DINOSAUR MODELS: THE GOOD, THE BAD, AND USING THEM TO ESTIMATE THE MASS OF DINOSAURS

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ABSTRACT—The methods for accurately restoring model dinosaurs in all dimensions are outlined. It is shown that most errors in the volume of dinosaur models are not due to differing interpretations of muscle bulk and fat deposits, but to gross errors in proportions, especially of the trunk. Comparison of commercial dinosaur models with technical, multiview skeletal restorations show that with few exceptions the former are marred by serious errors in proportions and volumes. It is concluded that the models are toy caricatures, should not be used in scientific studies, and that they often mislead the public as to the body forms of dinosaurs. A series of technical skeletal restorations and mass estimates of herbivorous dinosaurs is presented. The status of the largest predatory and herbivorous dinosaurs is assessed, and it is concluded that the former approached 10 tonnes in mass, with the latter exceeding 100 tonnes and approaching the mass of blue whales.

INTRODUCTION

OFTEN big and always spectacular, dinosaurs have strong visual appeal, so people wish to see more than just defleshed skeletons. Dinosaur images are therefore common in the non-scientific realm, much more so than most other fossils (such as trilobites or titanotheres). As a result many people learn most of what they know about the extinct archosaurs via images. Multitudes who never read a dinosaur book have seen *King Kong* and/or *Jurassic Park*.

There are two classes of dinosaur representations. One is a deliberate caricature in the manner that a stuffed teddy bear is an altered image of a bear. The other is representations intended to be realistic to a greater or lesser extent. The latter can be problematic, because they may not be as accurate as they are purported to be. In recent years, attempts to improve the accuracy of commercial models have focused upon obvious errors such as tail and limb posture. This study will concentrate on more subtle, but equally important, sources of error in dinosaur models.

In the post war era the new plastics allowed manufacturers to mass produce lines of commercial dinosaur figures, which have become more numerous as the popularity of dinosaurs has increased in recent years. These products are often promoted as being anatomically accurate and educational, in fact some lines are produced under the auspices of natural history museums and are frequently sold in museum shops. The need for the models to be accurate does not solely concern their public educational value, because commercial and artistic models have been used by some paleontologists in scientific studies.

In particular, the great size of some dinosaurs has long inspired attempts to estimate their masses. Aside from the it-looks-about-so-big method, two primary procedures are used to restore the mass of extinct forms: mass/skeletal element relationships, and volumetric models. Colbert (1962) made the pioneering attempt to mass a number of dinosaur taxa with models; Alexander (1989), Paul (1988a,b) and others have continued this work. The results, however, appear disappointing because mass estimates for the same specimen often vary widely (example: 32 to 78 tonnes for the Berlin *Brachiosaurus* skeleton). This study will show that the problem with volumetric modeling is not the basic concept, but the use of demonstrably inaccurate models. It will test the accuracy of volumetric modeling versus dimension based estimates, and detail the protocol needed to do the former accurately.

PROCEDURES AND PROBLEMS

Scaling Up and Scaling Down

Regardless of the method for employed estimating mass, it is usually necessary to do so using models and/or animals of different size. This is scaling. Doubling the dimensions of an object does not double its volume. In isometric objects that have identical proportions regardless of size, volume and mass are cubed because they increase eightfold with every doubling in dimensions. This rule applies when converting the mass of a model to that of the original animal. Assume that a 100 gram model's mass is too high by 3%. If the animal is ten times as long, and the estimated body mass is 100 kilograms, then it is still only 3% too high. Farlow's (1980) concern that scaling up the volume of a small model may result in a substantial error at full scale is therefore misplaced; any error is the same percentage at any scale, and accurate models can be constructed at any scale.

Allometric objects change their proportions in a fairly consistent manner with size. This is generally true of land animals, which tend to become stockier as they become bigger (there are important exceptions to this rule). No simple relationship describes animal allometry. Different body parts scale to mass in different ways, and different animal groups scale the same body part in different ways. The manner in which a given group of animals scales body mass to a given bone dimension can be determined by measuring a number of individuals from different species—the larger the number examined the better—and deriving a formula that describes the relationship with whatever plus or minus error is observed.

Bone Dimensions Versus Models

A common way to estimate mass is to measure body mass/bone dimension relationships (M/BDR) in living forms and extrapolate them to an extinct form (Anderson et al., 1985; Damuth & MacFadden, 1990; Gingerich, 1990; Campbell & Marcus, 1992; Fortelius & Kappelman 1993). Example: the circumference of the femur and tibia is measured in a fossil and a living deer, the latter is also weighed, and the mass of the former is then calculated. A better method is to derive an allometric scaling formula from a large number of living deer and apply it to the fossil form. Even closely related forms, however, can have significantly different M/BDR values. Haynes (1991) noted that mastodonts have much thicker limb bones than elephants of equal size, to the point that the mass of the former will be overestimated by 100% if they are assumed to have the same M/BDR as elephants.

M/BDR vary even more in tetrapods as a whole (Anderson et al., 1985; Damuth & MacFadden, 1990). In principle, circumference of the humerus and/or femur is a critical strength factor tightly linked to body mass. In reality, limb bone strength is not constant in land animals, but varies greatly in forms with different limb designs and locomotory abilities. So much so, that body mass varies by a factor of two relative to any given value
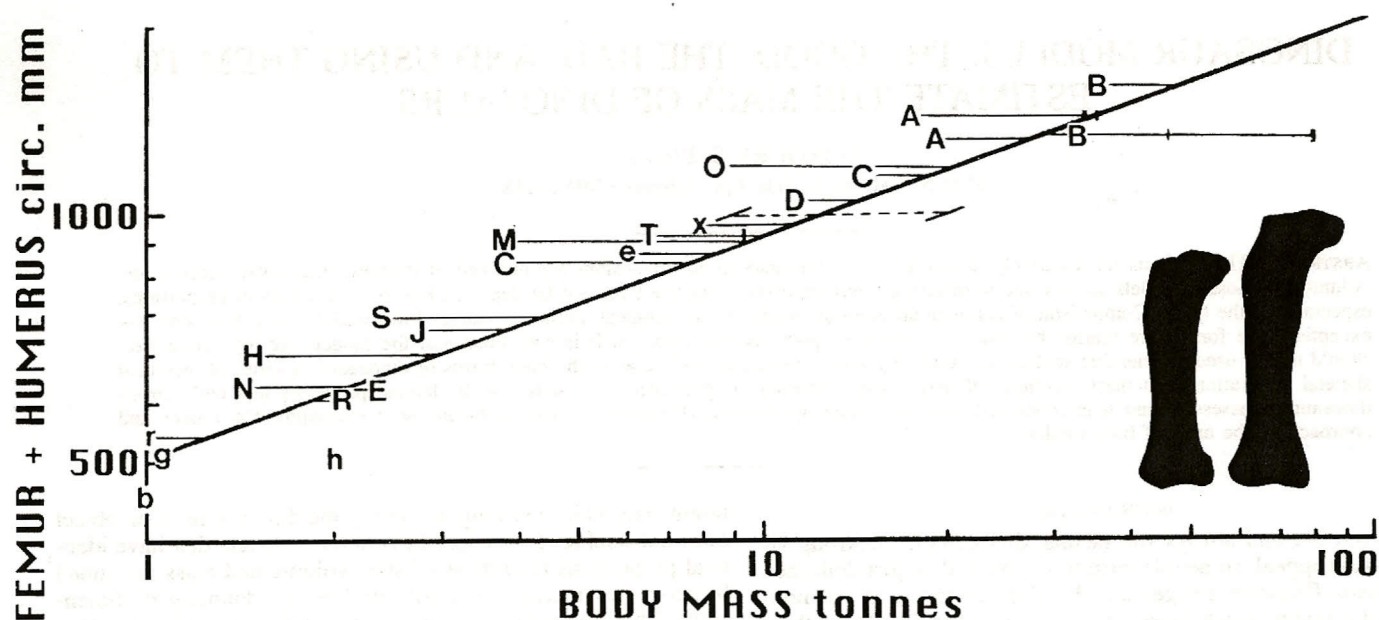
FIGURE *1*—This log-log plot shows how actual or modeled body mass is correlated to the combined circumference of the humerus plus femur in large quadrupedal mammals (small case) and dinosaurs (capitals). The sloping line is the correlation calculated by Anderson et al. (1985); horizontal lines connect the actual or modeled mass of each specimen to the predicted value (example: the mass predicted for an elephant with a combined circumference of 872 mm is about 8 tonnes, but its actual mass is about 6 tonnes). Note that only one mammal actually falls on the line, other mammals are either much lighter or heavier than predicted; the dashed horizontal line shows the two fold variation in body mass that can occur at any given circumference of limb bones in primarily terrestrial mammals (based on data in Anderson et al., 1985). Also indicated are the masses modeled by Colbert (1962, thick short vertical line) and Alexander (1989, thinner short vertical line). Sauropods—A, *Apatosaurus*; B, *Brachiosaurus* African and American (upper); C, *Camarasaurus* adult and juvenile; D, *Diplodocus*; M, *Amargasaurus*; O, *Opisthocoelicaudia*: stegosaurs—J, *Tuojiangosaurus*; S, *Stegosaurus*: ankylosaurs—E, *Euoplocephalus*; R, *Sauropelta*: ceratopsids—H, *Chasmosaurus*; N, *Centrosaurus*; T, *Triceratops*: mammals—b, bison; e, African elephant (Jumbo); g, giraffe; h, hippo; r, Indian rhino subadult; x, mammoth and indricothere. Inset shows that a femur of *Apatosaurus* (left) is thicker than that of *Brachiosaurus* even though the latter is much larger, drawn to same scale.

of upper limb bone circumference among primarily terrestrial quadrupedal mammals (Figure 1). Therefore, Anderson et al. (1985) should have included large plus or minus margins in their mass estimates of extinct forms.

