of volume was investigated, using the apparatus shown in Fig. 2. The model was suspended by a fine wire from one arm of a balance, so that it hung inside a large glass tank. Another fine

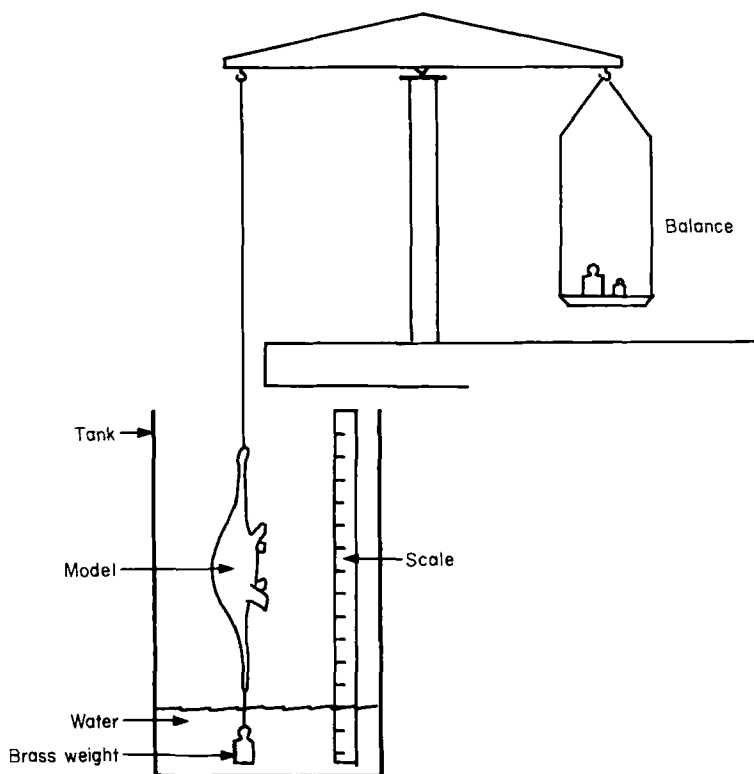


Figure 2. The apparatus used to investigate the distributions of volume along the dinosaurs.

wire connected a brass weight to its tail, so that what would have been the horizontal anterior-posterior axis in walking was instead vertical. Thus quadrupedal dinosaurs were suspended so that the plane of the soles of the feet was vertical. Bipedal dinosaurs were suspended so that the long axis of the body was vertical.

Initially, the brass weight was submerged in water but the model was wholly above the water. The weights in the balance pan were adjusted so that the beam was balanced. Water was then added to the tank to raise the water surface by increments of 1 cm or (for *Diplodocus* only) 2 cm. As it rose, Archimedes' upthrust supported more and more of the weight of the model, and weights had to be removed from the balance pan to rebalance the beam. Thus the volume of each 1 or 2 cm segment of the model was determined. The volumes of the corresponding segments of the dinosaur were calculated.

The distribution of weight along the dinosaur was calculated from the distribution of volume, in two different ways. First, it was assumed that the dinosaur had a uniform density of 1000 kg m^{-3} . Secondly, it was assumed as before that the lungs occupied 10% of the volume of the body and that the other tissues had a uniform density of 1111 kg m^{-3} . The volume of the lungs was assigned, as nearly as could be judged, to appropriate segments of the body.

Engineering textbooks (e.g. Warnock & Benham, 1965) explain how the bending moments in a beam can be calculated from the distribution of weight

along it and the forces acting at its supports. The same method was used to calculate the bending moments in dinosaurs. Bipedes were assumed to be supported at a single point vertically under the centre of mass. Quadrupeds were assumed to be supported at one point for each pair of feet, located midway between the midpoints of the soles of the left and right feet of the model.

The weights of supporting legs do not contribute to bending moments in the back. The legs of the *Triceratops* model were therefore amputated (at the elbow and the knee) prior to the experiment illustrated in Fig. 2. The experiments on *Diplodocus* and *Iguanodon* were nevertheless performed on intact models: amputation of supporting legs would have changed the calculated bending moments very little, because the legs lie entirely in segments close to the assumed points of support.

RESULTS AND DISCUSSION

Masses

Both here and in Colbert (1962a), body masses of dinosaurs are inferred from the volumes of models. It was argued in the Materials and Methods section that the densities of dinosaurs were probably nearer 1000 kg m^{-3} than the 900 kg m^{-3} assumed by Colbert. The former value has therefore been used, and Colbert's estimates have been adjusted accordingly.

Table 1 shows that the new estimates of mass for *Tyrannosaurus* and *Iguanodon* agree well with Colbert's estimates. The new estimate for *Diplodocus* is much larger than the one derived from Colbert (1962a), but refers to a larger specimen. Colbert assumed that his model represented a dinosaur of height 3.6 m (in the sacral region) but the model used in this investigation represents a specimen of height 3.8 m. The Colbert estimate would have been 13.8 tonnes if it had been calculated for a dinosaur of this height. The new estimate for *Stegosaurus* is greater, and that for *Triceratops* is less, than the Colbert estimate for the same genus. Colbert's (1962a) paper includes photographs of his models which show that his *Stegosaurus* was more slender and his *Triceratops* more portly than the models used in this investigation.

Table 1. Heights and estimated masses of dinosaurs of linear dimensions 40 times those of the models studied in this paper. Height is measured to the most dorsal point in the mid-line of the sacral region. Colbert's (1962a) estimates of mass, re-calculated for dinosaurs of density 1000 kg m^{-3} , are shown for comparison

	Height (m)	Mass (t)	
		This investigation	Colbert (1962a)
<i>Tyrannosaurus</i>	3.6	7.4	7.7
<i>Diplodocus</i>	3.8	18.5	11.7
<i>Iguanodon</i>	2.5	5.4	5.0
<i>Stegosaurus</i>	2.1	3.1	2.0
<i>Triceratops</i>	2.6	6.1	9.4

The masses given in Table 1 may be compared with Meinertzhagen's (1938) mean masses of 1.1 t for Black rhinoceros, *Diceros bicornis*, and 2.4 t for *Hippopotamus amphibius*. Also, most mature male African elephants, *Loxodonta africana*, have masses of between 2 and 5 t (Laws & Parker, 1968).

Centres of mass

Centres of mass are shown in Fig. 1. If the dinosaurs, like the models, were made of material of uniform density, their centres of mass would be at the positions **O**. Non-uniformity of density, due to lungs occupying 10% of body volume, would shift the centres of mass to the positions **Q**. Notice that the shifts are small, showing that the results obtained in this paper would not be altered much by assuming grossly different lung volumes.

