

DETERMINING THE LARGEST KNOWN LAND ANIMAL:
A CRITICAL COMPARISON OF DIFFERING METHODS
FOR RESTORING THE VOLUME AND MASS OF EXTINCT ANIMALS

GREGORY PAUL

3100 St. Paul Street 604, Baltimore, Maryland, 21218
GSP1954@aol.com

ABSTRACT

Recent claims regarding what is and is not the largest known sauropod dinosaur are tested via dimensional comparisons of the most critical metrics of relative size—especially, when possible, the functional lengths of the dorsal vertebral centra and the articulated length of the combined trunk vertebrae—and analog volumetric models based on technical skeletal restorations. The Cretaceous *Argentinosaurus* massed 65–75 tonnes, and its dorsal vertebrae and dorsal–sacral series are much larger than those of any other described titanosaur. Specimens of *Patagotitan* indicate a 50–55 tonne titanosaur, and the less complete *Notocolossus*, *Puertasaurus*, and ‘*Antarctosaurus*’ *giganteus* appear to have occupied a similar size range. *Paralititan* weighed between 30 and 55 tonnes. The juvenile *Dreadnoughtus*, as well as *Futalognkosaurus* and *Alamosaurus*, were in the area of 30 tonnes, with the possibility that the last was substantially larger. Entirely analog, skillfully produced, high-anatomical-fidelity skeletal restorations and volumetric models representing a prime-lean condition are approximately as scientifically objective and accurate, as well as more realistic than, analog-digital, crudely-formed convex hull volumetric models, which are based on subjectively and often inconsistently or erroneously mounted skeletons and digitized skeletal reconstructions. The need to ensure that skeletal restorations are as anatomically correct and consistent as the data allow is stressed, which requires that researchers and illustrators be sufficiently skilled in animal and especially dinosaur anatomy, and the procedures and standards for achieving the best possible results are detailed. When properly executed, analog and digital volumetric models produce adequately similar results that can be used to cross-check one another, and both produce accurate masses much more reliably than do methods based on strength factors such as limb bone circumferences or certain other skeletal dimensions that suffer from inherently very high plus-minus factors.

KEY WORDS: *Argentinosaurus*, convex hulling, mass estimation, *Patagotitan*, Sauropoda, skeletal restorations, Titanosauria, volumetric models

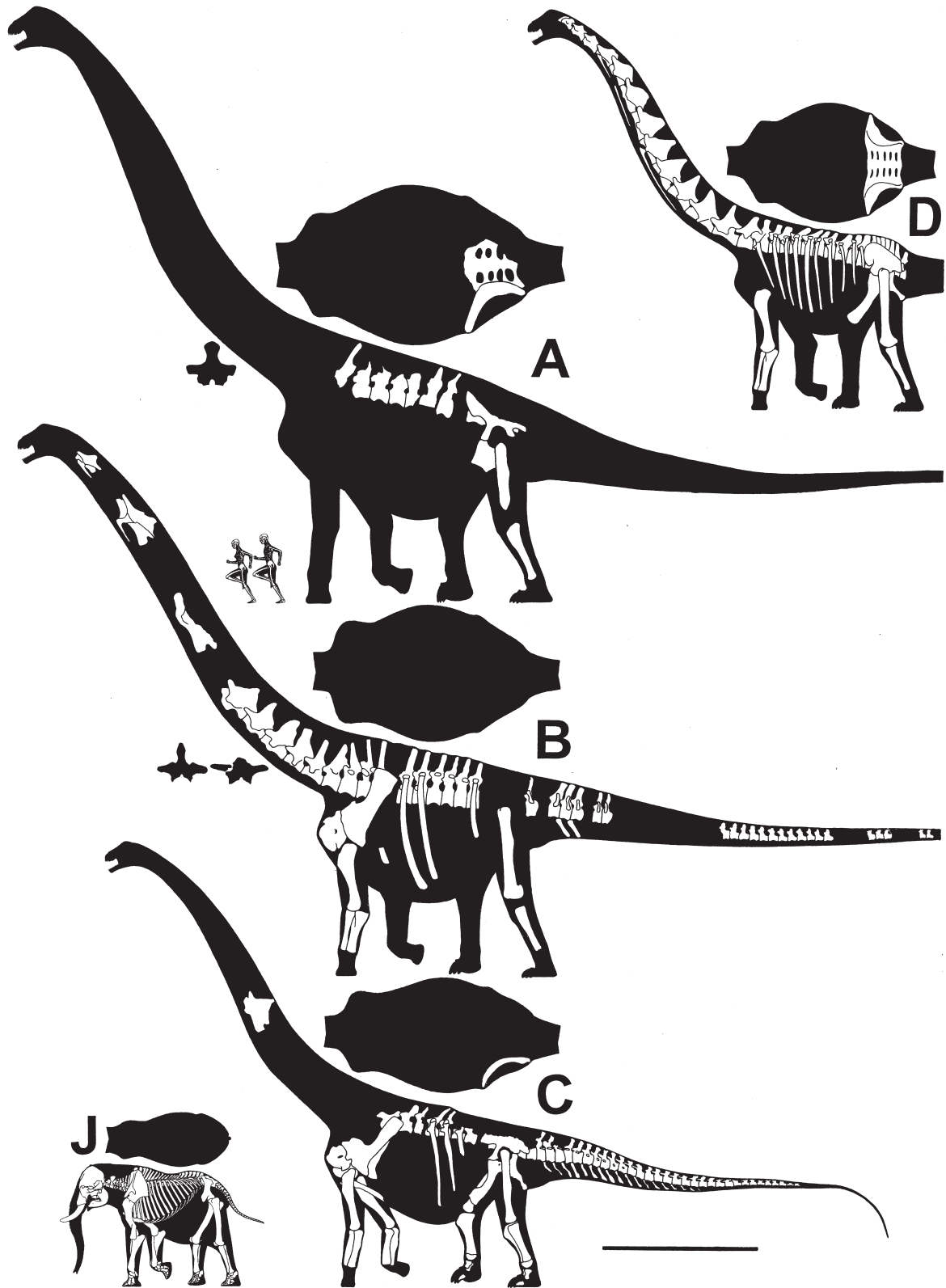
INTRODUCTION

Titanosaurs were a group of derived titanosauriform sauropodomorphs that became the dominant sauropod dinosaurs of the Cretaceous, especially during the latest Cretaceous when they were apparently the only surviving sauropods. Herbivorous as were other sauropods, two related features that distinguish titanosaur from other members of this clade are their exceptionally broad pelves and abdominal ribcages, mimicking the fat-bellied armored ankylosaurian dinosaurs in these respects. Titanosaurs also had atypically large pubes, another apparent adaptation for supporting unusually massive guts. Some titanosaur were not especially gigantic, being comparable to or lower than proboscideans in mass (Figs. 1F–H, J). But during the mid- and Late Cretaceous, other titanosaur—most but not all of which are known from southern South America—achieved colossal masses of over 50 tonnes, similar to those of gigantic whales, positioning them at least among the biggest known land animals of all time (Figs. 1A–B). Titanosaurs, however, may not have been the very largest sauropods, as a few Jurassic fossils hint at the existence of non-titanosaurian sauropods of truly extraordinary dimensions.

Determining the mass of the largest land animals is of particular biological importance, because assessing why and how these animals evolved the structural and physiological adaptations necessary to be so huge in 1G requires knowing the absolute values of their tonnage to the highest

accuracy possible. Doing so is also useful for examining the ecological evolution and impact of the biggest terrestrial tetrapods. Conversely, due to their stupendous size that is embodied in exotic anatomical forms, the masses of which cannot be simply extrapolated from living tetrapods, sauropods have, from the beginning of their study (e.g., Gregory 1905) been a primary focus of efforts to estimate the masses of extinct tetrapods via methods that offer the potential of approximating the volumes of their huge bodies.

For much of the history of the study of titanosaur, highly complete skeletons of single individuals remained unknown for most taxa, hindering assessments of their size. Fortunately, however, this situation has improved in recent years, with the discovery, documentation, and in some cases mounting of a few, more complete titanosaurian specimens that finally allow for more definitive size comparisons (Figs. 1A–D). However, which of these titanosaur was the largest yet discovered has remained a matter of question. *Argentinosaurus* (Bonaparte and Coria 1993; Paul 1997; Mazzetta et al. 2004; Carpenter 2006) was long and often seen as being the most massive member of the group. Recently, however, *Patagotitan* was estimated to be about ten percent larger than *Argentinosaurus* based on limited and problematic comparisons of bone dimensions, with mass estimates for the former taxon via various means ranging from up to 84 tonnes to about half



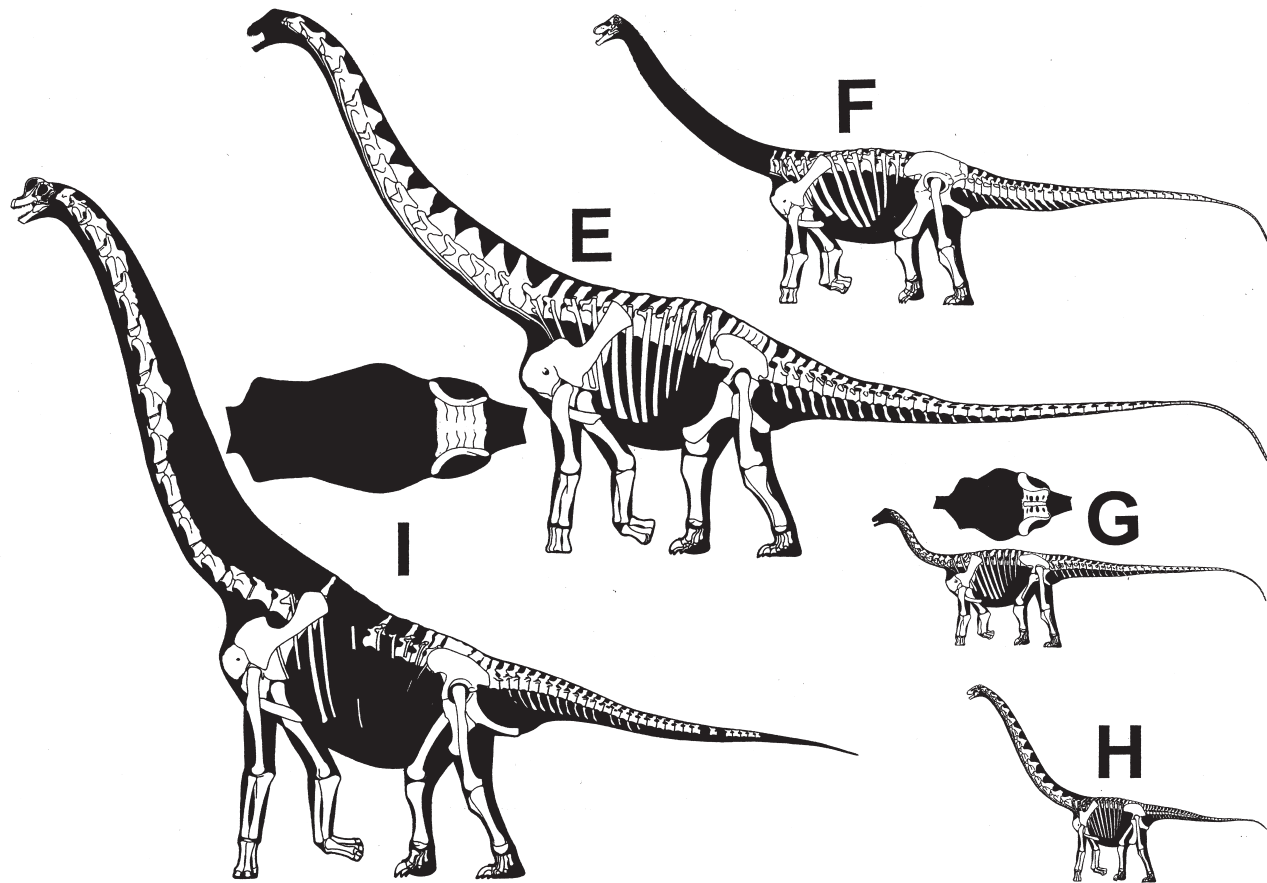


Fig. 1.—High-anatomical-fidelity analog profile-skeletal restorations with selected dorsal view trunk profiles of titanosauriform sauropods to same scale, bar equals 4 m, specimen(s) to which each reconstruction is scaled listed in Table 1. **A**, *Argentinosaurus huinculensis* holotype MCF-PVPH-1 with *?Argentinosaurus* femur MLP-DP 46-VIII-21-3 included, and anterior dorsal neural arch of holotype in anterior view, 70 t; **B**, *Patagotitan mayorum* composite with anterior dorsal neural arches of holotype MPEF-PV 3400 in anterior view, 52 t; **C**, *Dreadnoughtus schrani* holotype MPM-PV 1156 (immature), 31 t; **D**, *Futalognkosaurus dukei* holotype MUCPv-323, 29 t; **E**, *Alamosaurus sanjuanensis* composite, 27 t; **F**, *Nemegtosaurus mongoliensis* (= *Opisthocoelicaudia skarzynskii* holotype ZPAL MgD-I/48), 8.5 t; **G**, *Saltasaurus loricatus* composite, 2.5 t; **H**, *Rapetosaurus krausei* composite juvenile, 0.8 t; **I**, *Giraffatitan brancai* composite, 32 t; **J**, African bush elephant Jumbo AMNH 3283, 6 t. More complete and/or larger scale versions of F–I are provided in Paul (2016).

that (Carballido et al. 2017). Carballido et al. (2017) did not attempt to determine which of their estimates was the most accurate, but thankfully, such limited dimensional cross-comparisons, extreme plus-minus variations, and uncertainty in mass estimates are not necessary because sufficient skeletal material is available to arrive at a much narrower anatomically possible volume and mass range for *Patagotitan*. The Internet site of the Chicago Field Museum, which exhibits a mounted replica skeleton of this titanosaur, explicitly claims that, at 70 tonnes, *Patagotitan* was the largest dinosaur that ever lived (Anonymous

2018). Are such claims scientifically valid?

Regrettably, gigantic non-titanosaurian sauropods are also very incompletely represented. The recent taxonomic reidentification of a partial dorsal vertebral neural arch led Carpenter (2018) to propose a reduced mass estimate for the diplodocoid *Maraapunisaurus*, regarding that animal as broadly similar in size to the largest titanosaurs. A pair of cervical vertebrae from China imply a mamenchisaurid of similarly great dimensions and mass (Paul 2016).

The comparison of gigantic titanosaurs presented here—in firmly establishes that the dorsal vertebral centra of

Argentinosaurus are so much larger and especially longer than those yet known for any other titanosaur that it is at the least highly probable and in some cases virtually certain that this sauropod was considerably bulkier and possibly longer than the next-largest titanosaurs, *Patagotitan*, *Puertasaurus*, *Notocolossus*, and '*A.*' *giganteus*, whereas *Futalognkosaurus* and the immature holotype of *Dreadnoughtus* were markedly less massive. The mass of the *Argentinosaurus* type specimen can be confidently estimated at 65–75 tonnes. A carefully-proportioned volumetric model of the relatively completely known *Patagotitan* produces a reliable body mass range of 50–55 tonnes, approximately one-quarter less than that of *Argentinosaurus*, and the same value less than the maximal probability estimate based on the robustness of its proximal limb bones (Carballido et al. 2017). A model of the large but immature *Dreadnoughtus* holotype shows that this specimen was in the area of 30 tonnes, about half the maximal probability calculation based on proximal limb robustness (Lacovara et al. 2014). A *Futalognkosaurus* model results in a mass approaching 30 tonnes, again well below calculations based on limb bone strength by Benson et al. (2014) and Carballido et al. (2017). Concerning the most massive non-titanosaurian sauropods, the aforementioned mamenchisaurid may have surpassed the largest titanosaurs at 60–80 tonnes. If *Maraapunisaurus* actually existed (as argued by Carpenter 2018), then the diplodocoid was exceptionally huge, at 80–120 tonnes or more, and fragmentary remains suggest that the diplodocid *Barosaurus* may have been enormous as well.

This paper was initiated primarily to compare the dimensions and masses of the largest titanosaurs, in response to Carballido et al. (2017), but in the process of doing so, issues arose concerning methods of mass estimation that expanded the study into a larger comparative analysis of these differing procedures (matters that will be further examined by Larramendi and Paul in prep.).