For example, Anderson et al.'s 29 tonne mass estimate for *Brachiosaurus* is really in the middle of a range that extends from 20 to 40 tonnes, assuming its M/BDR are the same as those observed in quadrupedal mammals. Actually, the problem of estimating the mass of extinct exotic forms like dinosaurs is even more severe, because their proportions often differ radically from living forms. Although birds are direct descendants of predatory dinosaurs, the flight heritage of tailless birds radically altered the proportions of their thin-walled hindlimb bones compared to those of long tailed predatory dinosaurs, so the latter have longer, more slender femora and shorter distal leg bones. Therefore, attempts to estimate the mass of *Tyrannosaurus* via avian M/BDR (Anderson et al., 1985; Campbell & Marcus, 1992) resulted in values that were 20–40% too low. Anderson et al. (1985) estimated that *Apatosaurus* weighed a little more than *Brachiosaurus* because the former has more robust long bones (Figure 1). This cannot be correct, because the volume of the former's skeleton is about half that of the brachiosaur's (Figure 2, AppendFigs. 9,11).

Bone dimensions can be used to accurately estimate body masses when the forms being compared are very similar in form and function. They can also be used to expose implausibly high mass estimates. Example: the maximum mass compatible with the bone circumference and strength of the Berlin *Brachiosaurus* skeleton is about 45 tonnes (Figure 1), assuming it was a primarily terrestrial animal, so a higher mass estimate should be

examined critically. Otherwise, M/BDR produce initial and useful but broad "ball park" estimates that are inherently imprecise.

Minimal Criteria and Documentation for Modeling Volumes and Masses

Paul (1988a, b, 1990) and Haynes (1991) concluded the best way to restore the mass of extinct creatures is with a model based on a technical skeletal-muscle reconstruction. A mass estimate is only as accurate as the model, and to be accurate a model's proportions must closely conform to the original skeleton. It has been the author's observation that restorations based on gross dimensions of body proportions are usually proven to be in error by a more detailed bone-by-bone restoration. Also, in science it is critical to properly document the information— whether it be numbers, descriptions, illustrations or models— upon which conclusions are based. It is suggested that the minimal requirement for documentation of a volumetric mass estimate includes a bone-by-bone skeletal restoration. The skeletal restoration should include at least direct side, and preferably multiple, view/s (oblique views are acceptable only in addition to direct plan views). It is important that at least one member of a group be restored in multiple view as a guide for other group members of similar form (if the members of a group are similar in form, then multiple views for all may be redundant). The skeleton may be restored in either two or three dimensional media, and either made of real world materials or reside in virtual digital technology. The exact scale of the figure should be indicated (if a scale bar is included, it should be long enough to be easily used).
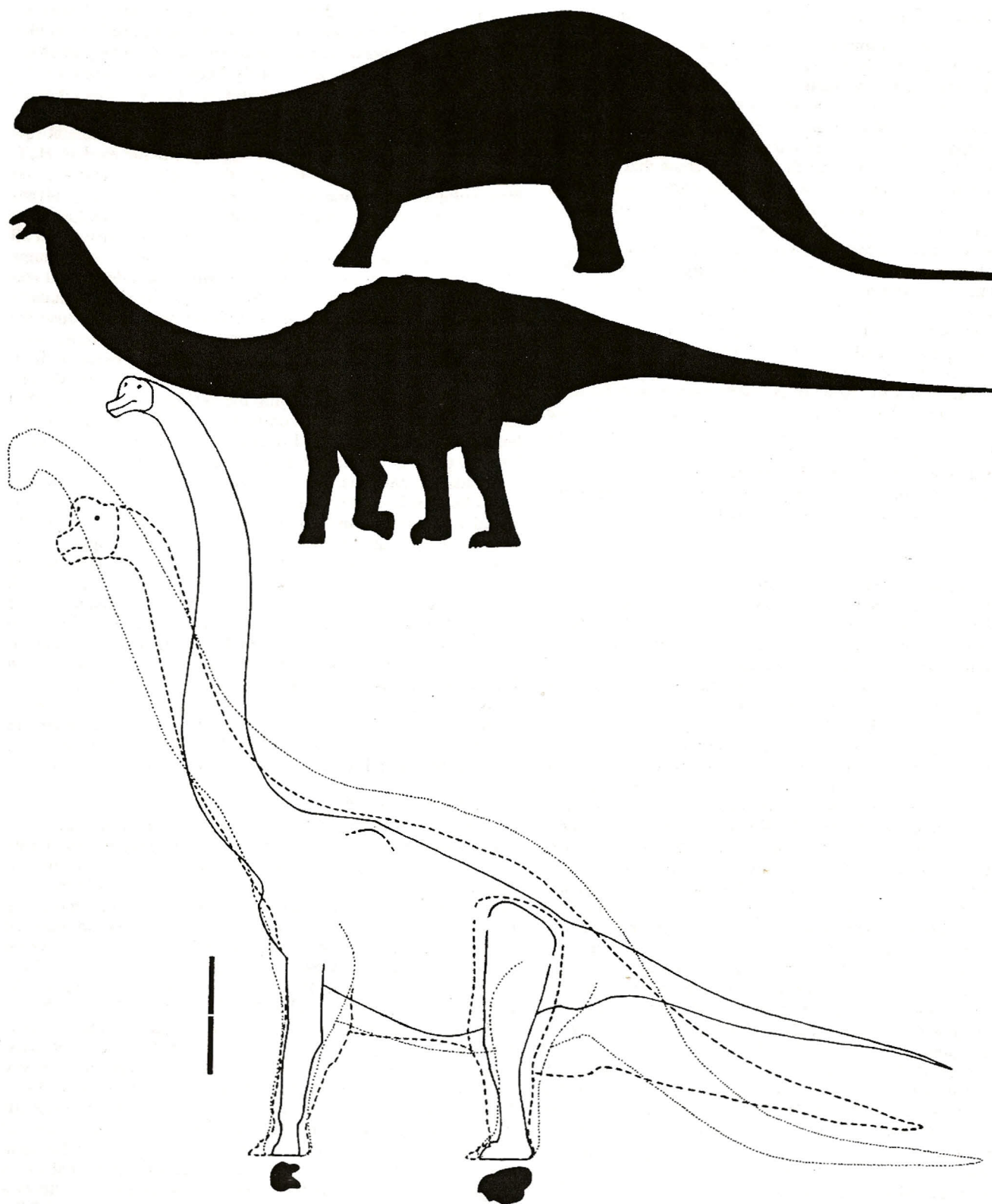
FIGURE 2—A comparison of volumetric restorations of sauropods; to same scale, scale bar equals 2 m. Outlines are *Brachiosaurus* HMN SII; solid after rigorous skeletal restoration, restored volume 37 m³; dashed BMNH model, 47 m³; dotted after obsolete skeletal restoration, 74 m³ (Gunga et al., 1995); fossil probable brachiosaur prints indicate modest size of feet. Solid profiles *Apatosaurus* CM 3018; upper profile after rigorous skeletal restoration, 20 m³; lower profile BMNH model, 34 m³.

Where Models—Especially Commercial Examples—Go Wrong

Most artistic and commercial dinosaur models do not meet the above criteria, mainly because any skeletal restorations they are based upon are rarely published. In order to assess the accuracy of some inadequately documented models, the profiles of British Museum of Natural History (BMNH) commercial models are compared to same scale technical skeletal-muscle restorations (Figures 2 & 3). The results not only show that the models are inaccurate to the point of being caricatures (Paul, 1990), they also reveal why. Major variations in restored volume are not, as commonly thought (Alexander, 1989), primarily due to the differing interpretations of muscle and other soft tissue bulk that result from "artistic license". Overly large chests (see below) inflate trunk volume by only 10–15%. It is the trunk that makes of most of an animal's volume, so mass estimates are not highly dependent upon the volume of appendages. Example: in sauropods big necks and tails usually make up about 20% of total mass, so arbitrarily increasing their volumes by half only increases total mass by 10%. If as much muscle and fat as is marginally conceivable is applied to dinosaurs, total volume can be boosted by at most 20% above the values presented in this study. By the same token, if a marginally emaciated condition is accepted about 20% can be shaved off. Greater differences in volume are due to gross errors in proportions and/or scale of the degree observed in the commercial models.

Protocol Employed in This Study

The methods for rigorously restoring fossil skeletons and musculature are detailed in Paul (1987, 1988a,b) and Paul & Chase (1989). Restorations are based on figures and/or photographs of bones and/or complete mounts, careful attention has been paid to reproducing the dimensions of both. The more complete a skeleton is the better, there is no simple cut off point at which a species' skeleton becomes too poorly known to be modeled accurately. The absence of dozens of tail vertebrae is less serious than the absence of the dozen vertebrae that make up the trunk. A skeleton that lacks 55% of its bones, but whose remaining 45% includes almost all elements from one side (which can be used to model the missing side) is superior to a skeleton that lacks the front 30%. When modeling a dinosaur, it is especially critical to properly articulate and space the vertebrae so that the length of the articulated spinal column is correct (in general, the spool-shaped centra of vertebrae are separated by thin cartilagenous disks in life). When parts from different skeletons of different sizes have to be put together they must be "cross-scaled" so that they are drawn to a common size. This produces a composite skeleton whose proportions are as accurate as possible with the remains on hand. Beware skeletal mounts that include unmodified parts from individuals of different sizes.