Table 2. Estimates of the fraction of body weight supported by the hind feet. Estimates are given both for animals of uniform density (with centres of mass in positions **O** of Fig. 1) and for animals with lungs (with centres of mass in positions **Q**). It is assumed in every case that the tail was held off the ground. The two neck positions of *Diplodocus* are as shown in Fig. 1D, E

	Fraction of weight on hind feet	
	Uniform density	With lungs
<i>Diplodocus</i> , neck low	0.78	0.83
<i>Diplodocus</i> , neck high	0.80	0.85
<i>Stegosaurus</i>	0.73	0.82
<i>Triceratops</i>	0.49	0.52

When an animal stands or runs at constant speed, the mean force on its feet must be vertical and must act through its centre of mass. The centre of mass of *Tyrannosaurus*, in the position of the model (Fig. 1A) lies posterior to one hind foot but anterior to the other. The animal could stand in this position without resting the tail on the ground if the feet exerted the appropriate forces. Since a vertical line through the centre of mass would pass nearer the more posterior of the two hind feet, that foot would have to support the major part of the animals weight. If the tail were shorter, as suggested by Newman (1970) the centre of mass would be more anterior and the weight would be more evenly divided between the feet. In either case, walking with the tail off the ground in (approximately) the position illustrated by Newman (1970; Fig. 1D) seems feasible.

Table 2 shows fractions of body weight supported on the hind feet. The weight of *Diplodocus* and of *Stegosaurus* was apparently supported mainly on the hind feet. In contrast, most quadrupedal mammals support only about 40% of body weight on their hind feet (Rollinson & Martin, 1981).

Bakker, (1968, 1978) suggested that some sauropods may have held their necks much more erect than in conventional restorations. Fig. 1E and Table 2 show the effects of such a posture on the position of the centre of mass and on the distribution of weight between the feet.

Table 2 refers to positions with the tail off the ground. Most restorations of long-tailed sauropods show the tail trailing on the ground, although most fossil tracks show no tail mark (Bird, 1944). It is impossible, without further assumptions, to calculate the distribution of weight between the feet when the tail is on the ground: if it were pressed down firmly enough, the weight could in principle be supported entirely by the tail and forefeet. A more plausible assumption might be that the posterior three-quarters of the length of the tail might be supported directly by the ground and that the remainder of the body might be supported entirely by the feet. The posterior three-quarters of the tail of the *Diplodocus* model was amputated and weighed, and its centre of mass was located by suspension. From the results it was calculated that a *Diplodocus* walking with its neck in the low position (Fig. 1D) and its tail trailing on the ground might have about 5% of body weight supported by the tail, 71% by the hind legs and 24% by the forelegs (the calculation took account of the lungs).

Bakker (1978) suggested that *Diplodocus* and *Stegosaurus* (and some other quadrupedal dinosaurs) reared up on their hind legs to browse on trees. To do this, they would have had to adopt a posture with the centre of mass over or behind the hind feet. Fig. 1 suggests that this would have been possible. The *Diplodocus* in Fig. 1D has its centre of mass over the left hind foot. If the right hind foot were brought forward alongside the left one, body weight would be supported entirely on the hind feet, and the forefeet could be lifted. Moving the right hind foot forward would of course move the centre of mass slightly forward but this could be compensated for if necessary by moving the right forefoot posteriorly. A similar argument applies to *Stegosaurus* (Fig. 1B). This paragraph has considered only problems of balance. Haemodynamic problems would also arise if *Diplodocus* raised its head far above its heart (Hohnke, 1973).

The centre of mass of *Iguanodon*, in the position of the model (Fig. 1C) lies posterior to the feet. The body must therefore be supported partly by the tail. Norman (1980) criticized restorations showing *Iguanodon* in this position. He suggested that *Iguanodon mantelli* walked bipedally and *I. bernissartensis* quadrupedally, both with their tails off the ground. The model appears to represent the latter species. It will balance in a quadrupedal position when tilted forward on its fore feet, and would still do so if the centre of mass were moved to the position that takes account of the lungs. However, such a posture looks unnatural. Comparison of Fig. 1C with Norman's (1980) drawing of *Iguanodon* walking quadrupedally indicates that in the latter drawing, the centre of mass would lie approximately midway between the two hind feet. The animal would have balanced on the hind feet alone and would not have needed support from the forefeet. Norman (1980) illustrates a trackway believed to show both fore and hind footprints of *Iguanodon*. However, the fore prints are small and lie remarkably far laterally, on either side of the line of hind prints. This is a striking difference from trackways of large quadrupedal mammals, which support a large fraction of their weight on their fore feet. It seems unlikely that the fore feet of *Iguanodon bernissartensis* supported more than a very small fraction of body weight, in normal walking.

Bending moments in the back

In this section, dinosaurs are considered as long beams, supported on legs. Figure 3A–C shows a flexible beam supported on knife edges in three different ways. When supported only at its ends (Fig. 3A) it sags: that is to say, it bends so that its initially straight upper surface becomes concave. When supported only at the middle (Fig. 3B) it bends so that its upper surface becomes convex. This is called hogging. Support at intermediate positions may result in hogging at the ends and sagging in the middle (Fig. 3C).

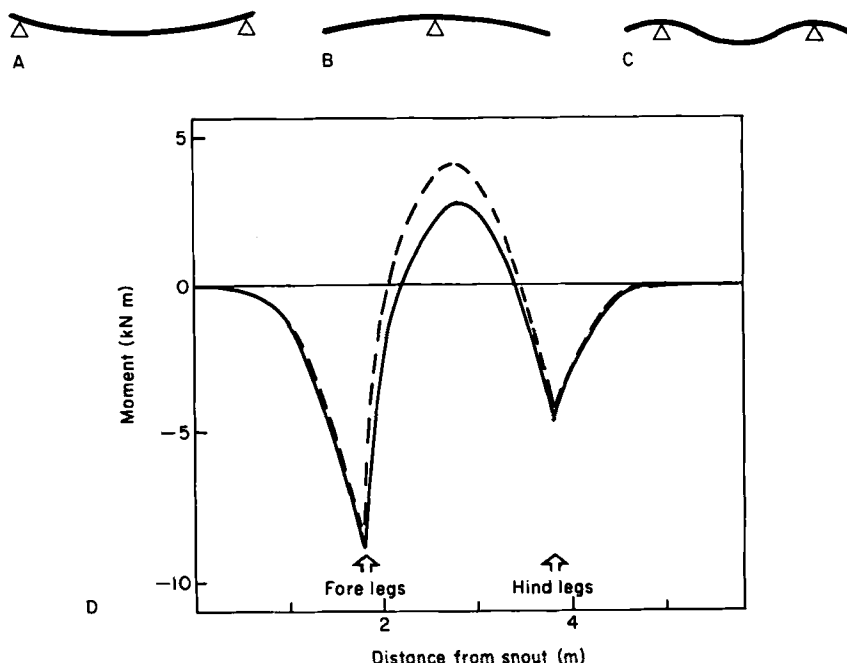


Figure 3. A, B, C, Diagrams of a beam supported in three different ways. D, A graph showing calculated bending moments in the back of *Triceratops*. Bending moment is plotted against distance from the anterior end of the body. The broken line shows estimates for dinosaurs of uniform density and the continuous line shows estimates that take account of the lungs.

