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ARTICLE

MY THEROPOD IS BIGGER THAN YOURS . . . OR NOT: ESTIMATING BODY SIZE FROM SKULL LENGTH IN THEROPODS

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ABSTRACT—To develop a widely applicable method to estimate body size in theropods, the scaling relationship between skull length, body length, and body mass was investigated using 13 strictly carnivorous, non-avialan theropod taxa ranging in size from the 1-m *Sinosauropteryx prima* to the 12-m *Tyrannosaurus rex*. Body length was obtained from the literature for complete to nearly-complete specimens and body mass was obtained from three-dimensional mathematical slicing of those same specimens to ensure accurate body length-body mass associations. Least-square regressions reveal a tight correlation between skull length and body length (SK-BL) and skull length and body mass (SK-BM). The SK-BL regression is negatively allometric, which indicates that skulls become longer relative to body length with increasing body size. In contrast, the SK-BM regression is positively allometric, indicating that body mass increases faster than skull length with increasing body size. These conclusions confirm that the common practice of scaling isometrically smaller relatives of a given taxon to obtain body length and body mass estimates is not valid. Although predictive equations derived from the regressions fail to predict accurately body size in abelisaurids and juvenile theropods due to their different head/body proportions, they produce accurate body size estimates for theropods of known body size, thus validating their applicability. Body size estimates for *Carcharodontosaurus* and *Giganotosaurus*, approaching 13 m and 14 tons, suggest that they may have surpassed *Tyrannosaurus* in size. A revised body size estimate for a large *Spinosaurus* specimen suggests a much shorter and heavier animal than recently suggested.

INTRODUCTION

Most large theropods are known from incomplete skeletal remains, which give free course to the imagination when it comes to estimate the body length and body mass of the "largest terrestrial predators to have ever existed." Whereas relatively simple ways exist to estimate body size among diapsids (e.g., snout-vent length; see Blob, 2000) and mammals (e.g., Van Valkenburgh, 1990; Anyonge, 1993; Ruff, 2003; Anyonge and Roman, 2006), similar methods are lacking for dinosaurs. Current body size estimation methods for dinosaurs require either accurate scale models of the specimen considered (Colbert, 1962; Alexander, 1985a; Farlow et al., 1995; Paul, 1988; Christiansen and Fariña, 2004), well-preserved postcranial material (Anderson et al., 1985; Christiansen and Fariña, 2004), or a high degree of mathematical prowess (Seebacher, 2001; Henderson, 1999; Hurlburt, 1999), all of which prevent widespread application to a large number of specimens.

Recently, a 1-m-long *Spinosaurus* snout was described by Dal Sasso and colleagues. (2005). These authors claimed that it pertained to a 16-m to 18-m-long individual weighing between 7 and 9 tons, an animal that would have been longer than any theropod known but that would have weighed less than a 12-m-long *Tyrannosaurus rex* (see Henderson and Snively, 2004). This unexpected association of great body length with small body mass triggered our interest in conducting a detailed analysis of the correlations between head and total body length, and between total body length and body mass, in theropod dinosaurs to derive a method to estimate body size from skull length.

MATERIALS AND METHODS

To develop a simple method to estimate body size in theropods, the scaling relationship between skull length, body length, and body mass was investigated using 13 strictly carnivorous, exclusively terrestrial, non-avialan theropod taxa (represented by 19 individuals) known from complete to nearly complete specimens (Table 1). Ornithomimids, oviraptorosaurs, and therizinosaurs were not considered in this study because their skull and overall body proportions differ from the common theropod *Bauplan* (see Clark et al., 2004; Makovicky et al., 2004; Osmólska et al., 2004). Body length of each individual, ranging from the 1-m *Sinosauropteryx prima* to the 12-m *Tyrannosaurus rex*, was obtained from the literature. Skull length, defined as the distance between the tip of the premaxillae and the occipital condyle, of each individual was obtained either from the literature or measured on actual specimens or museum-quality casts/reconstructions. Body mass was derived from three-dimensional mathematical slicing (Henderson, 1999) of illustrations of 11 individuals (9 taxa) to ensure accurate body length-body mass associations. Because three-dimensional mathematical slicing has reproduced accurately the body mass of animals of different body size, body proportions, and phylogenetic affinities (Henderson, 1999, 2004; Henderson and Snively, 2004), it is considered a highly reliable body mass estimation method. Body mass estimates derived from three-dimensional mathematical slicing for theropod taxa are generally compatible with those derived from other methods (Table 1).

Skull length, body length, and body mass were $\log_{10}$ transformed to reduce the effects of allometry (Smith, 1984, 1993) and subsequently plotted as body length versus skull length (SK-BL) and body mass versus skull length (SK-BM) plots (Fig. 1). Al-

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*Corresponding author.

