

Body mass estimations for *Plateosaurus engelhardti* using laser scanning and 3D reconstruction methods

Hanns-Christian Gunga · Tim Suthau ·
Anke Bellmann · Andreas Friedrich ·
Thomas Schwanebeck · Stefan Stoinski ·
Tobias Trippel · Karl Kirsch · Olaf Hellwich

Received: 12 July 2006 / Revised: 11 February 2007 / Accepted: 15 February 2007 / Published online: 14 March 2007
© Springer-Verlag 2007

Abstract Both body mass and surface area are factors determining the essence of any living organism. This should also hold true for an extinct organism such as a dinosaur. The present report discusses the use of a new 3D laser scanner method to establish body masses and surface areas of an Asian elephant (Zoological Museum of Copenhagen, Denmark) and of *Plateosaurus engelhardti*, a prosauropod from the Upper Triassic, exhibited at the Paleontological Museum in Tübingen (Germany). This method was used to study the effect that slight changes in body shape had on body mass for *P. engelhardti*. It was established that body volumes varied between 0.79 m³ (slim version) and 1.14 m³ (robust version), resulting in a presumable body mass of 630 and 912 kg, respectively. The total body surface areas ranged between 8.8 and 10.2 m², of which, in both reconstructions of *P. engelhardti*, ~33%

account for the thorax area alone. The main difference between the two models is in the tail and hind limb reconstruction. The tail of the slim version has a surface area of 1.98 m², whereas that of the robust version has a surface area of 2.73 m². The body volumes calculated for the slim version were as follows: head 0.006 m³, neck 0.016 m³, fore limbs 0.020 m³, hind limbs 0.08 m³, thoracic cavity 0.533 m³, and tail 0.136 m³. For the robust model, the following volumes were established: 0.01 m³ head, neck 0.026 m³, fore limbs 0.025 m³, hind limbs 0.18 m³, thoracic cavity 0.616 m³, and finally, tail 0.28 m³. Based on these body volumes, scaling equations were used to assess the size that the organs of this extinct dinosaur have.

Keywords Dinosauria · Sauropoda · Paleophysiology · Body mass estimation · Specific tissue density · Paleoecology

H.-C. Gunga (✉) · T. Trippel · K. Kirsch
Department of Physiology, Center of Space Medicine Berlin,
Charité Universitätsmedizin Berlin,
Campus Benjamin Franklin,
Berlin, Germany
e-mail: hanns-christian.gunga@charite.de

T. Suthau · A. Bellmann · A. Friedrich · T. Schwanebeck ·
S. Stoinski · O. Hellwich
Computer Vision & Remote Sensing,
Berlin University of Technology,
Franklinstrasse 28/29,
10587 Berlin, Germany

T. Suthau
e-mail: suthau@cs.tu-berlin.de
e-mail: dino@fpk.tu-berlin.de

H.-C. Gunga
Amimallee 22,
14195 Berlin-Dahlem, Germany

Introduction

Both body mass and surface area are factors determining the essence of any living organism. It can therefore be assumed that any estimates of the mass and surface of an extinct organism such as a dinosaur could also contribute to many other kinds of analyses dealing with paleobiological aspects. As the body masses of dinosaurs as presented in scientific literature differ considerably, in particular where large sauropods are concerned (Haubold 1990; Peczkis 1994), we began, in 1995, to use classical photogrammetry to assess the body mass and surface area of a large sauropod (Gunga et al. 1995). The highly disparate estimates that can be found in literature are mainly due to (1) the different methods used for mass estimations, such as

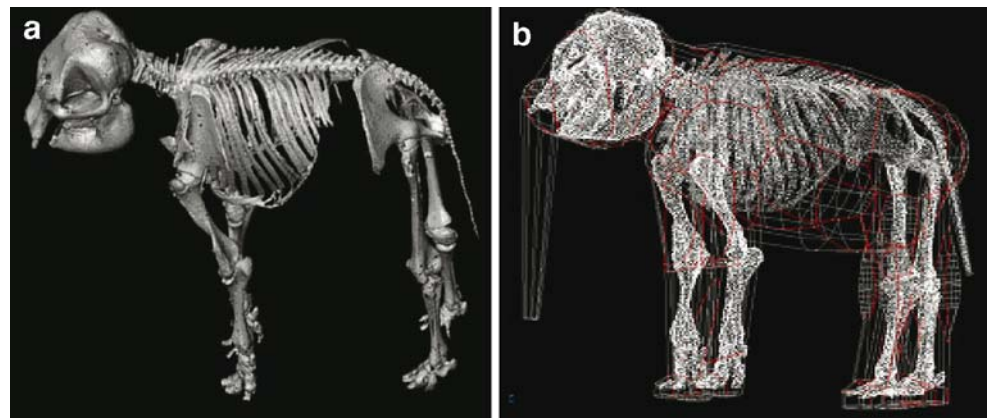
bone circumferences, and/or (2) the different assumptions made as to tissue density, which can range from 0.8 kg per 1,000 cm³ tissue to 1.2 kg per 1,000 cm³ tissue, depending on the anatomical part of the organism being investigated, such as neck, tail, or thorax (Colbert 1962; Lambert 1980; Schmidt-Nielsen 1984; Anderson et al. 1985; Withers 1992; Schmidt-Nielsen 1997; Gunga et al. 1999; Henderson 1999; Seebacher 2001; Motani 2001; Christiansen and Fariña 2004; Wedel 2003; Wedel 2005). The main advantages and disadvantages of some of these methods have already been subjected to intense scrutiny and discussion in previous papers (Anderson et al. 1985; Alexander 1989; Gunga et al. 1995; Gunga et al. 1999; Henderson 1999). In the meantime, the methodological approach has developed further, and more advanced laser scanners using 3D computer modeling software programs are available. In the present paper, we are presenting a study on the suitability of this 3D laser scanner (MENSI 25®) method for estimating the body masses and surface areas of an Asian elephant (*Elephas maximus*) exhibited at the Zoological Museum of Copenhagen (Denmark) and of *Plateosaurus engelhardti*, an extinct dinosaur from the Upper Triassic, exhibited at the Paleontological Museum in Tübingen (Germany).

