

Giants and Bizarres: Body Size of Some Southern South American Cretaceous Dinosaurs

GERARDO V. MAZZETTA^{a,*}, PER CHRISTIANSEN^{b,†} and RICHARD A. FARIÑA^{a,‡}

^aDepartamento de Paleontología, Facultad de Ciencias, Universidad de la República, Iguá 4225, 11400 Montevideo, Uruguay;

^bDepartment of Vertebrates, Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark

Body masses of some South American dinosaurs are estimated. The sauropod *Argentinosaurus huinculensis* reached 73 tonnes, and therefore, is the largest of all land animals whose mass has been rigorously obtained. Another sauropod, *Antarctosaurus giganteus*, was the second largest, at nearly 69 tonnes, while *Antarctosaurus wichmannianus* reached 34 tonnes. A third sauropod, the bizarre-looking *Amargasaurus cazauí*, was much smaller, with a body mass of only 2.5 tonnes. Among theropods, the body mass of the strangely looking, horned *Carnotaurus sastrei*, was volumetrically estimated at 1.5 tonnes, while allometric equations on limb measurements yielded overestimations. Moreover, the holotype specimen of *Giganotosaurus carolinii* (MUCPv-CH-1) was about as large as the average-sized *Tyrannosaurus rex*, and only marginally smaller than “Sue”, the largest specimen. However, a new dentary of *Giganotosaurus* (MUCPv-95) is 8% longer than that of the holotype. Assuming geometric similarity, that individual must have had a body mass above 8 tonnes and hence must have been the largest theropod ever found.

Keywords: South American dinosaurs; *Argentinosaurus*; *Antarctosaurus*; *Amargasaurus*; *Giganotosaurus*; *Carnotaurus*

INTRODUCTION

Dinosaurs were the dominant forms of the Cretaceous tetrapod faunas of southern South America, as they were in general throughout the Mesozoic ecosystems (Wing *et al.*, 1992). Among the dinosaurs, sauropods are particularly interesting from a biological point of view since some of them constituted the largest terrestrial vertebrates by a wide margin (Benton, 1990; Christiansen, 1997; 2002). The large-bodied Laurasian sauropods are generally the more well known, and some of these were of truly gigantic proportions, but some

sauropods from southern South America appear to have rivalled or even exceeded the hitherto largest known Laurasian forms.

It is difficult to say to what extent the known southern South American taxa might have characterised the Cretaceous continental assemblages of all of South America. However, it seems reasonable to suppose that most of the dinosaur groups recorded in southern South America were present in other regions of the continent as well, where relatively less palaeontological excavations have been made and where preservation conditions are not as favourable as in Patagonia. Bonaparte (1986) has pointed out that most of the dinosaurian taxa of the South American Cretaceous were indicative of the endemism observed throughout most of the southern supercontinent of Gondwana. This process was likely brought about by the relative geographic isolation of Gondwana and Laurasia, which probably began in the Middle Jurassic and lasted until the Campanian (Bonaparte, 1986, 1996a). However, this palaeobiogeographic issue still needs further study to be fully understood. The current knowledge of the dinosaur fauna of the South American Cretaceous indicates that it shows reasonably good affinities with the Cretaceous faunas of other Gondwanan landmasses: Africa, Indo-Madagascar, and Australia (Bonaparte, 1986; Sampson *et al.*, 1998), and more substantial differences with the Laurasian fossil record (Bonaparte and Kielan-Jaworowska, 1987).

Several of the southern South American dinosaurs appear different from their Laurasian relatives. The dicraeosaurine sauropod *Amargasaurus cazauí* appears to have taken the elongated, bifurcate neural

*E-mail: mazzetta@fcien.edu.uy

†E-mail: p2christiansen@zmuc.ku.dk

‡Corresponding author. E-mail: fari~a@fcien.edu.uy

spines, common in the neck and anterior dorsal regions of diplodocoids, to extremes, as they resemble large spikes. Among the most interesting forms of titanosaurian sauropods known to date are *Argentinosaurus huinculensis*, widely regarded as the largest dinosaur hitherto known (Bonaparte and Coria, 1993; Appenzeller, 1994; Paul, 1994, 1997), and *Antarctosaurus giganteus*, which appears to have been nearly as large. Aspects of the palaeobiology of these giants have not been investigated, nor have rigorous body mass estimates been attempted. Two recent theropod discoveries on Gondwana, although incomplete or fragmentary, appear to have equalled or even exceeded in size to the largest and complete *Tyrannosaurus rex*, the specimen FMNH PR2081 informally known as “Sue” (Horner and Lessem, 1993). One of them is the predatory dinosaur *Carcharodontosaurus saharicus*, a species first recognised in 1927 and represented by new material (a skull) discovered in the earliest Late Cretaceous (Cenomanian) of the Kem Kem region of Morocco (Serenó *et al.*, 1996). The other, and probably the largest terrestrial flesh-eater ever found, is *Giganotosaurus carolinii*, from the mid-Cretaceous (Albian-Cenomanian) of north-western Patagonia, Argentina (Coria and Salgado, 1995; Calvo and Coria, 1998).

Palaeobiological studies of South American dinosaurs are scarce (Casamiquela, 1978; Mazzetta *et al.*, 1998; Blanco and Mazzetta, 2001; Mazzetta and Blanco, 2001). From a biological point of view, many dinosaurian taxa of southern South America are interesting and in need of palaeobiological analysis, particularly the above-mentioned huge titanosaurian sauropods and the large-bodied theropod, as they appear to represent size maxima in dinosaur evolution. In this paper, we address the estimation of their body size to provide a basis for further palaeobiological studies related to locomotion and other palaeoecological issues. Additionally, some bizarre Patagonian dinosaurs like the small sauropod *A. cazau* and the moderately-sized theropod *Carnotaurus sastrei* are also included as they are specimens constituted by nearly complete skeletons.

MATERIALS AND METHODS

Included Taxa

An incomplete femur attributed to *A. huinculensis* (labelled MLP-DP 46-VIII-21-3), and skeletal material belonging to its holotype (PVPH-1) and also to

the holotype of another titanosaurian sauropod, *A. giganteus* (MLP 23-316), were used for this study.[†] The mentioned material is housed at the exhibition of the Museo de La Plata, Argentina, except for the holotype of *A. huinculensis*, which is exhibited at the Museo Municipal “Carmen Funes” of Plaza Huincul, Neuquén, Argentina. Additionally, the principal hindlimb bones of *Antarctosaurus wichmannianus* were included. The latter material was collected in Chubut, Argentina (Huene, 1929), but presently is housed at the Field Museum of Natural History in Chicago. At present it appears uncertain if *A. wichmannianus* is a different species from *A. giganteus*, but in this paper they are treated as two species (the impressive size difference may be considered another indication that they represent two species). The femur (FMNH P13019) and associated tibia (FMNH P13020) are not from the same hindlimb (the femur is a right side bone, unlike the tibia) but were found together, indicating that they must have belonged to the same animal. This is further corroborated by the fact that the size and proportions appear right for one individual, and since the texture and colour of the two bones is identical. Although the bones are of gigantic dimensions they clearly belong to an individual distinctly smaller than the colossal *A. giganteus* (the length of the femur in MLP 23-316 is 2350 mm compared to 1855 mm in FMNH P13019).

The skeletal cast of *A. cazau*, mounted at the exhibition of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina, and additional material housed at the same institution, labelled MACN-N 15 (holotype), were also used in the analyses. Additionally, limb bone measurements of the holotype specimen of *C. sastrei* (MACN-CH 894) published by Bonaparte *et al.* (1990), and measurements on appendicular bones of the disarticulated holotype specimen of *G. carolinii* (MUCPv-CH-1), were also considered.

