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New Data on the Dimensions of *Brachiosaurus brancai* and Their Physiological Implications

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There are highly divergent data on the body mass (M_b) of *Brachiosaurus* (*B.*). The range of the body-mass estimations lies between 14900 and 102000 kg for this giant dinosaur [1–6]. This is mainly due to the fact that different specimens and varying techniques are used for the volume (V) estimations, such as equations from the circumferences of femur and humerus [4] or from the volume of models [5]. The precise determination of V is important for calculating the body surface area (S_A) as well as for allometric equations, which are often based on M_b. Herewith, we present a photogrammetric method to determine the metrical dimensions of giant sauropods such as *B.*

The data presented here are based on the skeleton of *B. brancai* from the Upper Jurassic of Tendaguru (East Africa, Tanzania), mounted and exhibited at the Museum of Natural History in Berlin (Germany). The major part of the skeleton belongs to one single specimen of *B. brancai* recovered from the Middle Saurian Bed at Tendaguru. The tail originates from another individual of the same species of similar size found in the Upper Saurian Bed. In addition, skeletal remains of *B. brancai* excavated in different sites in the surroundings of the Tendaguru hill were used for the mounting, partly original and partly modeled. The presacral vertebral column (cervicals, dorsals) and the skull have been replaced by plaster copies modeled from originals of the main skeleton due to their extreme fragility and weight. The right shoulder blade, four dorsal ribs, and some bones of the left forefoot have been modeled in plaster according to counterparts of the other body side. Some missing elements are substituted by bones belonging to individuals of the same size such as the right ilium, the right ischium, and the left lower leg. Other missing items have been replaced by originals (e.g., left femur) or copies of bones from different-sized animals (e.g., sacrum, most hindfoot bones). At the very end of the tail four small pieces were added. Like the missing first caudal vertebra, most of the hemapophyses (chevrons) are plaster imitations [6].

As can be seen in Fig. 1, we divided the presumable shape of *B. brancai* into XI parts. Each part was separately calculated and the V_{I-XI} are given in Table 1. From the V found, the M_b was calculated assuming a density of 1000 kg per m^3 tissue [5, 7]. On the basis of the above findings, we investigated further whether the presumable organ volumes derived by allometric equations could be fitted into the anatomical dimensions given by the skeleton.

The advantage of the photogrammetrical approach is that when the values are taken from a specimen, the complete shape of the animal is stored in the computer. This allows later derivation of other forms and dimensions, which is almost impossible from a model. In the case of a small model being built from the data and later becoming enlarged, the smallest deviation is multiplied by a factor of 10–50 depending on the size of the model. Therefore, regardless of the size of a model, it is defined by these exact basal metric values.

The anatomical data of *B. brancai* derived by stereophotogrammetry and the presumable physiological data calculated after equations given for endotherms are summarized in Table 1, Table 2, and Fig. 2. According to these, the M_b of *B. brancai* is ca. 74420 kg (skeleton 11480 kg). Accordingly, the M_b estimations in [1] are similar to our findings, whereas those in [2, 4–6] are far too low. It is not clear whether the estimation in [3] for *B.* refers to the Berlin specimen. If so, it is far too high. The S_A (Table 2) was found to be at least (without any skin-