P. engelhardti belongs to the group of so-called large-bodied prosauropods. The discussion of the prosauropod interrelationships continues to be controversial. However, prosauropods and sauropods, such as the gigantic *Brachiosaurus brancai*, form a monophyletic group known as Sauropodomorpha (Klein 2004; Sander and Klein 2005). *Plateosaurus* is especially interesting because along with those of some other prosauropods, its skeletons have been discovered in several mass accumulations in the Upper Triassic to Lower Jurassic of central Europe. Digs include Trossingen (southern Germany) and Frick (northern Switzerland). Worldwide, the herbivorous *Plateosaurus* dominated this age (Galton and Upchurch 2004) and was one of the first high browsers to evolve. Therefore, the study of *P. engelhardti* can contribute towards a better understanding of the evolutionary tendency towards size increase, a phenomenon commonly known as Cope's rule. Recently, the discussion of this rule has been re-opened (Moen 2006). Furthermore, reconstructing *P. engelhardti* gave us the opportunity to evaluate the effect that slight changes in body shape have on body mass. Finally, we were able to test whether, in the size that we had derived from the body mass and calculated using scaling equations, the organs of this extinct dinosaur such as integument, lung, heart, gastrointestinal tract, liver, kidneys, and muscular system were actually anatomically able to fit into the thoracic and abdominal cavity of *P. engelhardti* as established in our 3D reconstruction, and this in the sizes which they are generally assumed to have.

Materials and methods

At the Zoological Museum of Copenhagen (Denmark), an Asian elephant (*E. maximus*) served as the reference object for evaluating the body mass and for establishing the modeling effects by changing the shape of the 3D model subsequently developed. This specimen (catalogue number 558) was a juvenile, male elephant, which had worked in "Circus Busch" and was given to the Zoological Museum in Copenhagen in June of 1890 after it died. While the local scientist in the Zoological Museum of Copenhagen knew the live weight of the Asian elephant, our team was not aware of it. The data were captured by a MENSI 25® laser scanner placed in seven different positions. Fifteen reference points were defined, and in total, about 920,000 points were measured at an accuracy of better than 1 mm (Fig. 1a). As a next step, the presumed shape (surface area) was added to the 3D simulation using CAD software (Fig. 1b; Jung 2002). Thereupon, *P. engelhardti* was measured using ten scanner positions and 17 reference points. The mounted skeleton (GPIT 1, often referred to in scientific literature as Skelett 1) is made up entirely of the bones of one single individual found at the Trossingen dig. It is complete but for the skull (modeled in plaster from Staatliches Museum für Naturkunde Stuttgart 13200) and a few manus and pes elements (replaced in plaster as symmetrical copies of the contralateral side). (Mallison 2007) A few elements are deformed, albeit only slightly (e.g., left tibia, left coracoid). Most of the dorsal and caudal vertebrae are slightly distorted, the transverse processes of the left side tilting downward and those of the right side tilting upward, each by roughly 20°. The first sacral vertebra exhibits a more distinct deformation, the cranial surfaces being tilted backwards quite considerably. The mount articulates all non-deformed bones well and takes the almost symmetrical deformation of the vertebrae into account. Thus, the ribs are positioned in a position that averages the position of the articulation surfaces on the right and left side. Sacral 1 is articulated with the last presacral, assuming the original proportions of sacral 1 to be similar to sacral 2, with parallel anterior and posterior faces. The only instance in which the mount is problematic in a significant way is the distal splaying of the metacarpals, which enlarges the palm of the hand to an unreasonable extent. Were they to be shown correctly, the metacarpals should be arranged sub-parallel and in close contact with one another, with equal contact both proximally and distally. This discrepancy in the hands has no significant influence on the distribution of mass of the animal as a whole; if anything, it makes the model heavier in the front than it should be. In total, the scanner recorded more than 3.2 million points on the skeleton, which were subsequently analyzed. The accuracy of the scanned points was less than 3 mm (Fig. 2). In a

Fig. 1 Results of evaluating the laser scanner image of the skeleton of an Asian elephant (*E. maximus*) mounted and exhibited at the Zoological Museum Copenhagen, Denmark (**a**, left panel) and presumable shape (surface area) added to the 3D simulation by using CAD software (**b**, right panel)