It is not possible to accurately restore individual muscles in extinct tetrapods (McGowan, 1979; Paul, 1987, 1988a,b; Bryant and Seymour, 1990), so the gross superficial musculature has been profiled in solid black (living animals were used as partial guides, sources include Knight [1947]; Ellenberger et al. [1949]; Kingdon [1979]). When not covered by feathers or thick fur, many predators and herbivores have a "bony" appearance. The tips of the neural spines and ribs lie just beneath the skin, the outermost edges of some girdle and limb bones such as the dorsal end of the scapula and the ilium form prominent contours, and the ribs are sometimes visible even when the animal is healthy. The figures represent the subjects in "prime-lean" condition, with healthy, full bodied muscles and little fat. In tropical nondomestic land animals, both small and large, fat is only about 4% of total mass (Ledger, 1968; Albl, 1971; Owen-Smith, 1988; Haynes, 1991; Shoshoni, pers. comm.; even hippos are only 10% fat; the heavy fat deposits postulated by Paul [1988a] are excessive). Predators are modeled with empty, hollow bellies (Paul [1988b]; otherwise, their latest victim would be part of the mass estimate!). Herbivores usually keep at least some fodder in their guts and are modeled in this manner, but this amounts to only about 2% of the total mass (Laws et al., 1975).

The dimensions and volume represented by the skeletal restorations were translated into half-figure plasticine models. Half-figure models save time—because they lack an armature, and their volume can be measured easily—but the primary advantage is that rendering the model directly atop a sagittal body plan facilitates accurate reproduction of body dimensions on all axes. Models were constructed solely to reproduce the volume of multi-view paper restorations; they were not independent restorations of volume, nor of artistic quality. The skeletal-muscle figures are the sole record of the volume estimate because the plasticine figures were cut into small sections, any holes were sealed, and their volume was measured at least twice with an accuracy of ±2% in water filled graduated cylinders. Results were further checked by copying the skeletal restorations either to the same scale, or to a common standard such as shoulder height or femur length, and overlaying the two skeletons on a back lit glass to visually compare relative volumes.

If land animals had the same density as water, their volume could be translated into mass on a one-to-one basis (as per Alexander, 1989). However, most animals float, so specific gravity (SG) is usually about 0.95. Pneumatic vertebrae suggest some dinosaurs were less dense. Early theropods are assigned an SG of 0.9, and the value used for more advanced theropods with more extensive air-sacs is 0.85 (Paul, 1988b). The main body of sauropods was probably less filled with air-sacs than birds, so their general SG is set at 0.9 (Paul, 1988a). However, the intensely pneumatic neck vertebrae mean their necks were even less dense. If this is not taken into account then the estimated mass of large necked sauropods will be too high relative to smaller necked forms. The SG of sauropod necks is therefore set at 0.6 (which may be too high, Paul [1988a]). In any case, the possible error involved with specific gravity is modest.

Using Living Animals to Test the Protocol

Farlow (1980) suggested that the accuracy of volumetric models be tested by modeling modern forms, and seeing how closely the resulting mass estimates correspond with reality. Carpenter (1988) expressed concern over the accuracy of half-figure models. Two large mammals were selected for modeling (AppendFigs. 6,8). In both the side views are based on mounted skeletons and photographs of living animals, the top views on aerial or fore-and-aft views of living animals. Secrecy and exaggeration by showman P. T. Barnum surrounds the size of the ponderous pachyderm Jumbo (Shoshoni et al., 1986). The restored height of 3.2 m is less than past height estimates, but is tall for a still growing bull of Jumbo's age. Despite great mass, slow moving proboscideans do not have an exceptionally heavy limb musculature (Knight, 1947; Kingdon, 1979; Haynes, 1991). Laws et al.'s (1985) data indicates a 5.8 ± 1.0 tonne mass for 3.18 m tall bulls in good condition. The model based estimated mass of 6.2 tonnes for Jumbo is therefore only 7% higher than the predicted mean, and within the range for an animal of its height. In rhinos the ventral profile of the abdomen follows a simple semi-circular arc down from the pubis (Figures 2.3,7.5 and others in Owen-Smith, 1988), rather than the more complex, baggier belly seen in elephants. Also, the leg muscles of galloping rhinos are more powerfully built than those of elephants. The estimated 1 tonne mass of an Indian rhino is only 5% higher than the mean value, and within the 0.8 to 1.0 tonne range, predicted for a specimen of its shoulder height.
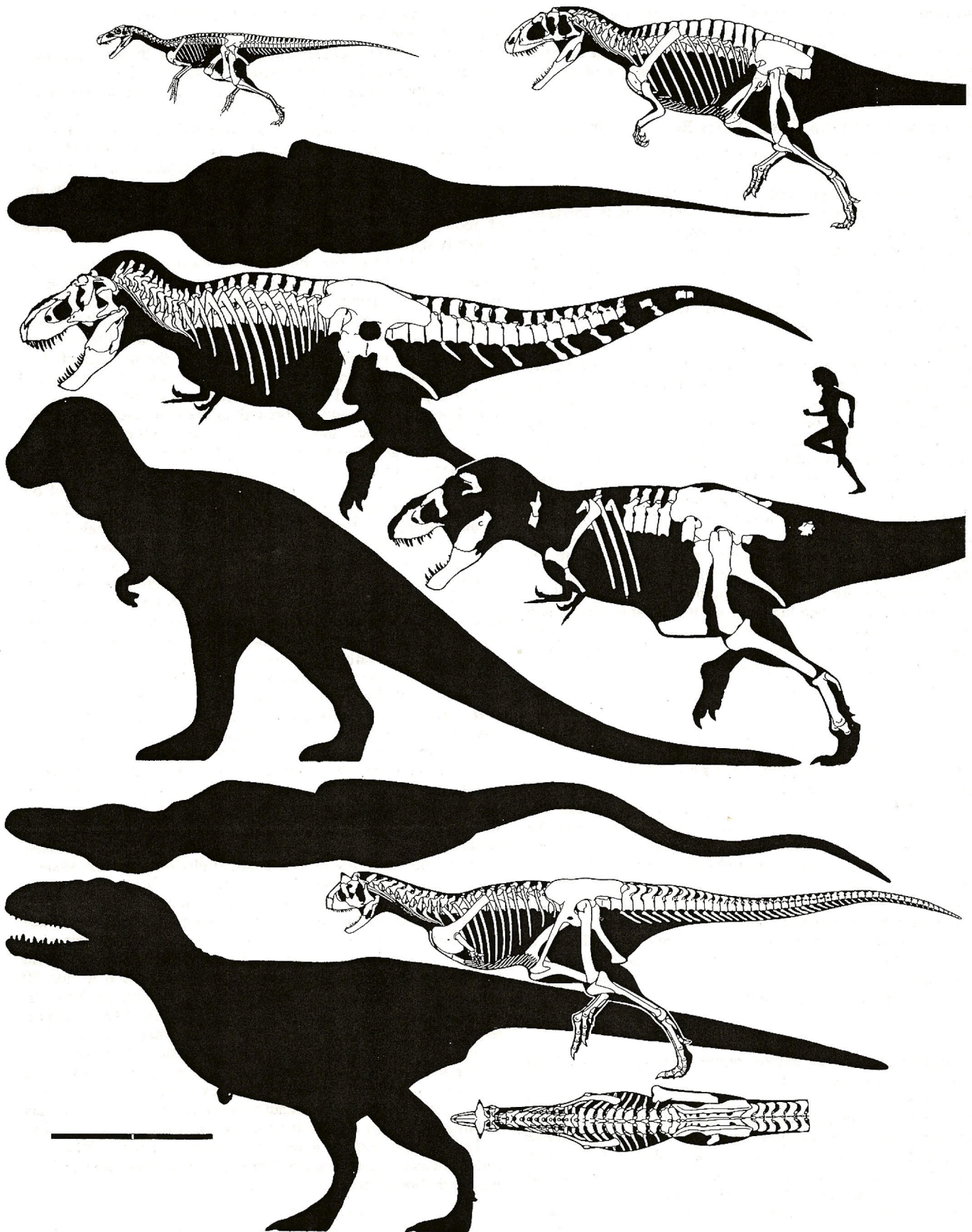
FIGURE 3—Volumetric restorations of predatory dinosaurs, to same scale, scale bar equals 2 m. *Tyrannosaurus*; rigorous skeletal restorations of AMNH 5027 (top center) and CM 9380 (center right), restored volume of both 6.7 m³ (5700 kg); BMNH model (center left), 7.4 m3; MOR 555 (bottom), 6.3 m³. *Herrerasaurus* (top left) PVL 2566, 124 kg. *Carnotaurus* (bottom right), 2070 kg. *Sinraptor* IVPP 10600 (top right), 1340 kg.

Had there been a large divergence between the estimated and actual masses, the protocol would have been falsified. As it is, the protocol is validated. Also, the modern figures can be used to compare and confirm figures and mass estimates of extinct forms.

Error Margins and Extrapolating Masses Between Individuals

It is not possible to assign a simple plus or minus margin of error to a mass estimate derived from an accurately restored model, but the range is probably about ±15% when the skeletal restoration is not missing any major sections. This is adequate in view of the fact that the mass of a nonpregnant adult animal can vary by a third within a year (especially in temperate regions where seasonal fat deposits are normal, less so in tropical inhabitants) and as they age (McEwen, et al., 1957; Sinclair, 1977; Damuth and MacFadden, 1990). Estimating the mass of a fossil species is not an exact science.

