

## Body Size and Body Volume Distribution in Two Sauropods from the Upper Jurassic of Tendaguru (Tanzania)

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With 3 figures, 4 tables and 1 map

### Abstract

Allometric equations are often based on the body mass of an animal because body mass determines many physiological functions. This should also hold for *Brachiosaurus brancai* and *Dicraeosaurus hansemanni*, two sauropods from the Upper Jurassic of Tendaguru/Tanzania (East Africa). Widely divergent estimates of body mass for the same specimen can be found in the literature for these two sauropods.

Therefore, in order to determine the exact body mass and volume distribution in these sauropods, classical three-dimensional stereophotogrammetry as well as a newly developed laser scanner technique were applied to the mounted skeletons of *Brachiosaurus brancai* and *Dicraeosaurus hansemanni* in the Museum für Naturkunde (Berlin, Germany). Thereafter, scaling equations were used to estimate the size of organ systems. In a second step it was tested whether the given data from photogrammetry could be brought in line with the results derived from the allometric equations. These findings are applied to possible ecological problems in the Upper Jurassic of Tendaguru/Tanzania.

**Key words:** Dinosauria, Sauropoda, palaeophysiology, evolutionary physiology, palaeoecology, body mass estimations, metabolism, nutrition, gait and posture.

### Zusammenfassung

Der Körpermasse eines Organismus werden oft allometrische Funktionen zugrunde gelegt, da von ihr viele physiologische Funktionen entscheidend abhängen. Dies sollte auch für ausgestorbene Organismen wie *Brachiosaurus brancai* und *Dicraeosaurus hansemanni*, zwei Sauropoden aus dem oberen Jura von Tendaguru/Tanzania in Ostafrika gelten. Da zu beiden Sauropoden nur sehr unterschiedliche Massenabschätzungen vorliegen, wurden die Körpermassen und Volumina von *Brachiosaurus brancai* und *Dicraeosaurus hansemanni* mit Hilfe der klassischen Photogrammetrie sowie einem neuentwickelten Laserscannerverfahren neu bestimmt. Basierend auf den so gemessenen Körpermassendaten wurden anschließend einige wichtige funktionell-morphologische Größen für eine paläophysiological Rekonstruktion dieser Sauropoden mit Hilfe der Allometrie berechnet. Die gewonnenen Ergebnisse sind u. a. wichtig für die Rekonstruktion eines Ökosystems im oberen Jura von Ostafrika.

**Schlüsselwörter:** Dinosauria, Sauropoda, Paläophysiology, Evolutionäre Physiologie, Paläoökologie, Körpermassenabschätzungen, Stoffwechsel, Ernährung, Bewegung und Haltung.

### Introduction

The German Tendaguru excavations in East Africa by the Friedrich Wilhelm Universität of Berlin from 1909 to 1913 were one of the most successful dinosaur excavations in the history of palaeontology (Janensch 1914a). The foremost

achievements in terms of exhibiting the discoveries were the reconstruction of the *Brachiosaurus brancai* and *Dicraeosaurus hansemanni* skeletons, which are on display today in the Museum für Naturkunde in Berlin (Janensch 1935a, 1950a, b). For the viewer of the skeletons the body mass of both sauropods is most impressive.

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Comparative physiology has frequently shown that to make simple, quantitative, and reasonably accurate predictions of physiological parameters, the total body mass is of particular importance (Peters 1983, Withers 1992, Schmidt-Nielsen 1984, 1997). This should also hold for palaeophysiological reconstructions for *Brachiosaurus brancai* (skeleton SII) and *Dicraeosaurus hansemanni* (skeleton m). Unfortunately, the body mass estimates found in the literature on these exhibited specimens are widely divergent, *Brachiosaurus brancai* 14.9–102 tons and *Dicraeosaurus hansemanni* 10–40 tons (Peczki 1994). These estimates were based on projections from models or circumferential measurements of the humerus and femur (Colbert 1962, Lambert 1983, Anderson et al. 1985, Alexander 1989). The disadvantage of these methods lies principally in the use of models, where, depending on the enlargement factor, the most minor inaccuracies can lead to differences with a multiplication factor of 10 to 50. When body mass is calculated by measuring the humerus and femur, it cannot be ruled out that the skeletal material examined actually comes from several different specimens. Furthermore there are still numerous gaps in the general comprehension of bone growth in dinosaurs (Reid 1984a, b; Sander 1999, in press). Moreover, extreme strain on the extremities, as occurs with the dynamic load of body mass walking and braking, plays a decisive role in bone growth. On this basis it is to be expected that the femur/humerus circumference in various species, which normally also differ in their skeletal patterns of movement, i.e. load patterns, does not always correlate necessarily with the body mass determined purely statistically. In addition, it is known that with an otherwise equal circumference and cross-sectional surface, the inner structure of bones can vary, so that the corticalis, for example, can be thickened overproportionally in order to increase stability. Last not least, the envelope describing the range of masses for mammals falls far short of the likely mass of the sauropods.

For this reason our group took a few years ago a new approach to the estimation of body mass and body volume distributions (Gunga et al. 1995). Meanwhile, Henderson (1999) published very recently a similar method to estimate the masses and centers of mass of extinct animals by a 3-D mathematical slicing technique.

To register the body mass we applied classical photogrammetry and a newly developed laser scanner for large-scale objects. Points of refer-

ence were mounted on the skeleton for the photogrammetry and a three-dimensional reconstruction was made with stereo projectors (Gunga et al. 1995, Wiedemann Wehr 1998, Wiedemann et al. 1999, in press). Then the dimensions of skeletons erected in the museum were determined by classical stereophotogrammetry either in the case of *Brachiosaurus* or scanned by a laser line by line in the case of *Dicraeosaurus*. On the basis of these photographic/electronic data the probable body contours of the skeletons were added (CAD technique) to calculate the body surface areas and masses. The reconstructions obtained in this way were cut up into larger parts and smaller elements and the volume and surface of each individual part was calculated from the usual geometric formulas according to Bronstein & Semendjajew (1985), which we have described in detail earlier (Gunga et al. 1995). It was found that the body mass and body volume distributions indicate a completely different life-style for these two sauropods.