All the species studied here were found in Patagonia, Argentina. *A. giganteus* is from the Río Neuquén Formation, Early Cenomanian, Neuquén Province (north-western Patagonia) (Huene, 1929), and *A. cazau* (Fig. 1) is from the La Amarga Formation, Late Neocomian, Neuquén Province (Salgado and Bonaparte, 1991). *A. huinculensis* and *G. carolinii* are both from the Río Limay Formation, mid-Cretaceous (Albian-Cenomanian), Neuquén Province (Bonaparte and Coria, 1993; Coria and Salgado, 1995), while the other theropod included in the study, *C. sastrei* (Fig. 2), was collected

[†]Institutional abbreviations: CN, Zoology Museum, Copenhagen University; FMNH, Field Museum of Natural History, Chicago, USA; HMN, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MLP-DP (and also MLP), Departamento Científico de Paleontología de Vertebrados of the Museo de La Plata, La Plata, Argentina; MUCPv-CH, Museo de Geología y Paleontología de la Universidad Nacional del Comahue, Paleontología de Vertebrados, El Chocón collection, Neuquén, Argentina; PVPH, Museo Municipal “Carmen Funes”, Plaza Huincul, Neuquén, Argentina.

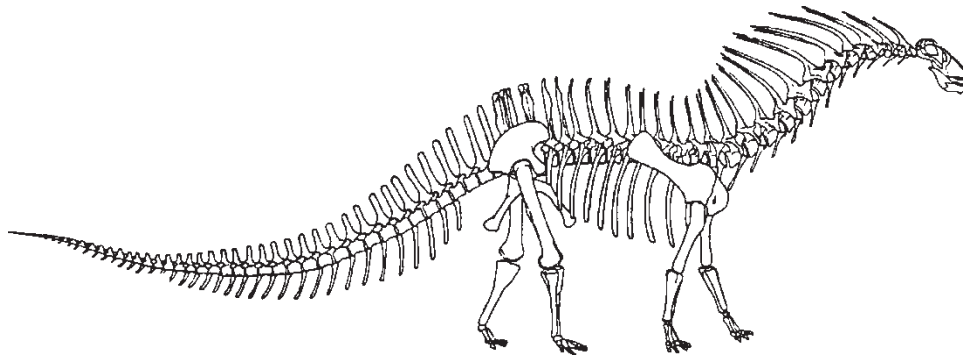


FIGURE 1 *Amargasaurus cazai*. Reconstruction of the skeleton. From Salgado and Bonaparte (1991).

from northern Chubut Province (Bonaparte, 1985; Bonaparte *et al.*, 1990). It was formerly believed to be from the Albian-Cenomanian Gorro Frigio Formation but later was referred to the lower section of La Colonia Formation, Late Cretaceous (Campanian-Maastrichtian) of Patagonia (Ardolino and Delpino, 1987).

Estimation of Body Mass

The body mass of the sauropod *A. cazai* was estimated by 3-D mathematical slicing (Henderson, 1999). For this purpose the width and height of its body (taking as reference its life-sized skeletal cast) was measured at regular intervals from the snout to the tip of the tail. Each pair of measurements was subsequently treated as the larger and lesser diameters of an ellipse. The outer surfaces between successive ellipses were smoothed to have a continuous outline of the body. Limb masses were calculated separately, and limbs were assumed to be cylinders. Following Alexander (1985), an overall density of 1000 kg m^{-3} was assumed for the body of *Amargasaurus*. Little difference is obtained considering a body density of 950 kg m^{-3} , as for the sauropods in Table I.

Unfortunately, the available skeletal material of the sauropods *A. huinculensis* and *Antarctosaurus* spp. (and the *G. carolinii*) is too fragmentary for a reliable model reconstruction to be made. Those sauropods are titanosaurs (e.g. Novas, 1997b; Salgado *et al.*, 1997a), which were the dominant sauropods in the Late Cretaceous (Upchurch, 1995). Although the detailed anatomy of the titanosaurs includes a great number of apomorphies compared to more archaic sauropods (Salgado *et al.*, 1997a,b), the overall body outline appears rather plesiomorphic for a sauropod, with rather long, but robust limbs (e.g. Borsuk-Bialynicka, 1977; Salgado *et al.*, 1997a; Wilson and Sereno, 1998), forelimbs not apomorphically shortened relative to the hindlimbs as in the diplodocoids, and lacking the apomorphically elongated neck and very elongated tail of these taxa with up to 82 caudal vertebrae (Christiansen, 1996). The few known fairly complete titanosaurs (e.g. *Saltasaurus loricatus*) appear to have been rather stoutly built with moderately long necks and tails, which has influenced popular reconstructions of *Argentinosaurus* (e.g. Appenzeller, 1994; Bonaparte, 1996b: p. 142). *Giganotosaurus* is a basal tetanurine theropod and most analyses indicate that it is a carnosaur (*sensu* Gauthier, 1986). It is most frequently placed alongside the almost equally

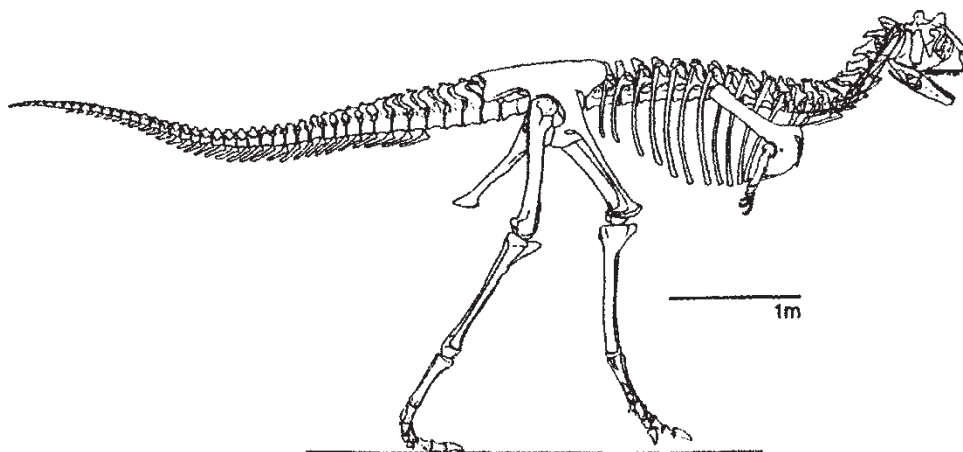


FIGURE 2 *Carnotaurus sastrei*. Reconstruction of the skeleton. From Bonaparte *et al.* (1990).

TABLE I Overall lengths, model-based body masses, and bone dimensions for a set of selected sauropods

Species	Overall length (m)	Body mass (kg)	Bone dimensions						
			fl	tl	fil	fw	fp	tp	va
<i>Amargasaurus cazau</i>	9.1	2600	1050	640	640	284	440	–	11,651
<i>Apatosaurus louisae</i>	22.8	20,600	1785	1115	1175	536	832	531	64,128
<i>Brachiosaurus brancai</i>	21.8	39,500	2028	1120	1190	590	945	518	148,597
<i>Camarasaurus supremus</i>	13.8	9300	1341	824	818	423	542	404	44,748
<i>Cetiosaurus oxoniensis</i>	16.5	15,900	1660	974	–	471	715	416	–
<i>Dicraosaurus hansemanni</i>	14.2	5700	1220	760	750	313	521	335	14,833
<i>Diplodocus carnegiei</i>	25.6	16,000	1540	1010	1050	412	589	356	43,004
<i>Euhelopus zdanskyi</i>	10.5	3800	955	602	618	261	400	264	12,441
<i>Haplocanthosaurus priscus</i>	14.8	12,800	1275	–	–	309	531	–	20,548
<i>Mamenchisaurus hochuanensis</i>	20.4	15,100	1275	860	865	380	621	331	61,850
<i>Omeisaurus tianfuensis</i>	20.2	9800	1215	855	860	331	526	432	–
<i>Opisthocoelicaudia skarzynskii</i>	11.3	8400	1395	810	830	430	644	424	26,507
<i>Shunosaurus lii</i>	9.9	3600	865	660	655	–	393	291	–

The body mass values shown were recalculated from Christiansen (1997), except for the cases of *Euhelopus*, *Haplocanthosaurus*, *Opisthocoelicaudia* (data taken from Paul, 1997), and *Amargasaurus* (datum calculated for this paper). Abbreviations: fl, length of the femur; tl, length of the tibia; fil, length of the fibula; fw, distal width of the femur across the condyles; fp, midshaft perimeter of the femur; tp, midshaft perimeter of the tibia; and va, cross-sectional area of the centrum of the second dorsal vertebra. All bone dimensions are in mm, except va (in mm²).

massive African *Carcharodontosaurus* in the Carcharodontosauridae (Serenó *et al.*, 1996), a taxon widely regarded as the sister taxon to the Allosauridae (Serenó *et al.*, 1996; Hutchinson and Padian, 1997; Novas, 1997b).