A model reproduces the mass of one individual in one condition, and mass/dimension relationships can vary substantially within a species, so applying the results of any model to other individuals should be done with care. Example: sexes often vary substantially, so it may be necessary to model both when they are known. The best measure of the size of the bulky trunk is the length of the articulated trunk and hip vertebrae, and this is the best dimension for extrapolating the mass of the modeled individual to others in its species or group. Total body length is less suitable because neck and tail length are highly variable relative to mass in individuals, and because consistently measuring the length of the often multi-curved spinal column is difficult. Also, spinal columns are often incomplete in fossils. Hindlimb elements are more often complete and can be substituted for spinal series when the latter are unavailable. The length of the humerus and especially the long femur are more tightly correlated with body mass than the more distal elements (Damuth & MacFadden, 1990), so femur length can be used as a standard dimension for estimating the approximate mass of individuals.

World Record Animals Today and in the Fossil Record

Among modern wild animals, very rare "world record" individuals are about twice as massive as the adult norm (McFarlan & McWhirter, 1989). For example, average African elephants weigh 3 to 7.5 tonnes, the largest bulls on record tip the scales at 10 to 12 tonnes. A typical blue whale weighs around 100 tonnes, the largest cows may reach 200 tonnes. The populations of which these giants are a part are very large, in the millions. In the fossil record the number of individual dinosaurs known from any particular species is much lower, from one to occasionally a few hundred. Among such small samples, it is very unlikely that the largest individuals represent a typical size for the species. The chance that individuals approaching or reaching "world record" class will be preserved is virtually nil.

SOME NONDINOSAURIAN MASS ESTIMATES

The large size of some extinct reptiles, mammals, and birds has elicited attempts to estimate their mass. A 420 kg mass estimate of one of the largest island ratites (AppendFig. 3) is in good agreement with past estimates. One of the largest continental reptiles was the poorly known giant monitor *Megalania* from Australia. A tentative 5.5 m long skeletal restoration (Rich & Hall, 1979) indicates that megalanians were typical lizards (long but narrow body, small legs) whose total volume was less than that of more robust bodied and bigger legged 1.3 tonne allosaurs (AppendFig. 5). A model shows that mass was 0.8 to at most 1.0 tonnes (using subadult komodo monitors as a scaling

data base, Auffenberg [1981] calculated 2.2 tonnes for a 4.5 m long individual).

Mammoths grew considerably larger than living elephants. The former tended to have shorter but broader bodies relative to their limbs than the latter. Many mounted mammoth skeletons are too tall because the shoulder is mounted too low on the chest, and claims that known individuals exceeded 4.5 m and 15 tonnes are excessive. The restoration of a nearly complete and very large (3.71 m tall) bull produces a mass estimate of 7.8 tonnes (AppendFig. 10). The tallest mammoth skeletons represent individuals a little over 4.0 m and 10 to 11 tonnes, about the size of modern world record elephants. World record mammoths probably approached 20 tonnes.

Bigger still were the long limbed indricothere rhinos. The skeletal restoration is based primarily upon a large juvenile or adult female (AppendFig. 9; Granger and Gregory, 1936). Combining this specimen with others (from Osborn, 1923; Borissiak, 1923a,b; Gromova, 1959) allowed the trunk and limbs to be accurately restored in all views, except for the number of dorsals. A large skull was scaled down to fit, and the incomplete neck was proportioned according to one partial vertebrae relative to its limb elements, and the breadth of the articulations in dorsal view. Restored flesh shoulder height is nearly 3.8 m. The biggest remains (two giant neck vertebrae and a partial central metacarpal) suggest males reached about 4.8 m. The completed restoration is neither as heavy in appearance as that published by Granger & Gregory, nor as extremely gracile as the Russian mount (Gromova, 1959). Granger & Gregory overscaled most of their classic figure (femur and vertebral column too long, hip too large), and placed the shoulder joint too low on the chest, making it too tall at 5.25 m. The mounted skeleton's errors (neck too long, pelvis too small, ribs too short, feet and humerus too long relative to femur, limbs too vertical) mainly stem from being made up of bones from individuals of different size (an example of the failure to cross-scale elements to a common size!). Because the new restoration has a very broad ribcage and hips, it is unlikely that the volume is too low. Neck musculature is restored as deep yet narrow, as in other ungulates. The massive abdomen is given a simple rhino-like semi-circular lateral profile. Limb musculature is restored as proximally powerful and distally light as per modern flexed limbed ungulates, using moderately fast rhinos, camels and workhorses as models. Mass for the medium sized specimen is restored as 7.8 tonnes, of which 10% is in the head and neck. The similarity in the size of the bodies of the tall rhino and the mammoth of the same mass confirms the accuracy of this result (indricotheres also share a similar mass/shoulder height relationship with proboscideans). Assuming isometry the biggest bulls should have exceeded about 16.4 tonnes, but this may be somewhat conservative since ungulates tend to become more massive relative to their neck and legs as they mature (Damuth & MacFadden, 1990). "World record" specimens are predicted to have reached 6 m and 30 tonnes. The results are in general agreement with the bone dimension/mass scaling calculations of Gingerich (1990) and Fortelius & Kappelman (1993), which offers further evidence of the accuracy of mass estimates based on technical data. Taken together, these studies also contradict extreme estimates of the size of known specimens. In particular, Alexander's (1989) 34 tonne mass estimate is too high because the trunk length (from Granger & Gregory, 1936) on which he based this estimate is excessive.

The recently extinct giant ape collected in the 1930's on a Indian ocean island stood 5.5 m tall, and is estimated to have weighed about 7 tonnes.

DINOSAUR MASS ESTIMATES

As in reptiles and birds, the volume of the dinosaur head and skull were essentially the same because they lacked extensive

facial muscles. In many dinosaur mounts and restorations the chest ribs are positioned vertically, like those of mammals, but Paul (1987, 1988a,b, 1996) and Carpenter et al. (1994) observed that all dinosaurs' chest ribs are swept back like crocodilians and birds (this can be seen in many articulated skeletons). Because the rib heads articulate with the vertebrae at an oblique angle, swinging the ribs backwards also swings them inwards. The shoulder girdle is accordingly both pulled back and narrowed (to the point that the coracoids almost meet on the midline). In quadrupedal reptiles the shoulder joint is just forward of or astride the first long dorsal rib, so the majority of the scapula is astride the chest ribs. The resulting tight fit between girdle and chest maximizes the amount of supporting muscles that connect the two, the same should have been true of fully or semi-quadrupedal dinosaurs. In a few dinosaur specimens (small ornithopods, AppendFig. 1) the sternal ribs are ossified and still connect the ribs and sternal plates, with the latter being just in front of the front ribs. In other articulated skeletons the sternals are set just forward of the first long dorsal rib (Pls. 7A, 18, 19 in Lull & Wright, 1942). Because the lower end of the shoulder blade articulates with the sternal plates the shoulder girdle is not far ahead of the ribs, and the shoulder joint is just forward of or astride the first ribs. This tight fit is seen in the best articulated dinosaur skeletons (see Pls. 9A, 12B, 13, 17B, 18, 22B, 24B, 27, 31 in Lull & Wright, 1942). The position of nerves that fed the forelimb also support a posterior position for the shoulder girdle (in predatory dinosaurs according to Giffin [1995], and the same configuration appears true of quadrupedal dinosaurs). In some skeletons the shoulder girdle is found more down and forwards, but sternal elements are displaced and the girdle was probably pushed out by bloating of the carcass (contrary to Carpenter et al. [1994] who indicates this was the life position in dinosaurs). These combined factors significantly reduce chest and shoulder volume both front and sides compared to traditional restorations.

In most dinosaurs the trunk and/or tail vertebrae were heavily braced in some manner, so it is probable that (as in stiff bodied birds) the back musculature was not as well developed as in more flexible bodied reptiles and mammals. The erect tail carriage that appears to be common to all dinosaurs implies that their tails did not bear massive burdens of flesh, but there is latitude in restoring this factor. Reptiles have short hips and narrow thigh muscles, the same appears to have been true of the most primitive dinosaurs. Birds and mammals have long upper hip bones that support broad thigh muscles, this applies to most dinosaurs (so the narrow thighs restored by Knight [see Paul, 1996b] are not correct). Fossil dinosaur footprints often help determine the volume of the soft tissues of the feet and lower limbs of various types. To a certain extent muscling dinosaurs is a matter of common sense. Neither the massive amounts of soft tissue draped over the skeletal frameworks in many traditional restorations, nor the extremely emaciated condition in some recent restorations (as per Russell, 1989) are plausible.

Predatory Dinosaurs, Those Lean Mean Fighting Machines

Restorations and mass estimates of predatory dinosaurs are detailed in Paul (1988b), some new and updated examples are presented in Figure 3. In top view chests were broader than waists, as in mammalian carnivores. Of all dinosaurs, the small-bellied predators are the ones in which the appendages have the most influence upon total body mass.