TABLE 1. Skull length, body length, and body mass of theropod specimens used to derive the SK-BL and SK-BM predictive equations

Taxon	Skull length (m)	Body length (m)	SK-BL estimate (m)	Body mass (kg)	SK-BM estimate (kg)	Published body mass estimates (kg)
Acrocanthosaurus atokensis NCSM 14345; Currie and Carpenter, 2000	1.230	11.50	10.55	5,672.00	5,864.65	
Allosaurus "atrox" UUVP 6000; Paul, 1988	0.845	7.90	7.65	?	1,516.84	1,320 (Paul, 1988)
Allosaurus fragilis YPM 1930; Paul, 1988	0.682	7.40	6.36	1,092.00	700.88	1,400 (Alexander, 1985a); 1,700 (Paul, 1988); 952 (Seebacher, 2001); 1,620 (Christiansen and Fariña, (2004)
Coelophysis bauri AMNH 7223; Paul, 1988	0.268	2.68	2.86	12.14	24.23	15.3 (Paul, 1988); 16 (Seebacher, 2001)
Coelophysis bauri AMNH 7224; Paul, 1988	0.216	2.86	2.38	?	11.14	19.9 (Paul, 1988)
Compsognathus longipes BSP 1563; Paul, 1988	0.076	0.89	0.97	0.32	0.26	0.58 (Paul, 1988)
Compsognathus longipes MNHN CNJ 79; Paul, 1988	0.105	1.25	1.28	?	0.83	2.5 (Paul, 1988); 3.5 (Seebacher, 2001)
Ceratosaurus nasicornis USNM 4735, Paul, 1988	0.625	5.69	5.90	647.50	511.81	670 (Anderson et al., 1985); 524 (Paul, 1988); 418.4 (Seebacher, 2001)
Daspletosaurus torosus CMN 8506; Paul, 1988	1.110	9.00	9.66	3,844.00	4,051.80	2,300 (Paul, 1988)
Deinonychus antirrhopus YPM 5232, Paul, 1988	0.330	3.26	3.43	56.67	52.41	45 (Paul, 1988); 75 (Spotila et al., 1991); 44.3–104.7 (Seebacher, 2001)
Dilophosaurus wetherilli UCMP 37302; Paul, 1988	0.523	6.03	5.07	355.20	269.38	283 (Paul, 1988)
Gorgosaurus libratus AMNH 5664; Paul, 1988	0.678	5.80	6.33	463.60	686.19	700 (Paul, 1988)
Gorgosaurus libratus AMNH 5458; Paul, 1988	1.040	8.60	9.13	2,795.00	3,204.37	2,500 (Paul, 1988); 2,465 (Seebacher, 2001)
Sinornithoides youngi IVPP V9612; Russell and Dong, 1993	0.109	1.20	1.32	?	0.95	2.5 (Russell and Dong, 1993); 1.2–1.9 (Seebacher, 2001)
Sinosauropteryx prima NIGP 127587; Currie and Chen, 2001	0.094	1.07	1.16	?	0.55	
Tarbosaurus bataar ZPAL MgD-1/3; Paul, 1988	0.745	5.80	6.86	?	963.60	760 (Paul, 1988)
Tarbosaurus bataar PIN 552-1; Paul, 1988	1.140	7.70	9.88	?	4,460.65	2,100 (Paul, 1988); 1,650 (Christiansen and Fariña, 2004)
Tyrannosaurus rex AMNH 5027; Paul, 1988	1.360	10.70	11.49	7,908.00	8,422.08	6,890 (Colbert, 1967); 7,400 (Alexander, 1985a); 4,500 (Anderson et al., 1985); 5,700 (Paul, 1988); 5,700 (Farlow, 1990); 7,224 (Henderson, 1999); 6,650 (Seebacher, 2001)
Tyrannosaurus rex FMNH PR2081; Brochu, 2003	1.390	12.00	11.71	10,200.00	9,110.74	

Body length and body mass are compared to estimates derived from the predictive equations and from the literature. "?" refers to values that were not computed by three-dimensional mathematical slicing.

though reduced major axis regressions are preferable when one of the considered variables is not clearly dependant on the other variable and that error exists around the quantification of both variables, it is generally agreed that the development of predictive equations should be done through least-squares regressions (Jungers, 1984; Martin et al., 2005). Furthermore, when the correlation coefficient between two variables is high, both regression models deliver nearly identical results (see Jungers, 1984; Martin et al., 2005). For these reasons, only least-square regressions were produced for the log-transformed data and used to derive the predictive equations. The precision and accuracy of each predictive equation was evaluated through the percent standard error of estimate (%SEE) and the percent prediction error (%PE), respectively (Van Valkenburgh, 1990). The %SEE represents the interval surrounding the line of best-fit in which 68% of the actual values occur, whereas the %PE represents the average difference between predicted values and actual values. The regressions were produced using the software PAST (Hammer et al., 2001) and statistics calculated with Excel 2003.