The first efforts to scientifically restore the masses of non-avian dinosaurs via volumetric models based on rigorously proportioned skeletal restorations were initiated in the 1980s (Paul 1988a, 1988b, 1997). Prior to then, the models used for mass estimation were often of uncertain scale and created to inconsistent anatomical criteria; moreover, these models were either produced by artists who did not base their sculptures on carefully measured plans of realistically articulated skeletons, or crafted by commercial sculptors with widely varying levels of paleobiological and anatomical skill. As such, when used for mass estimation, these models produced unreliable and often highly errant results (Paul 1997). More recently, digital convex hulling of skeletons has been offered as generating more objective results than do subjective, artistic analog methods (Sellers et al. 2012; Bates et al. 2015; Carballido et al. 2017). The analysis and results herein demonstrate that the traditional analog method of meticulously restoring the proportions and detailed form of skeletons, and then using those as the basis for technical volumetric models of

exotic fossil taxa largely by hand, is as least as accurate as analog-digital based efforts, which are themselves more subjective than widely portrayed. The results further confirm that both techniques produce the most accurate mass estimates possible much more reliably than do those that rely on the minimum circumference of the humerus and/or femur, or other bone dimensions.

METHODS AND NOTES

To determine the absolute masses of selected titanosaurs, analog, rigorously executed, high-fidelity, 'blueprint format' profile-skeletal reconstructions have been produced (Figs. 1A–H). Utilized for some extant mammals by Knight (1947, who never produced skeletal reconstructions of dinosaurs) and for prehistoric animals including dinosaurs by Scheele (1954, 1955), profile-skeletal reconstructions show the skeleton articulated in a life-like posture rather than a death pose, and set within an outline of, or immersed within the solid profile of, the restored primary soft tissues. For the purposes of optimal volume estimation, profile-skeletal reconstructions should be 'anatomical blueprints' executed without showing perspective between left and right elements in side views, or dorsal or ventral elements in top and bottom views, and need to be rigorously produced such that the dimensions and details of the elements are as accurate as possible given the information at hand. Also, the articulation of the elements must be as anatomically well informed as possible, especially regarding the trunk. For example, the anterior dorsal columns of hadrosaurid dinosaurs are strongly arched downwards (Paul 1987, 1997, 2016), shortening and reducing the volume of the trunk relative to what it would have been if the dorsal series was straighter. As detailed below, correct placement of the shoulder girdle is of prime importance in this regard, as is the consistent application of anatomical articulations between and within taxonomic groups.

The skeletal elements in the titanosaur profile-skeletal reconstructions in Figures 1B and 1D were derived primarily from lateral view photographs of mounted specimens adjusted when necessary by measurements and illustrations of individual elements, whereas Figure 1C was based on a digitized skeleton (from Lacovara et al. 2014). Also used were illustrated individual elements, sometimes in non-lateral views that helped to determine the transverse or mediolateral dimensions of the skeletons. The titanosaur bones were proportioned via measurements, either previously published (Bonaparte and Coria 1993; Calvo et al. 2001, 2007a, 2007b, 2008; Carpenter 2006; Bonaparte 2007; Calvo 2014; Lacovara et al. 2014; Ullmann and Lacovara 2016; Carballido et al. 2017; Voegelé et al. 2017) or from unpublished data provided by other researchers (Lamanna pers. comm.; Larramendi pers. comm.). The methods used herein for restoring analog profile-skeletal reconstructions and translating them into three-dimensional technical volumetric models of tetrapods in general and

TABLE 1. Quantitative size comparisons between titanosauriform sauropods. Specimens of *Argentinosaurus*, *Puertasaurus*, *Dreadnoughtus*, *Futalognkosaurus*, *Alamosaurus*, *Nemegtosaurus* (= *Opisthocoelicaudia*), *Saltasaurus*, *Rapetosaurus*, and *Giraffatitan* indicated are those to which the profile-skeletal reconstructions in Figures 1A–I were scaled. Abbreviations in order of appearance: DVFCL, dorsal vertebrae functional centrum length; ADSL, articulated dorsal series length; ADSSL, articulated dorsal–sacral series length; HL, humerus length; FL, femur length (all lengths in mm); H+NV, head + neck volume; T+LV, trunk + limbs volume; TV, tail volume (all volumes in kiloliters); Tonnes, total mass utilizes specific gravity (SG) for neck 0.6, rest of body 0.9 (Paul 1988a, 1997); ~ indicates estimated and/or approximate, volume and mass values are rounded, tonnage estimates are specific to the results of the models after application of the SG scaled up to the size of the specimens and have a plus-minus error of ~5–10 percent when projected to the living animals.

	DVFCL	ADSL	ADSSL	HL	FL	H+NV	T+LV	TV	Tonnes
<i>Argentinosaurus</i> MCF-PVPH-1 MLP-DP 46-VIII-21-3	~420–450	~4470	~6170		~2575	~8.3	~67.8	~5.9	~70
<i>Patagotitan</i> MPEF-PV 3400	~290–315	~3670		1675	2380	~6.5	~48	~5.6	~52
<i>Puertasaurus</i> MPM 10002	~290								
<i>Notocolossus</i> UNCUYO-LD 301	~220			1760	~2070–2515				
<i>Paralititan</i> CGM 81119				1690	~1990–2415				
'A.' <i>giganteus</i> MLP 26-316					2310				
<i>Dreadnoughtus</i> MPM-PV 1156	~200–350	~3700	~5050	1600	1910	~3.4	~29.1	~2.5	~31
<i>Alamosaurus</i> SMP VP-1625					~1850	~2.8	~25.8	~2	~27
<i>Futalognkosaurus</i> MUCPv-323	~290	~2900	~3825	1560	1980	~4	~26.7	~2.7	~29
<i>Nemegtosaurus</i> ZPAL MgD-I/48		~2435	~3660	1000	1395	~0.6	~8.3	~0.68	~8.5
<i>Saltasaurus</i> PVL 4017-79					875	~0.1	~2.54	~.17	~2.5
<i>Rapetosaurus</i> FMNH PR 2209					657	~0.15	~0.73	~0.06	~0.8
<i>Giraffatitan</i> HMN MB.R.2181		~3820	~4800	2130	~2090	~4.7	~30.3	~1.58	~32

sauropods specifically, as well as tests of their accuracy, were detailed by Paul (1987, 1988a, 1988b, 1997, 2014, 2016) and Paul and Chase (1989).

The soft tissue profiles utilized by the present researcher/illustrator/modeler represent the subjects in the healthy prime-lean condition that is most suitable for mass estimation (Paul 1997). This standard incorporates minimal fat deposits and lacks the extraneous and often erroneous soft tissues that, as the illustrative technique became popularized and then normalized, often beset profile-skeletal reconstructions produced by illustrators (or the researchers advising these illustrators) who are insufficiently familiar with animal anatomy. 'Shrink wrapping' dinosaurs by rendering them overly thin to the point of emaciation has been criticized (as per Conway et al. 2012), justifiably in some cases (e.g., Russell 1989), but the reality is that tetrapods living under natural conditions are often lean. Numerous

online photographs show that the ribs are commonly visible on rhinoceros, elephant, and lion flanks, as is the ventral edge of the thin, fan-like latissimus dorsi muscle. Also normally visible, or at most covered by a modest veneer of tissues, are the dorsal tips of the dorsal and sacral vertebrae, the dorsal edges of the scapula and ilium, and various portions of the limbs, such as the proximolateral corner of the humerus, the epicondylar bulges of the distal humerus, the olecranon process of the ulna (contra Brassey 2017: fig. 2a, which is an example of insufficient anatomical knowledge by the illustrator), the anterior surface of the knee (contra Brassey 2017: fig. 2a), and the lateral sides of the ankle. The anterior parts of the shins of straight-kneed, short-footed, and relatively slow-moving proboscideans (Knight 1947; Paul 1987, 1988a, 1997; Larramendi 2016; Fig. 1J) (contra Brassey 2017: fig. 2a) and humans are nearly devoid of musculature, and this was probably true

of sauropods as well (Figs. 1A–I). Continental tetrapods that are more ensheathed in fatty soft tissues are atypical, and are apparently limited to semiaquatic, short-limbed forms such as hippopotamus that differ strongly in body form from the relatively long-limbed, primarily terrestrial sauropods. When observing giraffe necks in anterior view, the bulge of each cervical vertebra is readily visible (with the lack of heavy lateral musculature and other soft tissues presumably being a weight-saving adaptation), and the same configuration is herein applied to sauropod necks. The ventral edges of the cervical ribs of most sauropods are positioned well below the centra, and are set laterally far apart, such that there is so much space between the ribs that the trachea and esophagus must have coursed between them. There should, therefore, have been little soft tissue ventral to the cervical ribs, all the more so because that would have added unneeded mass to the neck (Paul 1988a, 1997; Larramendi and Paul in prep.).

Additional mass due to seasonal and other variations may be added, but with caution. Medium-sized Neogene herbivores living at temperate latitudes that experience extreme seasonal variations, such as adult deer, normally see a 30 percent mass variation from a very lean, marginally healthy early spring condition to a pre-winter, highly fattened condition in the fall (Delgiudice et al. 1992). Because of lower metabolic rates due to scaling relative to increasing mass, giant herbivores are more starvation-resistant, and Asian elephants dwelling at lower-latitude, less seasonal habitats vary in mass by only a few percent over the year (Mumby et al. 2015). African bush elephants may undergo somewhat greater mass changes in their more strongly seasonally wet-dry habitats (Albl 1971), but the variations appear less than are experienced by smaller-bodied, higher-latitude herbivores. As shown by Albl (1971), even when bush elephants are in prime condition, subcutaneous fat barely covers the dorsal edges of the ilia, which are, conversely, readily visible at the end of the dry season. To account for seasonal alterations in the mass of low- and middle-latitude Mesozoic sauropods, which should have had ready access to floral resources year-round (Gee 2011, 2016), the projected percentage of extra fat deposits may be added to the prime-lean results modeled herein.

The trunk contains the great majority of the volume and mass of a land animal, including long-necked and -tailed dinosaurs (Table 1; Paul 1988a, 1997; Bates et al. 2015; Larramendi 2016; Brassey 2017; Carballido et al. 2017; Larramendi and Paul in prep.), and especially in big-bellied herbivores, of which the very broad-hipped titanosaurs were exemplars. It therefore follows that determining and comparing the dimensions of the trunk is the most critical single factor in estimating the absolute and relative masses of sauropods. Because the trunk is largely ensheathed by only thin sheets of soft tissue as discussed above, its volume is tightly constrained by its length (as determined by the combined length of the dorsal–sacral vertebrae and the placement of the pectoral girdle, as explained below), the contours and breadth of the ribcage, and the width of the

pelvis. If these aspects are correctly restored, it is difficult to incorrectly estimate the volume of the trunk by a great amount via artistic license when applying superficial soft tissues; i.e., the technical anatomical limitations preclude the application of significant artistic license. Because the respective volumes of the neck, tail, and limbs constitute a minority of the total volume, restorations of their volumes as impacted by artistic license inherently cannot unduly influence the total either, all the less so if they are restored in prime-lean condition. For example, the inaccurate restorations of the proboscidean fore- and hind limb soft tissues by Brassey (2017: fig. 2a) noted above are very minor in volumetric terms compared to the great bulk of the trunk in the same figure, this being all the more true because although the tissues posterior to the elbow and anterior to the knee and shin are too thick, those anterior to the elbow and posterior to the knee are too thin, as can be seen by comparing Brassey (2017: fig. 2a) to Fig. 1J herein. In the end, the errors in Brassey's (2017: fig. 2a) reconstruction of proboscidean limbs would have virtually no impact on any final volume estimate of the animal in question as derived from this illustration, an example of how artistic license exerts little influence on mass estimation provided that the basic proportions of the subject are rendered accurately. That said, it should be a fundamental requirement of scientific illustration that all persons producing a profile-skeletal restoration be sufficiently knowledgeable regarding the soft tissue anatomy of modern animals to have the ability to render the profile of extinct forms with as much morphological plausibility as is feasible.

To generate volumetric models, the profile-skeletal reconstructions are reproduced to a common femoral length of 52.5 mm, a scale that is sufficiently large to allow for easy and accurate sculpting of the volume of a given reconstruction. A sheet of clear plexiglass is placed over the lateral view profile-skeletal restoration. A plasticine half-model is then built directly atop the restoration, ensuring an exact reproduction of its profile. A vertical transverse half-section of the trunk at its broadest is cut from a piece of cardboard and the abdomen is modeled anterior and posterior to it, ensuring that the bulk of the belly is accurately reproduced. The ilium is modeled separately in plasticine to ensure that its breadth is correct, and then put in place to ensure that the transverse breadth of the pelvis is accurate. The plasticine model is constructed to represent the dimensions of the profile-skeletal reconstruction to within about one mm. Upon completion, the half-model is cut into pieces so that it can be immersed in water in a 1000 ml graduated cylinder (occasionally 100 ml for small items) in order to measure its volume. This submersion procedure is performed twice to preclude mismeasurement. Multiplied by two, the volumes obtained for the neck, trunk and legs, and tail are each recorded separately (Table 1). Retention of the intact models is not practical because of the need to dismember them for measurement, because of the hundreds of models that have been and will be produced, because of the need to recycle the available clay

for new models, and because unused oil-based plasticine degrades over time, causing it to become brittle and change volume, presenting insurmountable conservation problems. It is emphasized that the volumetric models are not finely sculpted art, but instead are utilitarian technical mockups intended to replicate the basic volume of body parts. It is therefore the profile-skeletal reconstructions and the published results that are the actual record of the volume of the modeled vertebrates, the volume of which can be reliably replicated by new physical models, or by digitally scanning and calculating the volume, the two procedures producing similar results (Larramendi and Paul in prep.).

That the volumetric models are straightforward, utilitarian rather than artistic, direct translations in three dimensions of multi-view profile-skeletal reconstructions that merely record the volume of the latter prevents the models from being significantly influenced by artistic license relative to the profile-skeletal reconstructions. In order to test the consistency of the results, a few models have been redone after a period of time has passed (Paul 2011; Larramendi and Paul in prep.). In all cases the second results have matched the first within a percentage in the low single digits, much less than the error range inherent to restoring the volume of animals, or the mass variation of a living adult animal. An attempt to deliberately exaggerate the mass of a volumetric model well beyond lean condition found that at most ten percent could be added before the results were so awkward and incompatible with the skeletal dimensions that they were not realistic; this amount accords with the fluctuations in the mass of living adult individuals detailed above (Paul 2011). Ergo, errors that occur in the present researcher's volume estimates originate in the profile-skeletal reconstructions, not the models.

Further aborting efforts to deliberately or unconsciously produce results that differ from those indicated by the profile-skeletal reconstructions is the fact that each model is produced one at a time in series, with the plasticine recycled for the next, so the models cannot be cross-compared and consequently adjusted in some manner. Nor is the human neural network capable of assessing the volume of profile-skeletal restorations or models of exotic creatures of variable proportions and from them predicting a final, specific quantitative result that can be consciously or subconsciously influenced. Every time the present researcher performs the calculations derived from water immersion measurements, he is curious as to what the results will be, and they are often surprising. The ability of volumes derived from profile-skeletal reconstructions to produce reasonably accurate results has been further supported by Paul (1997), Larramendi (2016), and Larramendi and Paul (in prep.) by consistently correctly restoring the known mass of a number of modern tetrapod specimens, including obtaining essentially the same correct result via independent profile-skeletal reconstructions of the famed circus elephant Jumbo (Fig. 1J). If attempts to restore the mass of extant vertebrates with the above techniques instead frequently

generated highly erroneous or varying results, then the method would be refuted.

Convex hulling is supposedly superior to allegedly arbitrary and subjective artistic license regarding volumetric modeling (Sellers et al. 2012; Bates et al. 2015; Carballido et al. 2017). However, when conducted by a worker with sufficient knowledge of animal anatomy, traditional analog methods are more correctly termed anatomical realism. The last is not present in convex hulling, which is neither as non-analog nor as non-subjective as it has been presented. Convex hulling involves a major subjective analog aspect because, like traditional analog methods, it too is ultimately dependent upon skeletal restorations, the accuracy of which depends on the efforts of persons of differing anatomical proficiency and opinions.

