Posture and Mechanics of the Forelimbs of *Brachiosaurus brancai* (Dinosauria: Sauropoda)

Andreas Christian[1], Wolf-Dieter Heinrich[1] & Werner Golder[2]

With 5 figures

Abstract

The posture and mechanics of the forelimbs of *Brachiosaurus brancai* were analysed with the help of biomechanical models. Peak forces in the joints due to acceleration of the fraction of body weight carried on the shoulder joints are critical in models with completely straight, column-like limbs and a rigid shoulder girdle. During fast walking, either the forelimbs were flexed at the elbows during the middle of the support phase or the apparently rigid shoulder girdle allowed movements of the shoulder joints relative to the trunk. The overall construction of *Brachiosaurus* was related to an extreme task, browsing high above the ground. Consequently, versatility was very restricted.

Key words: Dinosaurs, sauropods, *Brachiosaurus*, locomotion, limbs, limb posture, functional morphology, biomechanics.

Zusammenfassung

Die Stellung und die Mechanik der Vorderbeine von *Brachiosaurus brancai* wurden mit Hilfe von biomechanischen Modellen untersucht. Kraftspitzen aufgrund von Beschleunigungen des von den Schultern getragenen Anteils der Körpermasse erscheinen in Modellen mit völlig geraden, säulenförmigen Vorderbeinen und einem unbeweglichen Schultergürtel problematisch. Während des schnellen Gehens waren entweder die Vorderbeine in der Mitte der Stützphase in den Ellenbogengelenken gebeugt oder der scheinbar rigide Schultergürtel erlaubte Bewegungen der Schultergelenke relativ zum Brustkorb. Die Gesamtkonstruktion von *Brachiosaurus* war auf die Ausübung einer extremen Tätigkeit, die Nahrungsaufnahme in großer Höhe, ausgerichtet. Die Konsequenz war eine geringe Vielseitigkeit.

Schlüsselwörter: Dinosaurier, Sauropoden, *Brachiosaurus*, Fortbewegung, Extremitäten, Extremitätenstellung, Funktionelle Morphologie, Biomechanik.

Introduction

Brachiosaurus brancai from the Late Jurassic of East Africa is one of the most fascinating dinosaurs. Even though many details of the skeleton are well-known (e.g., Janensch 1935, 1950, 1961), the posture and the life-style of this creature has been disputed for many years. In some early reconstructions, *Brachiosaurus* is shown with semi-extended forelimbs (Janensch 1950; Figs 1, 2, 3A) and even some modern popular books on dinosaurs show *Brachiosaurus* with the elbows protruding to the sides. However, among most recent workers there is little doubt about a fully extended fore- and hindlimb posture in *Brachiosaurus* and other sauropods (Charig 1979, Alexander 1985a, 1989, Bakker 1986, Paul 1987, Weishampel et al. 1990, Fastovsky & Weishampel 1996; Fig. 3B).

One important argument in favour of this idea is the high body weight of sauropods. In geometrically similar shaped animals of different size, body weight increases to the third power of linear dimensions (e.g. body length) whereas maximum muscle forces and strength of bones, tendons and ligaments increase only with the square of linear dimensions. Therefore, larger animals tend to be less forceful with respect to their body weight than smaller animals. This implies that vertebrates of different sizes may have a different limb posture. Generally, the limbs tend to be more extended in larger vertebrates, so that the lever arms of external forces are reduced (McMahon & Bonner 1983, Schmidt-Nielsen 1984, Alexander 1985a, b, 1989,

---

[1] Museum für Naturkunde, Institut für Paläontologie, Invalidenstr. 43, 10115 Berlin, Germany.
[2] Freie Universität Berlin, Universitätsklinikum Benjamin Franklin, Fachbereich Humanmedizin, Radiologische Klinik und Poliklinik, Hindenburgdamm 30, 12200 Berlin, Germany.