## Methods

The study was performed on the specimens, i.e. *Brachiosaurus brancai* (skeleton II) and *Dicraeosaurus hansemanni* (skeleton m), mounted and exhibited at the Museum of Natural History in Berlin (Germany). Preliminary results concerning body mass and volume distribution in *Brachiosaurus brancai* were published earlier (Gunga et al. 1995). Therefore, a detailed description of the palaeontological setting and the classical photogrammetrical method applied on *Brachiosaurus brancai* is omitted here.

Briefly, the mounted specimens of *Brachiosaurus* and *Dicraeosaurus* were divided into elements (Figs 1, 2), which were treated, according to their geometry, as spherical caps, cylinders or truncated cones (*Brachiosaurus* head 2 spherical caps and 1 cylinder, other elements truncated cones; *Dicraeosaurus* head spherical caps, other elements truncated cones). The mathematical formulas used are given in Figs 1, 2. The different number of elements were compiled to parts I to XI in *Brachiosaurus* and I–VI in *Dicraeosaurus*.

## Palaeontological settings

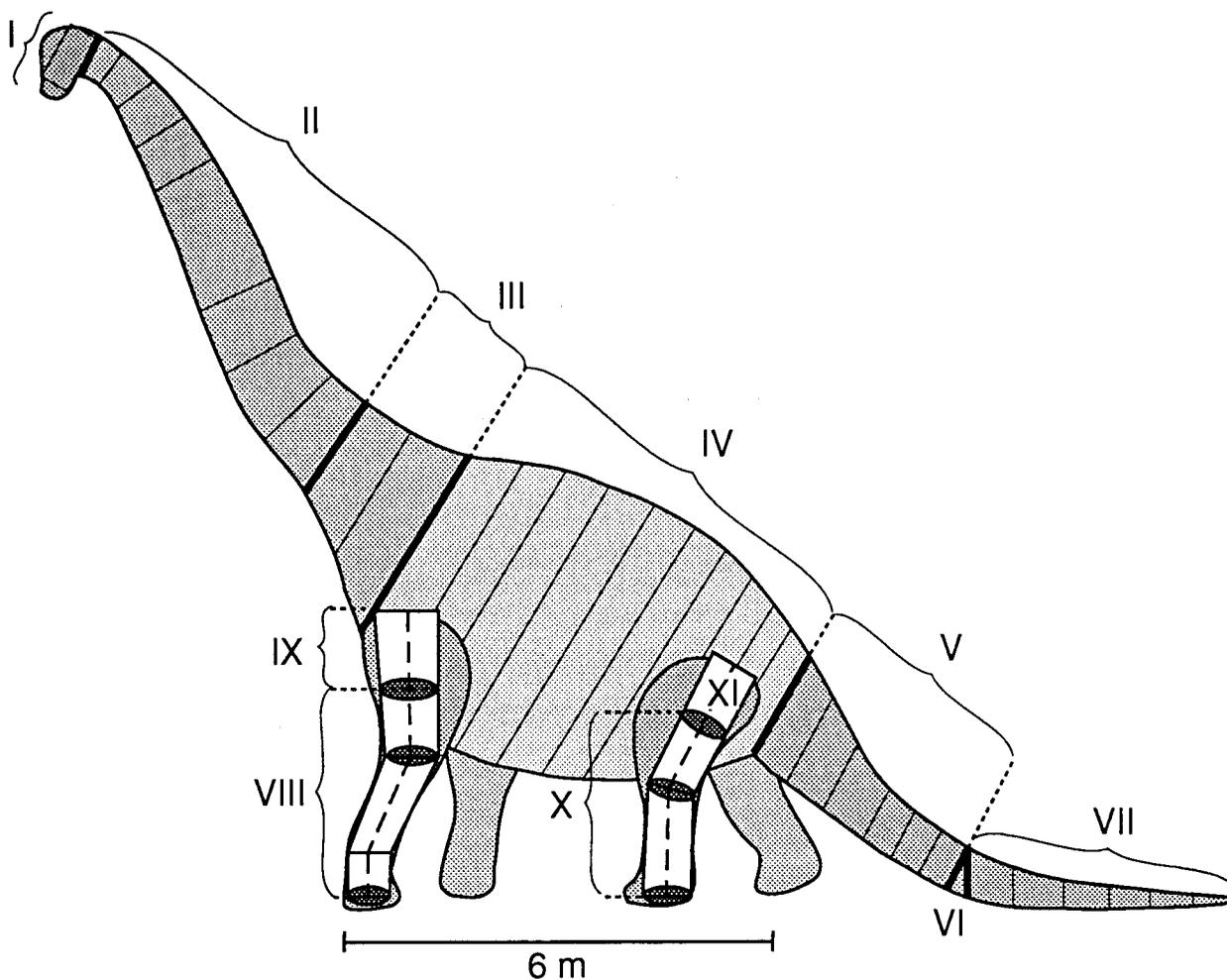
The skeletons of *Brachiosaurus brancai* (skeleton SII) and *Dicraeosaurus hansemanni* (skeleton m) are from the Upper Jurassic of Tendaguru/Tan-

zania, East Africa (Map 1). The skeleton of *Dicraeosaurus hansemanni* was mounted in the Museum für Naturkunde, Berlin, in 1930 (Janensch 1935a), that of *Brachiosaurus brancai* in 1937 (Janensch 1950b).