Traditionally, the largest predatory dinosaur has been *Tyrannosaurus*. Mass estimates as high as 12 tonnes (Paul, 1988b) are excessive. New large specimens are either too incomplete or have not been published in sufficient detail to allow accurate skeletal restorations and mass estimates, what has been revealed
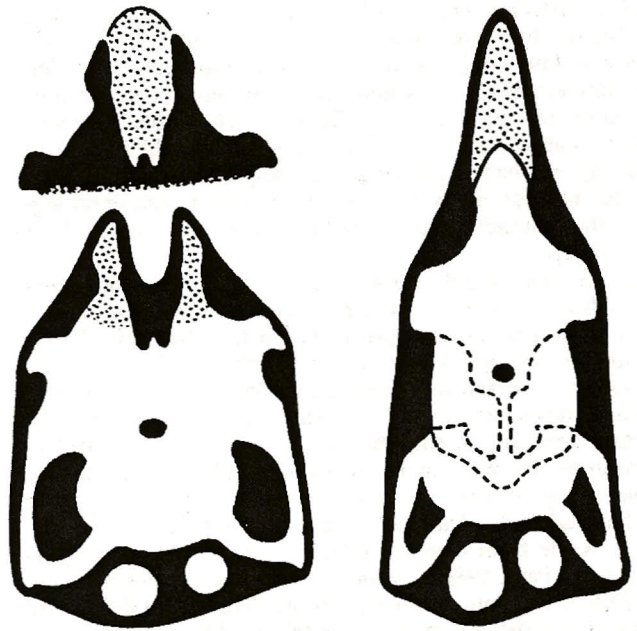

FIGURE 4—Supporting tissues of sauropod neck cross sections, to same approximate scale. Two left figures are *Diplodocus,* on right is *Brachiosaurus.* The top left figure shows the large nuchal ligament (stippled) lying between the V-spines restored by Alexander (1989), who assumed a heavy solid neck. Lower figure shows that ligaments (stippled) probably connected spines of succeeding vertebrae directly to one another, and that they did not need to be so thick because the neck was pneumatic, so a groove may have lain between the V-spines. The nuchal ligament (stippled) that may have helped carry the neck of brachiosaurus is shown, note that it was probably narrow. Also indicated are the excavations that lightened sauropod vertebrae (dotted lines) to the point that their centers consisted of a thin vertical wall, and the restored gullet and trachea (smaller passage) on the underside of each neck. Note the complex cross sectional shapes of sauropod necks, unlike the simple semi-circles shown in most restorations.

suggests that the biggest specimens approached 8 tonnes. Recently, new predatory dinosaurs have challenged the status of *Tyrannosaurus* as the biggest, again we await more details. The largest unpreserved world record individual predatory dinosaurs probably approached 15 tonnes.

Herbivorous Dinosaurs

Restorations and mass estimates of herbivorous dinosaurs are presented in the Appendix. In top view the chest was narrower than the belly, as in herbivorous mammals, and restorations that show the plant eating dinosaurs with hollow bellies are in serious error.

Therizinosaurs, Heavily Weird

Therizinosaurs are the dinosaurs designed by the committee on psychedelics. No complete skeleton is known, so mass estimates are imprecise. The front portion of the pelvis was extremely broad, indicating that the belly was equally so. *Therizinosaurus* had arms 2.5 m long, and weighed about 3 tonnes.

Sauropods, the Land Whales

It is not surprising that the largest land animals of all time have been the focus of many attempts to estimate their bulk. Did any approach or equal the size of the largest whales?

The now stony neck bones are often restored with a massive musculature, but the actually lightweight pneumatic vertebrae were probably supported by a musculature so minimal that the

individual vertebrae were visible, as in giraffes and long necked birds. Nuchal ligaments may have been present in a few sauropods with fairly tall shoulder spines (brachiosaurs, some Chinese examples), but these would have been slender and had little effect on overall mass (also see Figure 4). The rather slow sauropods probably had fairly slender leg muscles like those of nonrunning elephants, indeed fossil footprints (Figure 2) disprove the muscles artists are fond of applying to sauropod legs (such as the "Gumby" legs of the brachiosaurs in *Jurassic Park* [Paul, 1996a]).

Sauropods were highly variable in form and proportions. *Apatosaurus* had a strikingly stout neck (which few artists reproduce), but the pneumatic organ made up less than 9% of total mass. In most sauropods strongly curved ribs bore broad bellies, more so than average in camarasaurs, *Opisthocoelicaudia* and especially titanosaurs. In Chinese sauropods and the diplodocids (including apatosaurs), straighter abdominal ribs and narrower hips mean bellies were more compressed side to side (the abdominal cavity of a juvenile *Camarasaurus* is as capacious as that of an adult *Diplodocus* in the same display hall in the USNM). Aside from their big bellies, brachiosaurs are surprisingly gracile (Paul, 1988a), while camarasaurs, *Opisthocoelicaudia* and titanosaurs are unusually robustly built. Short diplodocid trunks had a reduced number of vertebrae; the apatosaur trunk was so short and deep (the enormous sacrum and pelvis is as tall as the dorsal column is long) that the body had a distinctive subcircular body in side view.

The restorations indicate that some well known sauropods weighed less than sometimes suggested. The mounted African *Brachiosaurus* skeleton in Berlin (along with its new partial copy in Chicago still the largest mounted dinosaur skeleton) is somewhat too large (Paul, 1988b) because the delicate trunk vertebrae (some only 9 inches long) were replaced by plaster models that are too long. The revised trunk column is nearly one fifth shorter. The revised skeletal restoration produces a mass under 32 tonnes (the somewhat stouter American species may have been 2–3 tonnes heavier). About 14% of the brachiosaurs' mass was in the neck and tail, so the body and legs massed 27 tonnes, and even doubling the mass of the appendages increases the overall estimate by only 6 tonnes. The artistic *Brachiosaurus* model Colbert (1962) used is inaccurate (its tail base is thicker than that of the *Apatosaurus* model used in the same study, when the reverse should be true), and the nearly as massive restoration by Gunga et al. (1995) is a bloated caricature whose trunk is much too long (Figure 2). The 74–78 tonne masses are probably over the limit that could be borne by the limbs (Figure 1). At the opposite extreme, a mere 15 tonnes of flesh (calculated by Russell et al., 1980) cannot be stretched over the great skeletons. The largest fragmentary remains of African and American brachiosaurs suggest individuals of 45–50 tonnes, not 190 tonnes as some suggest (Paul, 1988a).

Despite being one of the most strongly constructed sauropods (see below), the 13 to 19 tonnes typical of *Apatosaurus* are well under the 25 to 43 (Russell, 1989) tonne values often applied to the same specimens (because the big tail is one eighth the entire volume, doubling its mass adds only a couple of tonnes), but exceptionally large bones suggest individuals reached about 25 tonnes. *Opisthocoelicaudia* is just 38% the mass estimated by Anderson et al. (1989). Some sauropods were surprisingly light despite their great length. Gracile *Diplodocus* and *Barosaurus* are little heavier than the biggest living elephants despite being about four times longer (16 to 40 tonne estimates [Alexander, 1989; Russell, 1989] are excessive). *Omeisaurus,* with its extremely slender neck and narrow belly, is the most lightly constructed sauropod relative to its mass. Long necked *Mamenchisaurus* had the shortest limbs for its body mass of any sauropod

even though it is light bodied, shunosaurs have the longest limbs for their mass. Opposite the usual trend, the size of some sauropods has been understated. Because many *Camarasaurus* skeletons are juveniles it has often been considered a small sauropod, but big skeletons indicate individuals of 15 to well over 20 tonnes.

Cross comparisons of the sauropod and giant mammal skeletons confirm the above results. The Chicago *Brachiosaurus* is about half a dozen times more capacious than ~5 tonne African elephants mounted in the same hall, not ten to sixteen times bulkier (Kinzig, pers. comm.). The volume of the same and other museums' *Apatosaurus* skeletons is about half the brachiosaur's, so they did not exceed twenty tonnes (even though the apatosaur sacrum and pelvis are much larger). The *Diplodocus* and *Apatosaurus* skeletons restored here stand next to each other (p. 10 in McGinnis, 1982). Although the former had a larger tail, the apatosaur's trunk is 70% more capacious than the gracile diplodocid, so the former is not three times more massive (note that the visual "bulk" of *Apatosaurus* is exaggerated by tall spines above the hips). It is especially interesting to compare a 16 tonne indricothere to *Apatosaurus*. The trunk of the former is actually longer and broader, and the legs are of approximately similar volume, confirming the low mass estimates for apatosaurs (AppendFigs. 8,9,10). Likewise, the lightness of *Diplodocus* and *Barosaurus* is realistic because their trunk and leg volume is similar to the 8 tonne mammoth (AppendFigs 8,9). It was the long necks and especially the tails of the dinosaurs that made them heavier than the otherwise equally big bodied mammals. At over 2.5 tonnes, typical diplodocids tails were as large and powerful as allosaurs. Super sauropod tails (see below) weighed from 8 to 14 tonnes, equal to one or two giant theropods.

With accurately modeled mass estimates in hand, we can compare the skeletal strength of sauropods to each other, and to modern mammals (Figure 1). Despite its great size, *Brachiosaurus* had rather slender limb bones. The gracile diplodocids were more similar to proboscideans and giant rhinos in terms of bone strength. Modest sized *Apatosaurus* and smaller *Opisthocoelicaudia, Dicraeosaurus* and *Amargasaurus* were exceptionally strong boned for giant quadrupeds, much more so than big mammals. The results show that the correlation between sauropod body mass and bone dimensions is rather poor because there was a high degree of variation, probably more than observed in giant land mammals.

The mass/element relationships of well known sauropods can be used to make tentative estimates of the size of less well known giant relatives. The largest footprints record the passage of sauropods of about 50 tonnes (Paul, 1988a). Gillette's (1994) skeletal restoration of the diplodocid *Seismosaurus* is much shorter than his written estimates of 39–52 m, even though the restored distal tail vertebrae are overly long. Corrected length (with predicted diplodocid tail proportions) is about 32–34 m (assuming it had a long neck, less than 30 m if the neck was shorter). Gillette's 100 tonne estimate exceeds the volume of his own skeletal restoration three to four fold. A new sacro-pelvis attributed to the diplodocid *Supersaurus* (Olshevsky, 1988) is not much larger than that of *Apatosaurus* and *Seismosaurus,* and the smaller supersaur scapula is from an animal of similar or somewhat larger size. The largest supersaur scapula-coracoid is immense (Figure 5) and hints at a diplodocid of 40–50 tonnes and 35 (assuming apatosaur-like proportions, including tall vertebral spines that increased apparent size) to 45 (assuming Diplodocus-like proportions) meters long.

