

Long-bone circumference and weight in mammals, birds and dinosaurs

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The mid-shaft circumferences of the humerus and femur are closely related to body weight in living terrestrial vertebrates. Because these elements are frequently preserved in subfossil and fossil vertebrate skeletal materials, the relationship can be used to estimate body weight in extinct vertebrates. When the allometric equations are applied to the mid-shaft circumferences of these elements in dinosaurs, the weights calculated for some giant sauropods (*Brachiosaurus*) are found to be lighter than previous estimates.

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Introduction

When contemplating skeletons, the query ‘How large was the animal?’ often implies ‘How much did it weigh?’ Beyond its intrinsic interest, body weight provides a guide to the probable behaviour of animals (it correlates with the number and weight of eggs or neonates, growth rate, metabolic rate and home range—see summaries in Western 1979, Russell 1980). More than 20 years ago, E. H. Colbert estimated weights for dinosaurs using scale models. Since then, several authors have shown how the proportions of long-bones change rather precisely as power functions of body weight. It is certainly easier to obtain these measurements than to construct accurate scale models in order to assess body weight. We wish to demonstrate the utility of using the combined circumferences of the humerus and femur in quadrupeds, and the circumference of the femur in bipeds, as estimators of body weight.

Methods

The minimum mid-shaft circumferences of the humerus and femur can easily be compared in different individuals, for the measurements are relatively free of the ambiguity involved in selecting an orientation for making radial measurements. Furthermore, the shafts of the long-bones are frequently well preserved in otherwise incomplete fossil materials.

Circumference measurements were obtained from 225 mammals (representing 9 species) from Kruger National Park, South Africa and 3 specimens (1 species) from the Mountain Zebra National Park, South Africa. The animals were shot for research purposes or, in the case of hippopotamus, as part of routine population control exercises. The Impala, Bushbuck, Warthog, nyala, Grey duiker and hippo were weighed whole on spring balances. For hippos, the balance (Salter, 2000 kg capacity) was suspended from an hydraulic truck-mounted hoist which could lift the entire animal. The kudu, Burchell's zebra (*Equus burchelli antiquorum*), and Blue wildebeest from Kruger and the 3 Cape Mountain zebra (*Equus zebra zebra*) were first cut up and then weighed in pieces. Loss of weight due to lost body fluids was minimized but no compensation was made for such loss or evaporative water loss, which is unlikely to have exceeded 3% of total body weight (Smith & Ledger 1965, Laws *et al.* 1967, Skinner 1970, Huntley 1971). Similar data were compiled from skeletons of 74 mammals (representing 23 species) and 126 birds (representing 75 species), primarily from the collections of the University of Florida and the National Museum of Natural Sciences (Ottawa). Unfortunately, body weights are usually not available for skeletal materials stored in museum collections, and are very difficult to obtain for skeletons of large vertebrates. Because of the latter circumstances, data for a few ratites and elephants are tabulated in Table I. Drought conditions prevailed over Kruger Park during the early summer (September–November) of 1982 when rainfall amounted to only 22.3% of the long-term average for the season (30.6 mm vs. 137.1 mm). Animals which were culled during this time were therefore analysed separately.

TABLE I
Humeral and femoral circumferences in millimetres and body weight
in grams for ratites and elephants

	C_h	C_f	W
Ratites			
<i>Casuarus casuarius</i>	—	94	36 571
<i>Dromiceus novae-hollandiae</i>	—	95	40 667
<i>Struthio camelus</i>	—	134	80 920
<i>S. camelus</i>	—	166	80 970
Elephants			
<i>Loxodonta africana</i> ('Tiny')	196	209	927 600
<i>L. africana</i> ('Congo')	203	206	1 224 700
<i>L. africana</i> ('Jumbo')	459	413	5 896 700

In the case of quadrupeds, the circumferences of the humerus and femur in each specimen were combined, thereby smoothing variation in the relative proportions of these elements (and of the fore- and hind limbs) in different species. After transformation into logarithms, the data were used as the basis for least-squares regressions (cf. Bailey, 1981), first examining intraspecific allometry and then interspecific allometry. Confidence intervals of $\pm 95\%$ were calculated for the exponents. Circumference was treated as the dependent variable in all regressions except those in which it is used to predict weight. Circumference is measured in mm and body weight in g.