***Brachiosaurus brancai* Janensch 1914**

The skeleton is a composite. The major part of the skeleton belongs to one single specimen of *Brachiosaurus brancai* recovered from the Middle Saurian Bed at Tendaguru Site S (Map 1). The tail originates from another individual of the same species and similar size found in the Upper

Saurian Bed at Tendaguru Site no (Map 1). In addition, skeletal remains of *Brachiosaurus brancai* excavated in different sites in the surroundings of the Tendaguru hill were used for the mounting, partly original and partly modelled. The presacral vertebral column (cervical, dorsal) and the skull have been replaced by plaster copies modelled from originals. The right shoulder blade, four ribs, and some bones of the left fore-foot have been modelled in plaster according to counterparts on the other body side. Some missing elements were replaced by bones belonging to individuals of the same size, such as the right ilium, the right ischium, and left lower leg. Other



**Spherical Caps:**

$$V = \frac{1}{3} \cdot \pi \cdot h^3 \cdot (3r - h)$$

$$S_A = 2r \cdot h \cdot \pi$$

**Cylinder:**

$$V = \pi \cdot r^2 \cdot h$$

$$S_A = 2r \cdot h \cdot \pi$$

**Truncated Cone:**

$$V = \frac{h \cdot \pi}{3} (r_1^2 + r_1 \cdot r_2 + r_2^2)$$

$$S_A = (r_1 + r_2) \cdot \pi \sqrt{(r_1 - r_2)^2 + h^2}$$

Fig. 1. Lateral view of *Brachiosaurus brancai* showing the different parts taken for the volume and surface area calculations according to the formulas shown at the bottom of the figure

missing items have been replaced by originals (e.g. left femur) or copies of bones from different-sized animals (i.e. 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 haemapophyses (chevrons) are plaster imitations (Janensch 1950b).

### *Dicraeosaurus hansemanni* Janensch 1914

The skeleton of *Dicraeosaurus hansemanni* was recovered from the Middle Saurian Beds at Tendaguru site m (Map 1). The reconstructed skeleton consists mainly of bones from one single individual (specimen m). Some missing bones were replaced by skeletal remains of other individuals of the same species and similar size which were recovered in the Middle Saurian Beds at Tendaguru Site dd (Map 1). Other missing parts of the skeleton have been replaced by plaster copies modelled after the original bones of *Dicraeosaurus hansemanni* or of *D. sattleri*. All original bones included in the mount are remarkably well preserved. Their basic shape has not been altered by taphonomic and diagenetic processes.

The skull has been reconstructed. It was modelled in plaster on the basis of skull bones from Site dd (Janensch 1935a). The most important parts of the vertebral column of specimen m were recovered in their proper anatomical posi-

tion. The proatlas and atlas have not been found (Janensch 1929). The articulated part of the vertebral column comprises all vertebrae from cervical 2 to caudal 19. All of them were included in the skeletal reconstruction. With regard to the tail, only the anterior part was completely recovered (caudal 1 to 19). Except for three disarticulated caudal vertebrae, the posterior tail section (caudal 20 to 76) was apparently already missing when the skeleton was found. The missing items were either supplied by original caudal vertebrae from Tendaguru Site dd or replaced by plaster reconstructions.

The right coracoid and scapula come from Site dd. Their corresponding left counterparts as well as most of the cervical ribs, several left thoracic ribs, and the two sternal plates are plaster reconstructions. The right humerus included in the mount was recovered from the Middle Saurian Beds at locality Q near Kijenere, about 9 km north of Tendaguru hill (Janensch 1925). The left humerus, both forearms, and the five-toed forefeet are also substitutes made of plaster.

As with the shoulder girdle and forelimbs, the pelvic girdle and the hindlimbs of skeleton m have not been completely recovered. The ilium, the pubis, parts of the ischium of the left body side were modelled in plaster according to their preserved counterparts from the right side. With the exception of the two thigh bones, the left tibia,