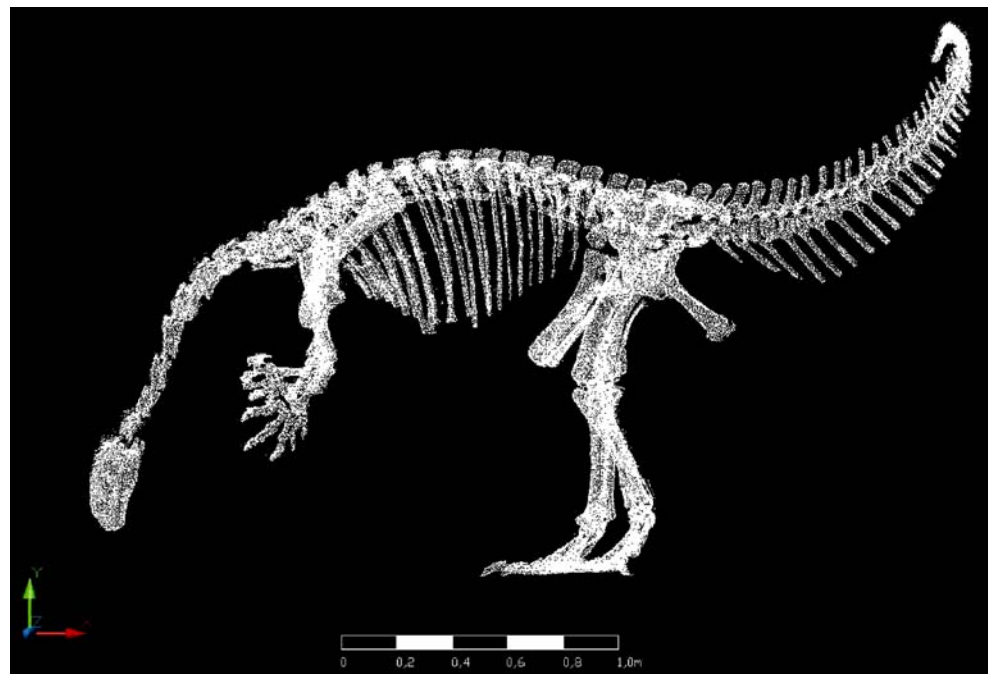
process similar to the method used for measuring the Asian elephant, the dinosaur's surface area was modeled with the aid of advanced CAD techniques. The basis for this CAD modeling is formed by the point clouds on these skeletons that are measured using the scanner. The presumable shape of the animals was then divided up into slices (rotational solids). Finally, *P. engelhardti* was given a slim (Fig. 3a) and a more robust shape in reconstruction (Fig. 3b, *P. engelhardti*). These solids have the advantage that they enable an enhanced accommodation to approximate the real shapes, and furthermore, allow complex changes of models at a reasonable expenditure of time and effort. Afterwards, the volumes were computed accordingly, the body weight was estimated, and the centers of gravity were determined by using MSC visualNastran 4D software. (Mallison 2007) For the Asian elephant, we assumed a specific density of the living tissue of 1.15 kg per 1,000 cm³, in accordance

with the results of a recent study by Bellmann et al. (2005) on the tissue density of a comparable mammalian organism (rhinoceros). However, in view of the extensive postcranial skeletal pneumaticity established for this type of sauropod by the data recently published by Wedel (2003, 2005), we proceeded from a much lower tissue density of 0.8 kg per 1,000 cm³ for *P. engelhardti*.

Results

The essential results of our work have been summarized in Figs. 1, 2, and 3 as well as in Tables 1 and 2. Figure 1a (left) shows the scan and Fig. 1b (right) the modeling result obtained for *E. maximus*, which has a computed volume of 0.622 m³. Based on the above-referenced assumption concerning the specific density of the living tissue of

Fig. 2 Results of evaluating the laser scanner image of the skeleton of *P. engelhardti* (Tübingen, Germany)