Discussion

Regressions for the mammalian data are listed in Table II. The exponent for intraspecific allometry is approximately 0.27, except in the case of hippos, where it is significantly larger (note

TABLE II

Allometric equations of the form $C = aW^b$ relating the circumference of the humerus and femur in millimetres to body weight in grams. The equations were obtained by least-squares regression after transformation to logarithms. The categories $\frac{1}{4}$ heaviest, $\frac{1}{2}$ heaviest and heaviest refer to interspecies regressions calculated from individuals with weights about $\frac{1}{4}$ as much, about $\frac{1}{2}$ as much or equal to the heaviest individual, here measured in 12 species for which data from some subadult specimens were available

	<i>n</i>	Factor <i>a</i>	Exponent <i>b</i> and 95% confidence limits
Mammalian species			
<i>Aepyceros melampus</i>			
(Impala)	57	10.64	0.24 ± 0.05
Nov. 1982	7	1.28	0.45 ± 0.21
Dec. 1982	6	13.78	0.22 ± 0.15
<i>Tragelaphus strepsiceros</i>			
(kudu)	49	11.45	0.24 ± 0.03
Oct. 1982	3	1.81	0.40 ± 0.11
Nov. 1982	4	4.69	0.32 ± 0.30
Dec. 1982	4	28.87	0.17 ± 0.31
1983	8	8.57	0.27 ± 0.11
<i>Tragelaphus scriptus</i>			
(Bushbuck)	4	24.23	0.15 ± 0.32
Nov. 1982	3	13.61	0.22 ± 0.26
<i>Phacochoerus aethiopicus</i>			
(Warthog)	20	5.54	0.29 ± 0.05
Nov. 1982	5	1.99	0.41 ± 0.21
<i>Equus zebra</i>			
(Cape Mountain zebra)	3	0.99	0.46 ± 0.17
<i>Hippopotamus amphibius</i>			
(hippo)	50	3.95	0.32 ± 0.03
<i>Urocyon cinereoargenteus</i>			
(Gray fox)	5	3.38	0.33 ± 0.27
<i>Canis laterans</i>			
(Coyote)	5	6.22	0.26 ± 0.59
<i>Canis lupus</i>			
(wolf)	9	5.55	0.29 ± 0.08
<i>Procyon lotor</i>			
(Raccoon)	9	7.87	0.23 ± 0.14
<i>Ursus americanus</i>			
(Black bear)	5	7.03	0.27 ± 0.19
<i>Erethizon dorsatum</i>			
(porcupine)	4	4.27	0.30 ± 0.27
<i>Bison bison</i>			
(bison)	11	3.50	0.33 ± 0.14
<i>Loxodonta africana</i>			
(elephant)	3	0.94	0.44 ± 0.24
$\frac{1}{4}$ heaviest	9	5.60	0.30 ± 0.07
$\frac{1}{2}$ heaviest	10	3.68	0.33 ± 0.04
heaviest	12	2.47	0.36 ± 0.03
herbivores (ungulates,			
Table III)	10	2.12	0.38 ± 0.05
carnivores (Table III)	13	2.70	0.36 ± 0.04
mammals (Table III)	33	2.64	0.36 ± 0.01
Reptilian species			
<i>Alligator mississippiensis</i>	12	2.72	0.34 ± 0.04
<i>Varanus</i> spp.	14	2.02	0.40 ± 0.05

TABLE III
Humeral and femoral circumferences in millimetres and body weight in grams for
individuals belonging to 33 species of quadrupedal mammals