To transform predicted log body mass estimates back into kilograms, a correction factor must be applied (Smith, 1993). The simplest correction method, the quasi-maximum likelihood estimator (QMLE), was applied to each regression equation.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **BMNH**, British Museum of Natural History, London; **BSP**, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; **CAGS**, Chinese Academy of Geological Sciences, Beijing; **CMN**, Canadian Museum of Nature, Ottawa; **FMNH**, Field Museum of Natural History, Chicago; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; **JME**, Jura-Museum, Eichstätt; **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **MNN**, Musée National de Niger, Niamey; **MSNM**, Museo di Storia Naturale di Milano, Milan; **MUCPv-CH**, Museo de la Universidad Nacional del Comahue, El Chocón collection, Neuquén, Argentina; **NCSM**, North Carolina State Museum of Natural Sciences, Raleigh; **NIGP**, Nanjing In-

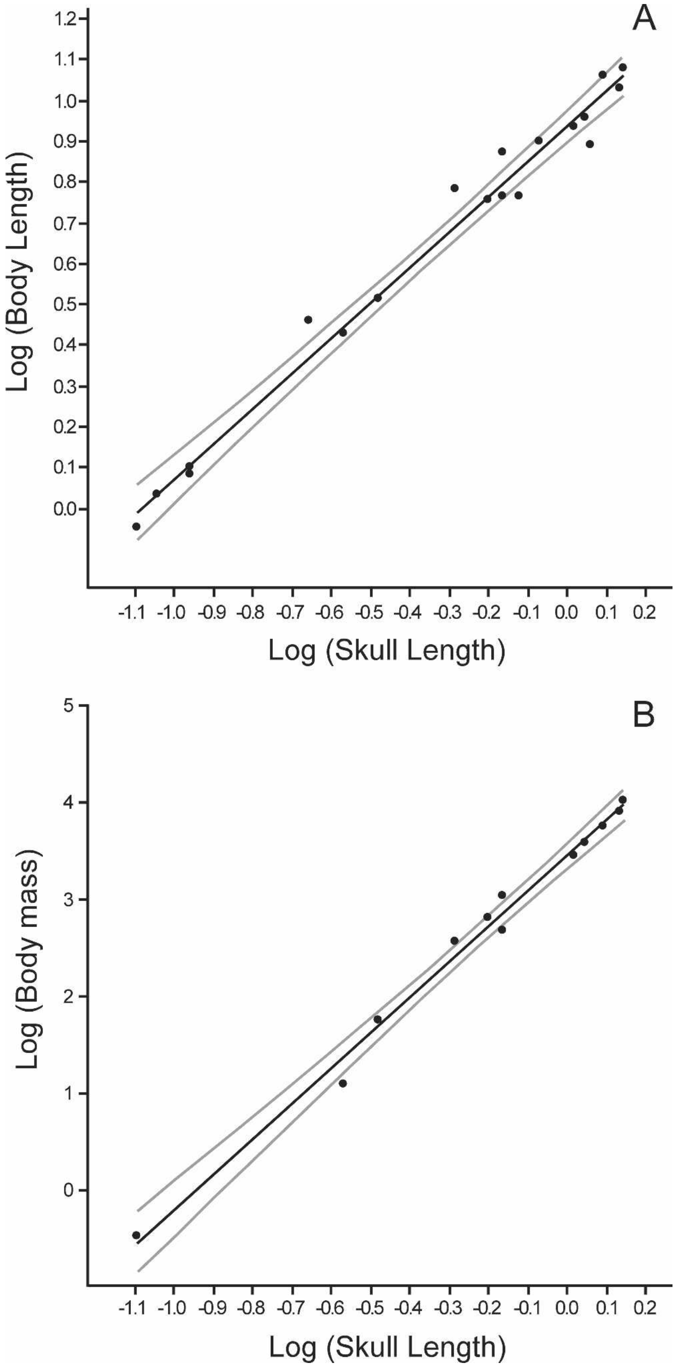

FIGURE 1. Least-squares regression of (**A**) body length versus skull length and (**B**) body mass versus skull length in theropods. Gray lines represent 95% confidence interval. Body length and body mass are highly correlated with skull length, which indicates that the latter is a good predictor of body size in theropods. See Table 1 for details.

stitute of Geology and Palaeontology, Nanjing; **PIN**, Paleontological Institute, Russian Academy of Sciences, Moscow; **SGM**, Ministère de l'Énergie et des Mines, Rabat, Morocco; **UCMP**, University of California Museum of Paleontology, Berkeley; **USNM**, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.; **UUVP**, University of Utah, Vertebrate Paleontology Collection, Salt Lake City; **YPM**, Yale Peabody Museum of Natural History, New Haven; **ZDM**, Zigong Dinosaur Museum, Zigong, Sichuan, China; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

RESULTS AND DISCUSSION

Body Length versus Skull Length

A logarithmic plot of skull length and body length (Fig. 1A) reveals that the two parameters are tightly correlated (r = 0.99083) and that skull length is an excellent predictor of total body length in theropods (%SEE = 11.57% and %PE = 9.41%). Significantly, body length is shown to be negatively allometric with respect to skull length, as the slope of the regression is lower than 1.0. This observation indicates that skull length increases proportionally faster than body length with increasing body size in theropods, that is, large theropods have relatively longer heads than small theropods (Fig. 2).