Bending moments that tend to cause sagging are conventionally considered positive, and those that tend to cause hogging are considered negative. Figure 3D shows the bending moments calculated for *Triceratops*. They are distributed along its length in the same way as in the beam of Fig. 3C: there are hogging (negative) moments at the anterior and posterior ends of the body, with sagging (positive) moments between. The largest hogging moments occur over the supporting legs. The differences between the moments calculated for an animal of uniform density, and those that take account of the lungs, are quite small.

Figure 4A shows bending moments calculated for *Iguanodon* standing bipedally. They are distributed as in the beam supported centrally (Fig. 3B). There are hogging moments along the whole length of the body with an extreme value at the centre of mass which must (for balance) be over the feet. *Iguanodon*

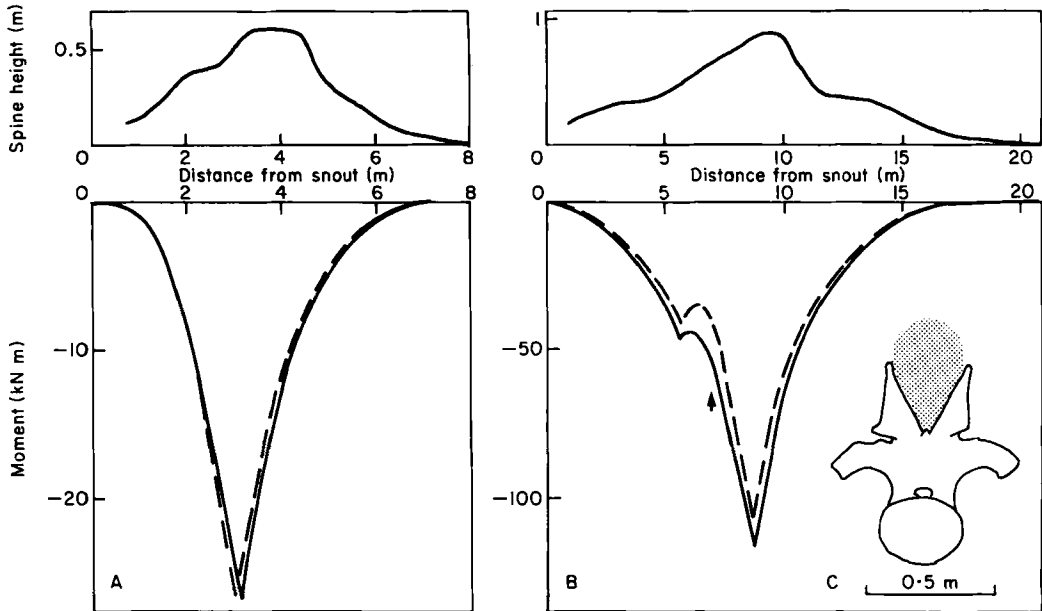


Figure 4. Graphs showing neural spine heights and estimated bending moments in A, *Iguanodon* and B, *Diplodocus*. In each case the upper graph shows neural spine height (measured from the axis of the centrum, from Norman, 1980 and Holland, 1906) and the lower one shows bending moments, both plotted against distance from the anterior end of the body. In the graphs of bending moments, a broken line shows estimates for dinosaurs of uniform density and the continuous line shows estimates that take account of the lungs. C, A posterior view of the third dorsal vertebra of *Diplodocus* (re-drawn from Hatcher, 1901). An arrow in B marks the position of this vertebra.

has a smaller estimated mass than *Triceratops* (Table 1) but its bending moments are much larger, because it is longer and has fewer supports.

Figure 4B shows bending moments for *Diplodocus*. The fore and hind legs are rather close together, and far from the ends of the body. For this reason, there are no sagging moments. Similarly, the beam shown in Fig. 3C would cease to sag in the middle if the supports were moved sufficiently close together. The hogging moments in *Diplodocus* are largest over the hind legs, which support most of the weight. The position of the forelegs is marked by a small cusp in the graph of bending moments.

Sagging moments in the trunks of dinosaurs such as *Triceratops* must have been counteracted by tension in hypaxial muscles. *Rectus abdominis* and *obliquus externus* may have been particularly important, as in mammals (Alexander & Jayes, 1981). Hogging moments in dinosaurs could in principle have been counteracted either by tension in epaxial muscles, or by elevated pressure in the body cavity due to contraction of the *obliquus internus* and *transversus* muscles (see Alexander & Jayes, 1981). However, an elevated pressure could not have been maintained while the dinosaur was breathing in, so the epaxial muscles by themselves must have been capable of counteracting the hogging moments. The forces required will be estimated, for *Iguanodon* and *Diplodocus*.

A longitudinal force F acting at a height y above the instantaneous centre of an intervertebral joint will counteract a moment $-Fy$ about that joint. It seems reasonable to assume that the instantaneous centres lay at the centroids of the

intervertebral discs, but the height y is uncertain. If the epaxial muscles were parallel-fibred, with all their fibres running longitudinally, their effective line of action would pass through the centroid of their cross-section, and y would be the height from the centroid of the intervertebral disc to the centroid of the epaxial muscle cross-section. If, as is more likely, the epaxial muscles were pennate, their effective line of action would probably lie close to the line of their principal tendons. This is because a given cross-sectional area of tendon will generally transmit much more force than an equal cross-sectional area of muscle. Alexander & Jayes (1981) argued that the line of action of the principal epaxial muscles in the lumbar region of mammals (*longissimus et iliocostalis*) lay approximately along their aponeurosis of insertion, very close to the surface of the back.

Tendons have been preserved alongside the vertebrae of some dinosaurs, but they were not necessarily the largest tendons of the back, or the tendons of the largest muscles. They may owe their preservation to their position, rather than their size. Norman (1980) described two layers of diagonally-arranged tendons in *Iguanodon*, which seem to have belonged to the multifidus and spinalis muscles (see Gasc's 1981, description of crocodilian muscles). The similarly-arranged multifidus and sacrococcygeus muscles of mammals make only a small contribution to lumbar bending moments (Alexander & Jayes, 1981). Longitudinal tendons have been found in *Triceratops*, close to the tips of the neural spines of the posterior trunk vertebrae (Hatcher, 1907). These resemble the aponeurosis of *longissimus et iliocostalis*, which is much the most important extensor of the back in mammals (Alexander & Jayes, 1981).

The greater the height y , the less the force F required to counteract any particular bending moment. It seems unlikely that the line of action of the epaxial muscles would be dorsal to the neural spines, which probably lay close under the skin. A position about level with the tips of the neural spines is suggested by the tendons preserved in *Triceratops*. It will be assumed in the following calculation that the line of action was level with the tips of the neural spines in the posterior part of the trunk. The values of y will therefore be the neural spine heights given in Fig. 4.