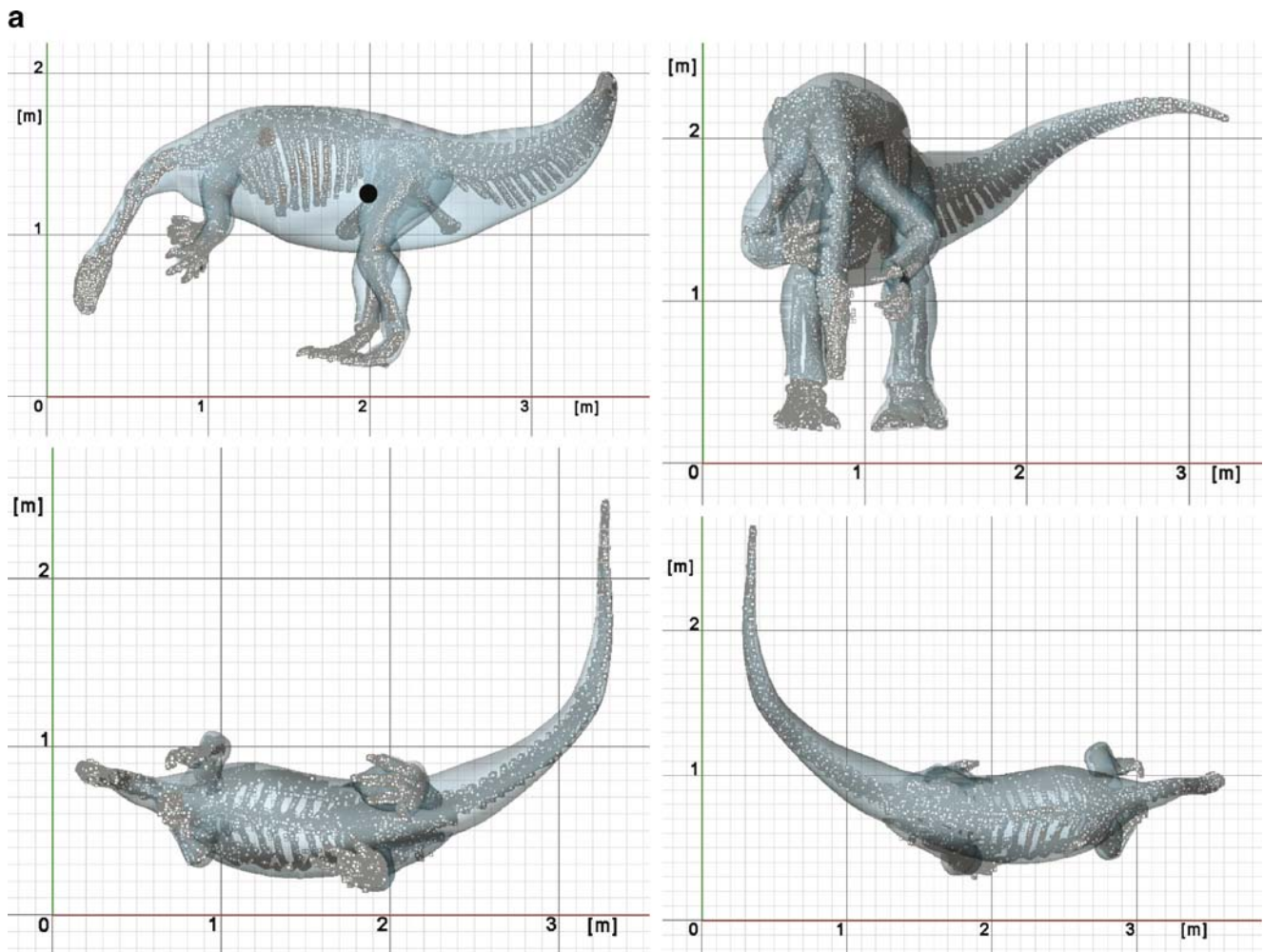


Fig. 3 The effect of modeling the surface of *P. engelhardti* on body mass in a slim (a) and robust type (b) of reconstruction and visualizations from different perspectives. The centers of gravity in

the slim and the robust reconstruction are marked (black dot) and were calculated by using MSC visualNastran 4D software

1.15 kg per 1,000 cm³ for this herbivorous mammal (Bellmann et al. 2005), a total body mass of 715 kg was calculated. The animal's actual live weight, known to the Zoological Museum of Copenhagen, was given to us later: It had been documented at 850 kg. This means that the deviation, which includes the modeling error of the computer modeling and/or a different specific density of the elephant's tissue, amounts to 16%. For *P. engelhardti*, body volumes of 0.79 (slim) up to 1.14 m³ (robust version) were determined, resulting in a likely body mass of 630 and 912 kg, respectively. These figures take into account the lower density of the tissues (Wedel 2005). The total body surface areas ranged between 8.8 and 10.2 m², of which, ~33% accounts for the thorax area alone in both reconstructions of *P. engelhardti*. The main difference between the two models lies in the tail and hind limb reconstruction. While the tail of the slim version has a surface area of 1.98 m², this part has a surface area of 2.73 m² in the robust version. Accordingly, the different surface areas account for

the different body volumes determined. The individual volume distributions from the head to the tail of *P. engelhardti* for the slim and the robust version have been summarized in Table 2. The sizes of major organs and organ systems for a slim and robust model of *P. engelhardti* based on allometric functions are given in Table 1.

Discussion

First, we will comment on the methodology used and will then describe the anatomical and physiological results of the study in a second part.

As it is based on the actual data points derived from skeletons, the methodological approach we have selected (Gunga et al. 1995; Gunga et al. 1999; Wiedemann et al. 1999) to estimate the body mass of large dinosaurs continues to be unique. It differs distinctively from the approaches recently taken by other researchers (Henderson