	C_h	C_f	W
<i>Microtus ochrogaster</i> (Meadow mouse)	4.9	5.5	47
<i>Cavia porcellus</i> (Guinea pig)	10	15	385
<i>Sciurus carolinensis</i> (Gray squirrel)	10	13	399
<i>Didelphis marsupialis</i> (opossum)	27	23	3 915
<i>Urocyon cinereoargenteus</i> (Gray fox)	28	26	4 200
<i>Procyon lotor</i> (Raccoon)	30	28	4 816
<i>Myocastor coypus</i> (Nutria)	21	28	4 836
<i>Lynx rufus</i> (Bobcat)	31	32	5 818
<i>Erethizon dorsatum</i> (porcupine)	30	34	7 200
<i>Lutra canadensis</i> (otter)	32	28	9 680
<i>Canis latrans</i> (Coyote)	35.5	36	12 701
<i>Neofelis nebulosa</i> (Cloud leopard)	44.7	41.4	13 478
<i>Sylvicapra grimmia</i> (duiker)	31	46	13 860
<i>Papio cynocephalus</i> (Yellow baboon)	55	57	28 576
<i>Acinonyx jubatus</i> (cheetah)	67	68.7	38 020
<i>Felis concolor</i> (Cougar)	62.1	60.25	43 999
<i>Canis lupus</i> (wolf)	62	61.5	48 081
<i>Tragelaphus scriptus</i> (Bushbuck)	56	62	50 900
<i>Aepyceros melampus</i> (Impala)	65	69	60 500
<i>Phacochoerus aethiopicus</i> (Warthog)	83	72	90 500
<i>Tragelaphus angasi</i> (nyala)	99	97	134 500
<i>Panthera leo</i> (lion)	103.6	93.5	143 450
<i>Ursus americanus</i> (Black bear)	98	93.5	217 724
<i>Ursus horribilis</i> (Grizzly bear)	124	106.5	256 117
<i>Connochaetes taurinus</i> (Blue wildebeest)	115	100	256 500
<i>Equus zebra</i> (Cape Mountain zebra)	132	143	262 000
<i>Tragelaphus strepsiceros</i> (kudu)	140	135	301 000
<i>Equus burchelli</i> (Burchell's zebra)	129	147	378 000
<i>Ursus maritimus</i> (Polar bear)	158	135	447 695
<i>Giraffa camelopardalis</i> (Giraffe)	192	173	710 000
<i>Bison bison</i> (bison)	191.5	167.5	1 179 000
<i>Hippopotamus amphibius</i> (hippo)	209	208	1 950 000
<i>Loxodonta africana</i> ('Jumbo')	459	413	5 896 700

confidence limits). During the drought months of October and November 1982, the intraspecific exponent increased about 1.5 times while the proportionality constant declined in five ungulate species from Kruger Park, indicating that the young animals at that time possessed relatively small bones. Recovery had apparently begun by December, after significant rains had fallen and veld conditions improved dramatically. The effect of using data from immature animals as a basis for estimating interspecific allometry can be seen in subsets of points taken from species where a relatively broad range of weights was available (Table II). The interspecific exponent declines as a function of the immaturity of the representatives of the species. Equations derived from adult carnivore and herbivore data are virtually identical. A regression based on the heaviest specimen available for a species (Table III) is here taken as a standard for quadrupeds, with weight as the dependent variable (C_h = circumference of humerus in mm, C_f = circumference of femur, W = weight in g):

$$W = 0.078 C_{h+f}^{2.73 \pm 0.09} \quad (1(a))$$

or $\log_{10} W = -1.11 + 2.73 \log_{10} C_{h+f}, \quad r^2 = 0.99. \quad (1(b))$