This figure shows extreme bending moments in the sacral region of about -25 kN m for *Iguanodon* and -120 kN m for *Diplodocus*. These may be overestimates because they assume point support: the cusps in the graphs would be blunted if supports of finite thickness were assumed, and this might be more realistic. Also, if the point of support lay below the sacrum, the bending moments at the immediately presacral and postsacral intervertebral joints might be appreciably less than the maximum. The maximum bending moments shown in Fig. 4 will nevertheless be used. The corresponding neural spine heights are about 0.6 m for *Iguanodon* and 0.9 m *Diplodocus* (Fig. 4). Thus the forces required in the epaxial muscles can be estimated as $25/0.6 = 40 \text{ kN}$ (4 t force) for *Iguanodon* and $120/0.9 = 130 \text{ kN}$ (13 t force) for *Diplodocus*.

These are tensile forces in the epaxial muscles, but equal compressive forces must have acted in the intervertebral discs. The area (projected on a transverse plane) of the posterior face of the penultimate dorsal centrum of *Iguanodon* is about 0.015 m^2 (Norman, 1980, the penultimate centrum is used because Norman illustrates it in end view). A force of 40 kN applied to this area would generate a stress of 3 MPa in the intervertebral disc. The area of the posterior

face of the last dorsal centrum of *Diplodocus* is 0.066 m^2 (Hatcher, 1901) so the calculated force of 130 kN would set up a stress of 2 MPa in the intervertebral disc.

These stresses do not seem excessive in comparison with the stresses developed in intervertebral discs of modern mammals. It can be estimated from Morris, Lucas & Bresler's (1961) analysis of weightlifting that stresses up to 6 MPa are liable to occur in human intervertebral discs.

The cervical and anterior dorsal vertebrae of *Diplodocus* have bifid neural spines (Fig. 4C). The notch between the two branches of each spine was presumably occupied by a tension member (either a ligament or a muscle) that supported the head and neck by counteracting the hogging moments due to their weight. The third dorsal vertebra will be considered because it has one of the biggest notches and because Hatcher (1901) supplied a scale drawing of its posterior face. The supposed tension member presumably at least filled the notch, but it seems quite likely that it may have projected above the neural spine as indicated by stipple in Fig. 4C. Calculations will be made for a member of the dimensions so indicated, but it should be remembered that it may have been larger or smaller. The stresses that will be calculated are subject to error for this reason, and also because of possible errors in the estimation of the hogging moment.

The centroid of the stippled cross-section is 0.66 m above the centroid of the face of the centrum. The hogging moment to be counteracted is about 50 kN m (from Fig. 4B). Hence the force to be transmitted by the tension member is $50/0.66 = 76 \text{ kN}$. The stippled area is 0.09 m^2 so the stress in a tension member of the dimensions shown would be $76/0.09 = 800 \text{ kPa}$. The compressive force on the centrum would also be 76 kN. It would set up a stress of 1.2 MPa in the intervertebral disc.

What kind of tension member could have exerted the estimated stress of 800 kPa? This stress is two orders of magnitude less than the tensile strength of collagen (Wainwright *et al.* 1976) so a collagen ligament would have had a ludicrously high factor of safety. It is the same order of magnitude as the tensile strength of elastin, which seems to be of the order of 2 MPa (inferred from data in Gosline, 1980). Thus an elastin ligament (like the *ligamentum nuchae* of many mammals) seems possible.

A passive tension member could have supported the neck in one position, but muscles would have been needed to raise and lower the neck. It seems possible that the member being discussed was itself a muscle. It cannot have been a parallel-fibred muscle, since vertebrate striated muscle cannot exert stresses greater than about 300 kPa in isometric contraction (Weis-Fogh & Alexander, 1977). It may, however, have been pennate. Tendon-like structures that may have belonged to a pennate muscle in this position were found associated with the neck vertebrae of the sauropod *Brachiosaurus* at Tendragu (personal communication from the late F. R. Parrington).

Suitably constructed pennate muscles can exert very much larger forces than parallel-fibred muscles occupying the same space, but they cannot shorten as much, because their fibres are shorter. If the structure in the notches of the neural spines was a pennate muscle, could it have shortened enough to have lifted the neck to an erect position? It seems easiest to tackle the question by considering the work required.

Suppose that a *Diplodocus* stood initially with its neck extended forward and downward, with the head resting on the ground. Suppose that it then raised its head and neck to the position shown in Fig. 1E. If a segment of the neck, of mass δm , is raised through a height h , the work done raising that particular segment is $hg\delta m$, where g is the acceleration of free fall. Different segments will be raised through different heights h , and the total work required is $\Sigma(hg\delta m)$. Estimates of segment mass had already been obtained from the experiment illustrated in Fig. 2. Thus it was possible to estimate the work required for the movement described above: the value obtained was 50 kJ. One kilogramme of vertebrate striated muscle, contracting slowly through its entire range, can perform about 0.22 kJ (Alexander & Bennet-Clark, 1977). Thus *Diplodocus* would have needed *at least* $50/0.22 = 230$ kg muscle to raise its neck.

The volume available for the supposed neck muscle has been estimated. Though Hatcher (1901) published a scale drawing of an end view of only one vertebra, he published small photographs of end views of them all. Measurements of the notches in the neural spines, taken from these photographs, show that the volume of the muscle would have been about 0.12 m^3 if its dorsal surface was everywhere level with the tips of the neural spines, or perhaps 0.25 m^3 if it projected above the neural spines as shown by stipple in Fig. 4C. The corresponding masses are about 120 or 250 kg. The muscle would at best have been barely large enough to have raised the neck to the position shown in Fig. 1E. It is of course possible that a muscle through the notches of the neural spines was supplemented by other muscles lateral to the neural spines. Alternatively, the structure in the notches may have been a ligament (probably an elastin ligament) and neck lifting may have depended entirely on muscles lateral to the neural spines. In either case, the animal may or may not have been able to raise its neck to the position of Fig. 1E.

Gaits

The speculations that follow are based partly on fossil footprints of dinosaurs, and partly on analogy with living animals. Since no living terrestrial animals are as large as the largest dinosaurs, the arguments by analogy depend on extrapolation to larger sizes. A plausible scaling rule was suggested by Alexander (1976). He argued that animals of different sizes should tend to move in dynamically similar fashion, whenever their Froude numbers u^2/gh were equal. Here u is the speed of walking or running, g is the acceleration of free fall and h is the height of the hip joint from the ground (a measure of leg length). Dynamic similarity implies that the movements of one animal could be made identical to those of the other, by uniform changes of the scales of length and time. Alexander & Jayes (1983) showed that the gaits of quadrupedal mammals, in the size range from cats to rhinoceros, depend on size and speed very much as predicted by the dynamic similarity hypothesis. Alexander (1976) had already shown that the stride lengths of ostriches (*Struthio*) and men were approximately the same as would be expected for a quadrupedal mammal of equal leg length, walking or running at the same speed.

Fossil footprints of bipedal and quadrupedal dinosaurs (for example, the footprints described by Bird, 1944) show that they walked or ran like modern birds and mammals, with their feet close to the median plane.