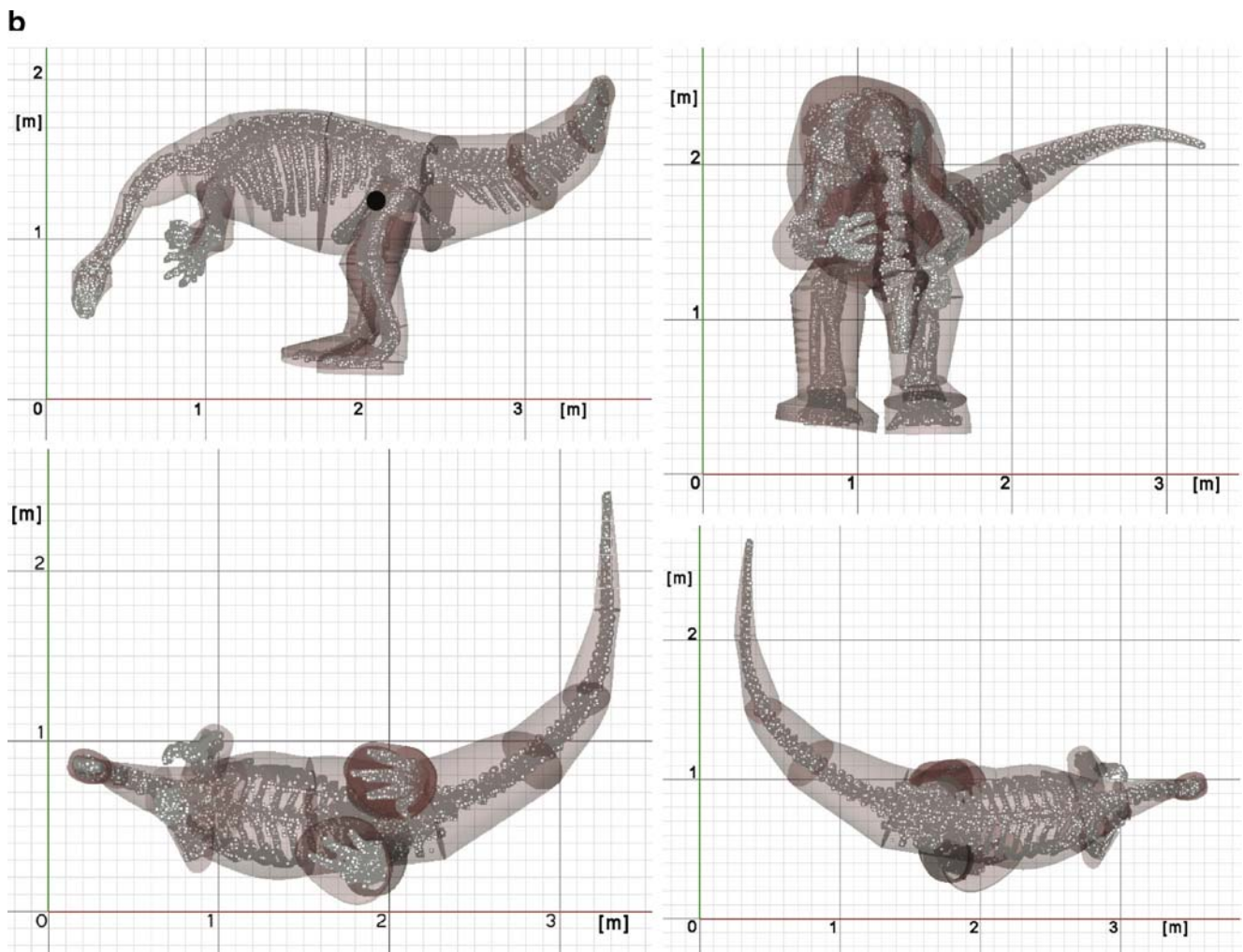


Fig. 3 (continued)

1999; Seebacher 2001; Motani 2001) in that the authors cited did not obtain three-dimensional data from the skeleton. Instead, they based their estimates on different views of the silhouettes developed on the basis of images and then used elliptical or super-elliptical solids. In our modeling, free-form geometrical bodies were used to ensure greater accuracy. In addition, as has already been pointed out by Blob (1998), any attempt at estimating body mass by studying changes in limb dimensions will also need to include body mass predictions based on features other than said limb dimensions to avoid analytical circularity. The process we use in modeling skeletons consists of two main phases. First, we collect data using a laser scanner, and second, we model the surface using CAD programs to compute the volume and weight of the dinosaurs. It has been shown that laser scanning provides complete ground truth data of a dinosaur skeleton at good accuracy. Individual details can be scanned at a higher resolution so that other research objectives can also be taken into

account. The main advantage of the photogrammetric procedure is that based on the respective body part, geometrical calculations can be made easily. If there are enough parts and elements available whose size is sufficiently large, any measurement errors for the total body mass can be kept to a minimum (Wiedemann and Wehr 1998; Wiedemann et al. 1999). To cite an example: Whenever a measurement error occurs in analyses using the humerus/femur circumference method, their direct result is that the total mass of the animal is calculated incorrectly. If, however, such a measurement error is made in determining the volume of the lower extremities using photogrammetrical methods, only the element measured is affected. Furthermore, data published by Sander (1999, 2000) show that the internal bone structure changes during growth. This means that bone circumference, for example, need not necessarily change at the same rate as the internal structure does. Recently, Henderson (1999) published a paper on studies using an approach similar to our photogrammetrical

Table 1 Changes of body mass, body surface, body surface area, and presumable physiological data of *P. engelhardti* mounted and exhibited at the Paleontological Museum of the University in Tübingen (Germany) in a slim and robust type of reconstruction