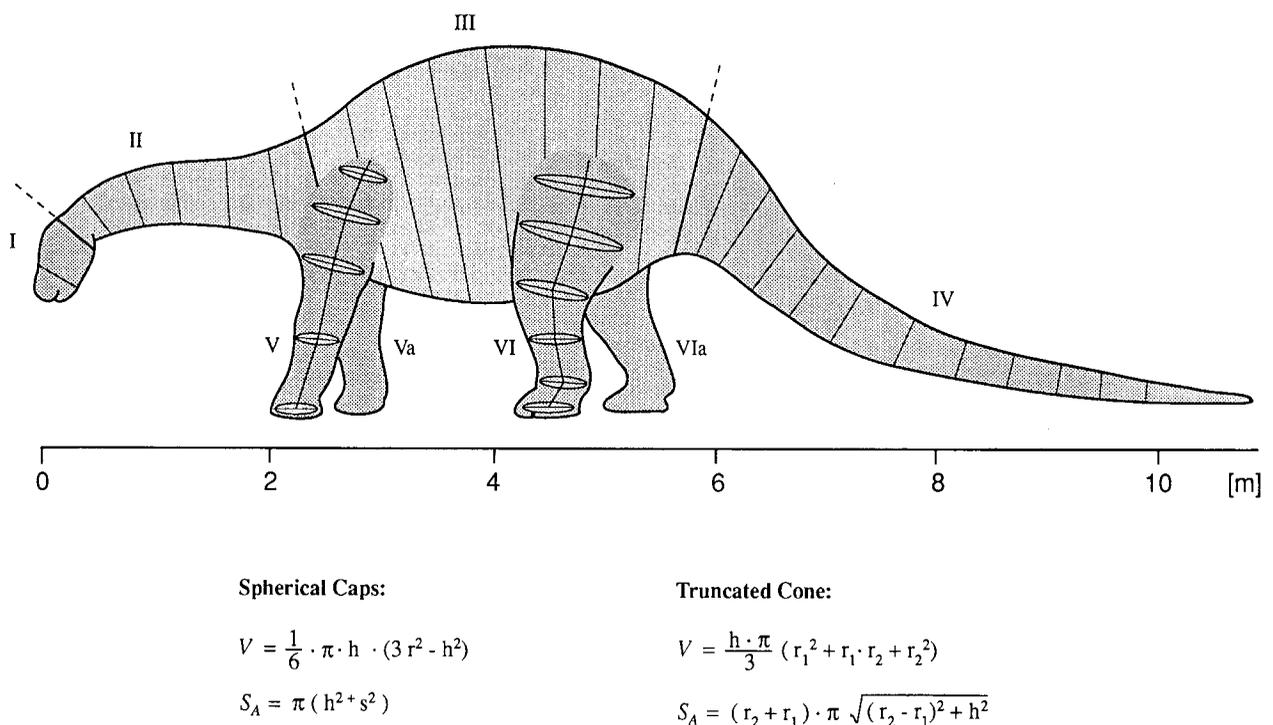
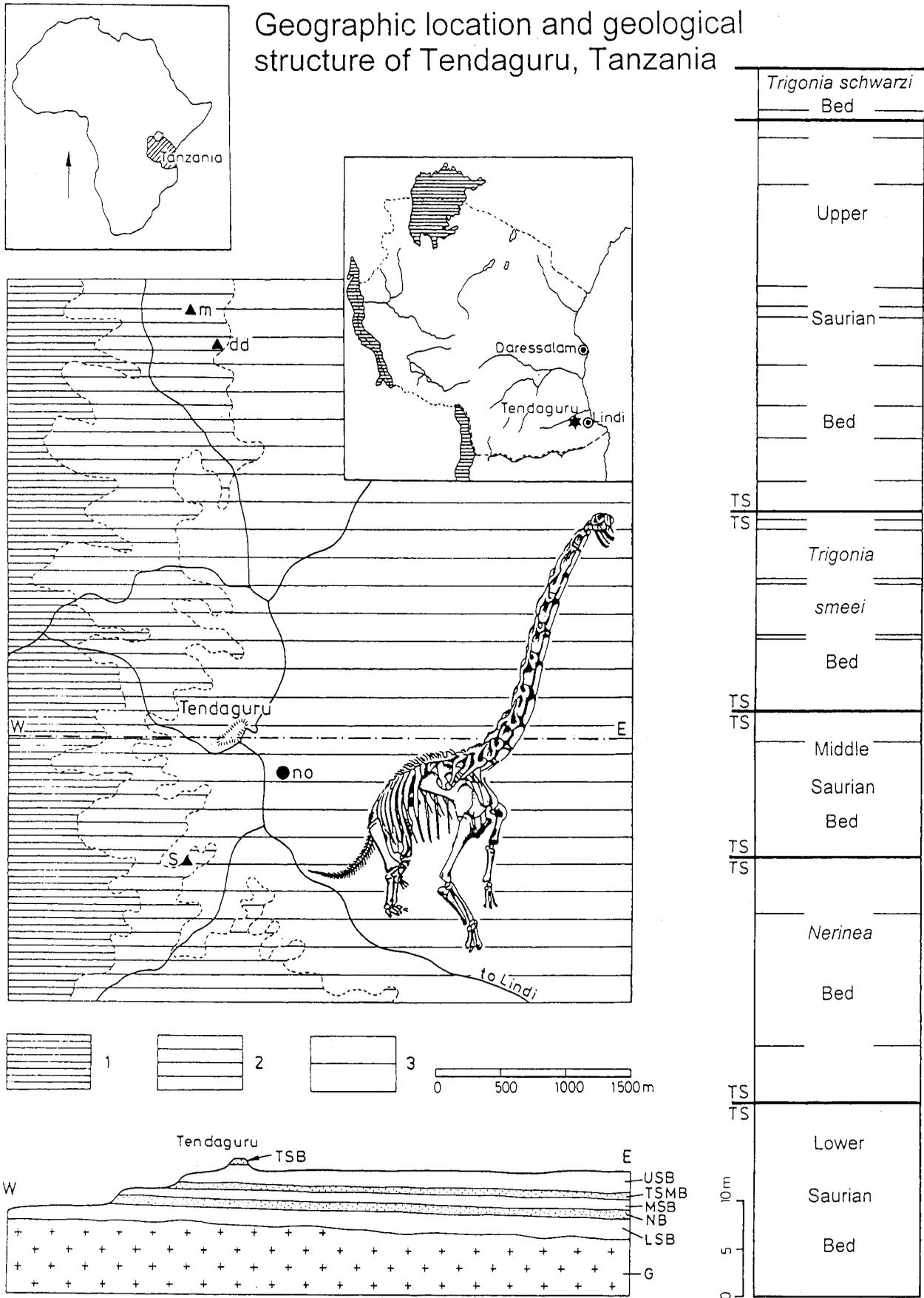


Fig. 2. Lateral view of *Dicraeosaurus hansemanni* showing the different parts taken for the volume and surface area calculations according to the formulas shown at the bottom of the figure

### Geographic location and geological structure of Tendaguru, Tanzania



Map 1. Tendaguru area with geological sections and the location of the sites that produced the major parts of the mounted skeletons of *Brachiosaurus brancai* (sites S, no) and *Dicraeosaurus hansemanni* (sites m, dd). Data from Hennig (1914), Janensch (1914a, b, 1925). For details see Heinrich (1999). **1**, Lower Saurian Bed; **2**, Middle Saurian Bed; **3**, Upper Saurian Bed; **TSB**, *Trigonía schwarzi* Bed; **USB**, Upper Saurian Bed; **TSMB**, *Trigonía smeei* Bed; **MSB**, Middle Saurian Bed; **NB**, *Nerinea* Bed; **LSB**, Lower Saurian Bed; **G**, gneiss; **TS**, Transitional Sands  
 ▲ – Sites in the Middle Saurian Bed, ● – Sites in the Upper Saurian Bed

fibula, and astragalus, all hindlimb elements included in the mount are plaster reconstructions.

Earlier opinions suggested for sauropods an aquatic way of life (e.g., Janensch 1935a, b; Gregory 1951). Today, however, the concept of a land-living life-style for sauropods is widely accepted (e.g., Alexander 1989, McIntosh 1997).