Fig. 1. Mounted skeleton of *Brachiosaurus brancai* from the Late Jurassic of Tendaguru (Tanzania) in the Museum of Natural History of the Humboldt University, Berlin. Frontal view, showing the huge semi-extended anterior limbs. The mounting was supervised by W. Janensch and completed in 1937
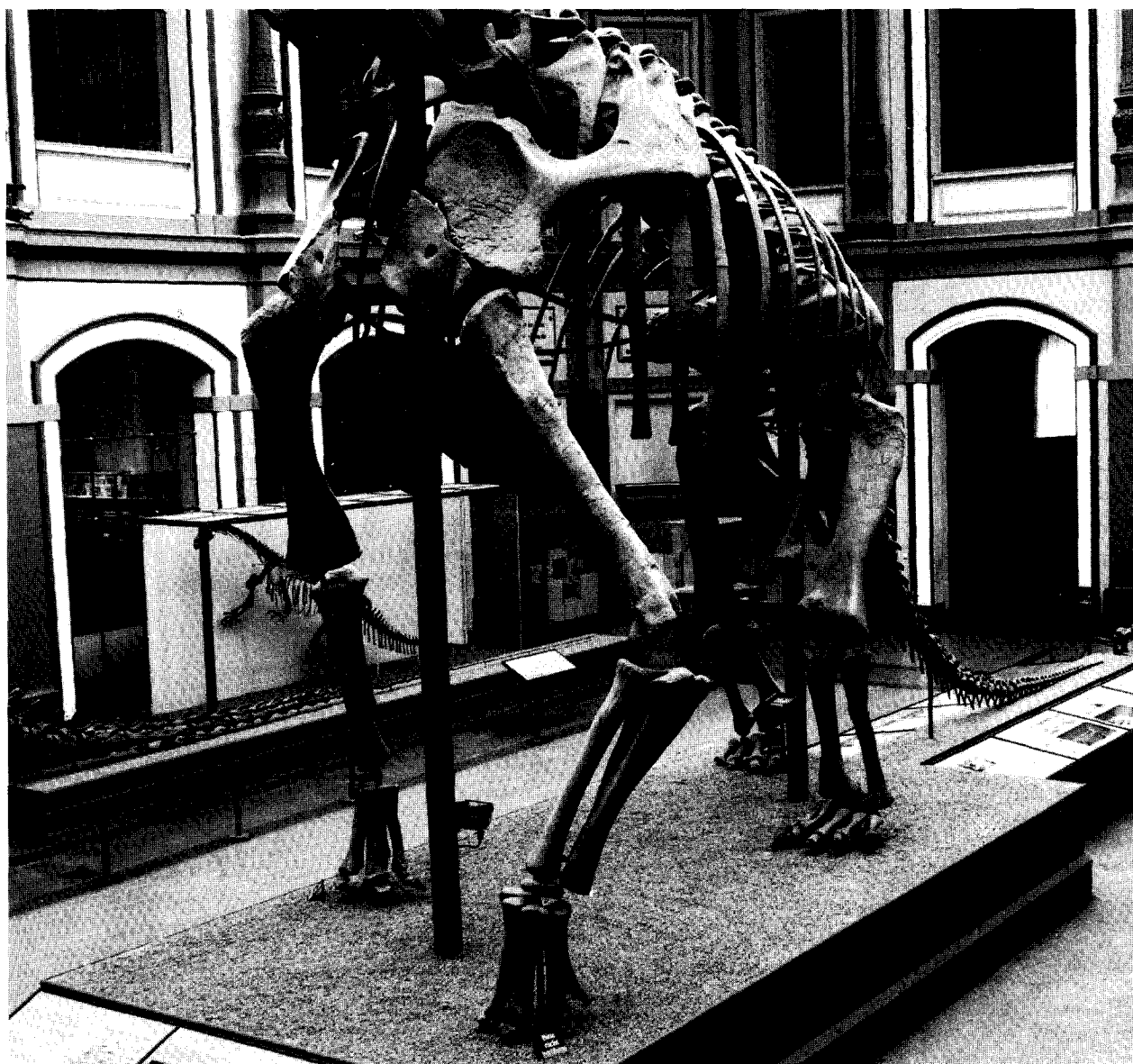
Fig. 2. Mounted skeleton of *Brachiosaurus brancai* from the Late Jurassic of Tendaguru (Tanzania) in the Museum of Natural History of the Humboldt University, Berlin. Anterolateral view, showing details of the shoulder girdle and anterior limbs