A badly damaged and now lost part of a trunk vertebra (Figure 5) tentatively assigned to the diplodocid *Amphicoelias* probably records the world's largest known dinosaur (Coe et al., 1987). The bone's original height is conservatively estimated to have
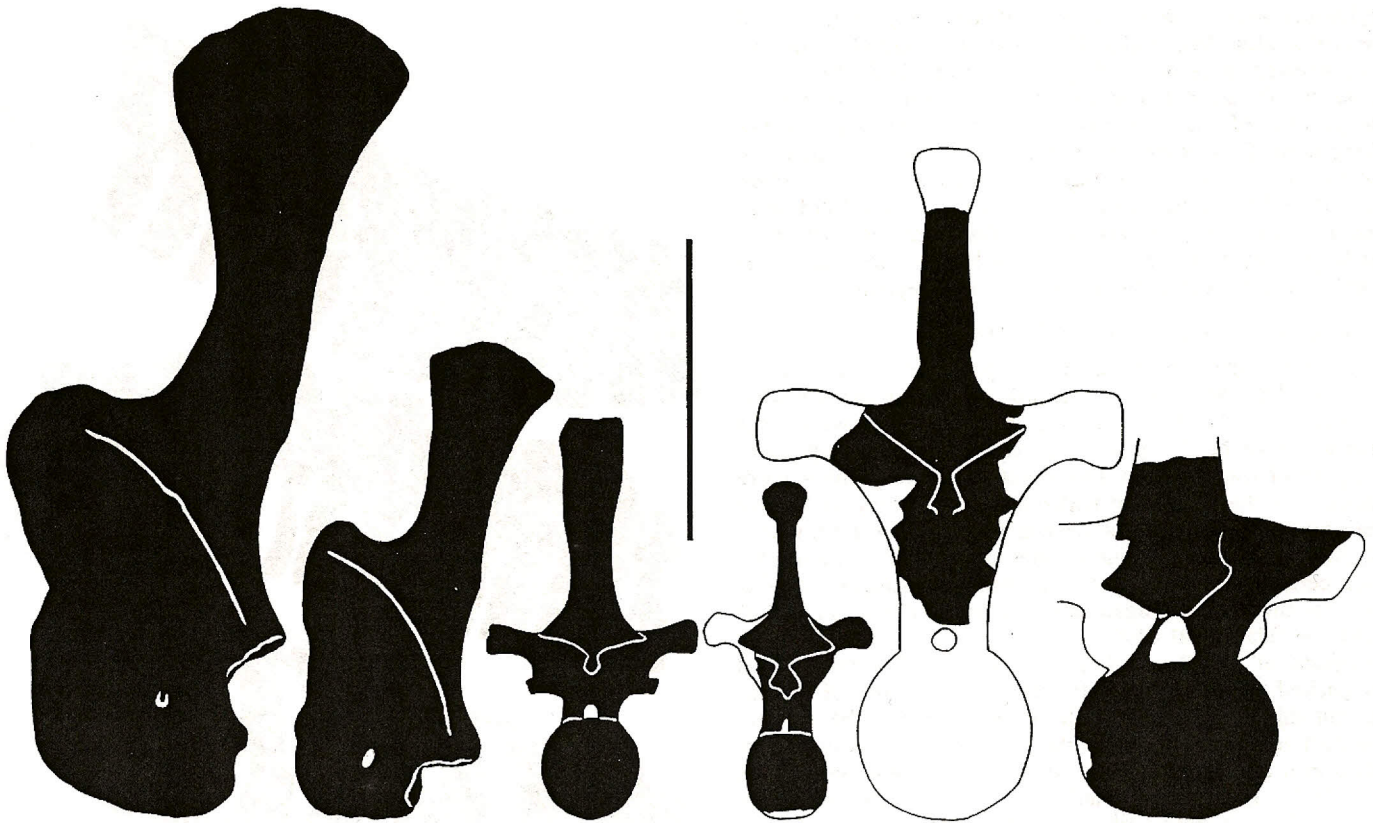
FIGURE 5—Shoulder blades and aft dorsal vertebrae of sauropods, to same scale, scale bar equals 1 m. From left to right, *Supersaurus* ~50 tonnes, *Apatosaurus* 18 t blade and vertebra, *Amphicoelias altus* ~12 t, *Amphicoelias fragillimus* ~125 t, *Argentinosaurus* ~90 t. Black parts are preserved.

been an astonishing 2.4 to 2.7 m tall, taller than a human and around twice that of the typical diplodocids (including *Seismosaurus*). Even prudent calculations imply a super-sauropod 40 m long and weighing 100 tonnes, figures of 60 m (equal to a blue and sperm whale combined) and 150 tonnes are equally plausible. These figures outclass even Late Cretaceous titanosaurs, whose limbs were heavily loaded by their very broad abdomens. The enormous dorsals (Figure 5) of *Argentinosaurus* (Bonaparte and Coria, 1993), although much shallower than those of *Amphicoelias* at about 1.5 m, were twice as long as those of *Apatosaurus, Seismosaurus,* and *Brachiosaurus,* and indicate that the dorso-sacral column was very long (about 7 m), even relative to the very long (1.6 m) fibula that was as long as the femur of some lesser sauropods. Using dorsal series/mass relationships of other broad bellied sauropods as a guide, the mass of *Argentinosaurus* is estimated at 80–100 tonnes. Some extremely long titanosaur femurs may represent animals of similar bulk (if so they are more massive than calculated by Paul [1988a]). Anderson et al. (1985) suggested that two thick shafted titanosaur femora represent exceptionally heavy individuals, but the other dimensions of the bones do not support this conclusion. In any case, titanosaurs demonstrate that sauropods did not experience a size decrease in the Cretaceous. Note that the downwards revision of sauropod masses in general limits the estimated masses of the largest fragmentary specimens. On the other hand, it is very unlikely that the largest sauropods have been discovered. Aside from the good possibility that one or more even more gigantic species remain unknown, occasional "world record" sauropods may have approached 200 tonnes, the mass of large blue whales (McFarlan and McWhirter, 1989).

Armored Dinosaurs, and the Moving Coffee Tables

Stegosaurs and ankylosaurs had small or modest sized skulls and necks that contributed little to their mass. The moderate sized tails were well muscled at the base, much less so distally. Hyper-elongated forward processes of the pelvic ilium bone probably helped support the gut, and any leg muscles anchored at the front end were probably thin. The assorted armor plates and spines were porous boned, often thin and/or hollow centered, and contributed little weight (so armored dinosaurs could probably float as well as armored crocodilians, land turtles, and armadillos).

Most stegosaurs have broad hips that supported similarly broad abdomens. The exception was narrower hipped *Stegosaurus,* but the slab sided gut was still capacious because it was deep. Large stegosaurs had moderate sized, elephantine nonrunning limbs. The mass of the biggest stegosaurs was comparable to Asian elephants and female African elephants.

The trunk vertebrae of ankylosaurs are long and numerous, so the trunk is long (as per Coombs, 1979; Paul, 1995). Some restorations have been too short-trunked, and this has forced the artist to narrow the hips (Carpenter, 1984). Ankylosaurs actually had almost unbelievably broad abdomens and bellies. Complete and little crushed hips consistently show that the front ends of the ilia flare far out to the sides and are supported by very long hip ribs. Undistorted abdominal ribs are also extraordinary for their strong sideways arc which made them as broad as the hips. The increase in body breadth from the narrow chest to the fat belly is so fast and extreme that the blade of the scapula is strongly twisted along its length in order to accommodate the strong helical curve of the top of the front part of the ribcage.

Ankylosaurs were so broad and flat bodied that one could almost serve coffee atop their backs. The Moscow mount of *Talarurus* has a narrower, more barrel-shaped, hippo-like body, but this is because the ribs are not articulated with the largely absent transverse process of the vertebrae—this ankylosaur was another walking table. Legs were rather short and moderately muscled, probably more heavily in the flexed limbed ankylosaurids (Paul, 1987, 1995). Mass estimates in this study are about a third higher than by Carpenter (1984) because of the longer, broader trunk. Most large ankylosaurs were the size of hippos and rhinos, bigger *Ankylosaurus* was as heavy as an Asian elephant.

Ceratopsians, the Dinosaurian Swelled Heads

In most dinosaurs the head makes up only a few percent of body mass. The exceptions are the little protoceratopsids and the big ceratopsids. In the latter, long frills combine with large snouts to create heads up to 3 m long, which make up about one eighth of total volume. Protoceratopsids are perhaps more remarkable in that their short frilled heads are enormous relative to their bodies, to the point of absurdity in *Leptoceratops,* whose head encompasses about one quarter of its total volume. Although ceratopsian necks were well muscled, suggestions that the nuchal muscles and ligaments attached to the upper end of the frill are false (Paul, 1987).

Burnham et al. (this volume) assert that *Triceratops* was sway-backed, which increases the length and volume of the ribcage, but this is not anatomically possible (Figure 6). In well articulated ceratopsid skeletons the trunk vertebrae correctly articulate in a dorsally convex arch as in other dinosaurs (Paul, 1987, 1996). In the Saint Paul *Triceratops* mount (Erickson, 1966) overly long sternal ribs make the chest too deep.