Maximal convex hulling (Sellers et al. 2012; Bates et al. 2015; Brassey et al. 2017; Carballido et al. 2017) swamps the subtle tetrapod topographic features listed above by ladling a thick layer of simulated flesh over most of the skeleton. The method is inherently unrealistic except in the cases of amphibious/aquatic forms (Fig. 2), and risks if not ensures producing highly excessive results for more terrestrially-adapted tetrapods. Consider that maximal versus minimal convex hull modeling results are presented with a variation as high as 75 percent (Bates et al. 2015; Carballido et al. 2017). Because maximal convex hull results are inherently excessive for land tetrapods, they are not viable plus or minus range values and should be discounted, so unless there is specific justification (such as analyzing and comparing methodologies) there is no apparent rationale for calculating and presenting them. At the opposite extreme, minimal convex hulling produces an emaciated, 'shrink-wrapped' body volume that represents starvation or close to it; as such, minimal convex hull volume results also lack scientific value and their use should be discontinued. Because the quantitative volume and mass results from both maximal and minimal convex hulling are inherently in error, they are ignored in the present analysis, which considers only the intermediate value. Specifically, in order to compensate for the latter underestimate, a correction value of 21 percent is added to the minimal convex hull volume estimate to arrive at what appears to approximate a prime-lean condition based on regression analysis of extant taxa (Sellers et al. 2012; Bates et al. 2015; Carballido et al. 2017). Although plausible, as acknowledged by Sellers et al. (2012), the sample size is limited, the correction value is subject to change, and the latter may vary substantially between body and trophic types. In particular, using the same correction value for all tetrapod forms may underestimate the masses of large-bellied herbivores relative to those of carnivores that are hollower-bellied, at least before they have gorged on a carcass.

A core truth regarding volumetric modeling of any type is that to produce results that are as optimal as possible in both absolute and relative terms, the model must be as anatomically correct as is possible given the data at hand. That, in turn, requires the application of anatomical knowledge

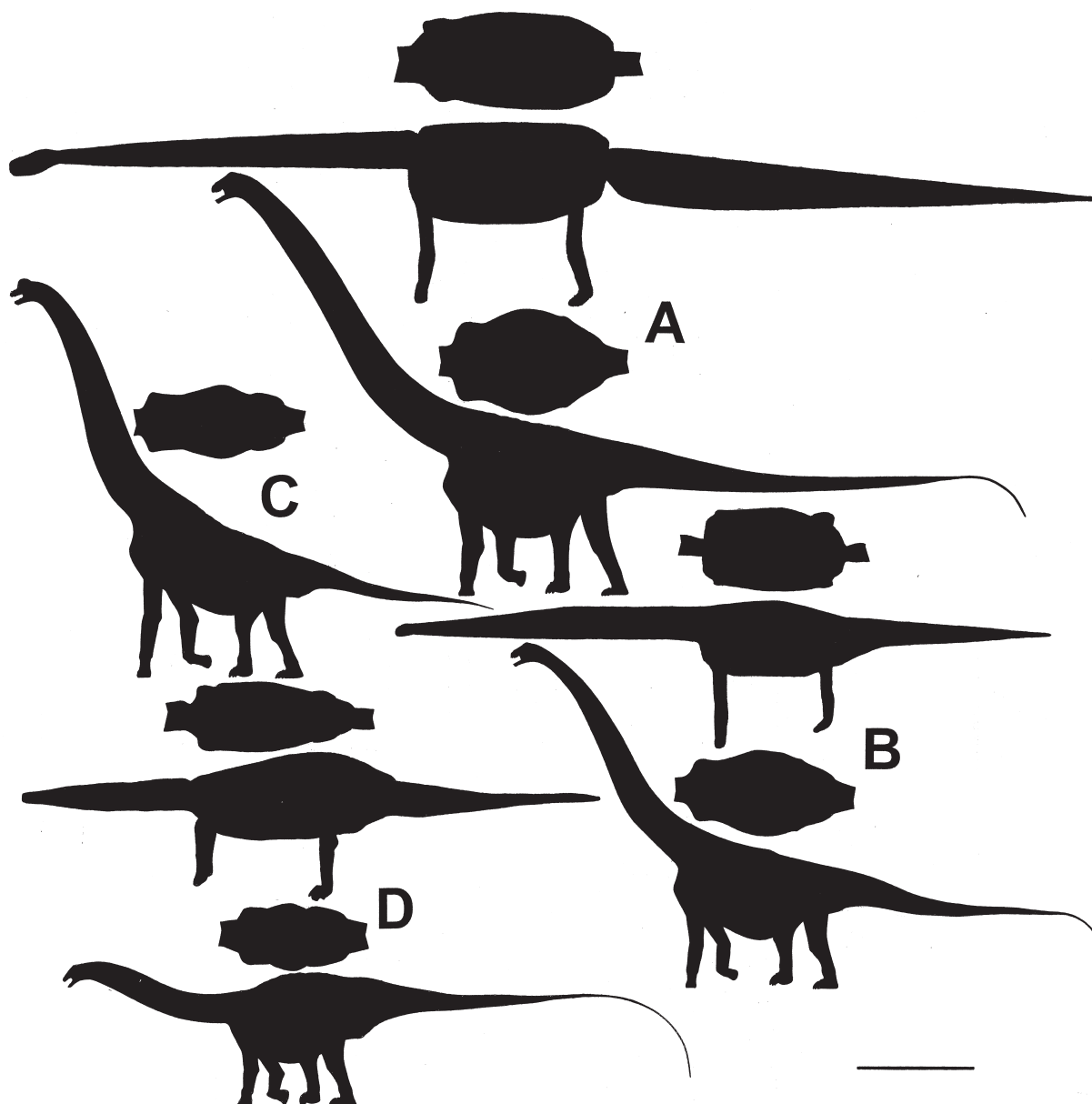


Fig. 2.—Profiles comparing volumetric corrected convex hull (at top when shown, by Bates et al. 2015 and Carballido et al. 2017) versus high-fidelity profile-skeletal (bottom or only) restorations of the same specimens to same scale, bar equals 4 m, tonnages listed are based on convex hulling and profile-skeletal reconstruction, respectively. **A**, *Patagotitan mayorum*, 51/52 t; **B**, *Dreadnoughtus schrani*, 28/31 t; **C**, *Giraffatitan brancai*, 25/32 t; **D**, *Apatosaurus* (or possibly *Brontosaurus*; see Paul 2016) *louisae* CM 3018, 27/18 t. A more complete version of D is provided in Paul (2016).

and common sense, which also, at times, requires the rejection of particulars of the sometimes erroneously mounted skeletons upon which convex hulling is typically based, and also demands consistency in the anatomical details of restorations of related taxa in order to generate consistent relative masses. Convex hulling provides a close, objective approximation of the body volume defined by the skeleton of a given fossil animal only in that it models the volume of that

skeleton as it has been reconstructed and proportioned—which may or may not be correct—rather than the volume of that skeleton when it was actually part of a living animal.

To wit, it has been repeatedly emphasized that estimates that project the most completely known apatosaurine diplodocid skeletons as massing more than those of large brachiosaurids cannot be correct; although made up of robust skeletal elements, apatosaurines had markedly shorter

trunks and narrower abdomens and hips than did brachiosaurids (Figs. 2C–D; Paul 1988a, 1997, 2016; various dimensions of these two sauropod clades having been well documented by Gilmore [1936] and Janensch [1950a, 1950b, 1961], respectively, supplemented by photographs of mounts of the Pittsburgh apatosaurine CM 3018 and the brachiosaurid *Giraffatitan brancai* [composite skeleton mounted at the HMN Berlin], including anterior and posterior views to further document the breadths of body elements). Yet, based on volumetric digital models, Bates et al. (2015) estimated the apatosaurine CM 3018 as massing 2 tonnes more than the Berlin brachiosaurid, and 10 tonnes more and half again as massive as an estimate for the same apatosaurine specimen by Paul (1988a, 1997, 2016), which was based on a more anatomically accurate profile-skeletal restoration that was itself derived from the detailed figures and measurements provided in the meticulous original description of the skeleton (Gilmore 1936), plus additional photographs of the mount. It is apparent that the trunk of the digital apatosaurine model employed by Bates et al. (2015) is much too large, particularly too long (Fig. 2D).

Because the original image of the model was reproduced at small size and low resolution by Bates et al. (2015), and a scale bar was not included, it is not possible to definitively ascertain how the error occurred, but it is clear that the pectoral girdle is placed far too anteriorly. Because there is no direct bone-to-bone connection between the axial skeleton and the scapulocoracoid, the placement of the pectoral girdle is inherently somewhat subjective, unlike that of the pelvis that is firmly attached to the vertebral column. In dinosaurs, the coracoid and glenohumeral joint are situated anterior to the dorsal ribs (Paul and Christiansen 2000), but because the chest is slung between the scapular blades via the serratus muscles (Hohn 2011), there must have been substantial overlap of the blade alongside the anterior dorsal ribs (Figs. 1E–I). In the CM 3018 model employed by Bates et al. (2015), the scapulocoracoid is oriented too close to subhorizontal for nonavian dinosaurs (Paul, 1987, 1988a, 2016, 2017; Paul and Christiansen 2000; Larramendi and Paul in prep.), and is placed so far anteriorly that much of the pectoral girdle is actually astride the posterior cervical vertebrae and ribs (that would, in life, have been in front of and free of the shoulders), leaving too little overlap between the scapular blade and the anterior dorsal ribs for a strong supporting connection. It also appears that proportional errors occurred, in that the length of the presacral–sacral series is about one-sixth greater than indicated by the data in the original description (Gilmore 1936). Whatever the cause(s), possibly in the mount and/or the scanning process and presentation, the trunk is over one-third longer than it should be, transforming an exceptionally short-bodied sauropod into a distinctly and incorrectly long-bodied animal. Because the Bates et al. (2015) apatosaurine mass estimate is based on this incorrect digital model, their result does not confirm the accuracy of the similar tonnage estimated for the same taxon via a non-rigorous artistic volumetric model by Gregory (1905; contra Brassey 2017).

Another mistake common to many dinosaur skeletal mounts (e.g., the apatosaurine in Bates et al. 2015) is that the anterior dorsal ribs are incorrectly oriented vertically, as they are in mammals (Fig. 1J); this error is most common in older mounts, but still occurs in some recent examples. Instead, all dinosaurs possessed posterodistally-angled anterior dorsal ribs that resulted not only in a reduced trunk volume lengthwise (Figs. 1D–I) but also a narrower chest (Paul 1987, 1988a, 1988b, 2016; Carpenter et al. 1995; Paul and Christiansen 2000). In comparison, the Berlin brachiosaurid skeleton was recently remounted with the scapulocoracoid more correctly subvertical, the blade of the scapula correctly extensively overlapping the anterior dorsal ribs, and these ribs properly swept posterodistally, producing a narrower, lower-volume shoulder region. The major divergence in the placing and spacing of the pectoral girdle in the two specimens precludes an accurate relative mass comparison as the skeletons are currently articulated.

A case that illustrates the subjective issues concerning skeletal restorations used for convex hulling can be found in Brassey et al. (2015). These authors' restorations of the stegosaur pectoral girdle in their figures 1a and 1b are plausible in both lateral and transverse views, including the coracoids being reasonably close to the body midline as has been well documented for dinosaurs (Paul 1987: fig. 19b; Carpenter et al. 1995; Paul and Christiansen 2000; Hohn 2011). By contrast, in Brassey et al.'s (2015) figures 1e and 1f, the skeleton is rearticulated such that the scapula is lateral to the dorsal series—a condition that never occurs in quadrupedal dinosaurs (Paul 1987, 2016)—and the coracoids are much too far from one another, resulting in the shoulders and chest being much too broad and therefore too great in volume. Brassey et al. (2015) did so in order to present a maximum possible skeletal volume, but the result is so anatomically incorrect that it is scientifically useless, and it should not have been produced other than as an example of how anatomical errors in a skeletal restoration can lead to errors in its associated volume estimate.

It is emphasized that the above observations and criticisms concerning digital restorations of volumes are not intended to entirely negate the utility of convex hulling, which is in fact a useful technique (Brassey 2017). They do, however, stress the need for more rigorous, skeptical analysis based on authoritative knowledge of dinosaur anatomy during the process. Their bones often distorted by the fossilization process (as cautioned by Brassey et al. 2015), mounted skeletons are analog structures that were subjectively assembled by a wide divergence of crews of differing levels of biological knowledge, opinions, and competency ranging from minimal to high over a span of more than a century. Virtual skeletal restorations based on scanned bones likewise involve the same subjective restorations of the articulations of ribs, pectoral elements, and other proportions that occur when mounting skeletons or preparing analog paper skeletal reconstructions. Therefore, digital volumetric models are actually highly subjective and

analog in their basis, much as digitized musical recordings are usually based on analog human performances. Estimating volumes without first modifying the digitized skeletons (whether they be physical or virtual) when necessary so that they are consistently anatomically correct literally guarantees inaccurate results that will be especially inconsistent when it comes to cross-comparisons of their dimensions and volumes. High-anatomical-fidelity analog skeletal restorations can reduce these sources of error and produce more consistent results when restored using uniform, accurate anatomical criteria. Brassey (2017) also noted that the very process of convex hulling itself requires subjective decisions. In sum, volumetric mass estimation via convex hulling is derived from a mixture of analog and digital methodologies that is no more objective or reliable than entirely analog methods, and may in fact be somewhat inferior. To put it another way, there is no ‘skill shortcut’ that eliminates the need for those involved in illustrating or mounting vertebrate skeletons to be highly knowledgeable animal anatomists who know how to make the most biologically realistic subjective decisions (Brassey 2017).

An assumption that underlies the supposed superiority of digitized restorations of volumes over more traditional analog methods is that three-dimensional scans of mounted skeletons are inherently accurate. While working to refine his profile-skeletal reconstructions of the *Tyrannosaurus* ‘Sue’ (FMNH PR 2081) for another project (Larramendi and Paul in prep.), the present author was surprised to realize that the digital scan of the specimen presented by Hutchinson et al. (2011: fig. 3) is incorrectly proportioned. Among other issues, the pelvis and other portions of the skeleton are too large relative to the femur when compared to both the measurements of the specimen published by Brochu (2003) and lateral view photographs of the mounted skeleton; these discrepancies apparently contributed to Hutchinson et al.’s (2011) extraordinarily high volume estimate for FMNH PR 2081 (Larramendi and Paul in prep.). Moreover, as noted above, the digital model of the apatosaurine skeleton CM 3018 presented by Bates et al. (2015) may have proportional issues. It appears that such unexpected errors can slip into three-dimensional scans in part because strategically-located physical scale bars are not always included in the scans. Doing so would allow those conducting the scan to ensure that they are presenting accurate results, and also for others to verify their accuracy. Until such procedures become the required norm (see Mallison and Wings 2014), the proportions of three-dimensional scans of skeletons must be regarded with caution unless the scans are presented at sufficiently large size so as to be verified by measurements of individual elements from various parts of the specimen.

Most of the profile-skeletal reconstructions illustrated in this study are shown incomplete. Note that, because information regarding exactly which bones have and have not been preserved in a given specimen or mount is often conflicting or unavailable, the widely used but inaccurate term “rigorous” restoration for incomplete profile-skeletal

reconstructions is best avoided in favor of “known bone only” (Paul 2016). Terms such as “rigorous” and “high-fidelity” should instead be reserved for skeletal reconstructions that are executed to a high degree of proportional and anatomical accuracy. In some of the profile-skeletal reconstructions presented herein, limb elements from one side have been replicated on the other. A few of the reconstructions are composites, and because it is not possible to fully determine which elements are and are not known in these cases, one of the profile-skeletal reconstructions is shown as complete. A limitation of convex hull modeling is that it requires the existence of an at least superficially complete skeletal reconstruction, be it physical or virtual. Conversely, an advantage of an artistically realistic physical volumetric model is that it can be rendered even when the remains are partial, so long as the specimen being modeled may be confidently presumed to be similar in form and proportions to related taxa (contra Carballido et al. 2017).