<i>Plateosaurus engelhardti</i>	Slim	Robust
Body volume (m ³)	0.79	1.140
Body mass (M_b) (kg)	630	912
Body surface area (m ²)	8.8	10.2
Skeleton (kg)	(0.0608 $M_b^{1.083}$)	97.6
Integument (kg)	(0.106 $M_b^{0.94}$)	64.2
Muscle mass (kg)	(0.45 $M_b^{1.0}$)	410
Fat mass (kg)	(0.075 $M_b^{1.19}$)	250
Lung mass (kg)	(0.011 $M_b^{0.99}$)	9.4
Lung volume (l)	(0.063 $M_b^{1.02}$)	65.8
Tidal volume (l)	(0.0062 $M_b^{1.01}$)	6.0
Respiration frequency (min ⁻¹)	(53.5 $M_b^{-0.26}$)	10.8
O ₂ consumption (l h ⁻¹)	(0.676 $M_b^{0.75}$)	112
O ₂ consumption (l h ⁻¹ kg ⁻¹)	(0.676 $M_b^{-0.25}$)	0.12
Basal metabolic rate [kJ (24 h) ⁻¹]	40 943	54 711
Respiration frequency (min ⁻¹)	(53.5 $M_b^{-0.26}$)	10.0
Blood volume (l)	(0.055 $M_b^{0.99}$)	32.5
Heart mass (kg)	(0.0058 $M_b^{0.99}$)	3.4
Heart rate (min ⁻¹)	(241 $M_b^{-0.25}$)	48.1
Kidney masses (kg)	(0.007 $M_b^{0.85}$)	1.7
Liver mass (kg)	(0.033 $M_b^{0.87}$)	9.0
Spleen mass	(0.003 $M_b^{1.02}$)	2.2
Gut mass (kg)	(0.053 $M_b^{1.02}$)	38.0

For mass estimations, it was assumed, in accordance with Wedel (2005), that 1,000 cm³ of tissue mass has a specific weight of 0.8 kg. Anatomical and physiological features were calculated pursuant to equations done by Anderson et al. (1979), Calder (1984), and Schmidt-Nielsen (1984), equating 1 l of oxygen consumption during oxidative metabolism (at 0°C, 760 mmHg) with 20.083 kJ

method. In the calculations, he made use of various reconstruction drawings from one or more angles, which were digitalized two-dimensionally. These primitives were then modeled using an AutoCAD program applied to truncated cones with ellipsoid sections and other geometric forms. The volume of the geometric primitives was calculated, and the primitives of the individual body parts and of the animal as a whole were brought in line with each other. Henderson's method has the advantage over our method, in which only circular cone segments were used,

resulting in a barrel-formed thorax, that the mathematical modeling is better, providing elliptical sections of truncated cones. Furthermore, his measurements have been validated on living species. On the other hand, our method arrives at a three-dimensional depiction of the original object, whereas Henderson only has two-dimensional drawings available. Finally, the reconstruction drawings Henderson used are of questionable geometric quality, whereas the methods our team used gave us precise measurements of the skeleton and three-dimensional data.

The anatomical and physiological results of the study are as follows. The overall body surface areas for integument without wrinkles of *P. engelhardti* amounted to approximately 8.8 m² for the slim version of the reconstructed dinosaur and to 10.2 m² for the robust version, the tail's integument making up 23–27% of the total amount, respectively. The body mass of *P. engelhardti* was determined as 630 kg (slim) and 912 kg (robust) in our reconstruction. This is distinctively lower than the estimations cited by Peczkis (1994) of 1,000–4,000 kg. The volume distribution indicates that 54–67% of the mass of *P. engelhardti* is located in the thorax (Figs. 2 and 3). Furthermore, and this finding contrasts with what has been established for later sauropods such as *B. brancai* (Gunga et al. 1995; Gunga et al. 1999), we find that *P. engelhardti*

Table 2 Different body volumes from the head to the tail of *P. engelhardti* mounted and exhibited at the Paleontological Museum of the University in Tübingen (Germany) in a slim and robust type of reconstruction

<i>Plateosaurus engelhardti</i>	Slim type (m ³)	Robust type (m ³)
Head	0.006	0.010
Neck	0.016	0.026
Fore limbs	0.020	0.025
Hind limbs	0.080	0.180
Thoracic cavity	0.533	0.616
Tail	0.136	0.280
Total body volume	0.79	1.14

has a very small neck volume of about 2% of the body mass and a relatively large body volume in the tail and hind limbs, i.e., ~26% in the slim version and ~40% in the robust version. These volume distributions strongly suggest that when feeding and high browsing, *P. engelhardti* used its tail and hind limbs as counterweights, the latter seems to be the case in the slim reconstruction. A specific analysis of the centers of gravity in both reconstructions revealed that in the slim reconstruction, a standing on the hind limbs could be achieved, whereas in the robust model, this seems to be difficult because the front part is too heavy. It is interesting to note that its head volume, in percentage of body mass, was about two times that of the mid-sized sauropod *Dicraeosaurus* and about four times that of large sauropods such as *B. brancai* (Gunga et al. 1999). It remains to be tested whether this type of negative correlation between head volume and body mass truly exists in herbivorous sauropods.