The combination of a short arched dorsal series and laterally arcing belly ribs means that ceratopsids had short but broad bellies, especially in chasmosaurs in which the femur bowed outwards to clear the rotund gut (Lehman, 1989). The sternals, and therefore the chest, were moderate in breadth. Because *Triceratops* was a big animal its shoulders were about 1 m broad, so its shoulder joints were directly above the manus during a normal walk (Figure 7) and forelimb posture was erect, albeit at a somewhat wider gauge than seen in large mammals. Massive limb bones and exceptionally large hips suggest that ceratopsid limbs were very powerfully muscled in these running forms. The 1.5 tonne masses of chasmosaurs and centrosaurs are similar to those of black and Indian rhinos. The 6+ tonne mass of *Triceratops* and *Torosaurus* is similar to that of Jumbo, a fact made readily apparent by a comparison of the two skeletal types. Skeletal remains suggest individuals approaching 10 tonnes, some very large but rather poorly preserved trackways (Figure 7) imply individuals in the 12 to 19 tonne range cited in Russell (1989).

Small Semi-Bipedal Ornithischians, From Slim and Trim to Pleasingly Plump

Many small ornithischians were semi-bipedal—lesothosaurs, heterodontosaurs, small ornithopods, pachycephalosaurs, psittacosaurs. Heads tended to be modest in size, necks short and rather slender. Bodies were compact, tails were fairly long and on the light side. Arms were short to moderate in length and not heavily muscled, legs were long, and the thighs and shanks were powerfully developed.

In most of these types the belly was not especially broad, as in kangaroos and antelope. Exceptions were psittacosaurs and pachycephalosaurs. The belly ribs of the former are more strongly arced, and articulated specimens confirm that the belly was rather plump. Pachycephalosaurs are much more unusual. The belly ribs are so strongly to the sides that that the belly is broader
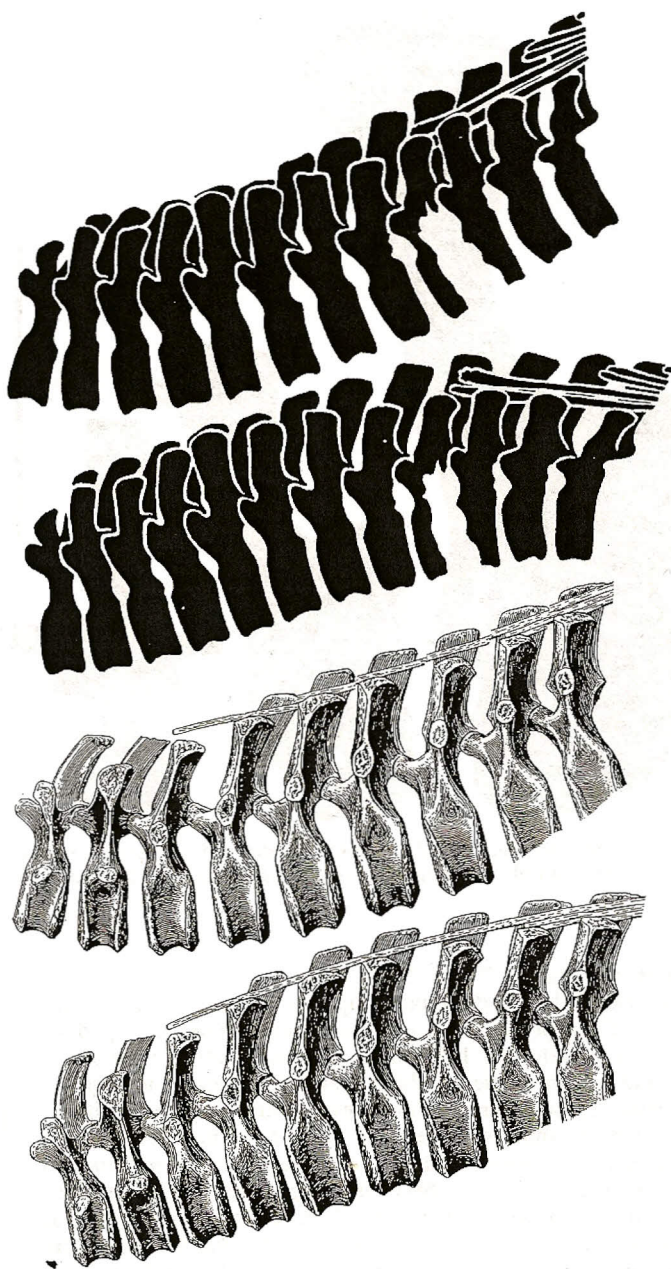

FIGURE 6—Curvature of the spine in ceratopsid dinosaurs. Solid profiles are vertebrae 10–21 of the medium sized *Centrosaurus* (AMNH 5351), shaded figures are 10–18 of the bigger *Triceratops* (from Hatcher et al., 1907). In all figures the zygapophysis that link each vertebra to its neighbor at mid level are fully articulated with one another. Pulling the vertebrae into a sway-back, as shown in the top figures of each example, separates their main bodies too much, and jams the neural spines too close together. Drying of the powerful dorsal musculature and ligaments often pulls the backs of dead animals into such a false sway-back. On the bottom the vertebrae are shown in proper articulation (and almost as originally found in the centrosaur), with the ossified tendons in place, the neural spines not crowded together, and most importantly the main, lower bodies flat on to each other and separated by a small distance (which was filled with a cartilage disc). The result is a gentle dorsally convex arch, which is shorter than the sway-back.

FIGURE 7—Front view of 6 tonne *Triceratops* fitted onto a large *Ceratopsipes* trackway. Note that although the chest ribs are narrow, and the foreprints are wider gauge than the larger hindprints, forelimb posture is erect. On the lower left are very large trackways that may have been made by oversized ceratopsids. Scale bar equals 1 m.

than the front end of the hips. The hips become broader progressing backwards, the reverse of the usual condition. It is extremely peculiar that the transverse processes at the base of the tail are so long that they form a set of functional ribs *behind* the pelvis. The false ribs' slenderness and dorsally convex arc, the posteriorly broad hips, and the absence of chevrons from the tail base suggest that there was a large extension of the digestive tract behind the hips, a rarity among vertebrates.

Iguanodonts and Hadrosaurs, Sometimes Bigger Than You Think

Big ornithopod heads and necks were moderate in size, bodies were compact and somewhat slab sided (except camptosaurs), tails were moderate in size, and hindlegs were long and powerfully muscled in these running forms. In some iguanodonts,

and all hadrosaurs, the front half of the trunk was strongly down-arched (Paul, 1987), which dramatically shortened the trunk and reduced its volume. If ungulate-like nuchal tendons helped support the head and neck in tall spined iguanodonts and in hadrosaurs (Czerkas, 1993) they were narrow and had little influence on mass. The belly was extremely deep in some iguanodonts, and the deep tails were very compressed from side to side. Although the arms were long, they were slender and had little influence upon overall mass.

Plump *Camptosaurus* seems a modest sized dinosaur because many skeletons are juvenile, but some individuals approached 2 tonnes (Erickson, 1988). Large *Iguanodon* exceeded 3 tonnes, higher values in Colbert (1962) and Alexander (1989) are based on inaccurate models. Also excessive, and often inconsistent, are mass estimates for typical American hadrosaurs as high as 4 tonnes. Colbert estimated that the New York *Corythosaurus* was heavier than the *Anatotitan* in the same hall, yet visual comparison on site shows that the latter is the bigger of the two specimens (AppendFigs. 7,8). Most American examples weighed about 2.5–3.0 or more tonnes (the 2.2 tonne estimate by Beland & Russell [1978] differs only in that their models were too hollow bellied). These masses are comparable to big white rhino bulls (AppendFig. 6–8), although the hadrosaurs tend to look larger because of their deeper body profile, large but thin tails, and taller stature. Hadrosaurs are unusually uniform and isometric in body design and proportions regardless of size, and some were surprisingly big. Some American hadrosaurs are two thirds or more longer than the norm (Morris, 1972) and suggest individuals of around 13 tonnes. Asian *Shantungosaurus* is modeled at 10–13 tonnes. The biggest hadrosaur trackways (Lockley et al., 1983) record individuals with feet about twice as large as those of typical examples, and imply weights as high as 20 to 25 tonnes. World record individuals approaching or exceeding 30 tonnes are probable. Giant hadrosaurs greatly outweighed ceratopsids, at least matched the biggest land mammals, and rivaled many sauropods—quite a feat for animals that bore most of their mass on two legs. Hadrosaurs were longer limbed than sauropods. Example: *Shantungosaurus* hindlegs were about as long as those of *Apatosaurus*, but the latter was about a third heavier.

Some Very Large Footprints

The 1.3 m long Jurassic *Gigantosauropus* footprints are the largest yet discovered (Mensink & Mertmann, 1984). They are so enormous, and ill defined in shape, that they are difficult to accept at face value. However, they do not show clear signs of distortion, and appear to represent a three toed biped of 20 to 30 tonnes and over 15 m length. No theropod is known to have reached more than a third of this bulk, such masses and dimensions are approached by some ornithopods skeletons and prints, and the prints' short, broad toes are most like those of ornithopods.

MASSIVE MISTAKES AND REVELATIONS

Many studies of dinosaur biology depend upon accurate mass estimates. Some examples of how mass estimates incorrect and correct can lead to results errant and useful are detailed below.

Rocking, Stomping Dinosaurs

Alexander (1989) used the inaccurate BMNH commercial models to measure the fore-and-aft mass distribution of dinosaurs. More accurate models would give better results, but there will always be a high degree of uncertainty because it is not possible to precisely restore the internal distribution (especially internal air-spaces) of mass in extinct forms. Just a modest error

in mass at the front or back end of an animal can have a major effect upon the center of gravity because of the lever effect.