Whatever means are used to restore a volume, it is then necessary to estimate the density of the subject to in turn calculate its mass. Because sauropod vertebrae were pneumatic, generally highly so in titanosaurs, the presence of internal air sacs must be accounted for. Paul (1988a, 1997, 2016) applied a specific gravity of 0.6 to the highly pneumatic neck and a value of 0.9 to the rest of the sauropod body. A revision of density values for sauropods is underway by Larramendi and Paul (in prep.), but any alterations will be too minor to significantly impact the final mass estimates for reasons discussed previously (Paul 1988a, 1988b, 1997, 2016).

The only measurements and estimates that are close to precise (in that they have very small plus-minus error ranges) in studies such as this are the dimensions of individual bones. All other values, including estimates of the collective length of articulated elements that would have been separated by cartilaginous tissues of often uncertain thicknesses, are approximate to varying degrees. The results of volumetric models, whether digital or entirely analog, inherently have significant plus-minus factors, perhaps 5–10 percent (for a total of 10–20 percent minimum to maximum) for profile-skeletal reconstructions when the remains of a given taxon are highly complete, and larger when the available specimens are less complete. The difficulty (or perhaps impossibility) of more precisely establishing a plus-minus value for mass estimates, the increasing error range as skeletal completeness decreases, and possible variations that may occur between animals of dramatically different form preclude a formal application of variation to the results (Paul 1997). Indeed, in her recent review of volumetric mass estimation techniques, Brassey (2017) did not offer a solution to this issue, and it is possible that one may never be forthcoming. Moreover, as also noted by Brassey (2017), reports of size estimates for lay audiences should always be similarly approximate rather than overly precise; for example, stating that *Patagotitan* massed 50–55 tonnes is preferable to stating that this same titanosaur massed precisely 52 tonnes. After all,

when alive, healthy, and fully mature, the mass of an individual varies over time, even over the short term.

In any case, the variation inherent in high-fidelity analog and digital skeleton-based volumetric mass estimates is far less than occurs when extrapolating from the dimensions of individual bones, because variation in mass relative to bone dimensions is often very substantial, and sometimes extremely so. For example, in principle, the ability of the limb bones of tetrapods to cope with the stress loads of bearing the mass of the body during locomotion could be tightly linked to overall body mass, on the assumption that natural selection persistently opts for maximum biostructural efficiency. But even in extant tetrapods, the variation of mass relative to the circumference of the humerus and/or femur varies by a factor of more than two, and does so even among animals of similar form such as extant proboscideans, even within species (Haynes 1991; Paul 1997; Campione and Evans 2012; Sellers et al. 2012; Bates et al. 2015; Larramendi 2016; Brassey 2017; Carballido et al. 2017; Larramendi and Paul in prep.). Furthermore, the extant fauna provides a very limited sample relative to all tetrapods that have existed through geologic time, so it is likely that exotic extinct forms exhibited even greater variation in their mass/stylopodial circumference ratios (Larramendi and Paul in prep.). Nor can limb bone strength be employed to calculate the masses of highly aquatic animals, which instead requires volumetric modeling.

Likewise, attempting to use the transverse dimensions of elements such as vertebrae to compare the sizes of different species is so problematic that it risks being misleading, given that such dimensions often vary greatly between species of equivalent mass even within a fairly morphologically uniform taxonomic group. For example, Carballido et al. (2017) did not first test their use of the lateral and vertical dimensions of dorsal vertebrae to estimate the relative sizes of titanosaurs, so their conclusion that *Patagotitan* was larger than all other known titanosaurs on this basis is unsubstantiated and potentially spurious; the Carballido et al. (2017) method is specifically related to the height and width of the shoulders, which do not necessarily closely relate to or impact the overall volume of animals of otherwise broadly similar size. Anterior dorsal neural spine height is likely to be a function of the dimensions and extent of the epaxial musculature, the means of dorsal neck support, and/or display rather than a close measure of overall size; consider, for example, the great differences in anterior thoracic neural spine height in bovids relative to mass, such as the tall-shouldered male American bison versus the more standardly proportioned Cape buffalo. Broader shoulders may be an adaptation for increasing the volume of the lungs, the increased air space of which does not add to the mass of an animal. In any case, Carballido et al.'s (2017: fig. S6) width estimate of the widest *Patagotitan* anterior dorsal vertebra, the transverse processes of which are not entirely complete (Fig. 1B), is plausible but may be in error, and moreover determining the exact positions and any corresponding dimensional comparability of the

anterior dorsals of this taxon and *Argentinosaurus* is difficult because of the incompleteness of their remains. Similar problems apply to varying degrees to using dimensions of individual cervical and caudal vertebrae and girdle and limb elements for the purposes of mass estimation (Paul 1997).

Because, as has been noted, the trunk contains the great majority of the mass of a land animal, it follows that the longer the trunk, the heavier the animal is likely to be when body proportions are otherwise generally similar. Accordingly, when comparing members of a fairly morphologically uniform tetrapod group such as South American titanosaurs in cases where at least some examples are fragmentary, the dimension for cross-comparisons intended to assess relative masses that is most likely to produce the most accurate results is likely to be the combined length of the articulated trunk vertebrae. Comparisons of trunk length would preferably be based on complete dorsal-sacral series, or if those are not available, partial series or individual dorsal vertebrae. When examining the last, the key longitudinal measurement for dimensional comparisons is functional length, as measured by the length of the lateral surface of the centrum without any anterior articular condyle that would have fit into the posterior cotyle of the preceding vertebra (Fig. 3).

Cross-comparison of the lengths of articulated dorsal series within Titanosauria is facilitated by a number of factors. Titanosaurs commonly possessed ten dorsal vertebrae (Campos et al. 2005; Calvo et al. 2007a, 2007b; Coria et al. 2013; Lacovara et al. 2014; Paul 2016; Carballido et al. 2017); although Borsuk-Bialynicka (1977) claimed that *Nemegtosaurus* (= '*Opisthocoelicaudia*,' Paul 2016; Currie et al. 2017) has 11 dorsals, the anteriormost preserved but damaged presacral vertebra appears to be the posteriormost cervical rather than the anteriormost dorsal, and the skeletal restoration in Borsuk-Bialynicka (1977) shows only ten long-ribbed dorsals (as followed in Fig. 1F). Within individual titanosaur specimens the length of the dorsal centra varies from very little to modestly. The former applies to the specimens examined herein (Bonaparte and Coria 1993; Calvo et al. 2007a, 2007b; Coria et al. 2013; Lacovara et al. 2014; Carballido et al. 2017; Figs. 1A–D). Greater variation is seen in other titanosaurs, although the degree of variation is difficult to quantitatively constrain because some of the measurements are approximations, and/or are not fully consistent with the accompanying figures (Borsuk-Bialynicka 1977; Campos et al. 2005; Curry-Rogers 2009; Coria et al. 2013). It is notable that in some titanosaur specimens the first dorsals can be somewhat shorter than are those that are more posterior, such as *Nemegtosaurus* and *Trigonosaurus*. Comparing the breadth of titanosaurian trunks is similarly facilitated by the fact that all titanosaurs with sufficiently preserved dorsal ribs and pelves are relatively broad-bellied and -hipped compared to other sauropods, with fairly consistent trunk length/pelvic width ratios (Figs. 1C–D, G–H; Borsuk-Bialynicka 1977; Powell 1992; Campos et al. 2005; Coria et

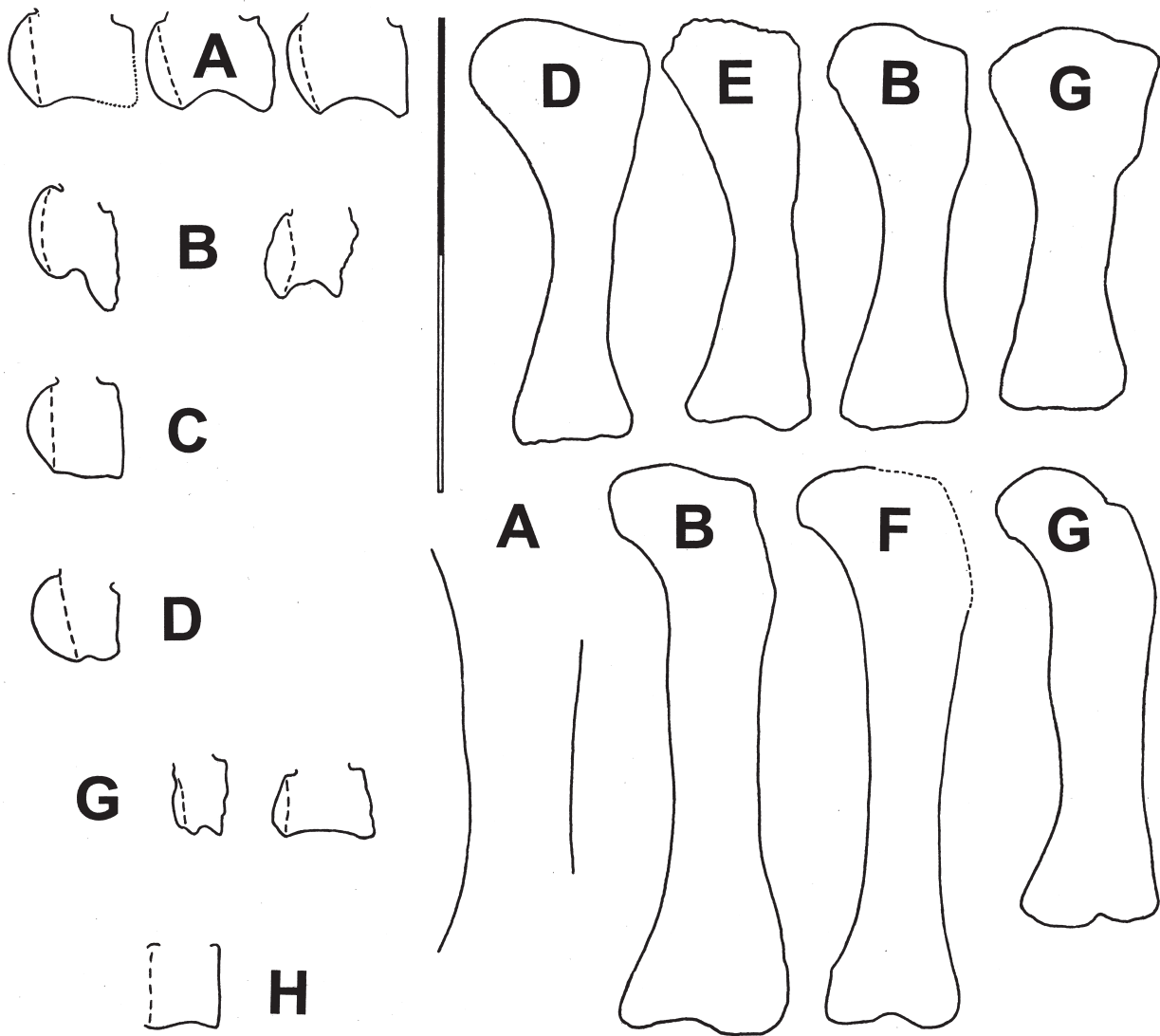


Fig. 3.—Titanosaurian dorsal centra (in left lateral view, dashed lines indicate anterior centroms from which dorsal vertebral functional centrum lengths were measured for Table 1), anterior or anteriormost, middle, and posterior (in that order) at left; humeri at upper right; and femora at lower right as preserved for a given taxon, to same scale; bar equals 2 m. **A**, *Argentinosaurus huinculensis*; **B**, *Patagotitan mayorum*; **C**, *Puertasaurus reuili*; **D**, *Notocolossus gonzalezparejasi*; **E**, *Paralititan stromeri*; **F**, *Antarctosaurus giganteus*; **G**, *Dreadnoughtus schrani* (immature); **H**, *Futalognkosaurus dukei*.

al. 2013; Lacovara et al. 2014; Paul 2016; Woodruff et al. 2016). In sauropod skeletons that were preserved in articulation, as well as in mounted specimens of these dinosaurs, the maximum breadth of the ribcage tends to be slightly greater than that of the anterolateralmost tips of the ilia. This is therefore presumed to be the case for the titanosaurs restored in this study, most restorations of which include pelvic material documented in dorsal view that allow for differences between taxa to be incorporated into the dorsal view restorations.

The very fragmentary nature of the one (formerly) known element of *Maraapunisaurus*, a gigantic but partial dorsal vertebral neural arch that is now missing (Cope 1878; Carpenter 2006, 2018) precludes volumetric modeling of the holotypic individual, so only gross approximations of its size are feasible. This calls attention to a problem that continues to afflict the presentation of skeletal restorations and volumetric models of extinct animals: these restorations and models are not always accompanied by scale bars, and even when they are, these bars are often inaccurate or too

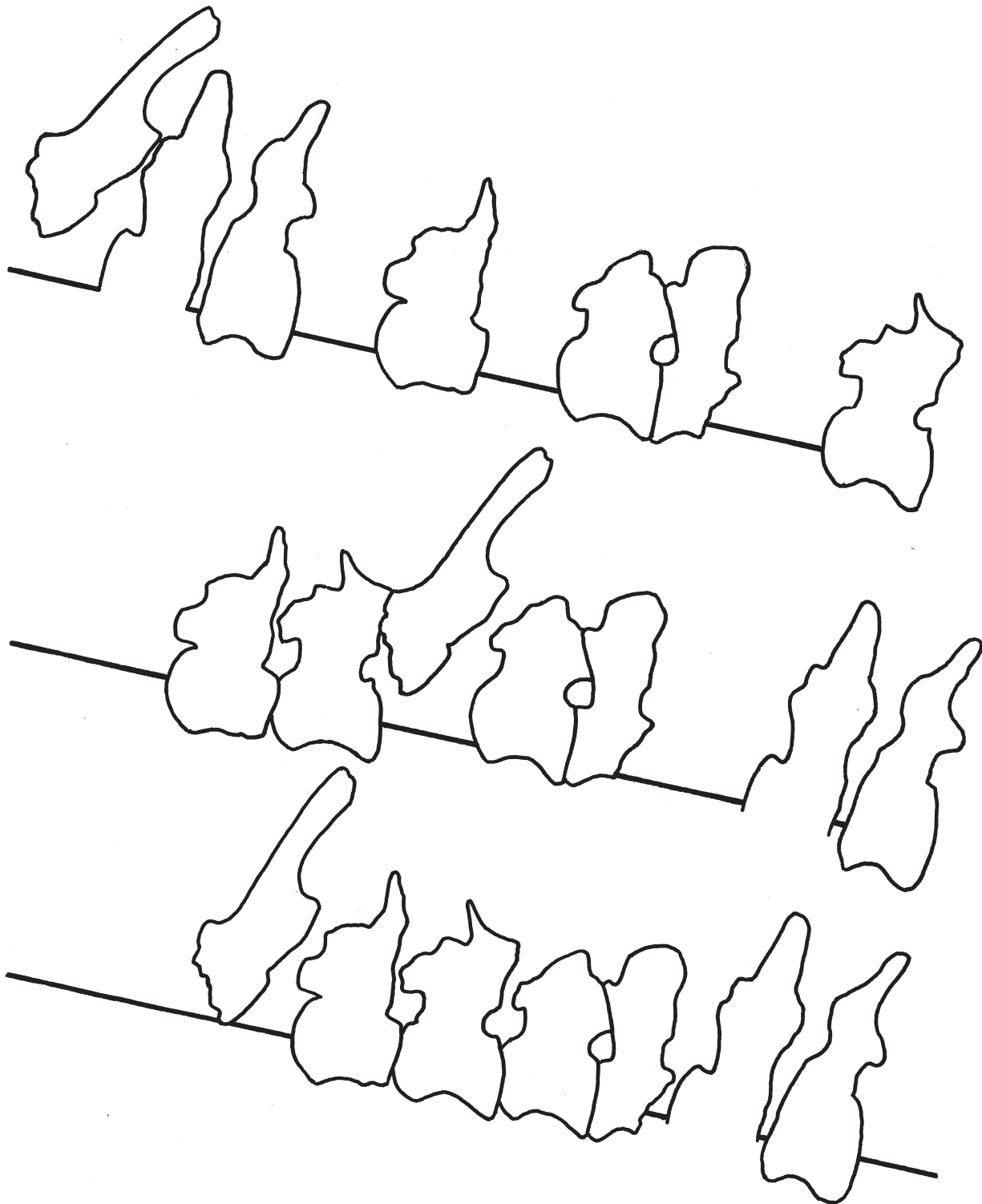


Fig. 4.—*Argentinosaurus* dorsal vertebral series articulated according to differing approximate sequences from top to bottom by Bonaparte and Coria (1993), Novas and Ezcurra (2006), and Salgado and Powell (2010; used here in Figs. 1A, 5C), showing that they all result in a similar total dorsal series length of ~4470 mm (presuming that all had a functional centrum length of 420–450 mm, with short intervening spaces for cartilaginous intervertebral discs). Dorsal vertebrae are figured after Bonaparte and Coria (1993) and unpublished photographs of MCF-PVPH-1 on display at the MCF-PVPH (Lamanna pers. comm., shared with permission from R. Coria). The ventral part of the centrum of the previously unpublished dorsal is obscured by another object in the photographs and as such it is not depicted here.