Alexander (1976) estimated speeds of dinosaurs from the stride lengths shown by their footprints. His estimates are about 1 m s^{-1} for sauropods, and $1\text{--}4 \text{ m s}^{-1}$ for bipedal dinosaurs of various sizes. Only two trackways of rather small dinosaurs had stride lengths long enough (compared to leg length) to suggest running. The other trackways apparently record walking. More recently, Farlow (1981) has described trackways which seem to have been made by moderate-sized bipedal dinosaurs running at up to 12 m s^{-1} .

Tracks of bipedal dinosaurs have the left and right footprints about equally spaced, showing that the gait was a walk or run and not a kangaroo-like hop. Tracks of sauropods show the left and right fore footprints about equally spaced, and similarly for the hind footprints (Fig. 5A). This shows that the gait was a symmetrical one, i.e. that the two feet of each pair moved half a cycle out of phase with each other. (Asymmetrical gaits would not in any case be expected at the low Froude numbers implied by the short strides. See Alexander & Jayes, 1983.)

The left and right scapulae of quadrupedal mammals are independently movable on the rib cage, and they rotate on the rib cage in walking and running (English, 1978). The effective length of the fore limb extends from the instantaneous centre of rotation of the scapula to the ground, and is generally approximately equal to the length of the hind limb. In contrast, quadrupedal or possibly quadrupedal dinosaurs seem to have had a sternum connecting the two halves of the pectoral girdle. In some of them it was partly ossified (for example, *Iguanodon*, Norman, 1980) and in others thickened edges on the coracoids suggests a cartilaginous sternum (for example, *Triceratops*, Hatcher, 1907). The pectoral girdle as a whole may have moved relative to the rib cage, but the scapulae cannot have moved independently and cannot have served as extensions of the forelimbs, at least in symmetrical gaits. The effective length of

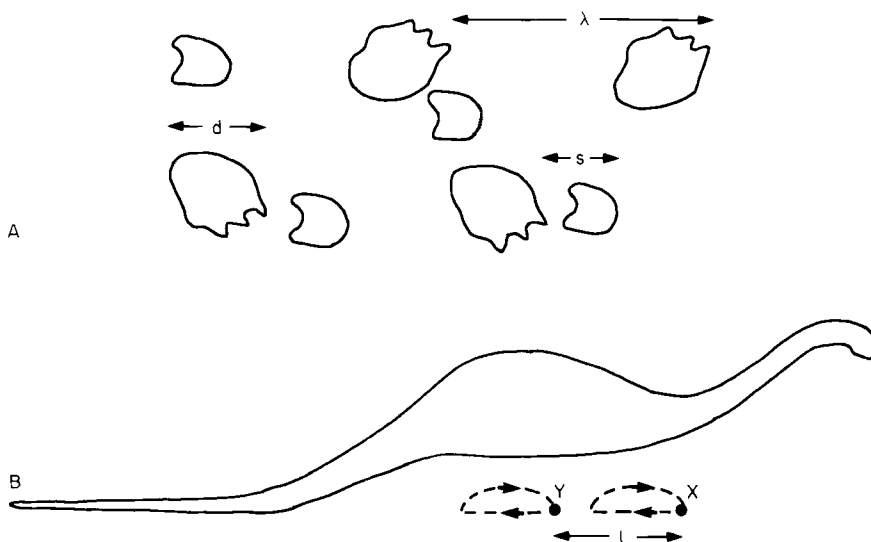


Figure 5. Diagrams showing dimensions used in the discussion of sauropod gaits. A, A plan of sauropod footprints, based on Colbert (1962b). B, A diagram showing movements of a sauropod's feet, relative to the trunk. Further explanation is given in the text.

the forelimb extended from the glenohumeral joint to the ground, and was much less than the length of the hind limb. Data compiled by Galton (1970) show that it was typically about 0.7 of the length of the hind limb.

Stride length is the distance travelled in a complete cycle of leg movements and step length is the distance travelled while a particular foot is on the ground. The fore and hind legs of dinosaurs must have taken strides of equal length but the short forelegs may have taken shorter steps than the longer hind legs. This possibility was discussed by Thulborn (1982).

Some lizards have forelegs much shorter than their hind legs. They run in typical reptilian fashion, placing their feet far lateral to the median plane, so detailed comparison with dinosaurs is inappropriate. It does, however, seem worth noting that, when they run quadrupedally, the forelegs generally take shorter steps than the hind legs (Rewcastle, 1981).

The footfall patterns of animals can be described by specifying the duty factor and relative phase of each foot. Duty factor is the fraction of the duration of the stride for which the foot remains on the ground, and is approximately (step length)/(stride length). Relative phase is the time at which the foot is set down, expressed as a fraction of the duration of the stride following the setting down of an arbitrarily-chosen reference foot. It has already been shown that surviving sauropod trackways indicate symmetrical gaits, that is gaits with relative phases that can be written thus:

$$\begin{array}{ll} \text{left fore: } 0 & \text{right fore: } 0.5 \\ \text{left hind: } \delta & \text{right hind: } \delta + 0.5, \end{array}$$

where δ is some fraction between 0 and 1. An attempt will be made to determine δ from the trackways.

Figure 5A shows part of a typical sauropod trackway. The distance λ is the stride length. The shorter distance s will be used to estimate the relative phase. It is measured between the anterior edges of a fore and a hind footprint.

Figure 5B represents the trunk of a sauropod dinosaur. Loops below the trunk represent the paths, relative to the trunk, of points on the anterior edges of the soles of the fore and hind feet. X and Y are the positions of the points, relative to the trunk, at the instants when the feet in question are set down on the ground. If the fore and hind feet of the same side of the body were set down simultaneously (i.e. if $\delta = 0$) the distance s in Fig. 5A would be equal to the distance l in Fig. 5B. If they are not set down simultaneously, the trunk advances a distance $\lambda\delta$ between the setting down of the forefoot and the next setting down of the hind foot. (It is assumed that speed remains fairly constant throughout the stride, so that the trunk advances $\lambda\delta$ in a fraction δ of the duration of the stride.) Consequently:

$$\begin{aligned} s &= l - \lambda\delta \\ \delta &= (l - s)/\lambda \end{aligned} \quad (1)$$

It will be convenient to express distances as multiples of hind footprint length, d . A typical large sauropod trackway (trail 8 of Bird, 1944) has $\lambda = 3.3 d$, $s = 0.6 d$. The trackway illustrated by Colbert (1962b) has $\lambda = 2.7 d$, $s = 0.9 d$. It is more difficult to estimate l/d . The model of *Diplodocus* (Fig. 1D) suggests $l = 3.5 d$. The drawing of *Apatosaurus* in Gilmore (1936) suggests $l = 3.0 d$. (This estimate was made after redrawing one foreleg in the position it would be likely

to occupy at the beginning of a step.) The drawing of *Brachiosaurus* in Charig (1979) suggests $l = 3.7 d$. Bakker's (1968) exceptionally small-footed restoration of *Barosaurus* suggests $l = 4.4 d$. It is unfortunate that the relative phase δ calculated from equation (1) depends critically on the value of l . For example the dimensions of Bird's trail 8 with $l = 3.0 d$ give $\delta = 0.73$ (representing a lateral sequence single-foot walk in the terminology of Hildebrand, 1976) but with $l = 3.7 d$ they give $\delta = 0.94$ (representing a walking pace). The lateral sequence single-foot walk is very commonly used by large mammals including elephants and rhinoceroses, but the walking pace seems to be used only by long-legged mammals such as the Gerenuk, *Litocranius*, and the Camelidae (Hildebrand, 1976).