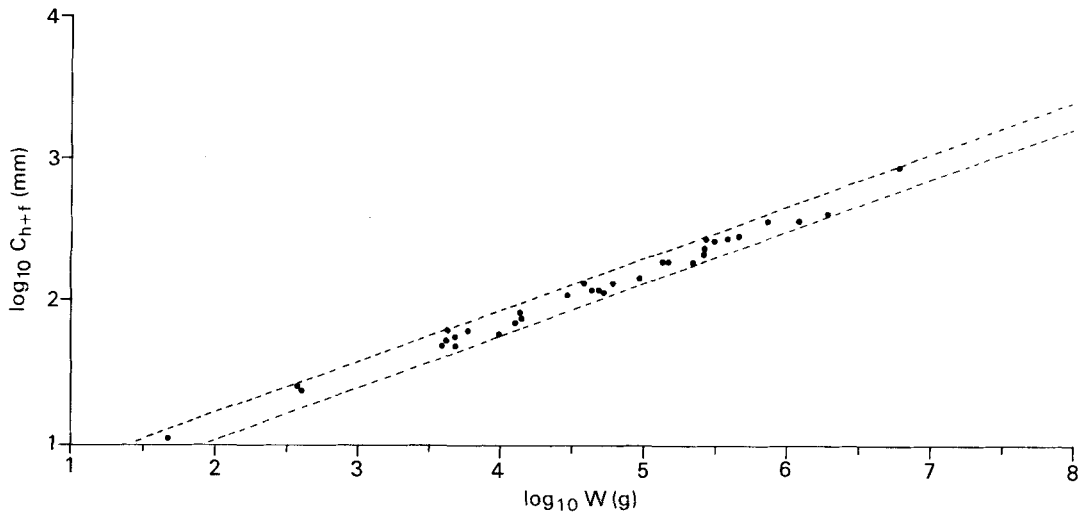


FIG. 1. A graph on logarithmic coordinates showing the combined circumferences of the humerus and femur plotted against body weight, based on data in Table III. Dotted lines represent 95% confidence limits for a single point.

Humeral and femoral circumference may be treated as two independent variables, where

$$\log_{10} W = -0.18 + 1.28 \log_{10} C_h + 1.46 \log_{10} C_f \quad (2)$$

but the residual variance is slightly greater than in equation 1 (b).

When separated into discrete humeral and femoral regressions, the data in Table III yield the following relationships:

$$C_h = 1.08 W^{0.38 \pm 0.02} \quad (3)$$

and

$$C_f = 1.50 W^{0.35 \pm 0.02} \quad (4)$$

The exponents are nearly identical to those observed by Alexander *et al.* (1979, 0.38 ± 0.01 and 0.36 ± 0.01 for the humerus and femur, respectively), who selected diameter instead of circumference as the dependent variable. The proportionality constants, when altered to correspond with the units used by Alexander *et al.* (1979) and divided by π , are also in good agreement (4.7 and 5.4 for the humerus and femur, respectively, versus 4.9 and 5.2 reported by Alexander *et al.*, 1979).

Prothero & Sereno (1982) found exponents of 0.45 and 0.39 from regressions of humeral and femoral diameter against estimated body weight in seven species of ceratomorphs. They suggested that the relatively large exponents were due to the large size of the species sampled relative to the weights of those examined by Alexander *et al.* (1979). The seven species in Table III represented by weights in excess of 300 kg yield the following relationships:

$$C_h = 1.09 W^{0.38 \pm 0.14} \quad (5)$$

and

$$C_f = 1.47 W^{0.35 \pm 0.13} \quad (6)$$

It would be useful to verify the ceratomorph trends using measurements on skeletal materials for which live weights are available.

Because of the limited range of available weights and small sample sizes, it was impossible to assess the intraspecific relationship between femoral circumference and body weight in flying

birds. Using single specimens or averages when more than one specimen was available for a species, the interspecific relationship was calculated from data pertaining to 72 species:

$$C_f = 1.11 W^{0.41 \pm 0.02} \quad (7)$$

The exponent is similar to those found by Maloiy *et al.* (1979) for running birds (0.43 ± 0.05) and Alexander (1983) for flying birds (0.42 ± 0.03). The proportionality constants, after modification for differing units and using diameter in the place of circumference, are also comparable (0.60 vs. 0.64 reported by Maloiy *et al.*, 1979 and Alexander, 1983). In four ratite specimens belonging to three species (Table I), the observed femoral circumferences are larger than those predicted by equation 7 by a factor of about 1.2. Interestingly, in two specimens of kangaroo (AMNH 197029 *Macropus irma*, $C_f = 42$ mm, $W = 7,500$ g; AMNH 197011 *Macropus fuliginosus*, $C_f = 69$ mm, $W = 28,500$ g; data provided by Paul Sereno), the observed femoral circumferences are similar to values predicted by equation 7. With weight as the dependent variable, the data used for equation 7 yield:

$$W = 1.08 C_f^{2.28 \pm 0.1} \quad (8 \text{ (a)})$$

$$\text{or} \quad \log_{10} W = 0.034 + 2.28 C_f, \quad r^2 = 0.94. \quad (8 \text{ (b)})$$

We are unaware of the reasons why the relationship between long-bone circumferences and weight should differ so greatly between birds (and kangaroos) and non-saltatorial mammals, but suspect it is linked to the relatively shorter and more horizontally oriented femur in the former (Coombs, 1978).