A number of Model II, Reduced Major Axis (RMA) or geometric mean regression analyses were performed (see Ricker, 1984, and Sokal and Rohlf, 1995 for computational background) in order to predict the body masses of *Argentinosaurus* and *Antarctosaurus* from measurements taken on their rather scarce skeletal remains (Fig. 3). Those analyses were performed on a log-transformed (base-10) database consisting of model-based body mass estimates and measurements of bone dimensions (such as lengths of the femur, tibia,

and fibula, distal width of the femur across the condyles, midshaft perimeter of the tibia, and cross-sectional area of the centrum of the second dorsal vertebra) in an array of 13 other sauropods listed in Table I. Clearly, both kinds of variables (that is, body mass and bone dimensions) are subject to measurement error as well as inherent, biological variability, thus requiring a Model II regression analysis (Sokal and Rohlf, 1995). Moreover, a geometric mean regression line is justifiable for prediction purposes when, as in this case, the sample (data) was withdrawn from a bivariate population whose frequency distribution is unknown.

The goodness of fit of the linear regression analysis was evaluated considering the correlation coefficient. A simple average (arithmetic mean) was

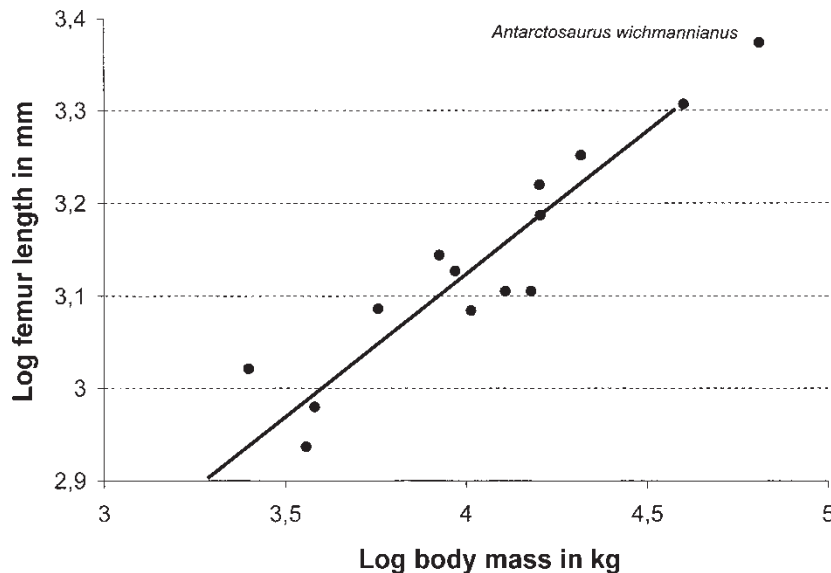


FIGURE 3 Two sample graphs (A, log body mass vs. log femur length and B, log body mass vs. log femur length cross sectional area of posterior articulating face of second dorsal vertebra), each showing the scatter of points on which a regression in Table II is based, the calculated regression line, and the predicted body masses of *Argentinosaurus huinculensis* and *Antarctosaurus wichmannianus*.

computed to estimate the body mass of the Patagonian sauropods taking into account the different body masses predicted by each equation.

The 13 sauropod species included in Table I represent a wide phylogenetic spectrum and their body masses had been found by weighing scale models in air and water in the case of *Apatosaurus*, *Brachiosaurus*, *Camarasaurus*, *Cetiosaurus*, *Dicraeosaurus*, *Diplodocus*, *Mamenchisaurus*, *Omeisaurus* and *Shunosaurus* (data from Christiansen, 1997). Commercially available models (see, e.g. Alexander, 1985, 1989) were avoided, as they are proportionally incorrect (Paul, 1997; Christiansen, 1997, 2000). However, the values from Christiansen (1997) were recalculated using a slightly higher overall density (950 kg m^{-3}), as the 900 kg m^{-3} used in that paper may be slightly too low. Most neosauropods have extensively pneumatized vertebrae, particularly the cervicals, which would tend to lower overall density. However, these animals are also very large, implying a proportionally greater amount of skeletal tissue (Christiansen, 2002), particularly appendicular skeletal tissue, and consequently, they should have had a higher overall density.

The body masses of *Euheleopus*, *Haplocanthosaurus*, and *Opisthocoelicaudia* were taken from Paul (1997). These were obtained from plasticine scale models, following a skeletal restoration. The body mass of *Amargasaurus* was also included in the database (see Table I) and its corresponding value was calculated by 3-D mathematical slicing (Henderson, 1999), as noted above. The right femur of the skeletal mount of *Brachiosaurus brancai* (HMN SII) consists of the original material proximally and distally (Janensch, 1950). Consequently, only the measurement corresponding to the distal part of the femur was included in the database. The diaphysis is lacking, and thus, the bone length is not available. Instead, the length of the femur of *B. altithorax* (FMNH 25107) was used, though this specimen appears to have been subequal in size to HMN SII (Paul, 1988; Christiansen, 1997).

Several of the dorsal vertebrae included in the holotype of *Argentinosaurus* appear rather well preserved (Bonaparte and Coria, 1993), which allowed the estimation of its body mass from regressions on the cross-sectional area of the centrum of the second dorsal vertebra. At present only the femoral diaphysis of *Argentinosaurus* is available (from the specimen MLP-DP 46-VIII-21-3), although a colossal femur (topotype) has also been referred to this species (Bonaparte, 1996b). Unfortunately, the latter specimen, which is exhibited at the Museo Municipal "Carmen Funes", has been anteroposteriorly compressed in fossilization, making it rather unreliable for body mass estimation based on its cross-sectional geometry. The "tibia" of the holotype (Bonaparte and Coria, 1993) is clearly not a tibia but a fibula. It lacks both the proportions and anatomical characters of a tibia.

The purported "cnemial crest" is merely the antero-proximal expansion common to sauropod fibulae, and the entire bone bears resemblance to the fibulae of other sauropods. Hence, the body mass of *Argentinosaurus* can also be regressed on its fibular length. Additionally, the fibular length (1550 mm), as well as the femoral midshaft perimeter of the specimen MLP-DP 46-VIII-21-3 (1180 mm), were used for prediction of femoral length in *Argentinosaurus*. This procedure was used to check the utility of the paratype material to predict the body mass of the holotype specimen. Accordingly, femoral length was regressed on fibular length and also on femoral midshaft perimeter considering the measurements taken on the 13 sauropod species mentioned in Table I plus *A. wichmannianus* (Table III). The extra measurement taken in *A. wichmannianus* was its femoral midshaft perimeter (873 mm).

Finally, multivariate regression analyses for prediction of sauropod body mass were performed on several "independent" variables with the aim of establishing if this technique would result in a better prediction of body mass than would be possible by any single "independent" variable. However, when a biological sample is considered, multivariate regression analysis of a "dependent" variable on a series of "independent" variables will inevitably lead to intercorrelation of the latter ones. Clearly, the proportions of an animal's backbone cannot be uncorrelated with the proportions of its limbs. Hence, tolerance values, eigen values and condition indices of the equation were computed to evaluate the intercorrelation of the "independent" variables. All data values were log-transformed (base 10) prior to statistical (bivariate or multivariate) analyses.