## Results

### The body mass of *Brachiosaurus* was found to be 74.4 t (Tab. 1) and that of *Dicraeosaurus* 12.8 t (Tab. 2).

The parts of *Brachiosaurus* (Tab. 1) show that the thorax occupies nearly (74%) of the body volume, together with the limbs even 80% (80.3%). The neck takes up 15%, the head only

0.20%, nevertheless the tail with 4.4% cannot balance neck + head. This imbalance suggests a vertical, not a horizontal position of the neck (Christian & Heinrich 1998).

In *Dicraeosaurus*, in contrast (Tab. 2), the head is 20 times larger compared to body volume than in *Brachiosaurus*; head + neck (6.4%) are also closer to being balanced by the tail (8.5% body volume). Still, body and limbs make up over 80% (85.2%) of the total volume. We have here two dinosaurs with different volume distributions (Tab. 3): in *Brachiosaurus* the neck takes up a much larger percentage (15%) of the total volume than in *Dicraeosaurus* (6%). This conforms with the reconstruction of a vertical neck in *Brachiosaurus* and a horizontal neck in *Dicraeosaurus*, where it could be balanced by the tail. The body of *Dicraeosaurus* is balanced on the strong hind limbs (8% of total volume).

Table 1

Parts, number of elements, parts of the body, body volumes and surface areas of *Brachiosaurus brancai*. I–XI, see Fig. 1 for identification of body parts; calculations of volume and surface area from formulas at the bottom of Figs 1, 2.

Part	Number of elements	Part of the body	Volume (V) [m <sup>3</sup> ]	Surface Area (S <sub>A</sub> ) [m <sup>2</sup> ]	Surface Area (S <sub>A</sub> ) [%]
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	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
<b>Total</b>	<b>50</b>		<b>74.42</b>	<b>138.9</b>	<b>100.0</b>

Table 2

Parts, number of elements, parts of the body, body volumes and surface areas of *Dicraeosaurus hansemanni*. I–VIa, see Fig. 2 for identification of body parts; calculations of volume and surface area from formulas below table.

Part	Number of elements	Part of the body	Volume (V) [m <sup>3</sup> ]	Surface Area (S <sub>A</sub> ) [m <sup>2</sup> ]	Surface Area (S <sub>A</sub> ) [%]
I	2	Head	0.05	0.7	0.9
II	6	Neck	0.75	4.8	7.1
III	8	Thorax	9.38	20.2	55.9
IV	12	Tail	1.09	8.1	11.7
V	5	Forelimb left	0.26	2.6	2.8
Va	5	Forelimb right	0.26	2.6	2.8
VI	6	Hindlimb left	0.51	3.7	9.4
VIa	6	Hindlimb right	0.51	3.7	9.4
<b>Total</b>	<b>50</b>		<b>12.81</b>	<b>46.4</b>	<b>100.0</b>

Table 3  
Body volume distribution [%] of *Brachiosaurus brancai* and *Dicraeosaurus hansemanni*.

	<i>Brachiosaurus brancai</i>	<i>Dicraeosaurus hansemanni</i>
Head	0.2	0.4
Neck	15.1	5.9
Thorax	74.1	73.2
Tail	4.4	8.4
Forelimbs	3.6	4.1
Hindlimbs	2.6	8.0
<b>Total</b>	<b>100.0</b>	<b>100.0</b>

A comparison with extant long-necked animals (Fig. 3) like the giraffe demonstrates the required pumping power, i.e. blood pressure in the left heart ventricle, in *Brachiosaurus*. In a male giraffe, which can be 5.5 m in height and up to 2000 kg in body mass (Owen 1988), the heart is located 2.4 m above the ground and has to pump a distance of 2.8 m to the brain. Taking the present mounting as scale, this compares to 3.8 m above ground in *Brachiosaurus* and 7.9 m from heart to brain. With a vertical neck position (Christian & Heinrich 1998) the distance from heart to brain increases by about 1.5 m. A more vertical position of the limbs also lifts the heart higher above the ground (Christian et al., this volume). The vertical heart-brain distance in humans is about 22%, in the giraffe 56% of

the total height, whereas in *Brachiosaurus* it is 66%.

From the disparity in body masses a different set of physiological data are deduced (Tab. 4) using allometric formulas given for endotherms.  $O_2$  consumption of *Brachiosaurus* should be about 4 times that of *Dicraeosaurus* from which we calculated a basal metabolic rate of about  $1.4 \times 10^6$  [kJ · (24 h)<sup>-1</sup>] for *Brachiosaurus* and  $0.4 \times 10^6$  [kJ · (24 h)<sup>-1</sup>] for *Dicraeosaurus*. We assume that *Brachiosaurus* has six times the lung volume of *Dicraeosaurus* and a blood volume difference in the same range.

## Discussion

First, we will comment on the methodology used. The main advantage of the photogrammetric procedure is that geometrical calculations can be easily made from each body part (Tabs 1 and 2). With a sufficient size and number of parts and elements, the error of measurement for the total body mass can be kept to a minimum (Wiedemann Wehr 1998, Wiedemann et al. 1999, in press). In contrast, when a measurement error appears with the humerus/femur circumference method, it results directly in a false calculation of the total mass. If a corresponding error is made when determining the volume of the lower