In addition to these determinations of general body volume and surface, the slim reconstruction of *P. engelhardti* was further analyzed with the intention of establishing whether the organs, in the sizes they are generally assumed by allometry to have, would actually fit into the thoracic cavity, or in other words, whether the skeleton established in our 3D reconstruction is in fact large enough. Within the thorax, the lungs represent a major volume. Using allometric scaling, a lung volume of ~45 l was established. However, this lung volume reconstruction remains questionable because it is still very difficult to say whether the type of respiration given in sauropods was similar to that of mammals, or whether it resembled the respiration of birds, which have air sacs (Perry 1989, 1992). It might well be that *P. engelhardti* had air sacs, meaning that sauropods had some of the respiratory and thermoregulatory advantages enjoyed by birds, a possibility that is consistent with the rapid growth rates observed in some sauropods (Wedel 2003; Klein 2004; Sander and Klein 2005). In general, air sacs permit the unidirectional flow of air through the lungs so that more oxygen is available for diffusion into the blood (higher efficiency, meaning that such a lung type can be smaller in relation to its body mass as compared to a mammalian lung type). If this were to be the case, the lungs of *P. engelhardti* were attached to a series of thin-walled air sacs that appear to have functioned something like bellows that move air through the body, as opposed to the diaphragm that forces air in and out of lungs. This assumption has recently been supported by Wedel (2005) who established that the vertebrae of sauropod dinosaurs are characterized by complex architecture involving laminae, fossae, and internal chambers of various shapes and sizes. He has interpreted these structures to be osteological correlates of a system of air sacs and pneumatic diverticula similar to that given in birds. Air sacs and skeletal pneumaticity probably facilitated the evolution

of extremely long necks in some sauropod lineages by overcoming respiratory dead space and reducing mass. The latter fact is the basis for our assumption of a tissue density of 0.8 kg per 1,000 cm³ tissue mass in *P. engelhardti*. Another major factor determining the volume in the thoracic cavity is the gastrointestinal tract. In the absence of any adaptive trend, the capacity of this organ should increase in direct proportion to body mass (Owen-Smith 1988). Very recently, Clauss et al. (2005) tested predictions on body mass and gut content in a dissected African elephant. They were able to confirm the above-referenced assumption by Owen-Smith (1988) and in fact established a remarkable uniformity, in mammals, of the relationship between body mass and the gastrointestinal tract. As a volume, respectively as a mass factor, the integument and the gut mass also play other, and essential, roles in the reconstruction of the thorax. As set out in Table 1, we arrived at an estimated integument mass of ~30 kg (two thirds of total mass) and a gut mass of about 38 kg. According to Calder (1984), it can be assumed that the full-gut capacity is usually approximately 3.4 times higher, i.e., 129 kg. To sum up the masses for the remaining organs and organ systems of the thorax segment of *P. engelhardti*, we determined a total fat mass of ~106 kg (two thirds of total mass), a muscle mass of ~95 kg (one third of total mass), a skeleton of ~21 kg (one third of total mass), a blood volume of 25 l (three fourths of total mass), heart mass of 3.4 kg, liver mass of 9.0 kg, spleen mass of 2.2 kg, and kidney mass of 1.7 kg. This adds up to a total weight of 454 kg, which would, in fact, correspond well to the anatomical limitations represented by the skeleton as estimated according to our methods, i.e., ~530 l. In contrast, at a total mass of 597 kg, the robust reconstruction seems to be at the upper limit of what could fit into the thorax segment. As no more structure is formed and maintained than is required to satisfy functional needs (Weibel and Taylor 1981), we assume that either the lungs and/or the gastrointestinal tract were actually larger than calculated in our slim version of the reconstruction. It would be interesting to compare, in a future project, short- and long-necked sauropods as well as small and large sauropods with one another as regards their volume distribution, mainly because these volume distributions are closely linked with physiological aspects such as heat balance and thermoregulation in a compact animal (elephant) in comparison to a more elongated animal shape such as *P. engelhardti*. In the latter, due to geometry, a heat dissipation/heat loss from the body to environment would have been facilitated.

Taken together, it seems to be possible, as already pointed out by Calder (1996), that in future allometry—a method that had its origins in applications serving ontogeny—can provide data in an evolutionary context rather than on an individual scale. Thus, this research

might pave the way for a better understanding of the evolution of gigantism in general.

Acknowledgments We wish to thank all the members of the DFG (Deutsche Forschungsgemeinschaft) Research Unit 533 “Biology of the sauropod dinosaurs: the evolution of gigantism”. Further thanks go to the staff of the institutions in which we measured the skeletons, the Paleontological Museum of Tübingen and the Zoological Museum of Copenhagen, in particular for their enthusiastic response to our project, their patience and their support, and H. Mallison (Tübingen) for his help to calculate the centers of gravity. The project has been granted financial support from the DFG-GU 414/3-1.