The lengths of the femora, tibiae and fibulae, as well as the midshaft perimeters of the femora and tibiae, were measured with a measuring tape. The distal widths of the femora across the condyles were measured with a large caliper. The cross-sectional areas of the centra of the second dorsal vertebrae were estimated from their diameters (dorsoventral and lateromedial) using the standard formula for the area of an ellipse.

The body masses of the theropods *Carnotaurus* and *Giganotosaurus* were estimated after the bivariate and multivariate regression equations in Christiansen and Fariña (2004). Those equations were obtained using a database of 16 theropod species, ranging in size from 16.5-kg *Ornitholestes* to 6300-kg *T. rex* and comprising a wide phylogenetic sample.

RESULTS

Sauropods

The estimated body mass for *A. cazau* was 2600 kg, when a normal vertebrate density of 1000 kg m^{-3} is used. The consideration of such a density value is

suggested by its stoutly built body, which does not show the common excavations (pleurocoels) found in the dorsal vertebrae of other sauropods. That figure is only slightly lowered to 2460 kg if the density assumed for the rest of the sauropods (950 kg m^{-3}) is used.

The rest of the sauropod species studied here are of very large dimensions. Indisputably, the largest dinosaur (and also the largest land animal) that is known from a reasonably complete skeleton is *B. brancai*. The skeleton of the specimen HMN SII is mounted at the Museum für Naturkunde in Berlin, and major portions of this skeleton can also be viewed (as casts) in the composite mount of *B. altithorax* at the Field Museum of Natural History in Chicago. The body mass of *Brachiosaurus* has been greatly exaggerated in many publications (e.g. Colbert, 1962; Norman, 1985; Benton, 1988; Gunga *et al.*, 1995; Christian *et al.*, 1999).

The fragmentary skeletal remains of *Argentinosaurus* (see Figs. 4 and 5) are distinctly larger than the corresponding parts of *Brachiosaurus*. For instance, some of its dorsal vertebrae are more than a meter

and a half tall (159 cm for the reconstructed first? dorsal) and the fibula is 155 cm long (described as a tibia by Bonaparte and Coria, 1993: Fig. 1), compared to 119 cm in HMN SII. Moreover, the fragmentary femoral diaphysis attributed to *Argentinosaurus* measures no less than 118 cm in its narrowest cross-sectional perimeter, compared to 94 cm in *Brachiosaurus altithorax* FMNH 25107 (203 cm long), and 82 cm in the rather slender specimen HMN XVI of *B. brancai* (211 cm long). Evidently, the body mass of *Argentinosaurus* was impressive. Some researchers have guessed its mass at close to 100 tonnes (Appenzeller, 1994), and Paul (1997) estimated its mass to be 90 tonnes.

When using a simple geometric scaling with fibular length in *Brachiosaurus* HMN SII (119 cm), which phylogenetically is the closest to *Argentinosaurus* in the database (Table I) (Salgado *et al.*, 1997a; Wilson and Sereno, 1998), a value of 87287 kg is obtained. *Camarasaurus* is the outgroup to the Titanosauriformes (*Brachiosaurus* + Titanosauria) (Salgado *et al.*, 1997a; Wilson and Sereno, 1998) and its overall body shape bears closer resemblance to



FIGURE 4 Cast of a vertebra of the giant sauropod *Argentinosaurus huinculensis*, as exhibited in the Museo Municipal del Chocón, Neuquén, Argentina (Photograph taken by L. Quagliotto).



FIGURE 5 Fragment of a huge femur of *Argentinosaurus huinculensis*, as exhibited in the Museo de La Plata.

those of known titanosaurs. A simple fibular scaling with the present specimen of *Camarasaurus supremus* (81.8 cm long) predicts a mass of 63273 kg for *Argentinosaurus*.

More reliable estimates should be obtained with the regression equations included in Table II. According to their correlation coefficients and s_v , the regressions computed on length of the femur (in a restricted sample without *Amargasaurus* and *Mamenchisaurus*), length of the tibia, length of

the fibula, and cross-sectional area of the centrum of the second dorsal vertebra (in a restricted sample without *Haplocanthosaurus*) constitute the most reliable equations for body mass prediction of all the equations. It should be made clear that, in the cases of *Antarctosaurus* and *Argentinosaurus*, we had to extrapolate beyond the range of our observational data to estimate the body masses of these huge sauropods.

The femoral length of *Argentinosaurus* predicted with the regressions on femoral midshaft perimeter and also fibular length are 2525, 2486, and 2659 mm, from equations 1, 2, and 3, respectively (Table III). When its average is computed, the final length estimate is 2557 mm. All of the above predicted lengths are highly similar, and are also nearly identical to Bonaparte's (1996b) length measurement for the complete femur referred to *Argentinosaurus* (250 cm). Thus, those values are within 2% of the length measured on that femur, which is considered a validation of the reliability of such predictions. On the other hand, those predictions indicate that the femoral fragment MLP-DP 46-VIII-21-3 and the complete femur belongs to individuals of the same size than the holotype. Consequently, the femoral midshaft perimeter measured in the former specimen and the femoral length measured in the latter were also used to estimate the body mass of *Argentinosaurus*.

Unfortunately, the length of the tibia and the distal width of the femur cannot be used to predict the body mass of *Argentinosaurus* (its tibiae were not found and the femur assigned to this species is distorted, as mentioned earlier). Hence, the body mass of *Argentinosaurus* has been computed from six regression equations, where the predicted values range from 60 to 88 tonnes (Table IV). When the average body mass is calculated, the result obtained is approximately 71 tonnes.

The multivariate regression equation of body mass on the length of the fibula and the cross-sectional area of the centrum of the second

TABLE II Bivariate (geometric mean) regression equations of log-transformed (base-10) data for prediction of body mass in sauropods

Equation	X	n	$\log u \pm 95\% \text{ CI}$	$v \pm 95\% \text{ CI}$	r	F
(1)	fl	13	-5.983 ± 2.780	3.195 ± 0.891	0.907	51.268**
(2)	fl*	11	-4.864 ± 2.120	2.838 ± 0.677	0.949	80.826**
(3)	fw	12	-3.589 ± 2.882	2.931 ± 1.116	0.842	24.274**
(4)	fw [†]	11	-3.881 ± 2.593	3.030 ± 1.000	0.899	37.964**
(5)	fp	13	-4.166 ± 2.291	2.955 ± 0.830	0.906	50.388**
(6)	tl	12	-7.342 ± 2.285	3.876 ± 0.782	0.958	111.994**
(7)	tp	11	-4.507 ± 3.829	3.288 ± 1.483	0.801	16.157***
(8)	fil	11	-6.521 ± 2.255	3.594 ± 0.771	0.959	102.008**
(9)	va	10	-0.438 ± 1.371	0.980 ± 0.304	0.925	47.303**
(10)	va [†]	9	-0.532 ± 1.009	0.994 ± 0.222	0.968	104.657**

v and u are the slope and antilog of the intercept in the regression equations, as $\log(\text{body mass}) = v \log X + \log u$. In all cases, body masses are calculated in kilograms and bone dimensions are considered in millimetres. Abbreviations as in Table I. (**, $P < 0.001$; ***, $0.001 < P < 0.01$). *Excluding outliers *Amargasaurus* and *Mamenchisaurus*. †Excluding outlier *Haplocanthosaurus*.