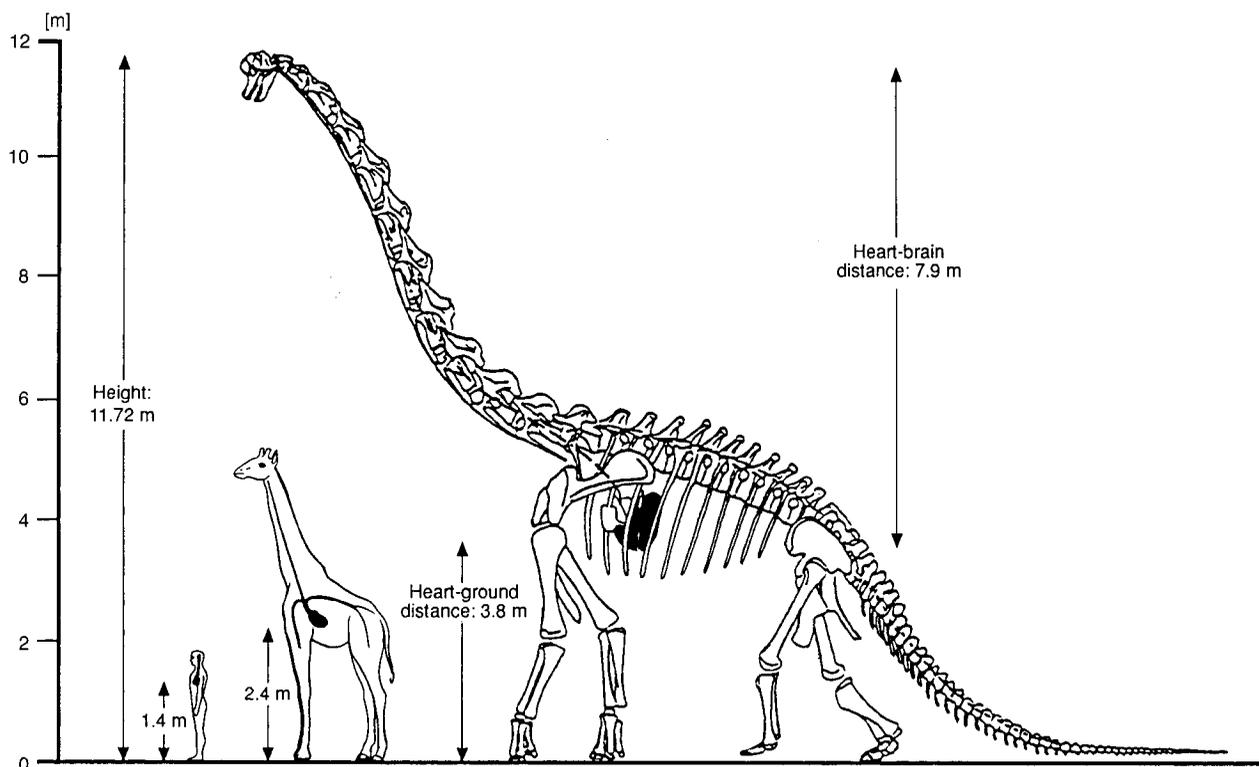


Fig. 3. A schematic view of the major hydrostatic distances acting on the heart and circulatory system in humans, giraffe and *Brachiosaurus brancai*

extremities photogrammetrically, only the element measured is affected. Furthermore, the new data published by Sander (1999, in press) show that the internal bone structure changes during growth, so that bone circumference, for example, might not alter to the same extent as the internal structure. Very recently Henderson (1999) published a similar approach to our photogrammetrical method. In his calculations Henderson (1999) made use of various reconstruction drawings from one or more angles, which were digitalized two-dimensionally. Modelling of primitives was accomplished with a AutoCAD programme applied to truncated cones with ellipsoid sections and other geometric forms. The volume of the geometric primitives was calculated and the primitives of individual body parts and of the animal as a whole were compiled. In comparison to our method in which only circular cone segments were used, resulting in a barrel-formed thorax, a strong point in Henderson's method is the improved mathematical modelling with elliptical sections of truncated cones. His approach also has the advantage that the measurements have been validated on living species. An advantage of our method is the three-dimensional registration of the original object as opposed to Henderson's approach of using solely two-dimensional drawings. Another weakness in our opinion is Henderson's application of reconstruction drawings of questionable geometric quality, whereas in our case precise measurements of the skeleton were made and three-dimensional data applied.

**Basic assumptions.** Besides the new photogrammetric method to estimate body mass, which provides a scientific base for allometric computations, palaeoecological data are of value for the most realistic palaeophysiological reconstruction. Besides body mass, the physical conditions are of the utmost importance in a physiological reconstruction. With these kinds of observations and calculations it must be ensured that the basic physical conditions during the Late Jurassic, like atmospheric pressure, temperature, gravitation and length of the day, were comparable with those existing today in order to justify their applicability. Once these environmental factors affecting the organism are known, it is certainly possible to arrive at specific physiological statements on the probable function of individual systems of organs (Dunham et al. 1989). For this reason it should first be clarified what exactly is known about these basic conditions.

**Atmospheric pressure and components.** There are indications that dramatic changes in the atmosphere of the earth took place during the Paleozoic Age, but no serious alterations in the earth atmospheric oxygen pressure have occurred in the last 250 million years (Gilbert 1996, Gans et al. 1999) as indicated in particular by sedimentology, morphological and structural investigations from palaeobotany and from studies on preserved fossil egg-shells. The ultrastructure of the biological material shows a high similarity to modern structures, especially with regard to the material used, the pore densities and the related diffusion properties according to Fick's Law. When we take a broader look at the oxygen content of the atmosphere in the course of geological history in general, we see dramatic changes in the atmosphere. But during the period in which the dinosaurs lived from 225 to 65 million years ago, the oxygen partial pressure at sea level was comparable to today's values (Gilbert 1996, Gans et al., 1999). This fact is decidedly significant in the efforts to reconstruct, as follows, the physiological capacity of the dinosaurs.

**Temperature.** According to measurements on belemnites, the palaeotemperature for mid-European waters was 20–27 °C in Malm (Upper Jurassic) (Brinkmann 1977, Barron 1983, Sellwood et al. 1994). Therefore, it can be assumed that the global temperature on earth during the Mesozoic Age was approximately 3–4 °C higher than today. It remained above today's mean global temperatures until the Cenomanian/Turonian (C/T) boundary, which is characterized by the "oceanic anoxic event" and a global cooling of several degrees Celsius (Kuypers et al. 1999).

**Gravitation.** According to Dirac's theory published sixty years ago (cited after Economos 1981), we have to assume a change in the gravitational constant of about 1.0–1.5% during the Mesozoic age, a difference that seems to be negligible for the present calculations. Furthermore, cosmologists recently showed that the theory of Dirac might only have an impact during the first moments after the origin of the universe and did not play a role afterwards (personal communication Reeves, Seuil, France).