Preuschoft & Demes 1985, Biewener 1989a, b, 1990, Steudel & Beattie 1993, Preuschoft et al. 1994, 1998, Christian & Garland 1996). These biomechanical arguments suggest a fully extended limb posture in animals as large as sauropods. In sauropods and other dinosaurs, the usually narrow trackways (Lockley 1991, Thulborn 1990, Lockley & Hunt 1995) indicate that limb movements indeed were restricted to parasagittal planes. Additionally, for most dinosaurs, a mammal-like limb posture can be modelled from skeletal features (Charig 1979, Bakker 1986, Paul 1987, 1988, Weishampel et al. 1990, Fastovsky & Weishampel 1996). Completely straight limbs, however, are not suitable for acceleration, as will be demonstrated below. Therefore, a fully extended limb posture with very little flexion in the elbow and knee joints can be expected only in heavy, graviportal animals

(Coombs 1978). The heaviest recent terrestrial vertebrates are elephants. In walking elephants, under load (during the support phase), the long limb bones remain more or less in line (Gambaryan 1974, Christiansen 1997). Because of the evidence listed above, the idea of fully extended limbs in *Brachiosaurus* is very attractive.

There is less agreement on the dynamics of the shoulder girdle. Whereas some workers favour the idea of a rigid shoulder girdle with a firm fusion between scapulocoracoid and sternum (Janensch 1961), others believe that scapular movement was utilised as a means of forward propulsion (Bakker 1975, Paul 1987, 1988, Christiansen 1997). In general, the function of the shoulder girdle and the transmission of weight force from the trunk onto the forelimbs is not understood in its principles.
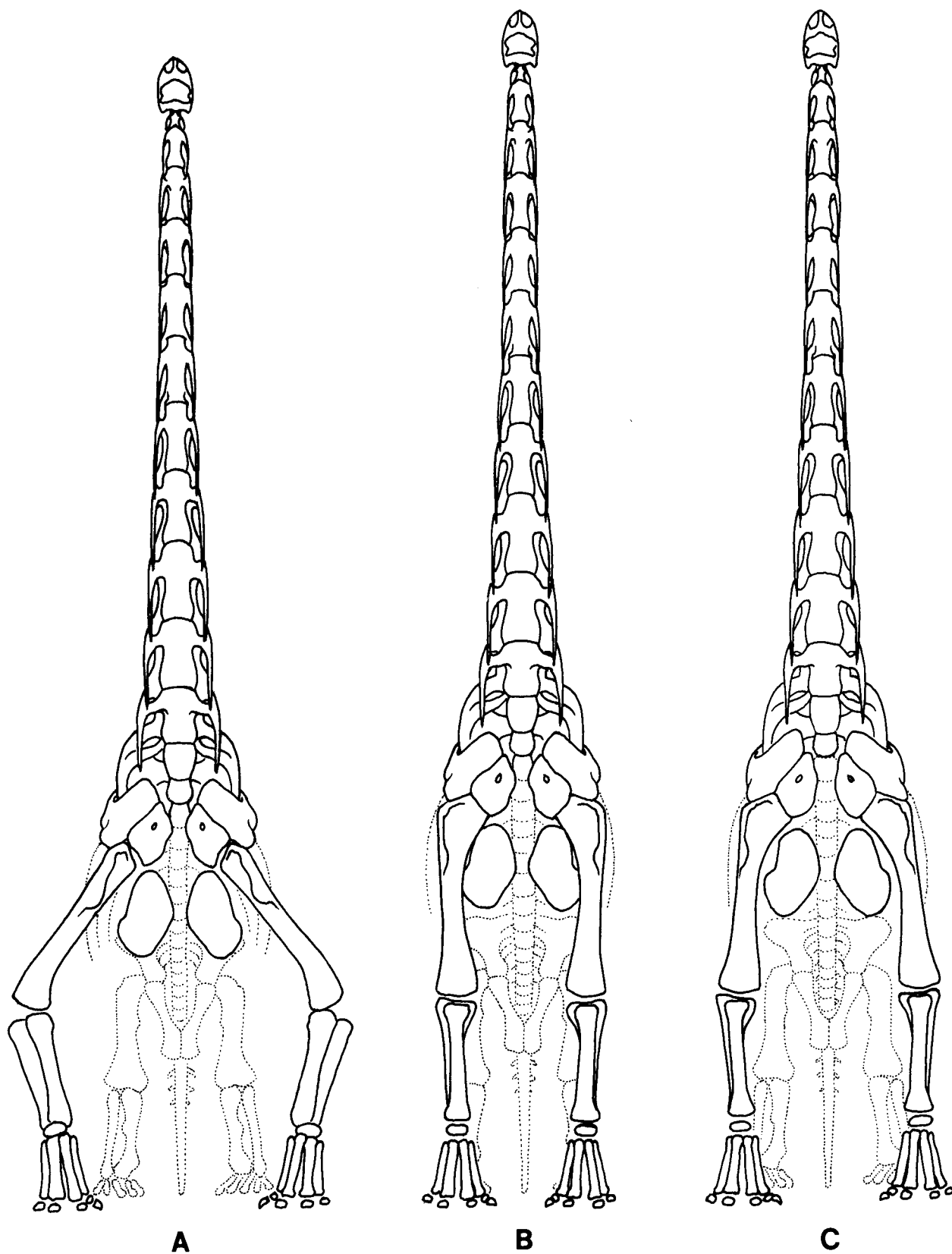
Fig. 3. *Brachiosaurus brancai* reconstructed with a semi-extended forelimb posture according to Janensch (1950) (**A**) and with an extended limb posture (**B**, **C**) with the long limb bones perfectly in line (**C**) or with the ellbow joints flexed slightly (**B**). Both reconstructions, **B** and **C** seem reasonable