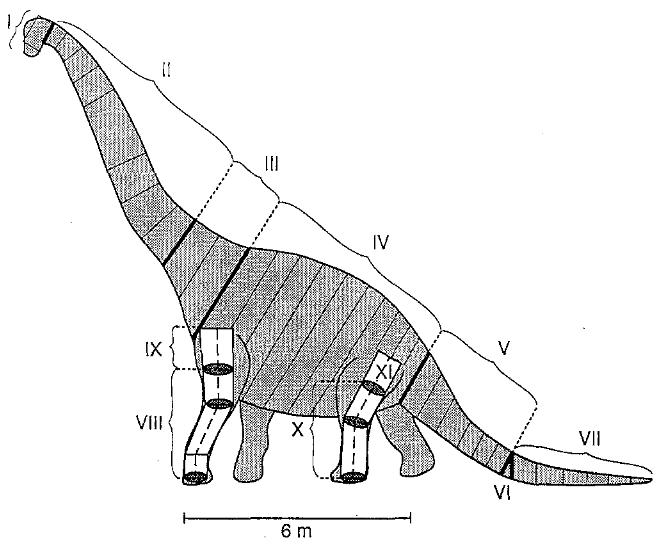

Fig. 1. For the calculation of the volume and the body surface area of *Brachiosaurus brancai* we divided the body into 11 parts, each consisting of a different number of elements. The *thick black lines* separate the parts (*I–XI*), the *light* ones the elements

folds) 138.9 m^2, which consists mainly of the S_A of the thorax-abdomen (66.7 m^2), neck (30.8 m^2), tail (14.1 m^2), and the extremities (25.8 m^2, Table 1).

M_b and S_A can be used to calculate the metabolic rate of an organism. If we assume that dinosaurs had a relatively high metabolic rate, similar to that of endotherms, for which we have very recently some strong new evidence [8], then *B. brancai* would have had an oxygen consumption of 3046 $l\,h^{-1}$ or 0.041 $l\,h^{-1}\,kg^{-1}$ and a basal metabolic rate (recalculated from the oxygen consumption) of approximately 16.9 $kJ\,s^{-1}$ or 1.47×10^6 kJ $(24\,h)^{-1}$. From the nutritional point of view, this means a food intake for *B. brancai* of approximately 1000 $kJ\,min^{-1}$. There are several good reasons why the nutrition of *B. brancai* depended mainly on plants [9]. Assuming first, a mean caloric content of 8.0 $kJ\,g^{-1}$ for the different plants (ferns, cycads, conifers, etc.) which were available for *B. brancai* in the Upper Jurassic, and second, a 50% digestive efficiency [10], then a food intake of at least 15 $kg\,h^{-1}$ or 360 kg $(24\,h)^{-1}$ was needed to fulfill the nutritional constraints. The actual free-living metabolism (foraging, migration, etc.) is hard to assume and might be 15–20% higher again [10]. Compared to living megaherbivores (African elephant), such a calculated energy expenditure seems to be thoroughly realistic. There is still open dispute as to whether anatomical limitations (size of the head) and/or feeding patterns allowed such an enormous daily food intake [9, 10]. Certainly, such a scenario requires constant, rich, and easily accessible local sources of food and fluid. Any factor disturbing this paleoecological equilibrium must have been disastrous for *B. brancai*.

Besides the nutritional aspects, thermal aspects of an endothermic model for *B. brancai* have also been frequently discussed [2, 5, 9]. Large animals, especially when they are moving, are in danger of becoming overheated. Four pathways exist to dissipate this additional heat load: radiation, conduction, convection, and evaporation. Since sauropods like *B. brancai* had reptile-like skin [5], evaporative heat loss seems to be unlikely, as also heat losses through the respiratory tract, because of the low respiration frequency (3 min^{-1}). Panting is also unlikely, due to the functional restriction given by the large dimension of the lungs (almost