short to be readily measurable. Examples of these issues are found in Calvo and Salgado's (1995) description of the rebbachisaurid diplodocoid *Limaysaurus* (originally *Rebbachisaurus*) *tessonei*. First, the scale bars associated with the humerus and the femur of the holotype (Calvo and Salgado 1995: figs. 12b, 15a) imply that both of these bones are ~7% longer than the measurements provided in the text (Calvo and Salgado 1995:23, 26). Next, although the humerus/femur length ratio cited in the text (Calvo and Salgado 1995:23) is in accord with both distinct sets of length measurements, this value is ~9% lower than the ratio illustrated in their skeletal reconstruction (Calvo and Salgado 1995: fig. 17; the correct ratio was used by Paul 2016:209). Calvo and Salgado (1995) noted the approximate relative sizes of the three specimens they described, but there are no cross-comparative measurements in the study with which to constrain quantitatively their differences. As a result, the size of the limb elements relative to the vertebral series is uncertain. Because of these problems, it is not currently possible to accurately restore the proportions of *L. tessonei*, and this confusing information appears to have contributed to Carpenter's (2018) estimate of the size of *Maraapunisaurus* being lower than might be expected. Examples of studies that present scale bars in a sufficiently long manner (Bonaparte and Coria 1993; Paul 1987, 1998a, 1988b, 2014, 2017; Campos et al. 2005; Carpenter 2018) need to be consistently replicated in technical paleozoological publications, with the accuracy of the bars verified before publication. Most ideal is the placement of actual metric bars in photographic or scanned images of the elements. Other than when cross-comparing elements to a constant dimension (e.g., in the case of femora, proximal length), elements in a given figure are best presented at the same scale when the size differential between them is small enough to do so, in which case only a single large scale bar is necessary. Maintaining a constant scale in different figures is also useful when feasible. Also necessary are extensive element measurements in the text and/or table(s) including specimens of differing sizes to allow cross comparisons, whereas magnification values for figures are no longer useful in the current age of online publication. Authors, illustrators, reviewers, and editors should pay careful attention that scientific manuscripts meet these standards, including the accuracy of scale bars.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York; CGM, Egyptian Geological Museum, Cairo; CM, Carnegie Museum of Natural History, Pittsburgh; FMNH, Field Museum of Natural History, Chicago; HMN, Humboldt Museum für Naturkunde, Berlin; MCF, Museo Carmen Funes, Plaza Huincul; MLP, Museo de La Plata, La Plata; MPEF, Museo Paleontológico Egidio Feruglio, Trelew; MPM, Museo Padre Molina, Río Gallegos; MUCPV, Museo de Geología y Paleontología de la Universidad Nacional del Comahue, Neuquén; PVL, Instituto Miguel Lillo, Tucumán; SMP, State Museum of Pennsylvania, Harrisburg; UNCUYO, Laboratorio de Dinosaurios de la Universidad Nacional de Cuyo, Mendoza;

ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

RESULTS

The axial skeletal remains of *Argentinosaurus* include seven preserved dorsal vertebrae, of which six include centra, three of them preserving their functional lengths, and five sacral vertebrae. As can be visually (Figs. 1A–D and 3A–H) and quantitatively (Table 1) observed, the dorsal centra of *Argentinosaurus* are clearly much larger than the preserved examples belonging to *Patagotitan*, *Puertasaurus*, *Notocolossus*, *Dreadnoughtus*, and *Futalognkosaurus* in bulk and most importantly length. Because the preserved centra are very similar in functional length, confidence in the conservative estimate of the length of the *Argentinosaurus* dorsal–sacral series is high, regardless of the different positional hypotheses for the dorsals (Fig. 4) proposed by Bonaparte and Coria (1993) versus Novas and Ezcurra (2006) or Salgado and Powell (2010), the last of which is used in the profile-skeletal restoration presented herein (Fig. 1A). Even if the anterior most two dorsals that appear to be missing were both one-fifth shorter than the rest, the reduction in total dorsal series length would be only 4%, and this value is at the high end of potential reduction if any was present. The reconstructed dorsal series of *Argentinosaurus* is about one-fifth longer than that of *Patagotitan* (Figs. 3A–B), the latter being based on dorsals of two specimens of similar size (Carballido et al. 2017). The lack of preservation of the sacrum in the latter taxon prevents a comparison of total dorsal–sacral length between the two, but is unlikely to greatly alter the results. With such a markedly shorter dorsal series, it is highly unlikely that *Patagotitan* possessed a trunk that was more or even as massive as that of the *Argentinosaurus* holotype. In this context, the probably greater width of a *Patagotitan* anterior dorsal (Figs. 1A–B) is too slight to conclude that the animals were equal in overall dimensions, much less to justify Carballido et al.'s (2017) calculation that the titanosaur they described is ten percent larger than *Argentinosaurus*. Had Carballido et al. (2017) measured and illustrated the dorsal centra of these two titanosaurs in lateral view to the same scale, this likely would have precluded their last claim.

At least two Patagonian titanosaur femora have been assigned to *Argentinosaurus* (Mazzetta et al. 2004; Bonaparte 2007; Benson et al. 2014), but whether or not any of these elements actually belong to this taxon is not yet clear. The incomplete femur illustrated by Mazzetta et al. (2004; Fig. 3A) is so long as preserved, and its shaft so robust, that it is of appropriate size to have belonged to an individual as large as the *Argentinosaurus* holotype (Fig. 1A). To accommodate normally proportioned proximal and distal articular ends, the bone must have been about one-twelfth or more longer than that of *Patagotitan*, and it is one-fifth broader-shafted (Figs. 3A–B).

For *Patagotitan* with its far smaller dorsal centra to have matched, much less exceeded, its larger-bodied relative *Argentinosaurus* in total mass would have required the neck, tail, and limbs of the former to be much larger than what its fossils actually show, and/or its abdominal region to be far broader than that observed in any titanosaur. Alternatively, these body parts would have to have been improbably petite in *Argentinosaurus*. The centrum of an anterior dorsal of *Patagotitan* is distorted (Fig. 3B), but even if it were somewhat longer in vivo, the addition in total dorsal length would be only a few percent. There is no dimensional evidence based on measurements that are strongly connected to body volume that indicates that *Patagotitan* was as large as—much less larger than—the *Argentinosaurus* holotype or the largest known titanosaurian femur. Instead, all available definitive measurements indicate that *Argentinosaurus* was considerably larger than *Patagotitan*, and correspondingly more massive.

The single known dorsal vertebra of *Puertasaurus*, regarded as dorsal 2 by Novas et al. (2005), is approximately the same size as that of *Patagotitan*, and suggests an individual of broadly similar mass (Figs. 3B–C). Because, based on the condition in many articulated titanosaurian dorsal series, the anterior dorsals of *Puertasaurus* may have been shorter than the unknown, more posterior dorsals of this taxon, this individual may have been larger than *Patagotitan* and closer to *Argentinosaurus* in mass, but no further conclusions can be determined with the very limited data on hand. The dorsals of the immature *Dreadnoughtus* holotype (Fig. 3G) and the *Futalognkosaurus* type specimen (Fig. 3H) are markedly smaller than those of *Patagotitan* and *Puertasaurus* and therefore indicate considerably less massive animals.

In some regards, *Futalognkosaurus* has become increasingly useful for restoring titanosaurian masses because the holotypic specimen (which apparently represents a single individual) possesses a more complete presacral–sacral series and pelvis than do most other titanosaurs, including some ribs (Fig. 1D); moreover, additional elements and measurements have become available in recent years (Calvo et al. 2001, 2007a, 2007b, 2008; Calvo 2014; Carballido et al. 2017). But inconsistencies between some measurements, including comparisons of published dimensions to those of mounted replica skeletons, leave some uncertainties, so the profile-skeletal reconstruction presented herein (Fig. 1D) must remain provisional until the specimen is the subject of a full description that includes extensive and fastidious measurements. According to Calvo et al. (2008), the sacrum and apparently the ilia are anteroposteriorly compressed, and this has been accounted for herein by moderately lengthening these elements in Figure 1D. The articulated presacral–sacral series is 11.9 m long according to Calvo et al. (2008), but this was not measured from a mounted skeleton, in which the measurement appears to be closer to 11.7 m; at any rate, this is a minor difference that has little impact on the final result. An unpublished photograph of articulated dorsal

centra in ventral view with an adjacent 10 cm scale bar (Lamanna pers. comm.) provides a ~290 mm functional length that is compatible with the abovementioned length of the presacral–sacral series. The width of the pelvis appears to be ~68 percent that of the length of the dorsal–sacral column. This uniquely high pelvic breadth to trunk length ratio is apparently a function of the short length of the dorsal–sacral series, which even after the above noted correction of the length of the sacrum is unusually abbreviated relative to the limbs of this comparatively long-legged titanosaur. As a result, even though *Futalognkosaurus* has a hind limb that is about as long as that of the ~32 tonne brachiosaurid titanosauriform *Giraffatitan*, as well as a broader belly and pelvis (Figs. 1D, I), its much shorter and perhaps shallower trunk result in a total mass of ~29 tonnes according to the volumetric model.

Lacovara et al. (2014) stated that elements from both known specimens of *Dreadnoughtus*—the larger-bodied but still immature holotype MPM-PV 1156 and the smaller paratype MPM-PV 3546—were used in both of their skeletal reconstructions of this taxon, and this is probably true of the dorsal vertebrae (Voegelé et al. 2017). If so, then the dorsal column length as restored herein may be slightly too short, but the impact of this possibility may be reduced by the trunk being longer relative to the limbs in the *Dreadnoughtus* restoration than in the other titanosaurs. The hind limbs of immature *Dreadnoughtus* and of *Futalognkosaurus* are of similar length, and their pelves appear similar in breadth (Figs. 1C–D; Table 1). The dorsal–sacral series of the former is 36 percent longer than that of the latter, and the belly seemingly deeper according to apparently longer ribs, so *Dreadnoughtus* was markedly heavier, the volumetric model producing a total mass of ~31 tonnes. That value is about one-sixth higher than the present author's previous estimate (Paul 2014), which was executed before the latest data became available (Ullmann and Lacovara 2016; Voegelé et al. 2017), and is slightly more than one-tenth higher than the prime-lean condition-equivalent (i.e., the '+21%') digital volumetric estimate of Bates et al. (2015; Fig. 2B). If, as is plausible, the pelvis was wider than was restored by Lacovara et al. (2014), then the mass of the *Dreadnoughtus* holotype may have been one tonne or so higher than ~31 tonnes.

That the *Patagotitan* fossils do not include sacral and pelvic material hinders but does not preclude restoring the mass of this taxon via volumetric modeling, especially for relative comparisons (Fig. 1B). The difference in the trunk breadth/dorsal–sacral length ratio in the large South American titanosaurs in which this value is highest and lowest, respectively—*Futalognkosaurus* and *Dreadnoughtus*—is about 20 percent, which translates into a difference in trunk volume of only about one-tenth. Moreover, because trunk capacity is about two-thirds of the total body volume in titanosaurs (as measured by Carballido et al. 2017), the range of trunk breadth observed in these sauropods translates to a difference in total mass of about seven percent. In lieu of the lack of the *Patagotitan* pelvis, the relative comparison

is achieved by using the same trunk breadth/length ratio restored for *Argentinosaurus*, which is intermediate between those of *Futalognkosaurus* and *Dreadnoughtus*. The shoulder region is restored as proportionally broader in *Patagotitan* than in *Argentinosaurus* in view of the probably longer transverse processes of an anterior dorsal vertebra of the former, but the effect this has on the total volume is trivial. The mass derived from the anatomically realistic model of *Patagotitan* (Fig. 1B) is 52 tonnes. The convex hull model of this taxon published by Carballido et al. (2017) has a trunk that appears too flat-sided for a titanosaur, and the incomplete neck and tail are extended to the very maximum length that may be plausible, but these authors' corrected, prime-lean mass estimate of 55 tonnes is not markedly different or egregiously excessive (Fig. 2A). That the two methods (analog volumetric modeling conducted in the present study and digital convex hull modeling by Carballido et al. 2017) produce similar results reinforces the probability that these results are approximately correct, and renders negligible the possibility that the known *Patagotitan* remains represent animals that massed nearly 70 tonnes (as favored by calculations derived from the midshaft circumferences of the humerus and femur; Carballido et al. 2017).

The preserved dorsal vertebrae and sacrum of *Argentinosaurus* are sufficient to restore the volume of the body core, the hind limb material is adequate for approximating the same for the limbs, and the volume of the neck and tail can (for the purposes of this study) be assumed to approximate those of other South American titanosaurs relative to the remainder of the body, their being fairly similar in these regards across various taxa (Fig. 1). Part of an ilium is preserved (Carpenter 2006), and, as in *Patagotitan*, the breadth of the pelvis is herein restored at the same proportion of 0.6 times the dorsal–sacral length, a ratio typical of titanosaurs. The resulting highest plausibility profile restoration confirms that *Argentinosaurus* was markedly more massive than *Patagotitan*, particularly regarding the trunk that, as previously discussed, made up the great majority of the mass of these herbivores (Fig. 1B). That *Patagotitan* appears to have had slightly taller and broader anterior dorsal vertebrae suggests that the anatomy and function of the musculature at the base of its neck differed somewhat from that of *Argentinosaurus*. Nevertheless, this in no way indicates that the former taxon was more massive than the latter, the mass of which is herein estimated at 65–75 tonnes after a substantial but uncertain plus-minus error is added to the 70 tonne calculated estimate in view of the highly incomplete nature of the fossil. This result accords with a previously published ~70 tonne estimate based on a set of dimensional regressions (Mazzetta et al. 2004); values that are significantly higher or lower (Paul 1997, 2016; Sellers et al. 2013; Benson et al. 2014) can be effectively ruled out by the results herein. Using the same, consistent criteria and procedures produces a mass estimate of *Argentinosaurus* that is about one-fourth higher than that of *Patagotitan*, a substantial difference that

is virtually impossible to overcome in any anatomically realistic manner. Demonstrating otherwise would require producing anatomically plausible volumetric restorations of these two titanosaurs that would render *Patagotitan* at least as voluminous as *Argentinosaurus* while realistically accommodating their respective skeletal elements. The shorter neck and tail restored herein—which is provisionally regarded as more plausible than the longer neck and tail restored by Carballido et al. (2017)—produce a total length of ~31 m for *Patagotitan* (Fig. 2A). *Argentinosaurus* may have been up to or more than 35 m long (Fig. 1A).

The humerus/femur length ratio in titanosaurs ranges from approximately 0.7 to 0.85 (Lacovara et al. 2014; Carballido et al. 2017). That of *Patagotitan* appears to be at the low end of this range, but this is not entirely certain because no single individual specimen of this titanosaur preserves both of these elements. The high variation in humerus/femur length ratios increases the uncertainty of the humerus length/total mass relationship in titanosaurs. If the lowest titanosaurian humerus/femur length ratio is applied to the enormous *Notocolossus* (González Riga et al. 2016) humerus, which is five percent longer than that of *Patagotitan* (Figs. 3B, D), then its femur would have been about as long as that of *Argentinosaurus*, and could therefore imply a similarly-sized sauropod. On the other hand, most titanosaurs have a higher humerus/femur length ratio, resulting in their trunks having a slight anterodorsal 'pitch'. That the *Notocolossus* anterior dorsal centrum (Fig. 3D) is in the *Patagotitan*/*Puertasaurus* size class suggests that the former titanosaur was a comparatively long-armed sauropod in the mass range of these latter two giants. Nevertheless, the anterior dorsal of *Notocolossus* may have been shorter than the still-unknown more posterior dorsals, in which case a body mass approaching that of *Argentinosaurus* would be viable.