TABLE III Bivariate (geometric mean) regression equations of log-transformed (base-10) data for prediction of femoral length in *Argentinosaurus*

Equation	X	n	$\log u \pm 95\% \text{ CI}$	$v \pm 95\% \text{ CI}$	r	F
(1)	fp	14	0.616 ± 0.378	0.907 ± 0.136	0.971	197.937***
(2)	fp*	13	0.640 ± 0.305	0.897 ± 0.110	0.983	310.375***
(3)	fil	11	-0.107 ± 0.760	1.107 ± 0.260	0.950	83.827***

All bone dimensions are considered in millimeters. Abbreviations as in Table I. (***, $P < 0.001$). *Excluding outlier *Diplodocus*.

dorsal vertebra is:

$$\begin{aligned} \log(\text{body mass}) = & -3.226 \pm 2.460 + 1.562 \\ & \pm 1.298 (\log \text{ fibular length}) \\ & + 0.581 \pm 0.362 (\log \text{ vertebral area}) \end{aligned}$$

where body mass is calculated in kilograms, and the bone measures, fibular length and vertebral area, are expressed in mm and mm^2 , respectively ($R=0.986$; $F=104.358$; $P<0.001$). As expected the tolerance values, eigen values and condition index indicated substantial intercorrelation of the “independent” variables (condition index up to 142 and tolerance values of 0.201), but this is probably unavoidable in a biological sample where multiple measures are taken on the same animal. However, the partial regression coefficients are significant (two-tailed t -tests yield P values of 0.029 and 0.009, for the coefficients of fibular length and vertebral area, respectively), so redundancy of the selected predictor variables can be ruled out.

The multivariate equation mentioned above predicts a body mass of 72936 kg for *Argentinosaurus*. As the multivariate regression analysis not only has a higher correlation coefficient than any of the bivariate analyses, but also incorporates more anatomical dimensions (i.e. more information), we consider the latter value of 73 tonnes as the most likely and will use this figure in further discussion.

Antarctosaurus was also an enormous sauropod (Fig. 6). Two complete femora of the largest

TABLE IV Computed body masses of *Argentinosaurus huinculensis* and *Antarctosaurus wichmannianus*. Numbered equations are those defined in Table II

Species	Equation used	Body mass (kg)
<i>A. huinculensis</i>	(1)	74,717
	(2)	60,166
	(5)	81,548
	(8)	88,115
	(9)	63,158
	(10)	60,432
<i>A. wichmannianus</i>	(1)	28,798
	(2)	25,797
	(3)	35,790
	(4)	34,419
	(5)	33,473
	(6)	47,611
	(7)	30,182

species, *A. giganteus*, are known. It seems, however, to have been smaller than *Argentinosaurus*, but clearly larger than *Brachiosaurus*. A simple geometric scaling of femoral and tibial lengths of the smaller species *A. wichmannianus* (measurements taken on specimens FMNH P13019 and FMNH P13020, respectively) to the specimen of *C. supremus* (Table I) yields body mass values of 24617 and 33410 kg, respectively. This is roughly comparable to the values obtained with the regression equations from Table II. In those cases, the body masses range from about 26 to almost 48 tonnes (Table IV). Regression equations related to femoral length yielded body masses of nearly 29 tonnes (equation 1) and almost 26 tonnes (equation 2) for

FIGURE 6 Femur of *Antarctosaurus giganteus*, exhibited in the Museo de La Plata besides a cast of *Diplodocus carnegiei*.

A. wichmannianus, which are in the range of the values obtained with the geometric scaling mentioned above. The average of the seven body masses computed in Table IV is almost 34 tonnes.

A number of multivariate analyses were also performed on the bone dimensions of the sauropods from Table I, but these only resulted in marginally higher correlation coefficients compared to the bivariate regression equations in Table II.

The femur of *A. wichmannianus* (FMNH P13019) is, however, distinctly smaller (1855 mm) than the gigantic femur MLP 23-316 of *A. giganteus* (2350 mm). Assuming a geometric scaling with the FMNH specimen, which is reasonable since they could even be from the same species, results in a body mass of nearly 69 tonnes for *A. giganteus*, befitting for the name. Thus, this colossus was evidently not that much smaller than *Argentinosaurus*.

Theropods

A body mass of 1500 kg was estimated for *C. sastrei* using a volumetric procedure (Mazzetta *et al.*, 1998). Here, its body mass was predicted from the appendicular bone measurements available in Bonaparte *et al.* (1990), using the regression equations obtained by Christiansen and Fariña (2004) (Table V). The average of the body mass values predicted is approximately 2100 kg and only one of them is about the value obtained through the volumetric estimation, while all the others are above that figure.

The disarticulated cranial bones of *G. carolinii* do not allow accurate size comparison with *T. rex*. A comparison between their respective appendicular bones shows that the femur of *Giganotosaurus* (1.43 m long) is about 5 cm longer than that of "Sue" (FMNH PR2081), although the tibia (1.12 m long) is 8 cm shorter, as is common in more plesiomorphic carnosaurs *sensu* Gauthier (1986) (see Christiansen and Bonde, 2002). Most bones included in the holotype of *Giganotosaurus* (MUCPv-CH-1) indicate that this species was at least similar in size to the largest known *Tyrannosaurus* specimens, or even bigger if one considers the fragmentary dentary

specimen MUCPv-95 (Calvo and Coria, 1998). Hence, assuming equal size between the holotype specimen of *Giganotosaurus* and the robust morph of *Tyrannosaurus*, a body mass of about 8 tonnes could be considered for the former taking into account reliable body mass estimates for the biggest specimens of *Tyrannosaurus* (Paul, 1997; Henderson, 1999). On the other hand, assuming geometric similarity with the holotype specimen of *Giganotosaurus*, a body mass of about 10 tonnes is estimated for the individual corresponding to the specimen MUCPv-95 (the ratio of dentary lengths between them is 0.926, therefore its body mass is $8 \times 1.08^3 = 10.1$ tonnes).

However, tyrannosaurids are very apomorphic, and therefore a better comparison should be made with the more plesiomorphic (and much closer related) carnosaurs *Allosaurus* and *Sinraptor* (data published in Christiansen, 1998). A simple length comparison between *Giganotosaurus* and *Allosaurus* predicts a body mass of 7796 kg using the femur and 5460 kg using the tibia. The latter may not be too reliable since big carnosaurs become more stubby-legged. When compared with the 1700-kg *Sinraptor dongi*, the body mass predictions for *Giganotosaurus* are 7196 and 4364 kg, using the lengths of femur and tibia, respectively.

More reliable body mass estimates for *Giganotosaurus* are shown in Table VI. Those estimates were obtained using the equations derived from the database of theropods cited above (Christiansen and Fariña, 2004). The average of bivariate equations is 5604 kg, but it includes a very low value predicted from the distal lateromedial diameter of the femur (2369 kg). If this outlier is excluded, the average amounts to 6143 kg. Multivariate equations, on the other hand, yielded an average of 6510 kg. Four equations yielded very low body mass estimates (between 3828 and 4418 kg), while two others produced very high estimates (9268 and 10,709 kg). If the four lower values in Table VI are excluded, the average is 6846 kg, while if the two higher values are not taken into account, the average is 6278 kg. Finally, the average without the six outliers is 6604 kg.

TABLE V Body mass estimates for *Carnotaurus sastrei*. Predictions based on bivariate and multivariate regression equations (Christiansen and Fariña, 2004). (Bone measurements are from Bonaparte *et al.*, 1990)

Bone dimension (kg)	Measurement (mm)	Body mass
Femoral length	1030	2626
Femoral midshaft anteroposterior diameter	~100	1795
Femoral midshaft lateromedial diameter	~100	-
Femoral distal lateromedial diameter	197.5	1488
Tibial midshaft anteroposterior diameter	70	-
Femoral length and Femoral midshaft lateromedial diameter	-	2415
Femoral length and Femoral distal lateromedial diameter	-	2361
Femoral length and Tibial midshaft anteroposterior diameter	-	2339
Femoral midshaft anteroposterior diameter and Femoral distal lateromedial diameter	-	1696
Average	-	2102

TABLE VI Body mass estimates for *Giganotosaurus carolinii*. Predictions based on bivariate and multivariate regression equations (Christiansen and Fariña, 2004)