The predictive equation to derive total body length from skull length (SK-BL), including the QMLE correction factor, is expressed as follows:

$$\text{Body Length} = 1.03161 * 10^{(0.85673*\text{Log(Skull Length)}+0.93482)} \qquad (1)$$

where both body length and skull length are in meters. This skull-body scaling relationship shows that estimating the total body length of a theropod by linearly extrapolating from the body and skull length proportions of a close relative of the taxon in question is overly simplistic and gives inaccurate results.

To test the validity of SK-BL, the equation was applied to taxa represented by specimens of known body length that were not used to derive the regression, namely the carnosaur *Sinraptor dongi*, the dromaeosaurids *Velociraptor mongoliensis* and NGCM 91 (unnamed taxon), the troodontid *Mei long*, and the abelisaurid *Carnotaurus sastrei* (Table 2). The body length estimates for *Sinraptor* and *Velociraptor* are extremely close to the published length for the specimens considered (<3.3%), which reinforce the validity of SK-BL. Interestingly, the body length of *Mei long* and of the small feathered NGMC 91 is overestimated (36% and 85%, respectively) by the SK-BL regression whereas that of *Carnotaurus* is underestimated (28%). These latter results reflect the facts that juvenile theropods have larger heads relative to their body size than adults (Ji et al., 2001; Xu and Norell, 2004) and that abelisaurids have shorter heads relative to their body size than other theropods (Bonaparte et al. 1990). Consequently, the SK-BL regression should not be used for abelisaurids or juvenile individuals.

Body Mass versus Skull Length

A logarithmic plot of skull length and body mass (Fig. 1B) reveals that the two parameters are tightly correlated (r = 0.99469) and that skull length is a reliable predictor of total body mass in theropods (%SEE = 34.38% and %PE = 22.23%), although it is not as accurate as for body length. Importantly, body mass is shown to be positively allometric with respect to skull length as the slope of the regression is greater than 3.0. In other words, body mass increases proportionally faster than skull length with increasing size among theropods (Fig. 2). Therefore, estimating the body mass of a theropod through isometric scaling of another taxon is invalid as theropod body shape changes with increasing size (see Henderson and Snively, 2004). A plot of body mass versus body length (not illustrated) reveals that the same conclusion is applicable to body length, that is, body mass increases proportionally faster than body length.

The predictive equation to derive total body mass from skull length (SK-BM), including the QMLE correction factor, is expressed as follows:

$$\text{Body Mass} = 1.00419 * 10^{(3.6022*\text{Log(Skull Length)}+3.4426)} \qquad (2)$$

TABLE 2. Body length and body mass estimates of incomplete theropod specimens.

Taxon	Skull length (m)	SK-BL estimate (m)	Published body length estimates (m)	SK-BM estimate (kg)	Published body mass estimates (kg)
Baryonyx walkeri BMNH R9951	0.91	8.19	8.5 (Charig and Milner, 1997), ~9.5 (Paul, 1988)	1,980.96	1,700 (Paul, 1988)
Carcharodontosaurus saharicus SGM-Din 1	1.60 (max)	13.28	12+ (Sereno et al., 1996)	15,125.05	6,173.2 (Seebacher, 2001)
Carnotaurus sastrei MACN-CH 894	0.52	5.07*	7.6 (Bonaparte et al., 1990)	263.88*	Mean 2,102 but varying between 1,488 and 2,626 (Mazzetta et al., 2004)
Dilong paradoxus IVPP V14243	0.166	1.91	1.6 (Xu et al., 2004)	4.32	
Dromaeosaurus albertensis AMNH 5356	0.24	2.61		16.29	~15 (Paul, 1988)
Giganotosaurus carolinii MUCPv-CH-1	1.56	13.00	12.5 (Coria and Salgado, 1995)	13,806.68	6,000+ (Coria and Salgado, 1995); 6,594.8 (Seebacher, 2001); mean 6,510 but varying between 2,639 and 9,268 (Mazzetta et al., 2004)
Guanlong wucaii IVPP V14531	0.3697	3.79	~3.0 (Xu et al., 2006)	77.22	
Huaxiagnathus orientalis CAGS-IG02-301	0.16 (min)	1.85	1.6 (Hwang et al., 2004)	3.95	
Huaxiagnathus orientalis CAGS-IG02-301	0.1753 (max)	2.00		5.25	
Juravenator starki JME Sch 200	0.082	1.04	0.75–0.80 (Göhlich and Chiappe, 2006)	0.34	
Mei long IVPP V12733	0.053	0.72†	0.53 (Xu and Norell, 2004)	0.07†	
Monolophosaurus jiangi IVPP V84019	0.63	5.98	5.1 (preserved length; Zhao and Currie, 1993)	391.05	
NGMC 91 (indet. dromaeosaurid)	0.1145	1.39†	0.75 (Ji et al., 2001)	1.13†	
Sinraptor dongi IVPP V10600	0.78	7.18	7.2 (Currie and Zhao, 1993)	1,136.89	1,009 (Seebacher, 2001); 1,700 (Christiansen and Fariña, 2004)
Sinraptor hepingensis ZDM0024	0.95	8.50	7.9 (preserved length; Gao, 1992)	2,312.98	
Spinosaurus aegyptiacus MSNM V4047	1.75 (max)	14.34	16–18 (Dal Sasso et al., M2005), ~15 (Paul, 1988)	20,887.55	~4,000 (Paul, 1988); 7,000–9,000 (Dal Sasso et al., 2005)
Spinosaurus aegyptiacus MSNM V4047	1.5 (revised)	12.57	16–18 (Dal Sasso et al., M2005), ~15 (Paul, 1988)	11,987.59	~4,000 (Paul, 1988); 7,000–9,000 (Dal Sasso et al., 2005)
Suchomimus tenerensis MNN GDF500, 501, 502	1.19	10.31	~11.0 (Sereno et al., 1998)	5,206.56	3,816.1 (Seebacher, 2001)
Velociraptor mongoliensis AMNH 6515	0.19	2.14	2.07 (Paul, 1988)	7.02	6.7 (Paul, 1988)