Estimates of the pressure exerted on the ground by the under surfaces of dinosaur feet in Alexander (1989) may be as excessive as the mass estimates used in the study.

Stand Up Sauropods and Stegosaurs

Some researchers assert that big sauropods were too heavy to stand on two legs, including Jensen (1988) who used mass estimates that were too high for the specimens cited. Alexander (1989) concluded that sauropod hindlimbs were strong enough to stand up on, even though the mass estimates he used were sometimes too high. That sauropods were less bulky than often thought aids the hypothesis that they reared up.

This study shows that the legs of dicraeosaurs, *Apatosaurus* and *Stegosaurus* and legs were unusually robust for animals of their mass, and so little of this strength was in the forelimb (in both the femur was one third thicker than the humerus) that hindlimb strength was as high as in bipeds. Additional bipedal features of *Stegosaurus,* dicraeosaurs and apatosaurs include unusually short arms and trunks, large sacrals and hips, and heavy tails. Giffin (1990) observed that neural control of the forelimbs is poorly developed in sprawling lizards, short armed bipeds, *Stegosaurus* and apatosaurs, and the same appears to be true of dicraeosaurs. Giffin suggested that the dinosaurs' arms were not erect, but stegosaur and sauropod arms could not articulate in a sprawling posture (Paul, 1987). It is more probable that dicraeosaurs, *Apatosaurus* and *Stegosaurus* arms were weak and poorly controlled because they used them less than previously realized, perhaps because they often walked on their strong hindlimbs alone.

Run Dinosaur Run

Faster moving animals need stronger limb bones that slower forms, so one way to assess the "athletic" ability of an extinct form is by comparing its limb strength vis-à-vis modern mammals (Alexander, 1989). This method is highly dependent upon accurate mass estimates (Farlow, 1990). Alexander calculated that a 12 tonne *Diplodocus* and a 34 tonne *Apatosaurus* were too weak-limbed to run. The last mass estimate is too high, and apatosaur legs were strong enough to run on (but lack of a proper limbs and feet prevented them from doing so [Paul, 1987]). Alexander calculated that the legs of 6 tonne *Triceratops* were strong enough to run on, this is plausible because the weight estimate is accurate and ceratopsid limbs and feet were suitable for running (Paul, 1987). Alexander and Farlow et al. (1995) calculated that two different *Tyrannosaurus* specimens (estimated mass 8 and 6 tonnes respectively) were too weak limbed to run. The model used by Farlow et al. (1995) has errors (Figure 3). Even so, the restored volume appears to be accurate because it is a little lower than that of the larger specimens, so its mass was probably 5.4 tonnes. Corrected mass for the specimen used by Alexander is less than 5.7 tonnes (Figure 3), at that value its limb bones appear to have been strong enough (Farlow, 1990) to bear the running gait its limbs were designed for (Paul, 1988b).

Dinosaur Brains

Many dinosaurs are famed for their "small" brains, others for being intellectually well endowed. Determining how big brained an animal was involves measuring the size of the brain, and plotting it as a function of body mass. Errors in estimating the latter have skewed the results. For example, a brachiosaur was plotted on the assumption that its owner weighed 78 tonnes (Hopson, 1980), but the skull belongs to a large juvenile of "only" 16 tonnes.
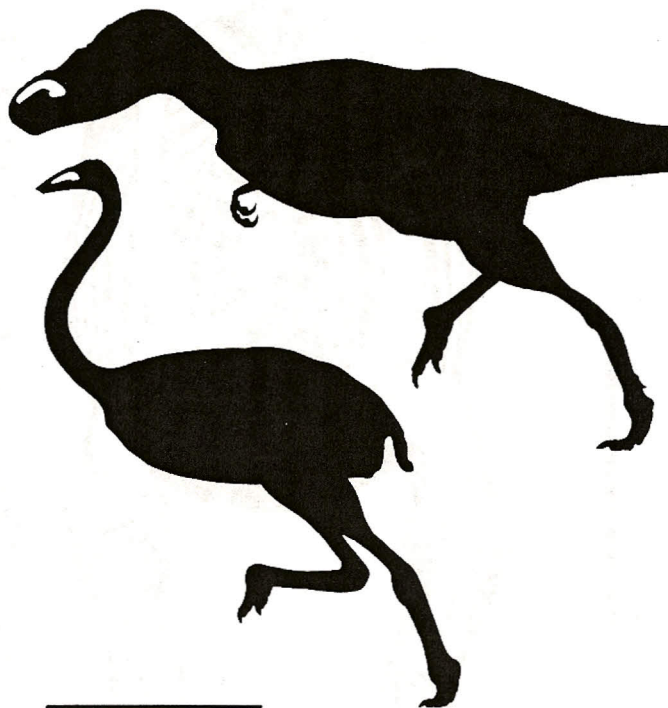

FIGURE 8—Profiles comparing the size of the body and nasal passage (in white) in a juvenile tyrannosaur (top) and elephant bird (bottom), to same scale, scale bar equals 1 m. Although the animals are roughly similar in bulk, the nasal passage of the dinosaur is larger than the bird, and could therefore contain equally well developed nasal scrolls.

Dinosaur Noses

Ruben et al. (1995) suggested that the nasal passages of predatory dinosaurs were too small to accommodate the bird-like nasal "scrolls" that may be necessary for a high metabolic rate. This hypothesis can be tested by estimating the mass of dinosaurs and birds of similar size, and seeing if the nasal passage of the former really is smaller than that of the latter. Figure 8 shows that a young tyrannosaur has a larger nasal passage than a giant bird of about the same weight, so Ruben's hypothesis is contradicted.

You Cannot Always Believe What You Perceive

Dinosaurs did not always appear to be the size they actually were. A horned ceratopsid looks smaller than a duckbilled hadrosaur or tyrannosaur of equal mass because it lacks the long tails and legs of the latter two, and the tall vertebral spines of the duckbill. The sauropod *Amargasaurus* looks about as large as *Dicraeosaurus,* which looks almost as large as *Opisthocoelicaudia,* but closer examination shows that the ribcage of the first is much smaller than its dicraeosaur relative, which in turn is less voluminous than the last sauropod, which lacks tall spines that would inflate its size. The big plates of *Stegosaurus* give it a profile as big as a ceratopsid two or three times as massive.

Being Huge in the Oceans is Good, Being Huge on Land is Better

A common cliché asserts that giant dinosaurs were misplaced on land, and that evolution more correctly placed whales in buoyant oceans. The reality is that super-sauropods were not only as big as whales, but thrived from about 150 to 65 Myr ago. Similarly massive whales appeared only 10 Myr ago, and the largest examples date back only a few Myr. So far the time tally favors the land giants.

CONCLUDING COMMENTS

The results of this study show that volumetric models must be based upon detailed, technically accurate, and well documented skeletal restorations. Off the shelf models, whether found in museums or shops, are prone to substantial error and may give misleading results. Despite advertisements to the contrary, many commercial models are toy caricatures that inaccurately represent certain dinosaur taxa, they are not scientifically reliable models. Unless their accuracy can be established it is best to avoid the use of such models in technical studies. Unfortunately most people who buy dinosaur models are not able to tell what is and is not as realistic as current science allow, it is up to those who produce and distribute the models to ensure that what is sold meets the highest standards of science.

In the future, the modeling of dinosaurs promises to go digital. As the ease of using computers rises and costs decline, extinct forms will increasingly be restored bone by bone (and perhaps muscle by muscle) in 3-D virtual reality. The volume of the final virtual model can be measured in the computer. The image can even be translated directly into hard form by various means of digital-plastic prototyping. Because traditional methods give accurate results, computer modeling is not expected to result in dramatic improvements in basic accuracy (indeed, the errant results in Gunga et al. (1995) show that bad data scanned into the computer results in equally bad results out). Where computer modeling may be most useful is in more precisely restoring the internal anatomy and weight distribution of the extinct subjects.

NOTE AND ACKNOWLEDGMENTS

Readers are reminded that the skeletal figures presented here are under the author's copyright, and that those who wish to base commercial images and products upon them need to make the proper arrangements. Among the many people who have provided discussion, information and other assistance are F. Boothman, M. Brett-Surman, K. Carpenter, J. Chevalier, J. Farlow, M. Fortelius, H. Jaeger, D. Kinzig, A. Lister, J. McIntosh, and S. L. Shoshoni.

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APPENDIX: SKELETAL RESTORATIONS AND MASS
ESTIMATES FOR HERBIVOROUS DINOSAURS

Most of the skeletons were restored on paper and modeled at constant femur lengths of 105 and 52.5 mm respectively. It would be ideal to present all skeletons at the same scale, but the great size range of dinosaurs makes this impractical. The skeletons and profiles are therefore reproduced in five common scales, one for each category of size—small (Figs. 1,2; scale bar equals 1 m), medium (3,4; 2 m), large (5–8; bar 2 m), sauropods (9–11; 4 m), super giants (12; 4 m). The human figure is 1.64 m tall (5′ 4″). Mass estimates (in large bold numerals) are in kilograms (= 2.2 lb.) for the small and medium category, tonnes (= 2.2 tons) for the rest. The symbol ~ means approximate, and applies to specimens that are too incomplete to estimate their mass more accurately. For some unusually large but fragmentary individuals profiles have been prepared (the preserved bones are sometimes included). These are not true rigorous restorations, but are intended to give a better idea of the possible dimensions and bulk of these giants.