Bone dimension	Body mass (kg)
Bivariate analyses:	
Femoral length	7532
Femoral midshaft perimeter	6167
Femoral midshaft anteroposterior diameter	6220
Femoral distal lateromedial diameter	2369*
Tibial midshaft perimeter	6704
Tibial distal lateromedial diameter	4884
Fibular proximal anteroposterior diameter	5353
Average	5604
Multivariate analyses:	
Femoral length and least perimeter	7017
Femoral length and Femoral midshaft lateromedial diameter	7204
Femoral length and Femoral distal lateromedial diameter	6053
Femoral length and Tibial midshaft perimeter	7296
Femoral length and Tibial midshaft anteroposterior diameter	6885
Femoral length and Tibial midshaft lateromedial diameter	7676
Femoral length and Tibial distal lateromedial diameter	6758
Femoral length and Fibular distal anteroposterior diameter	7901
Femoral length and Fibular distal lateromedial diameter	7955
Femoral midshaft perimeter and Tibial length	5332
Femoral perimeter and Tibial midshaft lateromedial diameter	6581
Femoral midshaft perimeter and Tibial distal lateromedial diameter	5808
Femoral midshaft anteroposterior diameter and Femoral distal lateromedial diameter	4255*
Femoral midshaft anteroposterior diameter and Tibial midshaft perimeter	6439
Femoral midshaft anteroposterior diameter and Tibial midshaft anteroposterior diameter	5525
Femoral midshaft anteroposterior diameter and Tibial distal lateromedial diameter	5598
Femoral midshaft anteroposterior diameter and Fibular midshaft perimeter	8470
Femoral midshaft anteroposterior diameter and Fibular midshaft lateromedial diameter	7370
Femoral midshaft anteroposterior diameter and Fibular distal anteroposterior diameter	6451
Femoral distal lateromedial diameter and Tibial midshaft perimeter	4868
Femoral distal lateromedial diameter and Tibial midshaft lateromedial diameter	4137*
Tibial length and Fibular midshaft perimeter	7184
Tibial length and Fibular distal anteroposterior diameter	4418*
Tibial midshaft perimeter and Fibular midshaft perimeter	7524
Tibial midshaft perimeter and Fibular midshaft lateromedial diameter	6898
Tibial midshaft perimeter and Fibular distal anteroposterior diameter	6404
Tibial midshaft perimeter and Fibular distal lateromedial diameter	6259
Tibial midshaft lateromedial diameter and Fibular midshaft perimeter	10709 [†]

TABLE VI – *continued*

Bone dimension	Body mass (kg)
Tibial midshaft lateromedial diameter and Fibular midshaft lateromedial diameter	9268 [†]
Tibial midshaft lateromedial diameter and Fibular distal lateromedial diameter	4758
Tibial distal lateromedial diameter and Fibular length	3828*
Fibular proximal anteroposterior diameter and Fibular distal anteroposterior diameter	5500
Average	6510

* Too low values. [†] Too high values.

DISCUSSION

Sauropods

Gregory (1905) was probably the first to report on body mass prediction in a sauropod. Based on the reconstruction designed by Charles Knight, a model of the skeletal mount of *Apatosaurus excelsus* was made, and the estimation of its body mass yielded 31 tonnes, clearly due to erroneous body proportions and a very portly design. Errors in model proportions are particularly liable to lead to inflated body mass estimates (Paul, 1997; Christiansen, 2000).

Among those sauropods studied here, *Amargasaurus* is clearly the smaller. As mentioned above, the estimated body mass of this bizarre-looking, small sauropod was about two and a half tonnes. The other sauropods in this paper are real giants, and must be compared with the largest known dinosaurs ever found. *Brachiosaurus* has traditionally been considered one of the largest, if not the largest, sauropod known, and for many years this was probably true. However, this is clearly not the case anymore. Colbert (1962) was the first researcher to report on the body mass of *Brachiosaurus*, but he also used a badly proportioned model. Additionally, he used a wrong scale. *Brachiosaurus* does not, as reported by Colbert (1962), stand 609 cm at the hips, but rather an estimated height of 540 cm (Paul, 1988), and the scaling error alone would lead to a body mass of 63,400 kg, not the widely cited value of 78,300 kg. More accurate reconstructions predict a body mass for *Brachiosaurus* of 32 (Paul, 1988; Paul, 1997) to 37 tonnes (Christiansen, 1997). However, note that in the latter paper the body mass is closer to 40 tonnes due to the higher density used in the calculations. Alexander (1989) computed a body mass of 47 tonnes for *Brachiosaurus*, based on the commercial model from the British Museum (Natural History), which is also proportionally inaccurate (Paul, 1997; Christiansen, 2000). Ironically, the new, lower body mass estimates for *Brachiosaurus* are very similar to the first estimate of 40 tonnes, based

simply on Werner Janensch's personal opinion (Janensch, 1938).

Impressive as this undeniably is, *Brachiosaurus* is, however, clearly not the largest dinosaur known. This title currently befalls to *Argentinosaurus*. It probably did not, however, reach the figure of 100 tonnes, proposed as the more conservative upper mass limit for a land tetrapod by Hokkanen (1986), unless some specimens were much larger than the holotype. Unfortunately, this cannot be checked until new findings are produced. Other dinosaurs are known, however, that may have approached *Argentinosaurus* in body mass. "*Ultrasauros*" (Jensen, 1985) was said to be of extraordinarily colossal dimensions, often credited with a body mass of 100 tonnes or more (e.g. Ostrom, 1978; Benton, 1988; Gillette, 1994). In reality, the scapulocoracoid (250 cm long, not 270 cm as stated in Jensen, 1985) of "*Ultrasauros*" cannot be shown to be different from those of the genus *Brachiosaurus* (Curtice and Curtice, 1996), and it could well belong to the type species *B. altithorax*. It is from a specimen larger than the holotype FMNH 25107, but not by more than around 10 or so tonnes (Paul, 1988; Curtice and Curtice, 1996). It probably had a mass of 45–50 tonnes. Additionally, equally large remains of *B. brancai* have been known, but clearly not discussed, for nearly a century. The scapula on HMN SII is nearly as large (193 cm, scapulocoracoid 238 cm), and an even larger scapula (203.5 cm) is on exhibition at the Museum für Naturkunde, Berlin (Christiansen, Personal observation). This is as large as that of "*Ultrasauros*". The reported dorsal vertebra of "*Ultrasauros*" is not even brachiosaurian but from a diplodocid (Curtice and Curtice, 1996). The type specimen of "*Ultrasauros*" was not the scapulocoracoid but that large diplodocid dorsal vertebra, now referred to *Supersaurus* (Britt and Curtice, 1997).

Supersaurus (Jensen, 1985) is a huge diplodocid, and at an estimated body mass of around 50 tonnes it is the largest diplodocid for which there are substantial remains (Paul, 1988, 1997). *Seismosaurus halli* (Gillette, 1987, 1991) is not as large, and claims of a body length of 50 m (Gillette, 1994) are based on dimensions other than vertebral lengths. Paul (1997) estimated that this animal would have had a body mass of around 30 tonnes, at an overall length of 32–35 m. The only other sauropods which could have been subequal in size to *Argentinosaurus* are known from only very fragmentary remains. *Sauroposeidon proteles* is a gigantic brachiosaurid (Wedel *et al.*, 2000a) that appears to have been substantially larger than *B. brancai* HMN SII. However, it would probably not have had a greater body mass than *Argentinosaurus*, and Wedel *et al.* (2000b) suggested that it probably had a mass of 50–60 tonnes, subequal to *A. giganteus*.

The incomplete vertebra of the diplodocid *Amphicoelias fragillimus* (Cope, 1878) apparently

was of colossal dimensions, indicating an animal potentially larger than even *Argentinosaurus* (Appenzeller, 1994; Paul, 1994, 1997). However, this vertebra has been lost for more than a century, making its true size and phylogenetic affinities uncertain.

Recently, Smith *et al.* (2001) described the partial skeleton of *Paralititan stromeri*, an extremely large titanosaurian sauropod from the Late Cretaceous of the Bahariya Oasis, Egypt. However, and according to these authors, this new species is probably not as large as *Argentinosaurus* but represents one of the biggest terrestrial vertebrates yet discovered.