Body length and body mass estimates are compared to published estimates.
*Indicates underestimated values.
†Indicates overestimated values.

where body mass is in kilograms and skull length is in meters. When applied to taxa not used to derive the regression, this scaling relationship provides a body mass estimate for *Sinraptor* that is within 13% of that predicted by Seebacher (2001) and a body mass estimate for *Velociraptor* that is very close (5%) to Paul's (1988) estimate (Table 2). Despite the scarcity of small, lightweight theropods available to derive the SK-BM regression, the similarity of our body mass estimates to that published for *Velociraptor* supports its validity even for small theropods. Because Seebacher (2001:table 2) failed to recognize the synonymy of "*Velociraptor*" *antirrhopus* with *Deinonychus antirrhopus*, he mistakenly attributed a body mass of 44.3 kg to the genus *Velociraptor*, a value that mysteriously differs from his body mass estimate for *Deinonychus* (Seebacher, 2001:table 4).

Estimating Body Size in Theropods Known from Incomplete Skeletons

Theropods are rarely known from complete skeletons, which, in the absence of accurate body proportions, prevent reconstruction of total length and computation of body mass. The SK-BL and SK-BM regressions offer the possibility to gain insight into body size for both small and large "incomplete" theropods, such as the compsognathids *Huaxiagnathus orientalis* and *Juravenator starki*, the tyrannosauroids *Dilong paradoxus* and *Guanlong wucaii*, the dromaeosaurid *Dromaeosaurus albertensis*, the carnosaurs *Monolophosaurus jiangi* and *Sinraptor hepingensis*, and the famous carcharodontosaurids *Carcharodontosaurus saharicus* and *Giganotosaurus carolinii* (Table 2).

The Solnhofen compsognathid *Juravenator* is represented by a nearly complete skeleton missing only the distal third of the tail (Göhlich and Chiappe, 2006). Estimated to have reached 0.75 to 0.80 m in length based on skeletal remains, the predictive equations developed above suggest a total length of 1.04 m and body mass of 0.34 kg for *Juravenator*. The greater body length estimate provided by the SK-BL regression could be related to the large head of this taxon (Göhlich and Chiappe, 2006).

Huaxiagnathus has been described as the second largest theropod taxon from the Jehol biota, being slightly larger than other compsognathids. Although the distal portion of the tail is missing, *Huaxiagnathus* has been assigned a conservative body length estimate of 1.60 m (Hwang et al., 2004). Because the posterior portion of the skull is crushed, skull length could only be bracketed between a minimum and maximum value (Table 2). From the predictive equations developed previously, *Huaxiagnathus* is estimated to have reached between 1.85 m and 2.00 m in length, values close to previous estimates, and to have weighed between 4 and 5 kg (Table 2).