In mammals, during locomotion, the effective limb length is changed by flexion and extension in the limb joints. In the forelimbs, peak loads are reduced by movements of the shoulder blades relative to the chest, so that the trajectory of the centre of gravity of the mass carried by the forelimbs is smoother than the trajectory of the shoulder joints. Like sauropods, the biggest living terrestrial animals, elephants, do not utilise true running gaits. Therefore, less mobility is necessary in the shoulder girdle of elephants compared to other mammals (Gambaryan 1974, Haynes 1991). However, the scapula is still suited for moderate movements relative to the underlying ribs, so that the shoulder joints can shift relative to the trunk during limb movements. Additionally, pads of soft tissue under the feet help to cushion impacts due to their compliance. These pads are compressed when the foot is placed on the ground and they extend at the end of the support phase. In addition, the long bones of the forelimbs (including the metacarpals) are not perfectly in line so that some changes in the joint angles are possible under load. These features help to cushion impacts thereby reducing peak forces acting on the limbs during locomotion.

The evidence put forward by Christiansen (1999) indicates very restricted movements in the forelimbs and little vertical displacements in the pectoral girdle under load in a walking *Brachiosaurus* (see also below). This concept, however, is critical with respect to the peak forces that occur in the locomotor apparatus, especially in the joint cartilage, as will demonstrated here. In order to reduce peak forces during fast walking either some flexion in the elbows of *Brachiosaurus* was necessary or the pectoral girdle must have allowed some mobility, so that vertical shifts of the shoulder joints relative to the chest were possible. This result confines the possible reconstructions of *Brachiosaurus*.