Weights for dinosaurs

Some earlier estimates of dinosaur weights have assumed that the cross-sectional area of the humerus and femur are proportional to body weight (cf. Bakker, 1972; Béland & Russell, 1980). However, Alexander *et al.* (1979), Maloiy *et al.* (1979) and Bakker (1980) have noted that the proportions of long-bones do not change with respect to body weight strictly according to models of geometric and elastic similarity. Equation 1 can thus be used in place of previous approximations as a means of estimating weights for quadrupedal dinosaurs. The proportions of the leg elements are similar in both non-saltatorial mammals and dinosaurs (Coombs, 1978). Sufficient data are not available from a broad enough range of weights and species of living reptiles to produce a general reptilian regression. An equation for alligators (Table II) resembles that for hippos. In both animals, the leg shafts are small relative to body weight, and it is tempting to consider this as the result of an amphibious mode of existence. The points from which the varanid equation (Table II) were calculated are centred on the mammalian regression line.

An equation for bipedal dinosaurs must be indirectly derived because of the lack of large living vertebrates with similar body shapes. The proportions of the posterior limb in bipedal dinosaurs resemble those in quadrupedal mammals more than those of birds and saltating mammals (Coombs, 1978, compare figs 5 and 9). An exponent of 2.8 was calculated from three cases where measurements of femoral circumferences can be related to weights estimated from models scaled from the same skeletons (*Stenonychosaurus*, Russell & Séguin, 1982; '*Anatosaurus*' and *Tyrannosaurus*, Colbert, 1962). Because this figure approximates the mammalian exponent, and because of similarities in limb proportions, the mammalian exponent is used with the

TABLE IV

Humeral and femoral circumferences in millimetres and estimated body weight in kilograms (rounded to two significant figures) for individuals belonging to 16 species of dinosaurs

	C_h	C_f	Estimated W (kg)	Calculated from scale models, a—Colbert, 1962 b—Bakker, 1972
Bipedal Dinosaurs				
<i>Parksosaurus warreni</i> (Ornithischia: Hypsilophodontidae; Parks, 1926)	—	103	50	
<i>Struthiomimus altus</i> (Saurischia: Ornithomimidae; AMNH 5339)	—	136	110	100 (<i>Dromiceiomimus</i> , b)
<i>Thescelosaurus garbani</i> (Ornithischia: Thescelosauridae; LACM 33542)	—	201	310	
<i>Ceratosaurus nasicornis</i> (Saurischia: Ceratosauridae; Madsen, 1976 p. 43)	—	267	670	
<i>Allosaurus fragilis</i> (Saurischia: Allosauridae; Madsen, 1976 p. 43)	—	348	1 400	1 000 (b) 2 090 (a)
<i>Hypacrosaurus altispinus</i> (Ornithischia: Hadrosauridae; NMC 8501)	—	400	2 000	3 000 (<i>Parasaurolophus</i> , b)
<i>Edmontosaurus regalis</i> (Ornithischia: Hadrosauridae; NMC 2289)	—	504	3 800	3 000 (<i>Parasaurolophus</i> , b)
<i>Anatosaurus copei</i> (Ornithischia: Hadrosauridae; AMNH 5730)	—	512	4 000	3 000 (<i>Parasaurolophus</i> , b) 3 380 (a)
<i>Tyrannosaurus rex</i> (Saurischia: Tyrannosauridae; CM 9380)	—	534	4 500	6 890 (a)
Quadrupedal dinosaurs				
<i>Leptoceratops gracilis</i> (Ornithischia: Protoceratopsidae; NMC 8889)	~95	~125	190	
<i>Styracosaurus albertensis</i> (Ornithischia: Ceratopsidae; NMC 344)	288	370	3 900	4 080 (a)
<i>Diplodocus</i> sp. (Saurischia: Diplodocidae; Mook, 1917)	320	405	5 000	10 560 (a) 15 000 (b)
<i>Opisthocoelicaudia skarzynskii</i> (Saurischia: Camarasauridae; Borsuk-Biatynicka, 1977)	565	680	22 000	
<i>‘Apatosaurus’ alenquerensis</i> (Saurischia: Diplo- docidae; Telles Antunes, pers. comm., 1979)	547	785	26 000	
<i>Brachiosaurus brancai</i> (Saurischia: Brachiosauridae; McIntosh, pers. comm., 1979)	654	730	29 000	78 260 (a)
<i>Apatosaurus louisae</i> (Saurischia: Diplodocidae; McIntosh, pers. comm., 1983)	629	845	35 000	27 870 (a) 30 000 (b) 32 420 (a)

Stenonychosaurus points ($C_f = 96$ mm, $W = 41,900$ g) to calculate the proportionality constant. The bipedal dinosaurian relationship becomes:

$$W = 0.16 C_f^{2.73}. \quad (9)$$

Representative dinosaurian weights are shown in Table IV.