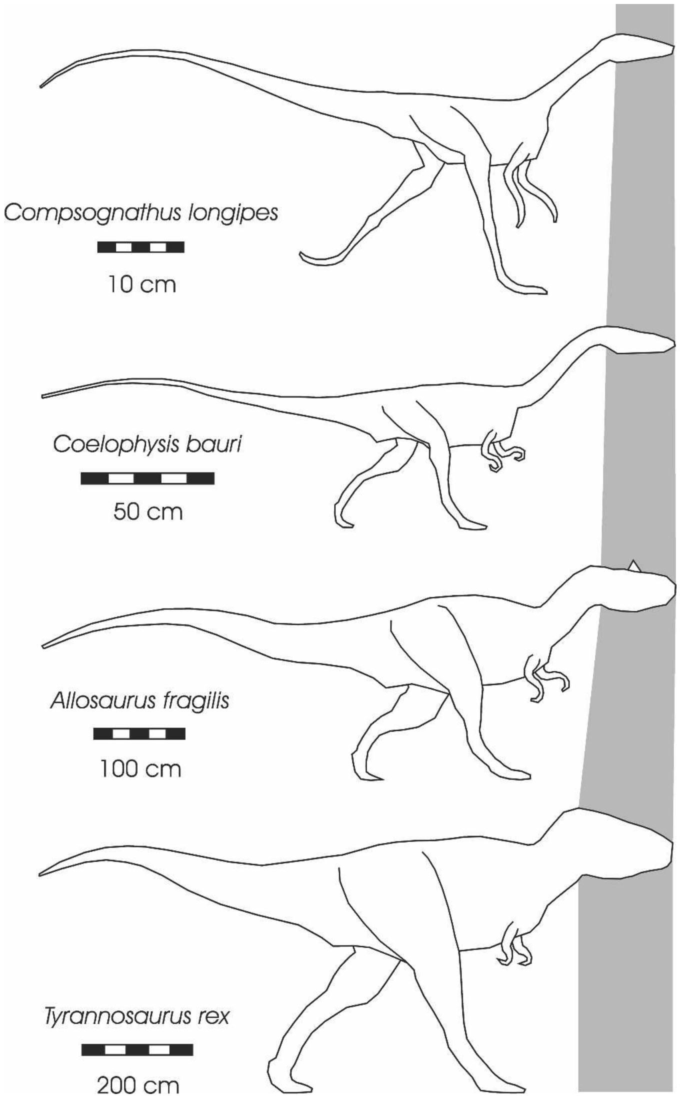

FIGURE 2. Schematic representation of four theropods in lateral view highlighting change in skull length (gray) with increasing body size. The skull becomes longer relative to body length with increasing body size among theropods, particularly visible between *Allosaurus* and *Tyrannosaurus*, due to the exponential scaling relationship between skull length and body length. Furthermore, the bodies of large theropods are relatively more rotund and deeper than those of small theropods, reflecting the positive allometry between body mass and skull length.

The basal tyrannosauroids *Dilong* and *Guanlong* are clearly smaller than their later relatives, but missing elements prevent accurate determination of their body size (Xu et al., 2004, 2006). The SK-BL regression predicts a body length of 1.91 m and 3.79 m for *Dilong* and *Guanlong*, respectively, estimates that are slightly greater than those previously suggested (Table 2). In terms of body mass, *Dilong* would have been much lighter (4.32 kg) than the larger *Guanlong* (77.22 kg) (Table 2).

To date, the best known specimen of *Dromaeosaurus* remains the holotype, represented by a nearly complete skull and fragmentary postcranial material (Colbert and Russell, 1969). Usually reconstructed with typical dromaeosaurid proportions, *Dromaeosaurus* is estimated to have reached 2.61 m in length and have weighed 16.3 kg; the body mass estimate is close (9%) to the estimate provided by Paul (1988).

Numerous large carnosaurs are known from China. The holotype of *Monolophosaurus*, a large crested Jurassic theropod, is represented by a nearly complete skeleton, which lacks the portion of the tail posterior to the sixth caudal vertebra; the holotype has preserved body length of 5.10 m (Zhao and Currie, 1993). The estimated body size of this individual, close to 6.00 m in length, is compatible with the preserved material. Based on SK-BM, *Monolophosaurus* is estimated to have weighed 390 kg. Another large Chinese theropod, *Sinraptor hepingensis* is represented by a nearly complete skeleton, lacking only the distal portion of the tail; the holotype of this taxon has a preserved body length of 7.90 m (Gao, 1992). Based on an estimated skull length of 0.95 m, the *S. hepingensis* holotype is estimated to be missing only 0.60 m of the tail. Based on SK-BM, *S. hepingensis* is estimated to have weighed 2,313 kg.

Carcharodontosaurids are widely recognized as theropods that approached, and possibly even surpassed, *Tyrannosaurus rex* in size; however, such claims are based solely on the dimension of various skeletal elements as nearly complete specimens are unknown for these taxa (Coria and Salgado, 1995; Sereno et al. 1996; Coria and Currie, 2006). Based on skull dimensions, *Carcharodontosaurus* and *Giganotosaurus* are both predicted to have approached 13 m in length and 14 tonnes in weight (Table 2). These body length estimates are comparable to previously published values but the predicted body mass surpasses previous estimates (Table 2). The body size estimates for *Carcharodontosaurus* should be considered as maximum values because the published skull length is for the distance between the premaxilla and the quadrate, a dimension longer than that used in our regressions (premaxilla-occipital condyle). Correcting for this difference is impossible without access to the specimen, but it is reasonable to assume that *Carcharodontosaurus* was approximately of the same size as *Giganotosaurus*. Finally, the body size estimates for these taxa are highly dependant on an accurate skull reconstruction, as small differences in skull length can result in major differences in body length and body mass estimates. Thus, until a complete skull of these theropods is discovered, these body size estimates should be considered with caution.