Finally, one of the included species in this analysis (*A. giganteus*) is also one of the largest dinosaurs ever discovered. The huge bones of the holotype have long been regarded as remains of one of the largest of all sauropods known. Paul (1988) estimated its body mass at 40–50 tonnes, but our results indicate that this value is too low. Janensch (1938) noted that its femora were the largest long bones from any known sauropod, and with the exception of the only known complete femur of *Argentinosaurus*, this still holds true today. However, its femoral length is 235 cm, not 231 cm as given by most previous authors. Van Valen (1969) estimated that *A. giganteus* had a body mass of around 80 tonnes, based mainly on comparisons with Colbert's (1962) inflated mass of 78 tonnes for *Brachiosaurus*. As explained earlier, our body mass estimation for *A. giganteus* yielded a figure of about 69 tonnes, which is intermediate to those pointed out for previous authors.

Theropods

As mentioned above, a volumetric procedure yielded a body mass estimate of 1500 kg for *C. sastrei* (Mazzetta *et al.*, 1998). The body mass overestimates obtained here by the usage of allometric equations based on limb bone dimensions may be due to the phylogenetic composition of the database in Christiansen and Fariña (2004), mostly integrated by very advanced forms, such as the very closely related tyrannosaurs and ornithomimids. As a primitive theropod (clade Abelisauridae), *Carnotaurus* is substantially different in several respects from the more advanced ones (Bonaparte *et al.*, 1990; Novas, 1997a,b). In any event, this discrepancy does not affect the conclusion on its locomotor capability proposed by Mazzetta *et al.* (1998). Such a conclusion states that the femoral strength indicator (quantity inversely related to the body mass) of *Carnotaurus* was high enough to endure strenuous activities, suggesting that it may have preyed upon fast-moving, rather small prey.

On the other hand, *G. carolinii* must have been one of the largest theropods ever found, and even the largest. With a body mass of about six tonnes and a half (when only the predictions based on

the multivariate regression equations are taken into account), its size must have been lower than those corresponding to “Sue”, the largest specimen of *T. rex*. Nevertheless, the individual corresponding to the dentary MUCPv-95 exceeds the size of “Sue”, even considering an estimation of its body mass based on a simple geometric scaling with a 6.5-tonnes holotype specimen. In this case, its body mass is $6.5 \times 1.08^3 = 8.2$ tonnes (since its dentary is 8% longer than that of the holotype, as mentioned above). Hence, with a body mass above 8 tonnes, this individual must have been the largest theropod ever found, as well as the largest terrestrial carnivore of all times.

Acknowledgements

The authors thanks R.E. Blanco for his assistance during body mass calculation. R.McN. Alexander and P.M. Barrett gave us useful advice and made comments on earlier versions of the manuscript. We are indebted to S.F. Vizcaíno and other staff from La Plata Museum, and J.F. Bonaparte from the Museo Argentino de Ciencias Naturales for their help in measuring the specimens. L. Quagliotto kindly provided us with the photographs of Fig. 3. L. Salgado and R.A. Coria warned one of us (G.V.M.) about the possibility that the “tibia” of the holotype of *Argentinosaurus* was actually a fibula.

References

- Alexander, R.McN. 1985. Mechanics of posture and gait of some large dinosaurs. *Zoological Journal of the Linnean Society* **83**, 1–25.
- Alexander, R.McN. 1989. *Dynamics of Dinosaurs and Other Extinct Giants*. Columbia University Press, New York.
- Appenzeller, T. 1994. Argentine dinos vie for heavyweight titles. *Science* **266**, 1805.
- Ardolino, A. and Delpino, D. 1987. Senoniano (continental-marino), Comarca Nordpatagónica, Provincia del Chubut, Argentina. *Actas X Congreso Geológico Argentino* **3**, 193–196.
- Benton, M.J. 1988. *Dinosaurs: An A–Z Guide*. Grisewood and Dempsey Ltd., London.
- Benton, M.J. 1990. Evolution of large size. In Briggs, D.E.G. and Crowther, P.R. (eds), *Palaeobiology: A Synthesis*, pp 147–152. Blackwell Scientific, Oxford.
- Blanco, R.E. and Mazzetta, G.V. 2001. A new approach to evaluate the cursorial ability of the giant theropod *Giganotosaurus carolinii*. *Acta Palaeontologica Polonica* **46**, 193–202.
- Bonaparte, J.F. 1985. A horned Cretaceous carnosaur from Patagonia. *National Geographic Research* **1**, 149–151.
- Bonaparte, J.F. 1986. History of the terrestrial Cretaceous vertebrates of Gondwana. *Actas IV Congreso Argentino de Paleontología y Bioestratigrafía* **2**, 63–95.
- Bonaparte, J.F. 1996a. Cretaceous tetrapods of Argentina. *Münchener Geowissenschaftliche Abhandlungen (A)* **30**, 73–130.
- Bonaparte, J.F. 1996b. *Dinosaurios de América del Sur*. Museo Argentino de Ciencias Naturales, Buenos Aires.
- Bonaparte, J.F. and Kielan-Jaworowska, Z. 1987. Late Cretaceous dinosaur and mammal faunas of Laurasia and Gondwana. In Currie, P.J. and Koster, E.H. (eds), *Fourth Symposium in Mesozoic Terrestrial Ecosystems*, Short papers, pp. 24–29.
- Bonaparte, J.F., Novas, F.E. and Coria, R.A. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Contributions in Science, Los Angeles County Museum* **416**, 1–42.
- Bonaparte, J.F. and Coria, R.A. 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiano-Cenomaniano) de la Provincia del Neuquén, Argentina. *Ameghiniana* **30**, 271–282.
- Borsuk-Bialynicka, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii* gen. n., sp. n. from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica* **37**, 1–64.
- Britt, B.B. and Curtice, B.D. 1997. Dry Mesa quarry. In Currie, P.J. and Padian, K. (eds), *Encyclopedia of Dinosaurs*. Academic Press, San Diego, p 196.
- Calvo, J.O. and Coria, R.A. 1998. New specimen of *Giganotosaurus carolinii* (Coria and Salgado, 1995), supports it as the largest theropod ever found. In Pérez-Moreno, B.P., Holtz, T.R., Jr., Sanz, J.L. and Moratalla, J.J. (eds), *Aspects of Theropod Palaeobiology, Gaia Special Volume*, pp. 117–122. Lisbon.
- Casamiquela, R.M. 1978. La zona litoral de la transgresión mastrichtiense en el norte de la Patagonia, Aspectos ecológicos. *Ameghiniana* **15**, 137–148.
- Christian, A., Heinrich, W.-D. and Golder, W. 1999. Posture and mechanics of the forelimbs of *Brachiosaurus brancai* (Dinosauria: Sauropoda). *Mitteilungen aus dem Museum für Naturkunde in Berlin. Geowissenschaftlicher Reihe* **2**, 63–73.
- Christiansen, P. 1996. The ‘whiplash’ tail of diplodocid sauropods: Was it really a weapon? In Morales, M. (ed), *The Continental Jurassic*, pp 51–58. Museum of Northern Arizona, Flagstaff.
- Christiansen, P. 1997. Locomotion in sauropod dinosaurs. *Gaia* **14**, 45–75.
- Christiansen, P. 1998. Strength indicator values of theropod long bones, with comments on limb proportions and cursorial potential. In Pérez-Moreno, B.P., Holtz, T.R., Jr., Sanz, J.L. and Moratalla, J.J. (eds), *Aspects of Theropod Palaeobiology, Gaia Special Volume*, pp. 241–255, Lisbon.
- Christiansen, P. 2000. Dinosaur biomechanics. In Paul, G.S. (ed) *The Scientific American Book of Dinosaurs*, pp 64–77. Byron Press Inc., New York.
- Christiansen, P. 2002. Mass allometry of the appendicular skeleton in terrestrial mammals. *Journal of Morphology* **251**, 195–209.
- Christiansen, P. and Bonde, N. 2002. Limb proportions and avian terrestrial locomotion. *Journal of Ornithology* **143**, 356–371.
- Christiansen, P. and Fariña, R.A. 2004. Mass prediction in theropod dinosaurs. *Historical Biology*.
- Colbert, E.H. 1962. The weights of dinosaurs. *American Museum Novitates* **2076**, 1–16.
- Cope, E.D. 1878. A new species of *Amphicoelias*. *American Naturalist* **12**, 563–565.
- Coria, R.A. and Salgado, L. 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* **377**, 224–226.
- Curtice, B.D. and Curtice, L.J. 1996. Death of a dinosaur—a reevaluation of *Ultrasaurus macintoshii*. *Journal of Vertebrate Paleontology* **16**(Suppl. 3), 29A.
- Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Science* **8**, 1–55.
- Gillette, D.D. 1987. A giant sauropod from the Jackpile SS Member of the Morrison Formation (Upper Jurassic) of New Mexico. *Journal of Vertebrate Paleontology* **7**(Suppl. 3), 16A–17A.
- Gillette, D.D. 1991. *Seismosaurus halli*, gen. et sp. nov. A new sauropod dinosaur from the Morrison Formation (Upper Jurassic/Lower Cretaceous) of New Mexico. *Journal of Vertebrate Paleontology* **11**, 417–433.
- Gillette, D.D. 1994. *Seismosaurus—The Earth Shaker*. Columbia University Press, New York.
- Gregory, W.K. 1905. The weight of the *Brontosaurus*. *Science (NS)* **22**, 572.
- Gunga, H.C., Kirsch, K.A., Baartz, F., Röcker, L., Heinrich, W.-D., Lisowski, W., Weidemann, A. and Albertz, J. 1995. New data on the dimensions of *Brachiosaurus brancai* and their physiological implications. *Naturwissenschaften* **82**, 190–192.
- Henderson, D.M. 1986. Estimating the masses and centers of mass of extinct animals by 3-D mathematical slicing. *Paleobiology* **25**, 88–106.