The humerus of *Paralititan* (Smith et al. 2001) is one percent longer than that of the apparently short-forelimbed *Patagotitan*, and five percent longer than that of *Dreadnoughtus* (Figs. 3B, E, G). Because humerus length to body mass ratios are so highly variable in titanosaurs, and lacking additional mass-related data, it can only be concluded that this African titanosaur massed somewhere between 30 and 55 tonnes.

The '*Antarctosaurus*' *giganteus* femora (Huene 1929; Powell 2003; Mazzetta et al. 2004; Lacovara et al. 2014) are almost as long as that of *Patagotitan*, albeit somewhat more slender, and the pubis of the former is slightly longer than that of the latter while being much longer than those of *Dreadnoughtus* (Lacovara et al. 2014; Carballido et al. 2017), so the remains probably record a titanosaur approaching the size of *Patagotitan* (Figs. 3B, F).

The notoriously ambiguous remains of *Bruhathkayosaurus* from the latest Cretaceous of India (Yadagiri and Ayyasami 1989; Galton and Ayyasami 2017), apparently poorly preserved and now lost, appear to represent a titanosaur, this being the only type of sauropod that is known from this geographic region and temporal interval. The

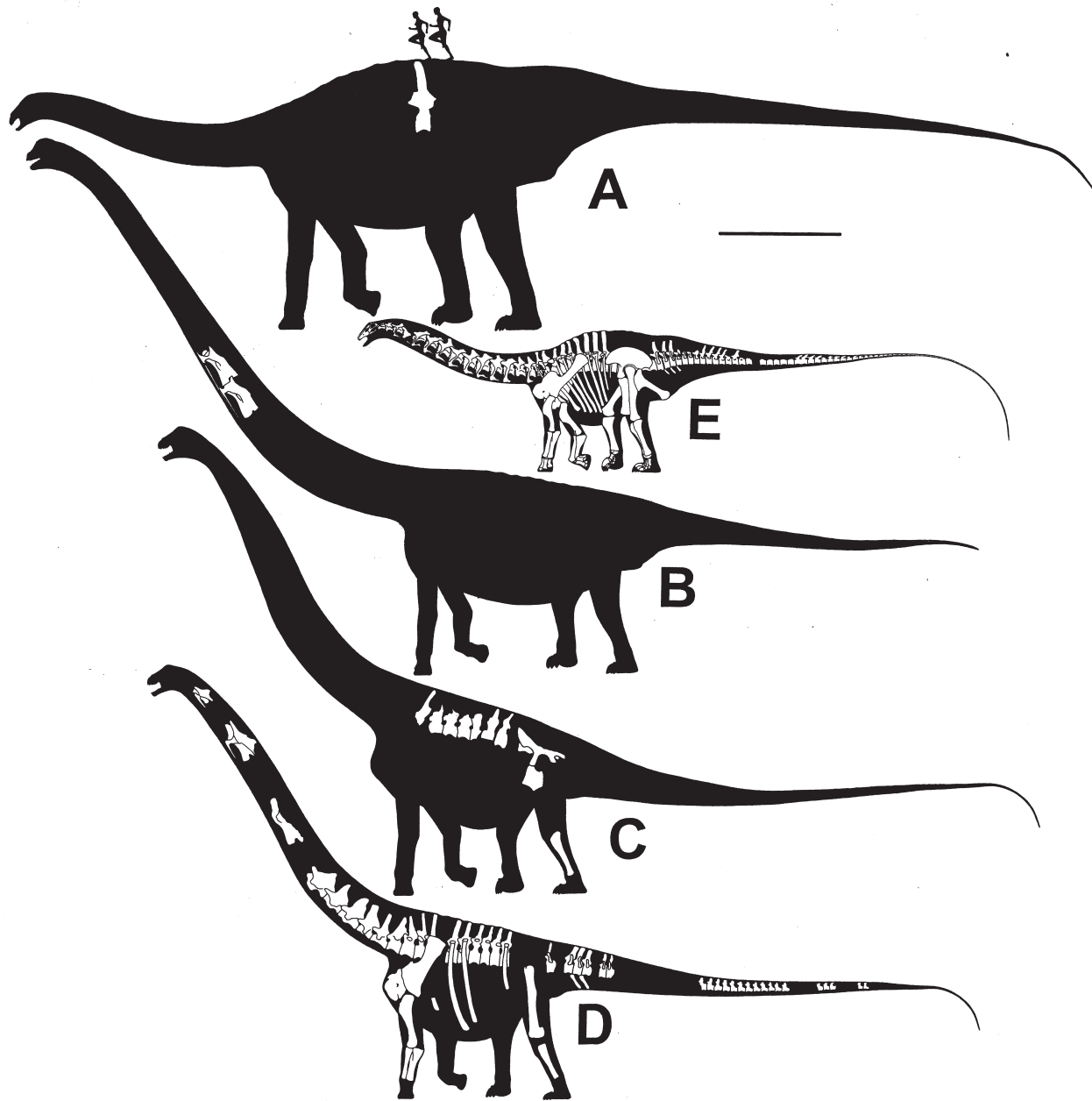


Fig. 5.—Known-bone-only sauropod profile-skeletal restorations to same scale, bar equals 4 m. **A**, *Maraapunisaurus fragillimus*, potentially the largest known land animal, restored as a robust, early-diverging diplodocoid at a mass of ~100 t; **B**, *Mamenchisaurus sinocanadorum?* restored as a long-necked mamenchisaurid at a mass of 75 t; **C**, *Argentinosaurus huinculensis*, the largest known titanosaur, 70 t; **D**, *Patagotitan mayorum*, the largest fairly completely known land animal, 52 t; **E**, *Apatosaurus* (or possibly *Brontosaurus*; see Paul 2016) *louisae* specimen CM 3018, the largest land animal known from a nearly complete individual skeleton, 18 t. A more complete version of E is provided in Paul (2016). Note that the elongate dorsal neural spines of the basal diplodocoid and the relatively narrow trunk of this animal and the mamenchisaurid result in these sauropods (especially the diplodocoid) appearing larger in profile compared to the broad-bellied titanosaurs relative to their respective total volumes.

ilium is similar in length to that of *Dreadnoughtus*, whereas the width of the distal femur appears to slightly exceed that of *Patagotitan*. The alleged tibia, if it is such, is almost one-third longer than the fibula of the *Argentinosaurus* holotype (Wilson and Sereno 1998). Nevertheless, if it is in fact fossil bone at all, the supposed *Bruhathkayosaurus* tibia is more probably a degraded femur, in which case its length is slightly greater than that of *Dreadnoughtus* and *Futalognkosaurus*. If so, this titanosaur was probably intermediate in mass between *Dreadnoughtus* and *Patagotitan*, and its status as an exceptionally gigantic land animal is therefore a myth (which is in some ways fortunate considering the extremely problematic status of its remains).

A fragmentary cervical vertebra attributed to the North American titanosaur *Alamosaurus* (Fowler and Sullivan 2011) may be similar in dimensions to that of *Puertasaurus*, but differences in neck dimensions relative to total mass in titanosaurs (Figs. 1B–E, G–H) render this information of limited value. A large partial anterior caudal vertebra (Jasinski et al. 2011: figs. 19a,b; Larramendi pers. comm.) suggests an *Alamosaurus* specimen that is about 15 percent dimensionally larger than the skeleton modeled herein (Fig. 1E), but individual variations such as these may not result in a correspondingly dramatic difference in mass. A partial femur (Fowler and Sullivan 2011) suggests an element approaching those of *Dreadnoughtus* and *Futalognkosaurus* in length, and therefore a similar body mass. A tibia that may pertain to *Alamosaurus* (Rivera-Sylva et al. 2006) also appears to be in this size class.

Assuming for the sake of size estimation it existed, a lost, fragmentary posterior dorsal vertebra of the Jurassic diplodocoid *Maraapunisaurus* has been restored at approximately 2.5 m in dorsoventral height on the presumption that its neural spine was not elongated into a tall, sail-like form (Paul 1997; Carpenter 2006, 2018). That the best estimated height of this vertebra, as tall as an ordinary room, roughly matches the lengths of the femora of the largest titanosaurs, and is almost twice as tall as their dorsals, is an indicator of the extraordinary size of this enigmatic and controversial sauropod. If *Maraapunisaurus* was a relatively gracile diplodocine, then it would have been in the area of 100–150 tonnes in mass and 50–60 m in length (Paul 1997, 2016; Carpenter 2006). *Maraapunisaurus* instead appears to have been a rebbachisaurid, in which the posterior dorsals are significantly larger relative to overall body mass and length (Carpenter 2018). In robustly-constructed diplodocoids—apatosaurines (Fig. 5E), rebbachisaurids, and dicraeosaurids (without prominent, hyperelongate neural spines such as those seen in the dicraeosaurid *Amargasaurus*)—for which dimensions are available, the posterior dorsal vertebral height/femur length ratio ranges from roughly two-thirds to three-quarters, implying a femoral length of 3 to 3.5 m or more in *Maraapunisaurus*. More importantly for estimating mass, dorsal–sacral series/posterior dorsal vertebral height ratios are about 3 to 3.5, indicating that the dorsal–sacral series

was 7.7 to nearly 9 m long in *Maraapunisaurus*, much longer than those of the largest titanosaurs. Although diplodocoids have narrower abdomens and pelvises than do titanosaurs, when envisioned as a robust diplodocoid (Carpenter 2018), the overall dimensions of *Maraapunisaurus* place this sauropod in the area of 80–120 tonnes in mass and 35 to 40 m in length (Fig. 5A). Accommodating such a tremendous vertebra within a smaller-bodied sauropod is implausible, and in the less likely but not impossible event that *Maraapunisaurus* had a lower, more typical (for sauropods) dorsal vertebral height/body size ratio, it might have been even larger. That extraordinarily gigantic diplodocoids on the scale of *Maraapunisaurus* existed may be supported by the titanic diplodocine cervical vertebra assigned to the gracile *Barosaurus* by Taylor and Wedel (2016) that may exceed the dimensions of the cervicals of the mamenchisaurid discussed in the next paragraph.

A pair of enormous vertebrae from the same Jurassic formation as, and that may belong to, ‘*Mamenchisaurus*’ *sinocanadorum* hint at a sauropod of 60–80 tonnes and ~35 m (Fig. 5B; Paul 2016; Xu pers. comm.); further analysis must await the formal description of these vertebrae. Interestingly, the Chinese basal titanosauriform ‘*Huangheititan*’ *ruyangensis* (Lü et al. 2007) has a dorsal rib that is about the same length as the exceptionally long rib of *Patagotitan*, and its sacrum may be similar in length, suggesting a broadly comparable mass. An alleged enormous footprint from the Early Cretaceous of Australia (Salisbury et al. 2016) seems to record a sauropod half again as dimensionally large as *Argentinosaurus*, which if correct would mean a dinosaur of 200 tonnes or more. Nevertheless, the depression in question is so poorly formed that it may not be an animal track at all, or if it is, degradation and perhaps partial overprinting of fore- and hind footprints may have exaggerated its apparent dimensions (Carpenter 2018). No well-preserved footprint suggesting an animal of such size has ever been reported. Finally, brachiosaurid titanosauriforms—of which the largest known, such as *Giraffatitan* and *Brachiosaurus*, were in the 30 to perhaps over 40 tonne range (Fig. 1I; Paul 1988a, 1997, 2016)—are not currently regarded to have been among the very largest sauropods.

DISCUSSION

Computational convex hulling may at first glance seem, and indeed has been promoted to be, less subjective and skill-dependent, and therefore more scientific, than analog methods of volumetric mass estimation in extinct animals. Nevertheless, the similar respective mass estimates for the giant titanosaurs *Patagotitan* and *Dreadnoughtus*—whether based on virtual corrected convex hulling or anatomically realistic, technical volumetric techniques—indicate that digital methods do not produce results that are inherently superior to those obtained via non-digital methods. This is not surprising because digital methods rely on subjective

and often inconsistent analog restorations of skeletons, sometimes produced by different workers of varying abilities and competency. Prime-lean volume results arising from carefully-constructed skeletal reconstructions based on consistently-applied principles of morphological realism by anatomically knowledgeable workers are at least as effective at generating accurate absolute and relative mass values, and may be readily modified in a plus-minus manner by removing or adding soft tissues in accord with patterns observed in appropriate modern analogs.

The consistent volume-mass estimates obtained herein result from the profile-skeletal reconstructions having been restored to consistent anatomical criteria. This result affirms that anatomical constancy is always required when producing mass estimates, whether the skeletons upon which these estimates are based are actual, physical mounts or otherwise. Therefore, when a previously-mounted skeleton is used as the basis for a volumetric estimate, it is always necessary to assess whether the anatomical configuration of the specimen is consistent with the most accurate, up-to-date knowledge; if it is not, then appropriate changes must be made to the virtual skeletal restoration (after all, there is little monetary cost to doing so in comparison to remounting the actual skeleton). There is a particular need to correctly restore the position and width of the dinosaurian pectoral girdle in its proper posterior location, and to ensure that the anterior dorsal ribs are given an appropriate posterodistal inclination that is reasonably consistent between specimens. It follows that those who produce virtual models must therefore have in-depth anatomical knowledge that is broadly comparable to that of those who produce technical skeletal illustrations. Moreover, these persons must correct for any anatomical errors in the mounted skeletons in question and carefully verify the proportions of their scans and virtual models to minimize the issues that can render digital models at least as subject to error as are their analog counterparts. Just as with recorded music, digital is not necessarily superior to high-fidelity analog, and in the case of estimating the bulk of extinct animals, it can sometimes result in an overreliance on computational procedures at the expense of knowing and paying keen attention to actual vertebrate anatomy.

The similar mass estimates derived from both analog and digital volume-based methods for *Patagotitan* and *Dreadnoughtus* also affirm and reinforce the soundness of restoring the dimensions and volumes of the skeletons and soft tissues of exotic extinct vertebrates to estimate their masses over using the dimensions of individual bones such as the humerus and/or femur. Though admittedly partly subjective and imprecise, volumetric methods boast plus-minus error ranges that are far less than those associated with mass estimates derived from inherently highly variable bone strength factors and other osteological dimensions. Consider that the tonnage calculated from the stylopodial circumferences of *Patagotitan* ranges from 52 to 86 tonnes (Carballido et al. 2017), a 65 percent change, far greater than the 10–20 percent variation that is inherent to

properly executed volumetric models. Although the lowest end of the limb bone circumference error range does include the volumetrically-derived mass estimate (which, again, is herein argued to closely approximate the actual mass of the animal), the median, ‘most likely’ value is very probably about one-third too great; similarly, the uppermost end of the stylopodially-derived range is probably two-thirds too high. The situation regarding *Dreadnoughtus* is worse in that even the lowest end of the 44 to 75 tonne estimate derived from limb bone circumferences (Lacovara et al. 2014; Bates et al. 2015) does not contain the mass value that fits within the volume of the skeleton (~31 tonnes as presented here); the lowest limb-bone scaling estimate is excessive by almost 50 percent, the median estimate is excessive by a factor of nearly two, and the uppermost by a factor of ~2.5. Such substantial overestimates by the stylopodial circumference method indicate that volumetric modeling is a superior means for estimating the masses of fossil animals in both absolute and relative terms, so long as the skeletons being used as the basis for these estimates are carefully restored to anatomical criteria that maximize the probability that the results will be as realistic and consistent as possible with the data at hand.