Estimating the Body Size of Spinosaurids

Recently, there has been renewed interest in the study of spinosaurids following claims that at least one member of this clade, *Spinosaurus aegyptiacus*, could have reached gigantic proportions (e.g., Dal Sasso et al., 2005). Given the elongate rostrum characteristic of spinosaurids, there exists the possibility that their skulls were longer, relative to total body length, than those of other theropods. Because this possibility would entail that the SK-BL and SK-BM regressions would overestimate the body length and body mass of spinosaurids, the applicability of the scaling relationships was tested with two better-known spinosaurids—*Suchomimus tenerensis* and *Baryonyx walkeri*. *Suchomimus*, known from a fairly complete skeleton lacking a major portion of the tail, has been estimated to have reached 11 m in length (Sereno et al., 1998) and to have weighed 3,816 kg (Seebacher, 2001). Based on the dimension of a skull reconstruction housed at the Chicago Children's Museum, *Suchomimus* is predicted to have been slightly smaller (10.31 m) and heavier (5,206 kg) than previously postulated (Table 2). *Baryonyx* is known from fragmentary, but associated, pre-caudal material of a single individual, from which a total body length estimate of 8.50 m was made (Charig and Milner, 1997:fig. 44). Based on the illustration of the reconstructed skull (Charig and Milner, 1997:fig. 1), *Baryonyx* is predicted to have reached a body length of 8.0 m—a value very close to that previously predicted—and to have weighed 1,980 kg (Table 2). Even though the skull of *Suchomimus* is only 47% longer than that of *Baryonyx*, the former animal is roughly 250% more massive. This disproportionate increase in body mass for a given increase in skull length is a direct result of the large exponent (3.6022) acting on skull length in the SK-BM regression. Given the close correspondence between published body size estimates based on skeletal remains and those derived from SK-BL and SK-BM, we believe that the predictive equations can be applied to spinosaurids.

Dal Sasso and colleagues (2005) described a one-meter-long isolated rostrum that they ascribed to *Spinosaurus*. Combining this rostrum with a scaled-up posterior cranial region of the South American spinosaur *Irritator challengeri*, these authors estimated that the skull of the large *Spinosaurus* reached a length of 1.75 m. Based on this tentative skull reconstruction and assuming body proportions similar to *Suchomimus*, Dal Sasso and colleagues (2005) estimated a total body length of 16 to 18 m and, following Seebacher's (2001) method, derived a body mass of 7 to 9 tons for their large *Spinosaurus*. These results are intriguing, not only because the animal would be the longest theropod known, but also because it would have been relatively lightweight, weighing less than a 12-m-long *Tyrannosaurus rex* (see Table 1; Henderson and Snively, 2004). Although Seebacher (2001) did not provide a body mass estimate for *Spinosaurus*, it is possible to derive one from his body mass estimate for *Suchomimus* (3,816 kg). Assuming geometric similarity (i.e., similar body proportions) between the two spinosaurids and that body mass is proportional to the cube of body length (Alexander, 1985), scaling an 11-m-long *Suchomimus* to the size of a 16-m to 18-m *Spinosaurus* provides body mass estimates ranging from 11,700 kg to 16,700 kg, values that are much higher (67% to 86%) than those suggested by Dal Sasso and colleagues (2005).

Because the SK-BL and SK-BM regressions provided good results for spinosaurids, published body size estimates for *Spinosaurus* can be appraised with these predictive equations. When the reconstructed skull length (1.75 m) for the large *Spinosaurus* is used in the SK-BL regression, a body length estimate of 14.34 m is obtained, a value appreciably lower (10% to 20%) than that previously proposed by Dal Sasso and colleagues (2005). A note of caution concerns the dimension of the reconstructed *Spinosaurus* skull. First, the proposed skull restoration (Dal Sasso et al. 2005:fig. 5B) is a composite reconstruction with the front and back halves being from different genera. Because skull shape varies among spinosaurids (i.e., the shape of the rostrum, the relative dimensions of the maxillae and premaxillae, and the shape of posterior region of the skull differ among spinosaurids; Fig. 3), there is potential for overestimating the length of a composite spinosaur skull. Second, Dal Sasso and colleagues' (2005:fig. 5) skull length estimate represents the distance between the premaxilla and the squamosal, which is greater than the measurement (premaxilla-occipital condyle) used in our predictive equations. Therefore, the body length estimate derived above (14.34 m) exceeds what must have been the total body length of the animal. It only takes a skull length (premaxilla-occipital condyle) of 1.50 m, that is, 0.25 m (14%) shorter than originally suggested, to predict a substantially shorter (22% to 31%) total body length of 12.57 m, a value very close to the body length of the largest theropods known (e.g., *Tyrannosaurus*, *Carcharodontosaurus*, *Giganotosaurus*). In terms of body mass, applying the SK-BM regression to the published reconstructed skull length of *Spinosaurus* predicts a body mass of 20,887 kg for a 14.34-m-long individual. This body mass estimate exceeds by 232% to 298% the previously published estimates of 7,000 to 9,000 kg for a 16-m to 18-m-long animal. For comparison purposes, the very large hadrosaur *Shantungosaurus* (Hu, 1973), estimated to have reached 17 m in length (Brett-Surman, 1997), is thought to have attained a mass of 22,467 kg (Seebacher, 2001). The published body mass estimate for a hadrosaur similar in length to that originally predicted for *Spinosaurus* emphasizes how the previous body mass estimate for this theropod (7 to 9 tons) was significantly underestimated. For a *Spinosaurus* with a shorter skull (1.50 m) and a body length of 12.57 m, a body mass estimate of 11,987 kg is obtained, a value 33% to 71% greater than previously suggested by Dal Sasso and colleagues (2005). The effects of allometric changes in skull shape, in combination with the non-linear nature of the skull-length to body-length and body-mass scaling function, suggest that body size estimates based on composite skulls must be treated with great caution.