Equation 1 predicts weights for *Allosaurus* and *Tyrannosaurus* which are about two-thirds those indicated by the models employed by Colbert (1962). This seems intuitively satisfactory for the models appear too ponderous in relation to the skeletons, in which the skulls are light, open structures and the vertebrae are penetrated by air cavities. Conversely, the ‘*Anatosaurus*’ model is

slenderer than the skeleton suggests. The sauropods *Diplodocus* and particularly *Brachiosaurus* are much lighter than indicated by the models. The *Diplodocus* limbs described by Mook (1917) are from a rather small animal. *Brachiosaurus* is well known for the extreme lightness of the bones of its axial skeleton, and the model used by Colbert may be too voluminous to properly reflect the bodily proportions of this giant giraffoid animal. The *Apatosaurus* models measured by Colbert produced weights lighter than that calculated for the type skeleton of *A. louisae* (CM 3018). Bakker (1980, p. 355, figs 4–5) also estimated weights for several dinosaurian species from scale models. His estimates for weights of an ornithomimid and a hadrosaurid compare well with those listed for similar animals in Table IV. The *Diplodocus* model, however, yielded a much greater weight and the *Apatosaurus* model a lighter weight than those indicated by the regression.

Although Van Valen (1969) cited appendicular elements of *Brachiosaurus brancai* (femoral circumference = 730 mm, Table IV) and *Antarctosaurus giganteus* (femoral circumference = 800 mm, pers. comm. J. S. McIntosh, 1983) as pertaining to the largest known dinosaurs, the femoral circumference in several sauropods is larger still. Among these are femora of *Titanosaurus falloti* from Laos (about 919 mm, Hoffer, 1942), a giant sauropod from the Algoa Basin, South Africa (about 921 mm, cf. McLachlan & McMillan, 1976, p. 202) and '*Brachiosaurus*' *ataliensis* from Portugal (about 998 mm, pers. comm. M. Telles Antunes, 1979).

There are many theoretical reasons why the circumferences of the humerus and femur might not accurately reflect body weight. Body weight is subject to short-term variations due to exercise, dehydration or seasonal changes in the abundance of food. Weight itself is less important than strenuous activity in generating high levels of stress within bones (Maloiy *et al.*, 1979). The elements in question usually vary in shape and orientation within the skeletal frameworks of different species, and mid-shaft circumference alone is clearly an incomplete descriptor of bone strength (cf. cantilever strength, Maloiy *et al.*, 1979). It was therefore gratifying to document the close relationship that apparently exists between circumference and body weight in various species of adult mammals and birds. A rapid and relatively accurate means is thus available for approximating the weight of extinct terrestrial vertebrates, which can in turn be incorporated into life-reconstructions and paleobiological analyses. However useful the above equations may appear to be as estimators of body weight in dinosaurs, their predictions should not be accepted uncritically. We anticipate that they will soon be superseded by more accurate combinations of estimators.

Conclusions

Within several species of carnivorous and herbivorous quadrupedal mammals, the combined circumference of the humerus and femur is proportional to (body weight)^{0.27}. In hippos, and particularly in starving populations of ungulates, the exponent is larger. Between species, the circumference of the humerus and femur scales according to the 0.38 and 0.35 power of body weight, respectively, including mammals weighing in excess of 300 kg. In flying birds, the circumference of the femur scales according to the 0.41 power of body weight. These interspecific exponents agree with values estimated previously for long-bone diameters. Two equations are proposed for estimating body weight in dinosaurs: $W = 0.078 C_{h+f}^{2.73}$ for quadrupedal dinosaurs; and $W = 0.16 C_f^{2.73}$ for bipedal dinosaurs. Some sauropods were not as heavy as implied by the volumes of some scale models; measurements of the circumferences in large articulated skeletons of *Brachiosaurus brancai* and *Apatosaurus louisae* indicate live weights of 29

and 35 metric tons, respectively. However, fragmentary skeletal materials belonging to other sauropods suggest that even larger animals may have existed.

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