Dimensions of bones

The dimensions of dinosaur leg bones will be compared to predictions for mammals of equal body mass, obtained from the allometric equations of Alexander, Jayes *et al.* (1979). These authors found that the lengths of major leg bones of mammals in general tended to be proportional to (body mass)^{0.35} but that leg bone lengths of Bovidae, considered separately, tended to be proportional to (body mass)^{0.26}. Economos (1983) suggested that the apparent peculiarity of Bovidae may be due to their large size. He showed that allometric equations relating body length to body mass for large (> 20 kg) mammals had smaller exponents than for small (< 20 kg) mammals. If his suggestion is correct, it may be more appropriate to compare dinosaur bone lengths to predictions for Bovidae of equal mass, than to predictions based on small as well as large mammals.

Figure 6A and C show that the femora and humeri of most of the dinosaurs were shorter than predicted for mammals in general of their estimated body mass, but longer than predicted for Bovidae. The femur of *Stegosaurus* seems rather long for the estimated body mass, but would lie much closer to the mammal line if the larger estimate of mass given in Table 1, were used. *Tyrannosaurus* and *Antrodemus* had remarkably short humeri. Figure 6B shows that the tibiae of the dinosaurs were shorter than predicted for mammals in general, and close to the lengths predicted for Bovidae. The ulnae of most of the dinosaurs were 50–70% of the lengths predicted for bovids by the equation of Alexander *et al.* (1979). Note that this comparison is potentially misleading, because the olecranon process is large in bovids but poorly developed in most dinosaurs.

Figure 6D shows that the femora of some dinosaurs have diameters close to those predicted for mammals of their body mass. The femora of *Tyrannosaurus* and *Apatosaurus* are a little stouter than predicted, but they carried a larger proportion of body weight than in mammals. *Tyrannosaurus* was bipedal and *Apatosaurus* (like *Diplodocus*, Table 2) probably carried most of its weight on its hind legs. The femur of *Diplodocus*, however, was rather slender. The femur of the moa *Pachyornis* is much more markedly stouter than predicted for mammals, than the femora of any of the dinosaurs.

The conclusions that have been drawn from Fig. 6 would not be altered materially if the new estimates of body mass, given in Table 1, were used instead of Colbert's (1962a) estimates.

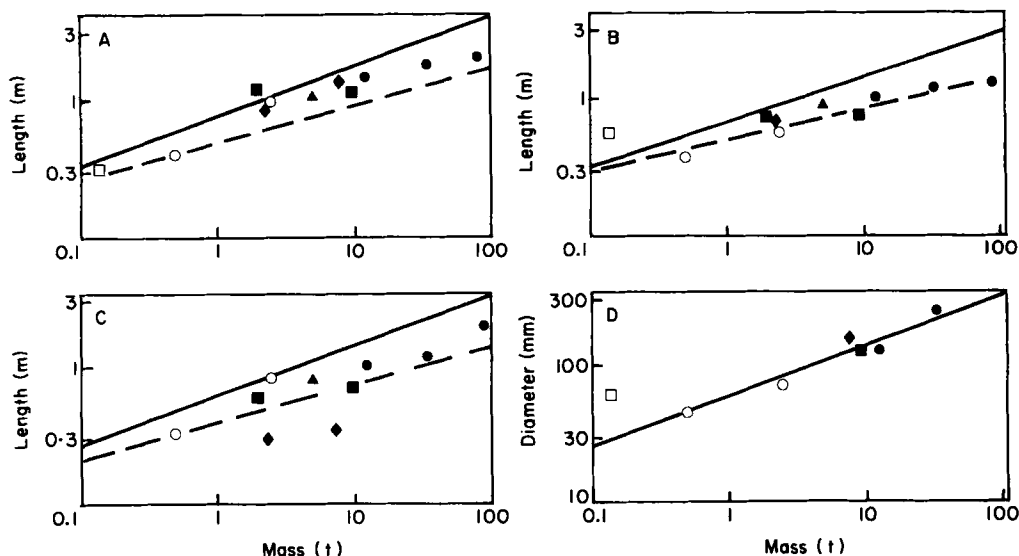


Figure 6. Graphs, on logarithmic coordinates, of limb bone dimensions against body mass. A, Femur length; B, tibia length; C, humerus length and D, the sagittal diameter of the femur midway between its ends. Continuous lines represent equations for mammals in general, and broken lines represent equations for Bovidae, from Alexander, Jayes, Maloiy *et al.* (1979). The points represent ●, sauropods (*Brachiosaurus*, 87 t; *Apatosaurus*, 34 t and *Diplodocus*, 12 t); ■, other quadrupedal dinosaurs (*Triceratops*, 9.4 t and *Stegosaurus*, 2.0 t); ◆, theropods (*Tyrannosaurus*, 7.7 t and *Antrodemus*, 2.3 t); ▲, *Iguanodon*, 5.0 t; ○, large mammals (*Loxodonta*, 2.5 t and *Syncerus*, 0.50 t. Data from Alexander *et al.*, 1979); □, a moa (*Pachyornis*, 0.14 t. Data from Alexander, 1983b). Sources for dinosaur bone dimensions are given in the Materials and methods section. Dinosaur body masses are from Colbert (1962a), recalculated for a density of 1000 kg m^{-3} .

Strengths of bones

Surviving footprints show that large dinosaurs could walk but give little evidence of running (see the section on Gaits). In mammals, and presumably also in dinosaurs, running imposes larger stresses on the leg bones than walking does (Rubin & Lanyon, 1982). The dimensions of dinosaur bones will be used now to assess their strength and particularly to consider whether they were strong enough to permit running. Biewener (1982) showed that bone from mammals and birds of a wide range of sizes was rather uniform in strength. It will be assumed that dinosaur bone had the same strength.

Leg bones, like other long slender structures, are particularly vulnerable to forces that impose bending moments on them. Stresses due to bending moments generally predominate, in the patterns of stress that act in leg bones in strenuous activities (Rubin & Lanyon, 1982; Alexander, 1983b). The most important components of the bending moments, in leg bones of mammals, birds and (presumably) dinosaurs, are components about transverse axes. This is because the long axes of the bones, and the principal forces on the bones, tend to lie more or less in parasagittal planes. The abilities of bones to withstand bending moments acting about transverse axes will be assessed.

Suppose that a force F acts on the distal end of a bone, at right angles to its long axis. The force and the long axis of the bone are assumed to lie in the same parasagittal plane. The force exerts a bending moment Fx on a section distant x

from the end of the bone, setting up stresses ranging from $-Fx/Z_1$ (a compressive stress) at one side of the section to $+Fx/Z_2$ (a tensile stress) at the other. Z_1 and Z_2 are the two section moduli for bending in a parasagittal plane (Warnock & Benham, 1965). They would be identical for a section that was symmetrical about its neutral axis, and are sufficiently nearly identical for the sections to be considered for mean values (Z) to be used.