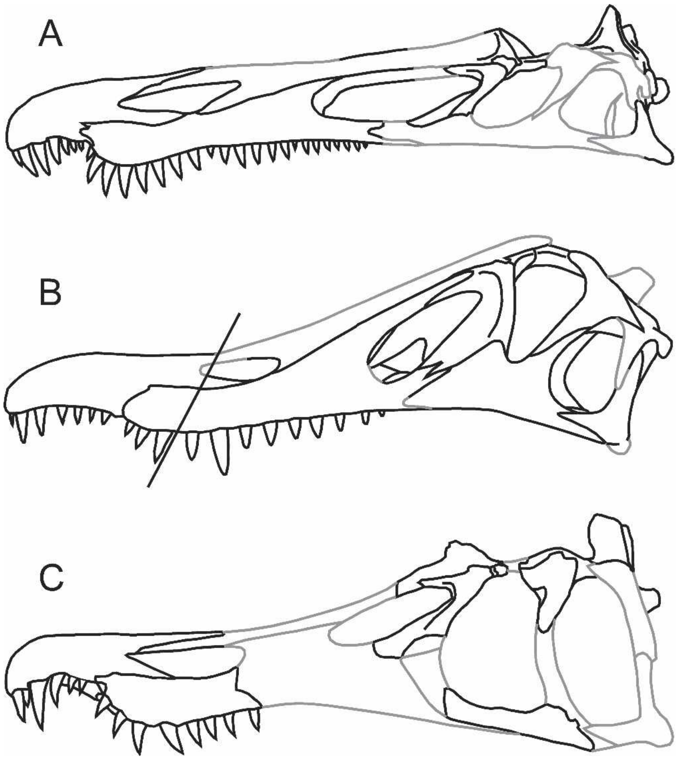

FIGURE 3. Comparison of the skull of (**A**) *Suchomimus tenerensis*, (**B**) *Angaturama limai*/ *Irritator challengeri*, and (**C**) *Baryonyx walkeri*. Skulls are scaled to the same dimension. Gray outlines represent missing elements. The relative proportions of the snout and of the posterior region of the skull vary among spinosaurids, which complicates the skull reconstruction and accurate determination of the skull dimension of *Spinosaurus aegyptiacus*. Modified from Sereno et al. (1998), Sues et al. (2002), and Dal Sasso et al. (2005).

It is generally accepted that large hadrosaurs, including those smaller than the 17-m-long *Shantungosaurus*, were primarily quadrupedal (Brett-Surman, 1997; Dilkes, 2001), which suggests that bipedalism at extremely large body size is impractical. In light of the results presented above, we conclude that it is doubtful that a bipedal theropod with a mass exceeding 20 tons could have existed. Although it was a large theropod, *Spinosaurus aegyptiacus* was probably no larger than the currently known largest tyrannosaurids and carcharodontosaurids, a size close to the biomechanical limit for strictly bipedal animals (Henderson, 2005).

CONCLUSION

The close correlation between skull length, body length, and body mass in theropods allows for the development of predictive equations to estimate body size. Their validity verified against theropods of known body size, the predictive equations provide a simple, statistically founded, and widely applicable method to estimate body length and body mass for incomplete theropod specimens.

Of particular interest, the SK-BL and SK-BM regressions give insight into the body size of large theropods, such as carcharodontosaurids and spinosaurids. The regressions reveal that *Carcharodontosaurus* and *Giganotosaurus* would have approached

13 m in length and 14 tons in weight, slightly surpassing *Tyrannosaurus rex* in body size. If a 1.75-m-long skull reconstruction for a large *Spinosaurus* individual is valid, our predictive equations indicate that such an animal would have been just over 14 m long, with an estimated body mass of 20 tons—an animal 10% to 20% shorter and 232% to 298% more massive than previously suggested. However, because the proposed skull reconstruction of *Spinosaurus* is based on limited material and comparisons with other incomplete spinosaurid skulls, large uncertainty surrounds the true skull length. Consequently, the body length and body mass estimates for this individual are subject to change and could be considerably lower—possibly 12.57 m and 12 tons—within the range of the largest theropods known. At present, it appears that theropods attaining a body length of 13 m and a body mass of 14 tons were approaching the upper limit for bipedal, terrestrial animals.

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