- Hokkanen, J.E.I. 1999. The size of the largest land animal. *Journal of Theoretical Biology* **118**, 491–499.
- Horner, J.R. and Lessem, D. 1993. *The complete T. rex*. Simon and Schuster, New York.
- Hutchinson, J.R. and Padian, K. 1997. Carnosauria. In Currie, P.J. and Padian, K. (eds), *Encyclopedia of Dinosaurs*, pp 94–97. Academic Press, San Diego.
- Janensch, W. 1938. Gestalt und grösse von *Brachiosaurus* und anderen reisenwüchsigen Sauropoden. *Der Biologe* **7**, 130–134.
- Janensch, W. 1950. Die Skelettrekonstruktion von *Brachiosaurus brancai*. *Palaeontographica* **3**(Suppl. 7), 95–103.
- Jensen, J.A. 1985. Three new sauropod dinosaurs from the Upper Jurassic of Colorado. *Great Basin Naturalist* **45**, 697–709.
- Mazzetta, G.V. and Blanco, R.E. 2001. Speeds of dinosaurs from the Albian-Cenomanian of Patagonia and sauropod stance and gait. *Acta Palaeontologica Polonica* **46**, 235–246.
- Mazzetta, G.V., Fariña, R.A. and Vizcaíno, S.F. 1998. On the palaeobiology of the South American horned theropod *Carnotaurus sastrei* Bonaparte. In Pérez-Moreno, B.P., Holtz, T.R., Jr., Sanz, J.L. and Moratalla, J.J. (eds), *Aspects of Theropod Paleobiology, Gaia Special Volume*, pp. 185–192. Lisbon.
- Norman, D. 1985. *The Illustrated Encyclopedia of Dinosaurs*. Salamander Books, London.
- Novas, F.E. 1997a. Abelisauridae. In Currie, P.J. and Padian, K. (eds), *Encyclopedia of Dinosaurs*, pp 1–2. Academic Press, San Diego.
- Novas, F.E. 1997b. South American dinosaurs. In Currie, P.J. and Padian, K. (eds), *Encyclopedia of Dinosaurs*, pp 678–689. Academic Press, San Diego.
- Ostrom, J.H. 1978. A new look at dinosaurs. *National Geographic* **154**, 152–185.
- Paul, G.S. 1988. The brachiosaur giants of the Morrison and Tendaguru with a description of a new subgenus, *Giraffatitan*, and a comparison of the world's largest dinosaurs. *Hunteria* **2**, 1–14.
- Paul, G.S. 1994. Is Garden Park home to the world's largest known land animal? *Garden Park Paleontology Society* **4**, 5.
- Paul, G.S. 1997. Dinosaur models: the good, the bad, and using them to estimate the mass of dinosaurs. In Wolberg, D.L., Stump, E. and Rosenberg, G.D. (eds), *DinoFest International Proceedings*, pp 129–154. The Academy of Natural Sciences, Philadelphia.
- Ricker, W.E. 1984. Computation and uses of central trend lines. *Canadian Journal of Zoology* **62**, 1897–1905.
- Salgado, L. and Bonaparte, J.F. 1991. Un nuevo saurópodo Dicraeosauridae, *Amargasaurus cazau* gen. et sp. nov., de la Formación La Amarga, Neocomiano de la Provincia del Neuquén, Argentina. *Ameghiniana* **28**, 333–346.
- Salgado, L., Coria, R.A. and Calvo, C.O. 1997a. Evolution of titanosaurid sauropods. I: Phylogenetic analyses based on postcranial evidence. *Ameghiniana* **34**, 3–32.
- Salgado, L., Coria, R.A. and Calvo, C.O. 1997b. Evolution of titanosaurid sauropods. II: The cranial evidence. *Ameghiniana* **34**, 33–48.
- Sampson, S.D., Witmer, L.M., Forster, C.A., Krause, D.W., O'Connor, P.M., Dodson, P. and Ravoavy, F. 1998. Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. *Science* **280**, 1048–1051.
- Sereno, P.C., Dutheil, D.B., Iarochene, M., Larsson, H.C.E., Lyon, G.H., Magwene, P.M., Sidor, C.A., Varricchio, D.J. and Wilson, J.A. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science* **272**, 986–991.
- Smith, J.B., Lamanna, M.C., Lacovara, K.J., Dodson, P., Smith, J.R., Poole, J.C., Giegengack, R. and Attia, Y. 2001. A giant sauropod dinosaur from an Upper Cretaceous mangrove deposit in Egypt. *Science* **292**, 1704–1706.
- Sokal, R.R. and Rohlf, F.J. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research.*, 3rd ed. W.H. Freeman and Co., New York.
- Upchurch, P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society (Ser. B)* **349**, 365–390.
- Van Valen, L. 1969. What was the largest dinosaur? *Copeia* **1969**, 624–625.
- Von Huene, F. 1929. Los saurisquios y ornitisquios del Cretáceo Argentino. *Anales del Museo de La Plata* **3**, 1–196.
- Wedel, M.J., Cifelli, R.L. and Sanders, R.K. 2000a. Sauroposeidon proteles, a new sauropod from the early Cretaceous of Oklahoma. *Journal of Vertebrate Paleontology* **20**, 109–114.
- Wedel, M.J., Cifelli, R.L. and Sanders, R.K. 2000b. Osteology, paleobiology, and relationships of the sauropod dinosaur Sauroposeidon. *Acta Palaeontologica Polonica* **45**, 343–388.
- Wilson, J.O. and Sereno, P.C. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology* **18**(Suppl. 2), 1–68, *Memoir* 5.
- Wing, S.L. and Sues, H.D. and eight others 1992. Mesozoic and early Cenozoic terrestrial ecosystems. In Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.D. and Wing, S.L. (eds), *Terrestrial Ecosystems through Time*, pp 327–416. University of Chicago Press, Chicago.