Consider two bipeds that are geometrically similar to each other in respect of bone lengths and positions of muscle attachment (but do not necessarily have geometrically similar bone cross-sections). Let them move in dynamically similar fashion. The components of force F tending to bend their bones will be proportional to their body weights mg , and the stresses due to bending moments in corresponding sections of their bones will be proportional to mgx/Z . Thus Z/mgx is a convenient measure of the ability of the leg bones of bipeds to withstand bending moments (Alexander, 1983b). A more general measure, applicable also to quadrupeds, is $Z/amgx$, where a is the fraction of body weight supported by the pair of legs being considered. This quantity will be calculated for various bones of dinosaurs and other animals.

Alexander (1983b) considered sections half way along bones, so that x was half the length of each bone. Some dinosaur leg bones have large processes for muscle attachment, about half way along their shafts. If the half-way section had been used in these cases, the value of $Z/amgx$ would have given an exaggerated impression of the strength of the bone as a whole. In such cases, a section of the shaft distal to the process has been used.

Section moduli were calculated from published drawings of sections through dinosaur bones, by the standard method of numerical integration (Warnock & Benham, 1965). The positions at which published sections were taken are not generally specified precisely, but ambiguities were resolved by referring to scale drawings of anterior or lateral views of the bones. The drawings of sections of *Triceratops* bones (Hatcher, 1907) do not show marrow cavities, and section moduli have been calculated from them as for solid bones. Values for hollow bones would be lower, but not much lower unless the marrow cavity occupied a large fraction of the diameter. The section moduli of *Apatosaurus* bones have been calculated for solid elliptical sections of the same sagittal and transverse diameters, because no drawings of sections were available. The femur has a slender marrow cavity and the other leg bones have only a cancellous centre, with no marrow cavity (Matthew, 1910), so little error has been introduced by calculating as for solid sections.

The estimates of $Z/amgx$ are shown in Table 3, together with values for some large modern animals (elephant, *Loxodonta*; buffalo, *Syncerus* and ostrich, *Struthio*). Remember that larger values of $Z/amgx$ indicate ability to withstand forces that are larger fractions of body weight, in any given posture. Large values of $Z/amgx$ suggest agility and the ability to use fast gaits involving low duty factors. Comparisons of dinosaurs with buffalo and ostrich have only limited value because of marked differences in the relative lengths of leg segments. Comparisons between the hind legs of sauropods, *Triceratops* and elephants seem likely to be more instructive, because these legs are similarly proportioned: all have relatively long femurs and short metatarsals. It seems likely that a sauropod or a *Triceratops* would have moved its hind legs very nearly in dynamically similar fashion to those of an elephant travelling with the

same Froude number. The stresses in homologous bones of the dinosaur and the elephant would then be inversely proportional to $\mathcal{Z}/amgx$.

Different bones, within the same animal, are held at different angles to the forces on the feet, and should not be expected to have identical values of $\mathcal{Z}/amgx$. The values for different bones of *Loxodonta*, in Table 3, range from 7 to 11 GPa^{-1} . The values for *Apatosaurus* span a wider but not very different range, 6 to 14 GPa^{-1} . This suggests that *Apatosaurus* may have been about as agile as *Loxodonta*; the fastest gait of *Apatosaurus* may have been similar to the fastest run of *Loxodonta*. Two values of $\mathcal{Z}/amgx$ are given for each bone of *Diplodocus* and

Table 3. Estimates of a measure of the bending strength of bones ($\mathcal{Z}/amgx$) for dinosaurs and some modern animals. Estimated body mass (m) and the fraction of body weight assumed to be carried by the hind legs (a_{hind} , Table 2) are also shown. Values given for dinosaurs are based on Colbert's (1962a) estimates of body mass, re-calculated for a density of 1000 kg m^{-3} . Values based on the new estimates (Table 1) are shown in parentheses. Data for elephant (*Loxodonta*), buffalo (*Syncerus*) and ostrich (*Struthio*) are from Alexander, Maloiy, Hunter *et al.* (1979) and Alexander, Maloiy, Njau *et al.* (1979), except that a_{hind} for *Loxodonta* is Thompson's (1917) value for *Elephas*

	$m(\text{kg})$	a_{hind}	$\mathcal{Z}/amgx \text{ (GPa}^{-1}\text{) for}$		
			Femur	Tibia	Humerus
<i>Apatosaurus</i>	33 500	0.70*	9	6	14
<i>Diplodocus</i>	11 700	0.83	5		
	(18 500)		(3)		
<i>Tyrannosaurus</i>	7 700	1.00	9		
	(7 400)		(10)		
<i>Triceratops</i>	9 400	0.52	13		14
	(6 100)		(19)		(22)
<i>Loxodonta</i>	2 500	0.42	7	9	11
<i>Syncerus</i>	500	0.40	22	27	21
<i>Struthio</i>	42	1.00	44	18	

* An estimate obtained from a crude model.

Triceratops, because two estimates of body mass are available for each, but both sets of values give the impression that *Diplodocus* was less agile than *Loxodonta* and that *Triceratops* was more agile. The higher estimates for *Triceratops* are close to the values for *Syncerus*.

The fastest gait of *Loxodonta* seems to be a rather slow run with duty factors of approximately 0.49, but *Syncerus* can gallop with duty factors as low as 0.27 (Alexander, Maloiy, Hunter *et al.*, 1979). The White rhinoceros, *Diceros simus*, is intermediate in mass between *Loxodonta* and *Syncerus* and is also capable of galloping, with minimum duty factors of about 0.4 (data of Alexander & Jayes, 1983). Thus the data in Table 3 could be interpreted very tentatively as suggesting that *Diplodocus* may have been capable only of walking; that *Apatosaurus* may have been capable of a slow elephant-like run and that *Triceratops* may conceivably have been capable of galloping like a rhinoceros

(though the gallop is commonly used only by mammals, it is occasionally used by crocodiles; Zug, 1974). These suggestions depend on the doubtful assumption that the factors of safety (the ratios of strength to maximum expected load) were about the same for dinosaur leg bones as for leg bones of modern mammals. Alexander (1981) argued that different ways of life could give rise to different optimum safety factors.

The estimate of $Z/amgx$ for the femur of *Tyrannosaurus* is close to the values for *Loxodonta* bones and might be interpreted as suggesting that *Tyrannosaurus* was capable only of slow running. However, *Tyrannosaurus* is so far from being geometrically similar to *Loxodonta* (or any other modern animal) that such a conclusion would be very tentative indeed. Further, the question whether optimum safety factors were the same as for modern mammals arises here, as in the discussion of quadrupedal dinosaurs.

Pressure on the ground

Geometrically similar animals of different sizes, made of the same materials, would have weights proportional to the cubes of their linear dimensions, but the areas of the soles of their feet would be proportional only to the squares of their linear dimensions. The larger animals would therefore exert larger pressures on the ground than the smaller ones and would be in more danger of getting bogged down in soft ground.