Methods

For the biomechanical analysis, body dimensions of *Brachiosaurus* were derived from the exhibited reconstruction in the Humboldt-Museum of Natural History, Berlin, Germany (Figs 1, 2). Despite its composite nature, this skeleton allows a reasonable reconstruction of the body proportions that are relevant for this study because sufficient bone material belongs to a single individual (SII) (Christian & Heinrich 1998). Estimates of the fraction of body mass that was carried on the shoulder joints are based on estimates of the mass distribution in the body of *Brachiosaurus* by Gunga et al. (1995). According to Gunga et al. (1995) the total volume of the body of the Berlin specimen of *Brachiosaurus brancai* was about 74.4 m^2. Gunga et al. (1995) assumed circular cross-sections in neck and tail thereby overestimating segment volumes by about 20% or 30%. Therefore, in this study, the volume of neck and tail was reduced by a factor of 0.8. The lungs and pneumatic cavities in the neck were also taken into account by assuming a mean density of the body of 900 kg/m^3 instead of around 1000 kg/m^3 as usual for many modern vertebrates (Alexander 1989). These reductions in estimated body mass mostly affect the fraction of mass carried on the shoulder joints. For comparison, the distribution of body mass was also derived from the scaled rubber model of *Brachiosaurus* produced by the British Museum of Natural History. If lung cavities were added to the rubber model, both estimates of mass distribution yielded essentially the same results with respect to the load on the forelimbs. The neck was modelled in vertical posture according to the findings of Christian & Heinrich (1998). With these assumptions a total body mass of about 63,000 kg was estimated. Of this mass a fraction m of approximately 20,000 kg was carried on the shoulder joints. To calculate the mass m, most of the mass of the limbs was subtracted from the total body mass because it was not carried on the shoulder and hip joints. Assuming that the lungs were located in the frontal part of the trunk, the centre of gravity of the rest of the body was located closer to the hip joints than to the shoulder joints. Therefore considerably less than half the total body weight was carried on the shoulder joints.

During locomotion, *Brachiosaurus* was assumed to be confined to walking gaits (Thulborn 1990, Christian et al. 1999). In accordance with modern speed estimates in the literature (Alexander 1976, 1989, Thulborn 1990, Christian et al. 1999), a maximum walking speed of 4.5 m/s (16.2 km/h) was estimated for a *Brachiosaurus* the size of the Berlin specimen. At this speed, stride length s was estimated to be twice the height of the hips h above the ground (Alexander 1976, Thulborn 1990). The footfall pattern in a walking *Brachiosaurus* was assumed to be similar to elephants during walking (Gambaryan 1974, own observations).

In order to estimate the strength of the humeri, the internal structure of the humeri of *Bra-*

chiosaurus and other Tendaguru-sauropods was analysed with the help of Computed Tomography scan reconstructions. The procedure and the basic results of this CT-study are described by Golder & Christian (1999). In the Berlin specimen of *Brachiosaurus*, the minimal cross-section in the middle fraction of the humerus (of the specimen SII) is around 29,000 mm^2 (at a distance 970 mm above its distal end). According to CT scan reconstructions, the diaphysis of the humerus of *Brachiosaurus* is nearly solid, with dense bone forming between 80% and 90% of the cross-section (Golder & Christian 1999), so that compressive forces could be distributed over approximately 25,000 mm^2 of dense bone. Compressive forces also acted in the joint cartilage. Forces acting in the cartilage of the shoulder joints can be used to estimate the maximum acceleration of the fraction of mass carried on the shoulder joints, as will be demonstrated below. With the help of the CT-data presented by Golder & Christian (1999) and the dimensions of the shoulder joints of the Berlin specimen of *Brachiosaurus*, it can be estimated that the forces exchanged between scapulocoracoid and humerus had to pass through an area of about 50,000 mm^2 or less ('surface area' of the shoulder joint).