### **Physiological data**

**Body mass.** The body mass of *Brachiosaurus* determined in our study as 74.4 t is similar to

the estimation of Colbert (1962), whereas those made by Béland & Russel (1980), Anderson et al. (1985), Alexander (1989) and Janensch (1950b) are much lower. Our body mass estimation for *Dicraeosaurus* (12.8 t), in contrast, is in the lower range compared to those estimations given by Janensch (1950b), who assumed a body mass from 10–40 t.

**Body volume distribution.** The volume distributions indicate that nearly 90% of the mass in *Brachiosaurus brancai* is located in the neck and particularly in the thorax (Tab. 3). In *Dicraeosaurus*, in contrast, we see a small neck volume and a large body volume located in tail and hindlimbs. This suggests that *Dicraeosaurus* used his tail and hindlimbs to balance a horizontal neck posture during feeding. Moreover, it is interesting to note that its head volume in percentage of body mass was twice that of *Brachiosaurus*.

Nevertheless, it should be mentioned here that we are especially critical regarding the volume reconstruction of the *Brachiosaurus* neck with about 11 m<sup>3</sup>. This seems to be very high, indeed, and therefore studies using a laser scanner method are in progress to re-evaluate the volume of this part of the sauropod again. The results will be presented in a separate publication.

**Body Surface Area.** The body surface area for the unfolded skin is 138.9 m<sup>2</sup> in *Brachiosaurus* and 46.4 m<sup>2</sup> in *Dicraeosaurus* (Tabs. 1 and 2). If we look at the *Brachiosaurus* surface area distribution in percentages, it is interesting to note that the neck, limbs and tail sum up to 51%

of the total skin (Tab. 1), in contrast to *Dicraeosaurus* with 43% (Tab. 2). These results are important in view of the basic metabolic rate and the heat exchange of large organisms with their environment (Haubold 1990, Carroll 1993). We will return to this point when discussing the respiration and metabolism, because the heat reflected from the ground does not reach the large surface area of *Brachiosaurus* as it does the surface area of the tail and large hindlimbs in *Dicraeosaurus* and probably other giant sauropods (Stevens & Parrish 1999). Thermoregulatory mechanisms must take care of this problem.

**Skeleton and Locomotion.** The major constraints on large size in a terrestrial vertebrate are the limits placed on bone strength and muscle power (Briggs & Crowther 1990, Weishampel et al. 1992). Animal skeletons are scaled allometrically with their body mass, so that the skeletons of large animals are more massive proportionally than those of small animals (Peters 1983, Schmidt-Nielsen 1997). If we assume that dinosaurs had a relatively high metabolic rate – especially in their juvenile phase (see below) –, similar to that of endotherms, for which we have some new strong evidence (Barrick & Showers 1994), we calculated a skeleton mass of 11.4 t for *Brachiosaurus* and 1.7 t for *Dicraeosaurus* (Tab. 4). Ricqlès (1980) has shown that the long bones in dinosaurs are characterized by a Haversian system, resembling that in mammals, rather than showing the more characteristic reptilian structure. In addition, Sander (1999, in press) determined the histology of the long bones, primarily the humerus and femur, from four different sauropod genera from Tendaguru. He found that

Table 4

Physiological data of *Brachiosaurus brancai* and *Dicraeosaurus hansemanni* (Museum für Naturkunde, Berlin) calculated from equations of Bronstein & Semendjajew (1985) and Schmidt-Nielsen (1984), and equating 1 l oxygen consumption during oxydative metabolism (at 0 °C, 760 mm Hg) with 20.083 kJ, according to Schmidt-Nielsen (1984).

			<i>Brachiosaurus brancai</i>	<i>Dicraeosaurus hansemanni</i>
Body mass (Mb)	[kg]		74420	12800
Body surface (SA)	[m <sup>2</sup> ]		138.9	46.4
Skeleton	[kg]	(0.0608 Mb <sup>1.083</sup> )	11480	1706
O <sub>2</sub> consumption	[l · h <sup>-1</sup> ]	(0.676 Mb <sup>0.75</sup> )	3046	814
O <sub>2</sub> consumption	[l · h <sup>-1</sup> · kg <sup>-1</sup> ]	(0.676 Mb <sup>-0.25</sup> )	0.041	0.064
Basal metabolic rate	[kJ · (24 h) <sup>-1</sup> ]		1468148	392342
Lung volume	[l]	(0.063 Mb <sup>1.02</sup> )	5866	974
Tidal volume	[l]	(0.0062 Mb <sup>1.01</sup> )	516	87
Respiration frequency	[min <sup>-1</sup> ]	(53.5 Mb <sup>-0.26</sup> )	3	4.6
Blood volume	[l]	(0.055 Mb <sup>0.99</sup> )	3659	641
Heart weight	[kg]	(0.0058 Mb <sup>0.99</sup> )	386	48
Heart rate	[min <sup>-1</sup> ]	(241 Mb <sup>-0.25</sup> )	14.6	23

the long bone cortex consisted almost exclusively of fibrolammellar bone tissue, suggesting uniformly high growth rates in long bones, comparable to those in mammals and birds. With one exception – a *Barosaurus* from Tendaguru – growth was uninterrupted as well. In all the taxa analysed, remodelling of the bone increases with age, and growth appears to slow down dramatically in individuals approaching their maximum size. According to the data published by Sander (1999), the *Brachiosaurus brancai* on exhibit at the Berlin Museum had not reached his ultimate size. We calculated the ultimate strength in compression of a similar *Brachiosaurus* femur. This femur had a length of 1.86 m, a circumference of 0.8 m and showed a cross-sectional area of 158.5 cm<sup>2</sup> at the middle part of the diaphysis. The cortex alone encompassed an area of 114.8 cm<sup>2</sup>. We found that the ultimate strength in compression for this femur lies around 180–190 t. Compared to a human femur showing a circumference/length ratio of 1:5.6, the ratio in the *Brachiosaurus* is only 1:2.3. Unfortunately, we have no comparable data up to now from *Dicraeosaurus*.