That the volume-delimited masses of *Patagotitan*, *Futalognkosaurus*, and especially *Dreadnoughtus* are well below those estimated via limb bone strength factors is in accord with how the skeletal strength of tetrapods is highly variable, as noted above, which in turn indicates that some of these animals are constructed considerably more robustly than others (Paul 1997; Larramendi and Paul in prep.). It is notable that titanosaurs are often much thicker-limbed relative to their overall body mass than is typical for sauropods, including other gigantic taxa, which raises the question of why this is so. Possibly the increased robusticity/greater circumference of the limb elements provided a means for these bones to cope with the exceptional loads imposed by the distinctly broad abdomens of titanosaurs; another possible factor is the wide gauge gait of titanosaurs (Wilson and Carrano 1999), though the structural stress mechanism for this putative biomechanical relationship is currently obscure. The same-scale comparison of titanosaurian humeri and femora (Fig. 3) reaffirms that, even by titanosaur standards, those of *Dreadnoughtus* are atypically overmassive relative to those of its larger-bodied relatives, perhaps because (based on osteohistological evidence presented by Lacovara et al. 2014) the holotype was a juvenile or subadult that would ultimately have matured into a much more massive adult. Sauropod, including titanosaur, limb bone growth appears to have been largely isometric (Bonnar 2007; Curry Rogers et al. 2016), and if adult *Dreadnoughtus* regularly approached or exceeded 100 tonnes, then beginning their lives with exceptionally robust limb bones may have been a means for such heavy-bodied herbivores to be structurally prepared for the extreme masses they may eventually have attained. The case of *Dreadnoughtus* reaffirms the risk inherent in relying on the robustness of limb elements to reliably estimate the

masses of dinosaurian taxa unless ontogeny is taken into account (see Brassey et al. 2015; Brassey 2017).

The limb bone robusticity of titanosaurs is not unique within Sauropoda, as the massively constructed apatosaurine diplodocids share this characteristic (Paul 1997; this is also indicated by the very high limb bone strength-based apatosaurine mass estimate in Benson et al. [2014] compared to those obtained from volumetric models), as did some other sauropods (Larramendi and Paul in prep.). Being ‘overbuilt’ in this way may have been a common adaptation of Gondwanan titanosaurs that often dwelled in habitats infested by gigantic carcharodontosaurid theropods, the additional strength perhaps allowing these sauropods to better resist predatory attacks (Paul 2016). Carballido et al. (2017) noted that titanosaurs reached a zenith in size during the middle Cretaceous of southern Argentina, though the possibly similarly great masses potentially reached by the North African *Paralititan* and (less probably, given the significant issues associated with its holotype) the Indian latest Cretaceous *Bruhathkayosaurus* suggest that the ‘supertitanosaur’ phenomenon may have been more widespread and generally late Mesozoic (i.e., middle–Late Cretaceous) in nature. The evolution of ‘supertitanosaurs’ may have been driven in part by the same need to better resist attacks from giant carcharodontosaurids that contributed to these sauropods having been so strongly constructed, although it is not certain that all such titanosaurs would have lived alongside these enormous predators. Conversely, Asian and North American titanosaurs apparently did not respond to the evolution of colossal, *Tarbosaurus*/*Tyrannosaurus*-sized tyrannosaurid theropods with the exceptional, >50 tonne gigantism that was seen south of the Cretaceous paleoequator. Earlier ‘supersauropods’ did not dwell in paleoecosystems that would also have included exceptionally large predators. The largest theropod known from the upper Morrison Formation that could potentially have preyed upon huge diplodocoids, such as *Maraapunisaurus*, is an allosaurid that was only about one-thirtieth its estimated adult mass (Paul 2016). Giant mamenchisaurids had to contend only with similarly modest-sized theropods.

When they first appear in the fossil record, apparently during the Late Triassic (Lallensack et al. 2017), sauropods were not gigantic, but they quickly reached elephantine bulk by at least the Early Jurassic (McPhee et al. 2015) and came to exceed all known proboscideans and indri-cotheres in mass by the Middle Jurassic (Paul 2016). The results of the present analysis confirm that Late Jurassic sauropods (e.g., *Maraapunisaurus* and the above mentioned giant mamenchisaurid) appear to have achieved the maximum dimensions and masses of Sauropoda, which may have been the greatest achievable by land animals, in which case there could not have been a trend towards ever-increasing size in the clade until its extinction at the end of the Cretaceous. If the stupendous Jurassic sauropods reached the largest possible sizes for land-living animals, it is unknown whether these size limitations

would have been due to structural or resource-related factors (note that even the largest land animals are dwarfed by the largest trees, which can be an order of magnitude heavier and six or more times taller). Determining whether or not there were significant decreases in sauropod body size and perhaps the eventual reattainment of these animals’ maximum possible size during the Cretaceous must await a larger, more statistically informative sample of remains. Extremely large sauropods were extant for approximately 100 million years; by comparison, similarly massive whales, and for that matter comparably gigantic marine animals in general, appeared only during the last few million years in response to atypical oceanic conditions that were apparently related to the advent of the Quaternary Ice Age (Slater et al. 2017). The titanic proportions of the largest sauropods probably evolved due to a complex set of selective advantages that accrued from being very tall and massive terrestrial herbivores, combined with the biological ability of sauropods to become as heavy as whales and as tall as trees in 1G ironically, in part, because of their small heads (Paul 1994, 2016, 2017; Sander et al. 2011). Basal diplodocoids had relatively short necks, and as such this may have aided *Maraapunisaurus* in attaining its extraordinary size by alleviating the potential issues with circulatory pressure that are associated with great height (Paul 2017). Another potential aid to diplodocoids becoming huge were their unusually tall-spined dorsal vertebrae, which may have conferred additional strength to the axial column.

CONCLUSION

Recent publications on the anatomy of the largest-bodied titanosaurian sauropod dinosaurs allow the sizes of these behemoths to be resolved to a level of accuracy that was not previously achievable. Regarding exceptionally large mid- and Late Cretaceous titanosaurs, the descriptions of the fairly complete skeletons of *Dreadnoughtus*, *Futalognkosaurus*, and *Patagotitan* provide data that document their dimensions and volume sufficiently thoroughly so as to finally enable the restoration of the masses of these titans with a reasonable degree of reliability. Using volumetric methods, it can now be firmly concluded that the *Argentinosaurus* holotype massed between 65 and 75 tonnes when healthy and not obese. Significantly higher and lower mass estimates for this taxon are no longer viable, and with the possible exception of a single femur, no other known titanosaurian specimen appears to be in its size class with regard to the pertinent dimensions of its colossal bones (Figs. 1A, 3A). For another titanosaur to have plausibly equaled or surpassed the size of *Argentinosaurus*, the anteroposterior length of its dorsal–sacral vertebral series must equal or exceed that of this latter taxon. Assertions that *Patagotitan* was in the same mass range as *Argentinosaurus*, or that it was the largest dinosaur, are currently untenable, and will remain so unless an

anatomically realistic volumetric model can be produced that plausibly accommodates the known skeletal elements within a significantly greater volume (which is improbable) or if future finds indicate the existence of substantially larger individuals. It is not even completely clear that *Patagotitan* is the second largest known titanosaur, with the masses of *Notocolossus*, *Puertasaurus*, and ‘*Antarctosaurus*’ *giganteus* also estimated in the 45–55 tonne range, and it being possible that *Notocolossus* and *Puertasaurus* were more massive. *Patagotitan* is, however, currently the largest land animal that is known from fairly complete (albeit composite) remains, with other titanosaurs of similar completeness being smaller. *Paralititan* and *Bruhathkayosaurus* (if the latter in fact existed) massed somewhere between 30 and 55 tonnes, and so may have *Dreadnoughtus*; however, because the largest known specimen of this last taxon pertains to a juvenile or subadult individual, it may even have attained a mass comparable to that of *Argentinosaurus* had it survived to adulthood. *Futalognkosaurus* and *Alamosaurus* were around 30 tonnes, with the possibility that the last was markedly more massive.

As enormous as many titanosaurs were, they were not the only sauropod group that attained truly gargantuan sizes. Though based only on two cervical vertebrae, a colossal mamenchisaurid from the Jurassic of China (perhaps belonging to ‘*Mamenchisaurus*’ *sinocanadorum*) appears to have matched or exceeded the bulk of *Argentinosaurus*. And outmassing all of these may have been the diplodocoid *Maraapunisaurus*, which even after having recently been reassessed as a robust diplodocoid remains the most likely candidate for the largest known land animal. If *Maraapunisaurus* was a robustly-constructed diplodocoid, then it is likely to have matched all but the most massive whale (the blue whale, *Balaenoptera musculus*) in size, and if it was less robust, it might have matched even *B. musculus*. Even more remarkably, it is highly probable that even larger sauropods await discovery, and moreover that the very biggest species and individuals were not likely to have been preserved as fossils, so sauropods of such titanic mass cannot be entirely ruled out. That a few land-living sauropods appear to have equaled some of the biggest water-buoyed whales in mass was probably due to their possession of the high aerobic power capacity that would have been needed to move such exceptional mass without the support of water, and to pump blood so high, in accord with the terramegathery hypothesis (Paul 1994) that proposes that gigantic land animals must be tachyenergetic endotherms (also Seymour et al. 2000; Sander et al. 2011; Seymour 2016).

But as biologically extraordinary as these animals were, the skeletons of *Maraapunisaurus*, ‘*M.*’ *sinocanadorum*?, *Argentinosaurus*, *Patagotitan*, and many other ‘supersauropods’ are at worst very fragmentary (and in the case of *Maraapunisaurus*, currently lost) and at best composites. What, then, is the largest land animal that is known from a nearly complete skeleton of a single individual? That is the classic Pittsburgh apatosaurine (CM 3018, the holotype of *Apatosaurus* [or possibly *Brontosaurus*; see Paul 2016]

louisae) from the Carnegie Quarry at Dinosaur National Monument, which was only a few tonnes more massive than the biggest land mammals (Fig. 5E; Paul 1988a, 1997, 2016; Larramendi 2016; Larramendi and Paul in prep.). At approximately 12 tonnes, the largest nearly complete fossil land mammals are about two-thirds as heavy (Larramendi 2016). These observations indicate that the preservation of relatively complete skeletons of 20+ tonne sauropods is unlikely, presumably in part because ordinary taphonomic processes usually do not result in the rapid and sufficient burial and preservation of such tremendous bodies (Carpenter 2006).

To briefly summarize the broader picture of mass restoration in fossil taxa, estimates that are derived from the dimensions of one or a few skeletal elements of animals of variable proportions, including those based on limb bone strength factors, can, in many cases, only be used to produce ‘ballpark’ mass estimates; moreover, the transverse dimensions of elements are especially problematic. Owing to the limitations of bone dimension to body mass regression equations, skeleton-based volumetric restorations—despite their own associated issues—remain the most accurate means of estimating and comparing the absolute mass of a given extinct taxon when sufficient material is available to do so. As such, the question is not whether to use the volumetric method, but how, in so doing, to produce the best possible results (Brassey 2017). Volumetric methods can achieve that goal regardless of whether they are based on digital representations of actual skeletons or on technical profile-skeletal reconstructions; digital means for estimating body volumes are not markedly less subjective or reliable than entirely analog methods. In either case—digital or analog—restorations of skeletons and body volumes need to be carefully produced by persons with sufficient anatomical knowledge. Optimized, standardized, and more rigorous procedures for three-dimensionally scanning mounted skeletons are needed, among them the consistent inclusion of scale bars in the scans and the cross-checking of results with measurements and conventional two-dimensional images. Also necessary are more carefully-measured scale bars in figures that are appropriately large for the size of the bones or skeletons being depicted and that are carefully cross-checked with actual measurements of these elements. During the present author’s effort to re-estimate the size of *Maraapunisaurus*, he noticed the inconsistent measurements in Calvo and Salgado’s (1995) description of *Limaysaurus tessonei* noted above because these dimensions could not be reconciled with the profile-skeletal reconstruction of this same taxon by Paul (2016), which underscores the need for accurate skeletal restorations in many aspects of paleozoological work (Paul 1987, 1997). Skeletons mounted under different anatomical criteria cannot be used to determine and compare the volumes of the living animals to which they pertained without first assessing, and if necessary adjusting, for any potential inconsistencies and inaccuracies. Particular attention must be paid to the restoration of the

pectoral and anterior dorsal regions, ensuring that the anterior dorsal ribs are posterodistally inclined, the scapula is subvertical with the majority of its blade overlapping these ribs, and the medial edges of the coracoids approach the sagittal midline. Finally, analog and digital skeletal restorations must be presented at sufficiently large scale to allow researchers to readily assess their proportions and anatomical details.

ACKNOWLEDGMENTS

Sincere thanks to M. Lamanna, A. Larramendi, K. Carpenter, J. McIntosh, J. Porfiri, H. Jaeger, J. Nova, R. Coria, X. Xu, M. Tanimoto, F. Boothman, and an anonymous reviewer.

LITERATURE CITED

- ALBL, P. 1971. Studies on assessment of physical condition in African elephants. *Biological Conservation*, 3:134–140.
- ANONYMOUS?. 2018. Maximo the titanosaur. Field Museum of Natural History, Chicago, <https://www.fieldmuseum.org/at-the-field/exhibitions/maximo-titanosaur> (last viewed December 2019).
- BATES, K.T., P.L. FALKINGHAM, S. MACCAULAY, C. BRASSEY, AND S.C. R. MAIDMENT. 2015. Downsizing a giant: reevaluating *Dreadnoughtus* body mass. *Biology Letters*, 11:20150215.
- BENSON, R.B.J., N.E. CAMPIONES, M.T. CARRANO, P.D. MANNION, C. SULLIVAN, P. UPCHURCH, AND D.C. EVANS. 2014. Rates of dinosaur body mass evolution indicate 170 million years of sustained ecological innovation on the avian stem lineage. *PLoS Biology*, 12:e1001853.
- BONAPARTE, J.F. 2007. Dinosaurios y Pterosaurios de America del Sur, Sudamerica Prehistorica. Editorial Albatros y Fundación de Historia Natural, Felix de Azara.
- BONAPARTE, J.F. AND R.A. CORIA. 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río. Limay de la Provincia del Neuquén, Argentina. *Ameghiniana*, 30:271–282.
- BONNAN, M.F. 2007. Linear and geometric morphometric analysis of long bone scaling patterns in Jurassic neosauropod dinosaurs: their functional and paleobiological implications. *The Anatomical Record*, 290:1089–1111.
- BORSUK-BIALYNICKA, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii* from the Upper Cretaceous of Mongolia. *Acta Palaeontologica Polonica*, 37:1–64.
- BRASSEY, C.A. 2017. Body-mass estimation in paleontology: a review of volumetric techniques. *The Paleontological Society Papers*, 22:133–156.
- BRASSEY, C.A., S.C.R. MAIDMENT, AND P.M. BARRETT. 2015. Body mass estimates of an exceptionally complete *Stegosaurus*: comparing volumetric and linear bivariate mass estimation methods. *Biology Letters*, 11:20140984.
- BROCHU, C.A. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Society of Vertebrate Paleontology Memoir*, 7:1–138.
- CALVO, J.O. 2014. New fossil remains of *Futalognkosaurus dukei* from the Late Cretaceous of Neuquén, Argentina. 4th International Palaeontological Congress:325.
- CALVO, J.O., J.D. PORFIRI, C. VERALLI, AND F. POBLETE. 2001. A giant Titanosauridae from the Upper Cretaceous of Neuquén. *Ameghiniana*, 38:5R.
- CALVO J.O., J.D. PORFIRI, B.J. GONZÁLEZ-RIGA, AND A.W.A. KELLNER. 2007a. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *Anais da Academia Brasileira de Ciências*, 79:529–541.
- CALVO, J.O., J.D. PORFIRI, B.J. GONZÁLEZ-RIGA, AND A.W.A. KELLNER. 2007b. Anatomy of *Futalognkosaurus dukei* from the Neuquén Group, Patagonia, Argentina. *Arquivos do Museu Nacional, Rio de Janeiro*, 65:511–526.
- CALVO, J.O., R. JUÁREZ VALIERI, AND J.D. PORFIRI. 2008. Re-sizing giants: estimation of body length of *Futalognkosaurus dukei* and implications for giant titanosaurian sauropods. III Congreso Latinoamericano de Paleontología de Vertebrados:43.
- CALVO, J.O., AND L. SALGADO. 1995. *Rebbachisaurus tessonei* sp. nov. a new Sauropoda from the Albian-Cenomanian of Argentina: new evidence on the origin of the Diplodocidae. *Gaia*, 11:13–33.
- CAMPIONE, N.E., AND D.C. EVANS. 2012. A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC Biology*, 10:1–22.
- CAMPOS, D.A., A.W.A. KELLNER, R. BERTINI, AND R. SANTUCCI. 2005. On a titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru Group, Late Cretaceous of Brazil. *Arquivos do Museu Nacional, Rio de Janeiro*, 63:565–593.
- CARBALLIDO, J.L., D. POL, A. OTERO, I.A. CERDA, L. SALGADO, A.C. GARRIDO, J. RAMEZANI, N.R. CUNEO, AND J.M. KRAUSE. 2017. A new giant titanosaur sheds light on body mass evolution among sauropod dinosaurs. *Proceedings of the Royal Society B*, 284:20171219.
- CARPENTER, K. 2006. Biggest of the big: a critical reevaluation of the mega-sauropod *Amphicoelias fragillimus*. *New Mexico Museum of Natural History and Science Bulletin*, 36:131–138.
- . 2018. *Maraapunisaurus fragillimus*, n.g. (formerly *Amphicoelias fragillimus*), a basal rebbachisaurid from the Morrison Formation (Upper Jurassic) of Colorado. *Geology of the Intermountain West*, 5:227–244.
- CARPENTER, K., J.H. MADSEN, AND A. LEWIS. 1995. Mounting of fossil vertebrate skeletons. Pp. 285–322, in *Vertebrate Paleontological Techniques V* (P. Leiggi and P. May, eds.). Cambridge University Press, Cambridge.
- CONWAY J., C.M. KOSEMAN, AND D. NAISH. 2012. *All Yesterdays: Unique and Speculative Views of Dinosaurs and Other Prehistoric Animals*. Irregular Books.
- COPE, E.D. 1878. A new species of *Amphicoelias*. *American Naturalist*, 12:563–565.
- CORIA, R.A., L.S. FILIPPI, L.M. CHIAPPE, R. GARCÍA, AND A.B. ARCUCCI. 2013. *Overosaurus paradisorum*, a new sauropod dinosaur from the Late Cretaceous of Neuquén, Patagonia, Argentina. *Zootaxa*, 4:357–376.
- CURRIE, P.J., J.A. WILSON, F. FANTI, B. MAINBAYER, AND K. TSOGTBAATAR. 2017. Rediscovery of the type localities of the Late Cretaceous Mongolian sauropods *Nemegtosaurus mongoliensis* and *Opisthocoelicaudia skarzynskii*: stratigraphic and taxonomic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 494:5–13.
- CURRY ROGERS, K. 2009. The postcranial osteology of *Rapetosaurus krausei* from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, 29:1046–1086.
- CURRY ROGERS, K., M. WHITNEY, M. D'EMIC, AND B. BAGLEY. 2016. Precocity in a tiny titanosaur from the Late Cretaceous of Madagascar. *Science*, 352:450–454.
- DELGIUDICE, G.D., L.D. MECH, K.E. KUNKEL, E.M. GESE, AND U.S. SEAL. 1992. Seasonal patterns of weight, hematology, and serum characteristics of free-ranging female white-tailed deer in Minnesota. *Canadian Journal of Zoology*, 70:974–983.
- FOWLER, D.W., AND R.M. SULLIVAN. 2011. The first giant titanosaurian sauropod from the Upper Cretaceous of North America. *Acta Palaeontologica Polonica*, 56:685–690.
- GALTON, P.M., AND K. AYYASAMI. 2017. Purported latest bone of a plated dinosaur (Ornithischia: Stegosauria), a “dermal plate” from the Maastrichtian (Upper Cretaceous) of southern India. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 285:91–96.
- GEE, C.T. 2011. Dietary options for the sauropod dinosaurs from an integrated botanical and paleobotanical perspective. Pp. 34–56, in *Biology of the Sauropod Dinosaurs: Understanding the Life of Giants* (N. Klein, K. Remes, C. Gee, and P. Sander, eds.). Indiana