The analysis is based on the following assumptions about a *Brachiosaurus* the size of the Berlin specimen walking at its maximum speed. Some of the data presented below cannot be more than rough estimates. Errors of 10% or even 20% are possible, except in the forelimb lengths, but do not affect the general conclusions regarding forelimb posture and mechanics presented below. Inside the error rage, those values were chosen that gave the least support for the argumentation below.

Forelimb length (from ground to shoulder joint): 4.1 m
(upper arm ≅ 2.15 m; forearm ≅ 1.30 m;
foot ≅ 0.65 m)

Height h of the hips above the ground:	3.5 m
Maximum stride length s (= 2 · h):	7.0 m
Maximum speed of locomotion v:	4.5 m/s
Total body mass:	63,000 kg
Fraction m of the body mass carried on the shoulders:	20,000 kg
Minimum cross-section of dense bone in the humerus:	25,000 mm^2
'Surface area' of the shoulder joint (as defined above):	50,000 mm^2

Walking with fully extended limbs

Walking with fully extended limbs can be described with the help of the model of an "in-verted pendulum" (Mochon & McMahon 1980a, b, Alexander 1980, 1982, Fig. 4). To apply this model to a quadruped, the body of *Brachiosaurus* is modelled as two units, front and hind, each of which is carried by a single pair of limbs. With limbs that remain straight throughout the support phase, hip or shoulder joints move along arcs with the convex sides facing upwards there-
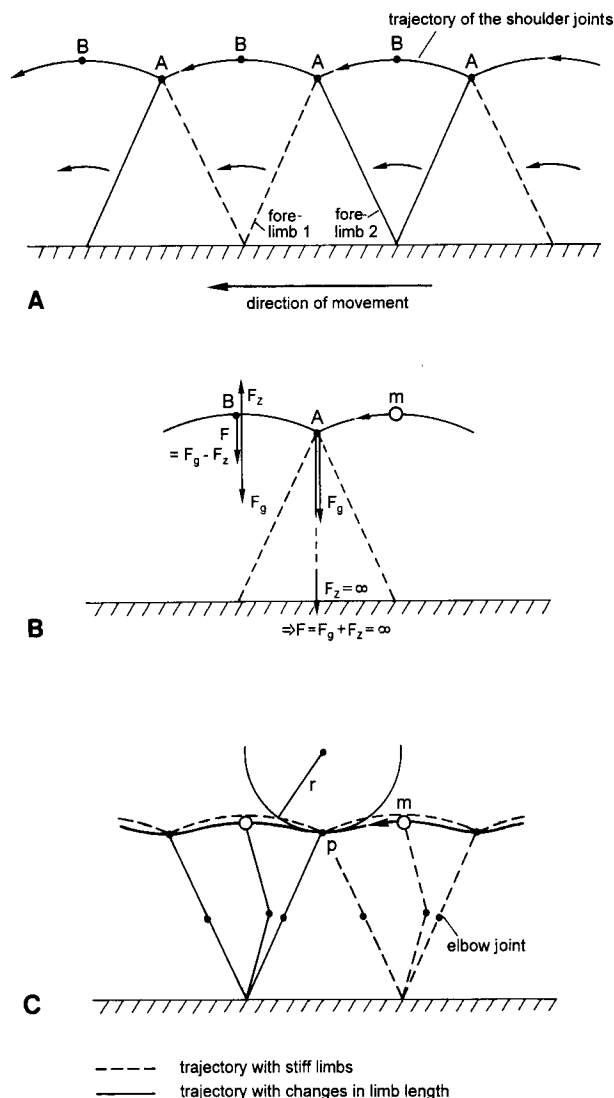