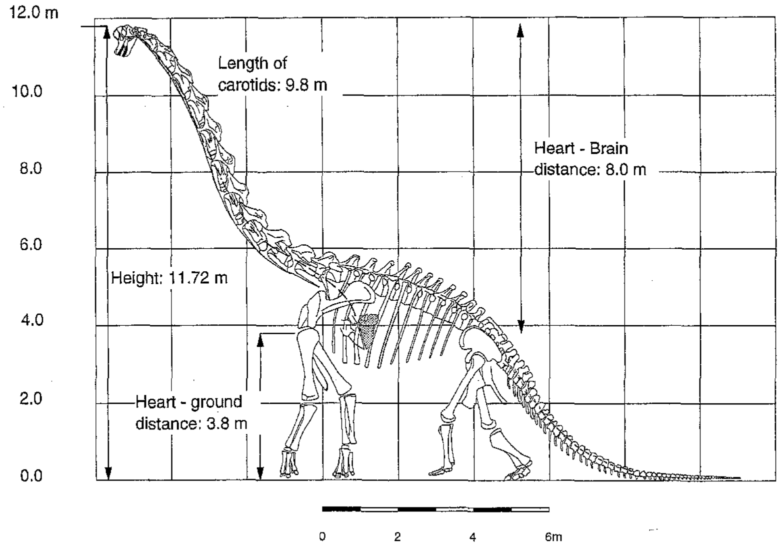

Fig. 2. Stereophotogrammetrically derived plot (side view) of the *Brachiosaurus brancai* from the Museum of Natural History in Berlin (Germany). Besides the height of the sauropod, the presumable position of the heart, heart-ground and heart-brain distances, as well as the length of the carotids are shown

Table 1. The parts (*I – XI*) of *Brachiosaurus brancai* used for calculation, the number of elements of each part, the anatomical term, the volume (V) and the body surface area (S_A). Part (*I*): The head was achieved as a sum of three elements: two caps of a sphere, one part being a cylinder. The radius of the spheres was calculated by geometric construction. First element (spherical cap, skull): r (radius) = 0.23 m, height (h) = 0.19 m; $V = 0.02\,m^3$, $S_A = 0.27\,m^2$. $V = 1/3\cdot\pi\cdot h^3\cdot(3r-h)$, $S_A = 2r\cdot h\cdot\pi$. Second element (spherical cap): (r) = 0.23 m, (h) = 0.13 m; $V = 0.01\,m^3$, $S_A = 0.18\,m^2$. Third element (cylinder): (r) = 0.21 m^3, (h) = 0.80 m; $V = 0.11\,m^3$, $S_A = 1.05\,m^2$. $V = \pi\cdot r^2\cdot h$, $S_A = 2r\cdot h\cdot\pi$. Parts (*II – XI*): V of the neck, thorax-abdomen, tail, and extremities: these parts of *B. brancai* have been calculated as sums of truncated cones, the only simplification being that the connection between the lower and the upper circle of each truncated cone element is a straight line. The (r) and (h) of each element have been taken from the sketches. For the S_A we used the cone shaped shell. $V = h\cdot\pi(r_1^2 + r_1\cdot r_2 + r_2^2)/3$, $S_A = (r_1+r_2)\cdot\pi\sqrt{(r_1-r_2)^2+h^2}$. Parts *IX* and *XI* have been divided by 2 because the fore- and hindlimbs are adjacent the trunk

Part	No. of elements	Part of the body	Volume (V) [m^3]	Surface area (S_A) [m^2]	Surface area (S_A) [%]
I	3	Head	0.14	1.5	1.1
II	8	Neck	5.04	19.5	14.0
III	2	Neck	6.16	11.3	8.2
IV	10	Thorax-abdomen	55.12	66.7	48.0
V	6	Tail	2.81	10.2	7.3
VI	1	Tail	0.10	0.1	0.1
VII	6	Tail	0.37	3.8	2.7
VIII	3	Forelimb right	1.07	6.1	4.4
IX	1	Forelimb right	0.29	1.2	0.9
X	2	Hindlimb right	0.80	4.9	3.5
XI	1	Hindlimb right	0.18	0.7	0.5
VIII	3	Forelimb left	1.07	6.1	4.4
IX	1	Forelimb left	0.29	1.2	0.9
X	2	Hindlimb left	0.80	4.9	3.5
XI	1	Hindlimb left	0.18	0.7	0.5
Total	50		74.42	138.9	100.0

Table 2. Presumable physiological data of *Brachiosaurus brancai* (Museum of Natural History, Berlin) calculated after equations from [a][14], [b][15], and [c]equating after [15] 1-l oxygen consumption during oxydative metabolism (at 0 °C, 760 mmHg) with 20.083 kJ