References

- Alexander RM (1989) Dynamics of dinosaurs and other extinct giants. Columbia University Press, New York
- Anderson JF, Rahn H, Prange HD (1979) Scaling of supportive tissue mass. *Q Rev Biol* 54:139–148
- Anderson JF, Hall-Martin A, Russell DA (1985) Long-bone circumference and weight in mammals, birds, and dinosaurs. *J Zool (London)* 207:53–61
- Bellmann A, Suthau T, Stoinski S, Friedrich A, Hellwich O, Gunga H-C (2005) 3D-modelling of dinosaurs. In: Grün/Kahmen (ed) Optical 3-D measurement techniques VII (Proceedings of the 7th Conference) Part 1, Vienna
- Blob RW (1998) Evaluation of vent position from lizard skeletons for estimation snout-vent length and body mass. *Copeia* 3:792–801
- Calder EH (1984) Size, function, and life history. Harvard University Press, Cambridge, Massachusetts
- Calder EH (1996) Size, function, and life history. Harvard University Press, Cambridge, Massachusetts
- Christiansen P, Fariña RA (2004) Mass prediction in theropod dinosaurs. *Historical Biology: Journal of Paleobiology* 16:85–92
- Clauss M, Robert N, Walzer, Vitaud C, Hummel J (2005) Testing predictions on body mass and gut contents: dissection of an African elephant *Loxodonta africana* Blumenbach 1797. *Eur J Wildl Res* 51:291–294
- Colbert EH (1962) The weights of dinosaurs. *Am Mus Novit* 2076:1–16
- Galton PM, Upchurch P (2004) Prosauropoda. In: Weishampel DB, Dodson P, Osmolska H (eds) *The Dinosauria* (2nd edn). University of California Press, Berkeley, pp 232–258
- Gunga H-C, Kirsch K, Baartz F, Röcker L, Heinrich W-D, Lisowski W, Wiedemann A, Albertz J (1995) New data on the dimensions of *Brachiosaurus brancai* and their physiological implications. *Naturwissenschaften* 82:190–192
- Gunga H-C, Kirsch K, Rittweger J, Clarke A, Albertz J, Wiedemann A, Mokry S, Suthau T, Wehr A, Clarke D, Heinrich W-D, Schultze H-P (1999) Body size and body volume distribution in two sauropods from the Upper Jurassic of Tendaguru/Tansania (East Africa). *Mitteilungen aus dem Museum für Naturkunde in Berlin. Geowissenschaftliche Reihe* 2:91–102
- Haubold H (1990) *Die Dinosaurier*. A. Ziemsen Verlag, Wittenberg
- Henderson DM (1999) Estimating the masses and centers of masses of extinct animals by 3-D mathematical slicing. *Paleobiology* 25:88–106
- Jung C (2002) Kernspintomographische Untersuchung der Relation zwischen Muskelvolumen, Muskelgeometrie und Knochengeometrie am Unterschenkel. FU Dissertation, Berlin
- Klein (2004) Bone histology and growth of the prosauropod dinosaur *Plateosaurus engelhardti* MEYER, 1837 from the Norian bonebeds of Trossingen (Germany) and Frick (Switzerland). Dissertation, Bonn
- Lambert D (1980) *A field guide to dinosaurs*. Avon, New York
- Mallison H (2007) *Virtual Dinosaurs - Developing Computer Aided Design and Computer Aided Engineering Modeling Methods for Vertebrate Paleontology*. Doctoral Thesis, Eberhardt-Karls-Universität Tübingen
- Moen DS (2006) Cope’s rule in cryptodiran turtles: do the body sizes of extant species reflect a trend of phyletic size increase? *J Evol Biol* 19:1210–1221
- Motani R (2001) Estimating body mass from silhouettes: testing the assumption of elliptical body cross-sections. *Paleobiology* 27:735–750
- Owen-Smith RN (1988) Megaherbivores. The influence of very large body size on ecology. Cambridge University Press, Cambridge
- Peczis J (1994) Implications of body-mass estimates for dinosaurs. *J Vertebr Paleontol* 14:520–533
- Perry SF (1989) Mainstreams in the evolution of vertebrate respiratory structures. In: King AS, McLelland J (eds) *Form and function in birds*, vol 4. Chapter 1. Academic, London, pp 1–67
- Perry SF (1992) Gas exchange strategies in reptiles and the origin of the avian lung. In: Wood SC, Weber RE, Hargens AR, Millard RW (eds) *Physiological adaptations in vertebrates. Respiration, circulation, and metabolism*. Marcel Dekker, New York, pp 149–167
- Sander PM (1999) Life history of the Tendaguru sauropods as deduced from long bone histology. *Mitteilungen aus dem Museum für Naturkunde Berlin, Geowissenschaftliche Reihe* 2:103–112
- Sander PM (2000) Long bone histology of the Tendaguru sauropods: implication for growth and biology. *Paleobiology* 26:466–488
- Sander PM, Klein N (2005) Developmental plasticity in the life history of a prosauropod dinosaur. *Science* 310:1800–1802
- Schmidt-Nielsen K (1997) *Animal physiology*. Cambridge University Press, Cambridge
- Schmidt-Nielsen K (1984) *Scaling: why is animal size so important?* Cambridge University Press, Cambridge
- Seebacher F (2001) A new method to calculate allometric length-mass relationships of dinosaurs. *J Vertebr Paleontol* 21:51–60
- Wedel MJ (2003) Vertebral pneumaticity, air sacs, and the physiology of sauropod dinosaurs. *Paleobiology* 29:243–255
- Wedel MJ (2005) Postcranial skeletal pneumaticity in sauropods and its implications for mass estimates. In: Wilson JA, Curry-Rogers K (eds) *The sauropods: evolution and paleobiology*. University of California Press, pp 201–228
- Weibel ER, Taylor CR (eds) (1981) *Design of the mammalian respiratory system*. *Respir Physiol* 44:1–164
- Wiedemann A, Wehr A (1998) *Vermessung von Dinosaurierskeletten mit Stereophotogrammetrie und Laserscanner*. *Publikationen der Deutschen Gesellschaft für Photogrammetrie und Fernerkundung* 6:301–308
- Wiedemann A, Suthau T, Albertz J (1999) Photogrammetric survey of dinosaur skeletons. *Mitteilungen aus dem Museum für Naturkunde Berlin, Geowissenschaftliche Reihe Band* 2:113–119
- Withers PC (1992) *Comparative animal physiology*. Saunders College Publishing, Fort Worth