That argument was too simple, for two reasons. First, soft mud may be underlain by a hard pan. A small animal may get bogged down but a larger one, with longer legs, may be able to walk satisfactorily, with its feet sinking to the hard pan. Secondly, the maximum load that soft ground can support is not simply proportional to the area of the foot. A circular foot of radius r (area πr^2) will support a maximum load W where

$$W = \pi r^2 (A + Br) \quad (2)$$

(Wong, 1978). A and B are parameters describing the properties of the particular soil. For a soil that depended entirely on cohesion to support loads, B would be zero and W would be proportional to r^2 . Wet clays are more or less like this. For a soil that depended entirely on friction between the grains, A would be zero and W would be proportional to r^3 . Dry sand is more or less like this. Therefore, if geometrically similar animals of different sizes walk on wet clay, the argument of the first paragraph holds and the larger animals will be more liable to get bogged down. If, however, they walk on dry sand, both body weight and W are proportional to the cubes of their linear dimensions: geometrically similar animals of different sizes will be equally well supported by dry sand.

The pressures exerted by the feet of some dinosaurs will be estimated. They will be compared to the pressures exerted by the feet of living animals and by the tracks of cross-country vehicles. Estimated body weight will be divided by the total of the area of all four feet (for quadrupeds) or the two hind feet (for bipeds) to obtain the mean pressure exerted on the ground in standing.

The tracks illustrated by Colbert (1962b) were apparently made by a Lower Cretaceous sauropod. They seem to be about the right size for *Apatosaurus* which is, however, known only from the Upper Jurassic. The total sole area (four feet) is 1.2 m^2 . If the animal that made them had a mass of 34 t (Colbert's 1962a,

estimate for *Apotosaurus*, adjusted to a density of 1000 kg m^{-3}) the standing pressure was 280 kPa.

It appears from the size of its foot skeleton that *Tyrannosaurus* must have made footprints 0.85 m long. No known footprints of bipedal dinosaurs are so large, but some smaller footprints have been attributed to smaller theropods (Bird, 1944). It can be estimated from them that the total sole area (two feet) of *Tyrannosaurus* was 0.6 m^2 . If the mass of the body was 8 t (Table 1) the standing pressure was about 130 kPa.

Charig (1979) illustrated a clear hind footprint attributed to a small *Iguanodon*. A pair of footprints of the same shape but of appropriate size for *I. bernissartensis* would have a combined area of about 0.4 m^2 . If the mass of the dinosaur was 5 t (Table 1) the standing pressure was about 120 kPa.

Laws & Parker (1968) give the masses and shoulder heights of elephants (*Loxodonta*) of stated age and sex. The ratios of foot diameters to shoulder height have been measured from photographs. It seems that a 4.5 t elephant would have a total sole area (four feet) of about 0.6 m^2 , giving a standing pressure of about 80 kPa.

Domestic cattle typically have masses of about 0.6 t and total footprint areas (four feet) of about 0.04 m^2 (D. Scholefield, Grassland Research Institute, pers. comm.). Thus their standing pressures are about 150 kPa. Ssemakula (1983) gives a smaller value, 100 kPa.

Leakey & Hay (1979) give dimensions of fossil footprints attributed to rhinoceros, *Diceros bicornis*, and giraffe, *Giraffa*, of similar size to the modern species. If the animals which made these prints had masses of 1.1 t in both cases (Meinertzhagen, 1938; Sachs, 1967) the standing pressures were 60 and 110 kPa respectively.

These data seem to show that large bipedal dinosaurs exerted about the same pressure on the ground as cattle, but that sauropods exerted much more pressure than cattle. The bipeds could have walked on soft ground as easily as cattle but the sauropods would have been rather likely to have got bogged down in predominantly cohesive soils such as wet clays. On soils with significant frictional properties (appreciable values of B in equation (2)) sauropods might have had an advantage over cattle, because such soils can withstand larger pressures from large feet than from small ones.

The pressures that have been calculated refer to standing and should be doubled to obtain estimates of peak pressures during walking. This is because the peak forces exerted by individual feet of walking mammals are typically about double the forces required for standing (Jayes & Alexander, 1978). Thus walking sauropods would probably exert peak pressures of 500 kPa. These are nominal ground pressures: the maximum pressure at the centre of the sole would presumably be larger (Wong, 1978).

Rowland (1975) recommended that maximum pressures under the tracks of off-road vehicles should not exceed 300 kPa (or 450 kPa for occasional off-road use), if they are to be used on wet, fine-grained soils. He noted that a selection of post-1945 tanks with masses of 37–51 t exerted maximum pressures of 200–270 kPa. Thus the feet of sauropods seem rather heavily loaded, by comparison with the tracks of tanks. There is no need, in this comparison, to distinguish between cohesive and frictional soils because the diameters of sauropod feet are comparable to the widths of tank tracks.

SUMMARY

(1) Dimensions of dinosaur bones and of models of dinosaurs have been used as the basis for calculations designed to throw light on the posture and gait of dinosaurs.

(2) New estimates of body weight, obtained from the models, are compared with previous estimates.

(3) *Diplodocus* and *Stegosaurus* probably supported about 80% of their weight on their hind feet and about 20% on their fore feet. It seems likely that they were capable of rearing up on their hind legs.

(4) The trunk of *Triceratops* probably tended to sag under gravity, requiring tension in hypaxial muscles to prevent this. *Diplodocus* had no tendency to sag because of the weight of the neck and tail. Like bipedal dinosaurs, it probably required tension only in epaxial muscles to maintain its standing posture. The stresses in the intervertebral discs, due to epaxial muscle tension, were probably no more than 2 MPa. (Stresses up to 6 MPa act in intervertebral discs of men lifting heavy weights).

(5) The long neck of *Diplodocus* was presumably supported by tension in a structure running through the forked neural spines of the cervical and dorsal vertebrae. It seems likely that this structure was either an elastin ligament or a pennate muscle. There is barely enough space for a muscle large enough to have lifted the neck to a vertical position.

(6) An attempt to use fossil tracks, to determine the relative phases of the feet of sauropods, gave ambiguous results.

(7) The femora of large dinosaurs, and also (in the case of quadrupeds) their humeri, were generally shorter than predicted for their body weight by extrapolation of allometric equations for mammals in general, but longer than predicted from equations for bovids. The tibiae of dinosaurs in general had about the lengths predicted for bovids.

(8) The principal leg bones of *Apatosaurus* seem to have been strong enough to permit the degree of agility shown by modern elephants. Those of *Diplodocus* may have been too weak for running, but those of *Triceratops* seem to have been strong enough for greater agility than shown by elephants.

(9) The pressures that acted on the soles of the feet of large bipedal dinosaurs were larger than for elephants, but about the same as for cattle. Such dinosaurs were probably no more likely than cattle to get bogged down in soft ground. Higher pressures acted on the feet of sauropods.

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