- University Press, Bloomington
- . 2016. Emerging data on the Morrison flora: opulent conifer forests or a hinterland xeriscape for the sauropods? *Journal of Vertebrate Paleontology, Program and Abstracts*, 2016:143.
- GILMORE, C.W. 1936. Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. *Memoirs of the Carnegie Museum*, 11:169–300.
- GONZÁLEZ RIGA, B.J., M.C. LAMANNA, L.D. ORTIZ DAVID, J.O. CALVO, AND J.P. CORIA. 2016. A gigantic new dinosaur from Argentina and the evolution of the sauropod hind foot. *Scientific Reports*, 6:19165.
- GREGORY, W.K. 1905. The weight of the *Brontosaurus*. *Science*, 22:572.
- HAYNES, G. 1991. *Mammoths, Mastodonts, and Elephants*. Cambridge University Press, Cambridge.
- HÖHN, B. 2011. Walking with the shoulder of giants: biomechanical conditions in the tetrapod shoulder as a basis for sauropod shoulder girdle reconstruction. Pp. 182–196, in *Biology of the Sauropod Dinosaurs* (N. Klein, K. Remes, C.T. Gee, and P.M. Sander, eds.) Indiana University Press, Bloomington.
- HUENE F. VON. 1929. Los sauriscios y ornitisquios del Cretáceo Argentino. *Anales del Museo de La Plata*, 3:1–196.
- HUTCHINSON, J.R., K.T. BATES, J. MOLNAR, V. ALLEN, AND P.J. MAKOVICKY. 2011. A computational analysis of limb and body dimensions in *Tyrannosaurus rex* with implications for locomotion, ontogeny, and growth. *PLoS ONE*, 6:e26037.
- JANENSCH, W. 1950a. Die Wirbelsäule von *Brachiosaurus brancai*. *Palaeontographica, Suppl.* 7:27–93.
- . 1950b. Die Skelettrekonstruktion von *Brachiosaurus brancai*. *Palaeontographica, Suppl.* 7:97–102.
- . 1961. Die Gliedmassen und Gliedmassengürtel der Sauropoden der Tendaguru-Schichten. *Palaeontographica, Suppl.* 7:177–235.
- JASINSKI, S.E., R.M. SULLIVAN, AND S.G. LUCAS. 2011. Taxonomic composition of the Alamo Wash local fauna from the Upper Cretaceous Ojo Alamo Formation, San Juan Basin, New Mexico. *New Mexico Museum of Natural History and Science Bulletin*, 53:216–271.
- KNIGHT, C.R. 1947. *Animal Drawing: Anatomy and Action for Artists*. McGraw Hill, New York.
- LACOVARA, K.J., M.C. LAMANNA, L.M. IBIRICU, J.C. POOLE, E.R. SCHROETER, P.V. ULLMANN, K.K. VOEGELE, Z.M. BOLES, A.M. CARTER, E.K. FOWLER, V.M. EGERTON, A.E. MOYER, C.L. COUGHENOUR, J.P. SCHEIN, J.D. HARRIS, R.D. MARTÍNEZ, AND F.E. NOVAS. 2014. A gigantic, exceptionally complete titanosaurian sauropod dinosaur from southern Patagonia, Argentina. *Scientific Reports*, 4:6196.
- LALLENSACK, J.N., H. KLEIN, J. MILAN, O. WINGS, O. MATEUS, AND L.B. CLEMMENSEN. 2017. Sauropodomorph dinosaur trackways from the Fleming Fjord Formation of East Greenland: evidence for Late Triassic sauropods. *Acta Palaeontologica Polonica*, 62:833–843.
- LARRAMENDI, A. 2016. Shoulder height, body mass, and shape of proboscideans. *Acta Palaeontologica Polonica*, 61:537–574.
- LÜ, J., L. XU, X. ZHANG, W. HU, Y. WU, S. JIA, AND Q. JI. 2007. A new gigantic sauropod dinosaur with the deepest known body cavity from the Cretaceous of Asia. *Acta Geologica Sinica*, 81:167–176.
- MALLISON, H., AND O. WINGS. 2014. Photogrammetry in paleontology – a practical guide. *Journal of Paleontological Techniques*, 12:1–31.
- MAZZETTA, G.V., P. CHRISTIANSEN, AND R.A. FARIÑA. 2004. Giants and bizarres: body size of some southern South American Cretaceous dinosaurs. *Historical Biology*, 16:71–83.
- MCPHEE, B.W., M.F. BONNAN, A. YATES, J. NEVELING, AND J.N. CHOINIERE. 2015. A new basal sauropod from the pre-Toarcian Jurassic of South Africa: evidence of niche-partitioning in the sauropodomorph–sauropod boundary? *Scientific Reports*, 5:13224.
- MUMBY, H.S., K.U. MAR, C. THITARAM, A. COURTIOL, P. TOWIBOON, Z. MIN-OO, J.L. BROWN, AND V. LUMMA. 2015. Stress and body condition are associated with climate and demography in Asian elephants. *Conservation Physiology*, 3:PMC4778474.
- NOVAS, F.E., AND M. EZCURRA. 2006. Reinterpretation of the dorsal vertebrae of *Argentinosaurus huinculensis*. *Ameghiniana*, 43:48R–49R.
- NOVAS, F.E., L. SALGADO, J.O. CALVO, AND F. AGNOLIN. 2005. Giant titanosaur from the Late Cretaceous of Patagonia. *Revista del Museo Argentino de Ciencias Naturales*, 7:37–41.
- PAUL, G.S. 1987. The science and art of restoring the life appearance of dinosaurs and their relatives: a rigorous how-to guide. Pp. 4–49, in *Dinosaurs Past and Present 2* (S.J. Czerkas and E.C. Olsen, eds.). Natural History Museum of Los Angeles County, Los Angeles.
- . 1988a. 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.
- . 1988b. *Predatory Dinosaurs of the World*. Simon & Schuster, New York.
- . 1994. Terramegathermy and Cope's Rule in the land of titans. *Modern Geology*, 23:179–217.
- . 1997. Dinosaur models: the good, the bad, and using them to estimate the mass of dinosaurs. Pp. 129–154, in *Dinofest International Symposium Proceedings*, Academy of Natural Sciences, Philadelphia (D.L. Wolberg, E. Stump, and G.D. Rosenberg, eds.). Academy of Natural Sciences, Philadelphia.
- . 2011. *Tyrannosaurus*, the lean killing machine. *PLoS ONE*: <https://journals.plos.org/plosone/article/comment?id=info:doi/10.1371/annotation/b76d947b-ec96-4954-84fa-31a558c17542>.
- . 2014. Not so gigantic after all: reply to Lacovara et al. *Figshare*. https://figshare.com/articles/Not_so_gigantic_after_all_Response_to_Lacovara_et_al/_1264019.
- . 2016. *The Princeton Field Guide to Dinosaurs* (Second Edition). Princeton University Press, Princeton.
- . 2017. Restoring maximum vertical browsing reach in sauropod dinosaurs. *The Anatomical Record*, 300:1802–1825.
- PAUL, G.S., AND T.L. CHASE. 1989. Paleontological illustrations. Pp. 239–256, in *The Guild Handbook of Scientific Illustration* (E.R.S. Hodges, ed.). Van Nostrand Reinhold, New York.
- PAUL, G.S., AND P. CHRISTIANSEN. 2000. Forelimb posture in neoceratopsian dinosaurs: implications for gait and locomotion. *Paleobiology*, 26:450–465.
- POWELL, J.E. 1992. Osteología de *Saltasaurus loricatus* (Sauropoda Titanosauridae) del Cretácico Superior del noroeste Argentino. Pp. 165–230, in *Los Dinosaurios y su Interno Biótico* (J. Sanz and A. Buscalioni, eds.). Actas del Segundo Curso de Paleontología, Cuenca.
- . 2003. Revision of South American titanosaurid dinosaurs: paleobiological, palaeobiogeographical and phylogenetic aspects. *Records of the Queen Victoria Museum*, 111:1–173.
- RIVERA-SYLVA, H.E., J.R. GUZMÁN-GUTIÉRREZ, AND F. R. PALOMINO-SÁNCHEZ. 2006. Preliminary report on a vertebrate fossil assemblage from the Late Cretaceous of Chihuahua, Mexico. *Hantkeniana*, 5:66–68.
- RUSSELL, D.A. 1989. *An Odyssey in Time*. University of Toronto Press, Toronto.
- SALGADO, L., AND J.E. POWELL. 2010. Reassessment of the vertebral laminae in some South American titanosaurian sauropods. *Journal of Vertebrate Paleontology*, 30:1760–1722.
- SALISBURY, S.W., A. ROMILIO, M.C. HERNE, R.T. TUCKER, AND J.P. NAIR. 2016. The dinosaurian ichnofauna of the Lower Cretaceous Broome Sandstone of the Walmadany area, Dampier Peninsula, Western Australia. *Society of Vertebrate Paleontology Memoir*, 16:1–152.
- SANDER, P.M., A. CHRISTIAN, M. CLAUSS, R. FECHNER, C.T. GEE, E.-M. GRIEBELER, H.-C. GUNGA, J. HUMMEL, H. MALLISON, S.F. PERRY, H. PREUSCHOF, O.W.M. RAUHUT, K. REMES, T. TÛTKEN, O. WINGS, AND U. WITZEL. 2011. Biology of the sauropod dinosaurs: the evolution of gigantism. *Biological Reviews*, 86:117–155.
- SCHEELE, W.E. 1954. *Prehistoric Animals*. The World Publishing Co., Cleveland.
- . 1955. *The First Mammals*. The World Publishing Co., Cleveland.
- SELLERS, W.I., J. HEPWORTH-BELL, P.L. FALKINGHAM, K.T. BATES, C.A. BRASSEY, V.M. EGERTON, AND P.L. MANNING. 2012. Minimum convex hull mass estimations of complete mounted skeletons. *Biology Letters*, 8:842–845.
- SELLERS, W.I., L. MARGETTS, R.A. CORIA, AND P.L. MANNING. 2013. March of the titans: the locomotor capabilities of sauropod dinosaurs. *PLoS ONE*, 8:e78733.

- SEYMOUR, R.S. 2016. Cardiovascular physiology of dinosaurs. *Physiology*, 31:430-441.
- SEYMOUR, R.S., AND H.B. LILLYWHITE. 2000. Hearts, neck posture and metabolic intensity of sauropod dinosaurs. *Proceeding of the Royal Society B*, 267:1883-1887.
- SLATER, G.J., J.A. GOLDBOGEN, AND N.D. PYENSON. 2017. Independent evolution of baleen whale gigantism linked to Plio-Pleistocene ocean dynamics. *Proceedings of the Royal Society B*, 284:20170546.
- SMITH, J.B., M.C. LAMANNA, K.J. LACOVARA, P. DODSON, J.R. SMITH, J.C. POOLE, R. GIEGENGACK, AND Y. ATTIA. 2001. A giant sauropod dinosaur from an Upper Cretaceous mangrove deposit in Egypt. *Science*, 292:1704-1706.
- TAYLOR, M.P. 2015. Almost all known sauropod necks are incomplete and distorted. *PeerJ PrePrints*, 3:e1418v1.
- TAYLOR, M.P., AND M.J. WEDEL. 2016. How big did *Barosaurus* get? SVPCA 2016 abstracts, <http://www.miketaylor.org.uk/dino/pubs/svpca2016/abstract.html#gsc.tab=0>.
- ULLMANN, P.V., AND K.J. LACOVARA. 2016. Appendicular osteology of *Dreadnoughtus schrani*, a giant titanosaurian (Sauropoda, Titanosauria) from the Upper Cretaceous of Patagonia, Argentina. *Journal of Vertebrate Paleontology*, 36:e1225303.
- VOEGELE, K.K., M.C. LAMANNA, AND K.J. LACOVARA. 2017. Osteology of the dorsal vertebrae of the giant titanosaurian dinosaur *Dreadnoughtus schrani* from the Late Cretaceous of Argentina. *Acta Palaeontologica Polonica*, 62:667-681.
- WILSON, J.A., AND M.T. CARRANO. 1999. Titanosaurs and the origin of "wide-gauge" trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology*, 25:252-267.
- WILSON, J.A., AND P.C. SERENO. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Society of Vertebrate Paleontology Memoir*, 5:1-68.
- WOODRUFF, D.C., N.J. ATWOOD, AND A. MADILL. 2016. The structural preservation of a titanosaurid vertebral ligament. *Cretaceous Research*, 60:253-266.
- YADAGIRI, P., AND K. AYYASAMI. 1989. A carnosaurian dinosaur from the Kallamedu Formation Tamilnadu. *Geological Society of India Special Publication*, 11:523-528.