What do we know about their locomotion? Fossil tracks of sauropods like *Brachiosaurus* show that these reptiles – completely different to recent modern reptiles – walked with their feet close to the midline beneath the body, similar to modern elephants (Norman 1991, Lambert 1993). Indeed, such a posture is the only practicable way for animals of this size to walk on dry land, because the force of gravity goes straight these to be the heavy limbs to the broad, rounded feet. We measured the circumferences of the fore- and hindfoot in *Brachiosaurus* and determined 2.20 m and 2.8 m respectively. Therefore, we assume a very slow locomotion due to its body mass, or also due to the limitations exerted by the thermoregulatory and circulatory systems.

**Respiration and Metabolism.** The oxygen from the environment travels via the respiratory tract to the alveoli and through their thin membranes reaches the blood. It is difficult to say whether the type of respiration that existed in *Brachiosaurus* was like that of a mammal or one more resembling that of birds, who have so-called air sacks at their disposal (Perry 1989, 1992). Nevertheless, in *Brachiosaurus* the so-called “dead space” alone – that is the gas volume in the mouth, nose, larynx, and the trachea with the branching bronchial tubes which needs

to be moved during respiration but which does not take part in the gas exchange – already amounts to a volume of about 20 l, compared to 150 ml in humans. Again, assuming a metabolism similar to that of endotherms because of its fast growing rates (Sander 1999, this volume and Sander 1999, in press) and homiothermy probably facilitated due its large body mass (Spotila 1980, Hotton 1980) we applied allometric equations based on data from mammals to calculate presumable organ sizes and physiological parameter (Peters 1983, Withers 1992, Schmidt-Nielsen 1984, 1997). Its lung volume must have been on the scale of 6000 litres and its tidal volume 520 l, with an estimated respiratory rate of around 3 breaths per minute (Tab. 4). From a gravitational point of view a mammalian lung type could create serious problems. The huge *Brachiosaurus* lung causes hydrostatic pressure differences between its top and bottom, amounting to possibly more than 60 mm Hg, which would seriously affect the capillary pressures in the lung.

With a body mass of 74 t, it follows that the *Brachiosaurus* oxygen consumption at rest was about 50 l per min compared to 0.3 litres in humans. Furthermore, we can assume a basal metabolic rate of approximately  $1.47 \cdot 10^6 \text{ kJ} \cdot (24 \text{ h}^{-1})$  (Tab. 4). The estimated amount of food ingested would probably have been less than 1% of the total body weight or approximately 350 kg. In all our calculations we assumed that approximately 70% of the plant intake is water and 30% represents the dry mass, of which 50% was actually absorbed by the gastro-intestinal tract, as is known from living megaherbivores (Owen-Smith 1988). Furthermore, with regards to the posture of its neck and longer forelimbs, it appears that this dinosaur must have been an extremely specialized high browser; the neck was positioned even more vertically than in the restored position (Christian & Heinrich 1998).

**Heart and Circulation.** The capacity of the cardio-circulatory system of *B. brancai* seems to be a critical point per se, as was first described by Hohnke (1973). Our measurements show that the vertical distance from the vault of the cranium to the ground is 11.7 m (Fig. 3) without a completely erect neck and front limbs (see Christian et al., this volume). We calculated a vertical heart-ground distance of 3.80 m and a heart-brain distance of 8.00 m in the mounted skeleton. The carotids were about 9.80 m long. These anatomical-morphological conditions place very tight restrictions on the level of physical exercise.

The blood volume was about 3600 l, the heart weight at least 386 kg with a stroke volume of approximately 17.4 l, and a heart frequency of  $14.6 \text{ min}^{-1}$  (Tab. 4). From our point of view this reconstruction of the cardiovascular system in *Brachiosaurus* with a completely four-chamber heart is the only plausible solution at present. The hypothesis recently published by Choy & Altman (1992) showing several muscle pumps located in the vascular system of the long sauro-pod neck should be rejected in our opinion. The chronological and volumetric coordination of several hearts with this type of pump mechanism would present extremely difficult physiological problems. Assuming a classical four-chambered heart, on the other hand, the left ventricle would have had to generate a pressure of about 600 to 750 mm Hg to surmount the enormous hydrostatic blood column of about 8.0 metres to reach the *Brachiosaurus* brain (Fig. 3). Such a cardiac pressure function is unknown in today's animal world. But in giraffes, 3–4 m tall, blood pressures from 260 to 360 mm Hg have been measured (Hargens et al. 1987). Nonetheless, the giraffe's cerebral blood vessels show a pressure of 100 mm Hg during changing neck positions. This is achieved by the intervention of a rete mirabile. We might assume that *Brachiosaurus*, especially, would have had such a structure as well in the head area.

The veins are a part of the low pressure system and contain by far the greatest portion of the total blood volume, which is usually between 5 and 10% of the body mass – leading in *Brachiosaurus* to a blood volume of about 3,659 litres (Tab. 4). 80%, or 3000 litres, were probably located in the veins, the right heart and the vessels of the pulmonary circulation. Because of the hydrostatic load at the level of the extremities, *Brachiosaurus* must have been equipped with an ingenious "oedema prevention mechanism". Venous valves, muscular venous pumps, extremely strong connective tissue and a thickened basal membrane, as seen in the extremities of giraffes and gazelles (Hargens et al. 1987, Withers 1992), could have developed in *Brachiosaurus*.

Finally, looking at the different organ sizes of *Brachiosaurus* and *Dicraeosaurus* the thoracic-abdominal cavity in both dinosaurs seems to be large enough to carry these organs and a gastrointestinal tract as well which is, surprising enough, in some megaherbivores, for example the African elephant, relatively small (Owen 1988). It can be concluded from these studies that sauro-pods like *Brachiosaurus* were highly specialized

with regards to their metabolism, circulation and temperature regulation. Even the most minor changes in their environment involving climate, food or fluid intake would have had catastrophic consequences for the survival of such huge organisms.

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