Body mass (M_b) [kg]		74420
Body surface area[a] (S_A) [m^2]		138.9
Skeleton[b] [kg]	$(0.0608 \cdot M_b^{1.083})$	11480
O_2 consumption[b] [l h^{-1}]	$(0.676 \cdot M_b^{0.75})$	3046
O_2 consumption[b] [l h^{-1} kg^{-1}]	$(0.676 \cdot M_b^{-0.25})$	0.041
Basal metabolic rate[c] [kJ (24 h)$^{-1}$]		1468148
Lung volume[b] [l]	$(0.063 \cdot M_b^{1.02})$	5866
Tidal volume[b] [l]	$(0.0062 \cdot M_b^{1.01})$	516
Respiration frequency[b] [min^{-1}]	$(53.5 \cdot M_b^{-0.26})$	3
Blood volume[b] [l]	$(0.055 \cdot M_b^{0.99})$	3659
Heart weight[b] [kg]	$(0.0058 \cdot M_b^{0.99})$	386
Heart rate[b] [min^{-1}]	$(241 \cdot M_b^{-0.25})$	14.6

6 m^3, tidal volume 516 l). We therefore favor the idea that *B. brancai* used behavioral adaptation to dissipate the metabolic heat load, like wallowing or immersing their body in water or mud, as is known from living megaherbivores [11]. Many variables affect the thermal conductivity of an animal, among them body size (S_A) for heat exchange, presence of insulation, and the nature of the environment (air or water). The thermal conductivity in an aquatic environment is 25 times and the thermal capacity approximately 3200 times greater than under atmospheric conditions [12]. Furthermore, for ridding itself of the heat, *B. brancai* was facilitated by the long neck, tail, and extremities, which could have served as efficient counter-current heat exchangers. These parts of the body still represent 50.9% of the total S_A (Table 1). Therefore, conductive and convective heat transport in these parts of the sauropod could have been very efficient, as is known from the fins and flukes of cetaceans, where a central artery is surrounded by many small veins [12]. Furthermore, those parts of the S_A which are mainly above the water, such as the upper thorax, could easily have been moistened and thus also used for cooling, since per liter evaporated water, 2500 kJ can be drawn from the body without putting a load on the overall fluid balance. An amount of 567 kg (24 h)$^{-1}$ or 0.007 kg s^{-1} evaporated water from the moistened skin would have been enough to dissipate the basal metabolic heat production of *B. brancai.* Therefore, such a behavioral adaptation in sauropods would seem to have been sufficient to overcome the thermoregulatory demands of endothermic metabolism.

This presumed behavioral adaptation would also effect the capacity of the cardio-circulatory system of *B. brancai.* This seems to be a critical point per se, as first described in [13], although the height of *B. brancai* was given as too tall. Our measurements show that the vertical distance between the vault of the cranium to the ground is 11.72 m (Fig. 2). A heart-ground distance of 5.32 m, as calculated in [13] for the mounted skeleton of *B. brancai,* is unrealistic, as can be seen in Fig. 2. We calculated a vertical heart-ground distance of 3.80 m and a heart-brain distance of 8.00 m in the mounted skeleton (Fig. 2). This means that already under resting conditions the left ventricle should have reached a blood pressure of 86.4 kPa (78.4 kPa hydrostatic pressure plus 8.0 kPa brain perfusion pressure), which is higher than formerly described [13]. The length of the carotids was ca. 9.80 m (Fig. 2). The heart weight should have been at least 386 kg, with a stroke volume of approximately 17.4 l (total blood volume 3659 l), assuming a heart frequency of 14.6 min^{-1} (Table 2) and an oxygen transport capacity of the blood of *B. brancai* which is not very different from that of existing endotherms (20 ml oxygen per 100 ml arterial blood).

Finally, looking at the different presumable organ sizes (lung, heart) the thoracic-abdominal cavity does indeed seem to be big enough to carry these organs (approximately 6 m^3) and a gastro-intestinal tract as well.

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