Fig. 4. With the forelimbs remaining straight throughout the support phase, the shoulder joints move along a series of arcs (**Fig. 4A**), thereby shifting the fraction of mass m that is carried on the shoulders from one limb to the other at the transition points A. At the tops of the arcs (B), the weight force F_g of the mass m is reduced due to the downward acceleration at this point resulting in a centrifugal force F_z. At sharp transitions (A) between consecutive arcs, however, the resulting force F would be infinite due to an infinite centrifugal force (equation (1, 2)) (**Fig. 4B**). Therefore, the trajectory of the mass m must be more level, with smooth transitions between the arcs (**Fig. 4C**). This, however, is possible only with changes in effective forelimb length during the support phase by flexion and extension in the joints or, with shifts of the mass m relative to the shoulder joints. (For further explanation see the text) r, radius of curvature of the trajectory of the mass m at point P

by forcing the fractions of mass carried on the shoulder or hip joints, respectively, to perform the same kind of movements.

To calculate the total load on a limb, forces due to acceleration have to be taken into account (Alexander 1982). The loading force F on a pair of limbs is given by:

$$F = m \cdot g + m \cdot a = m \cdot (g + a), \qquad (1)$$

where m = the fraction of body mass carried on the proximal limb joints, g = acceleration due to gravity, and a = acceleration that results from movements of the mass m on its trajectory (Figs 4B, 4C).

During walking at constant speed, at both the highest and the lowest positions along the trajectory, the horizontal acceleration of the mass m can be neglected. In order to calculate the total load on a limb, however, at the tops of the arcs the centrifugal force F_z has to be subtracted from the weight force (Alexander 1982) whereas a centrifugal force has to be added at the transition points of two consecutive arcs (Figs 4B, 4C). The centrifugal force F_z is given by the square of the speed v divided by the radius of curvature r of the trajectory:

$$F_z = v^2/r. \qquad (2)$$

With stiff limbs, the radius of curvature r is zero at the transition points of consecutive arcs (Fig. 4B), so that the total load on the limbs is infinite at these points. Therefore, walking with a fraction m of the body mass fixed to the proximal joints of absolutely stiff limbs is impossible. Thus, in the forelimbs of *Brachiosaurus*, even under axial loading conditions, either considerable flexion in the elbow joints or movements of the shoulder joints relative to the chest were necessary to reduce peak forces during the support phase, as will be demonstrated in more detail in the following.

The weight loaded on a limb results in forces acting in the limb bones. A minimum (compressive) force occurs under axial loading conditions and a homogeneous distribution of the force over the cross-sections of the bones. In the humerus of *Brachiosaurus* (SII), the minimum cross-section of dense bone is about 25,000 mm² (see methods). Assuming a maximum stress (yield stress, stress = force/cross-section) of about 200 MPa (Mega-Pascal, 1 MPa = 1 N/mm²) before breaking (Biewener 1982), each humerus was capable of sustaining a maximum axial compressive force of about 200 N/mm² times 25,000 mm² = 5,000 kN (equivalent to about

500,000 kg) which is 25 times the estimated total weight carried on the shoulder joints (see above) or approximately eight times the total body weight. In the forearm (radius plus ulna), the minimum cross-section of dense bone is not very different from the upper arm (humerus), so that the maximum sustainable compressive force is similar to the humerus. These results are only moderately affected by the limb mass. The limb mass is neglected here (see methods), but moderately increases the stress in the humerus and the stress in the bones of the lower limb.

In extant vertebrates, during regularly occurring activities, the maximum stress in bones, tendons and ligaments, is much lower than the yield stress. The ratio between the yield stress and the maximum occurring stress is called safety factor. Independent of body size, the safety factor is around three (between two and four) in bones (Alexander 1985, Biewener 1989a, b, 1990). Assuming a safety-factor of about 3 in the humerus of *Brachiosaurus*, as well, the maximum compressive stress that is likely to have occurred during regular movements was approximately 70 MPa (in accordance with Alexander et al. 1990), so that the maximum compressive force on each humerus was about 70 N/mm² times 25,000 mm² = 1,750 kN. With an angle of about 51° formed by both forelimbs at the transition points of consecutive arcs of the trajectory of the mass m carried on the shoulder joints (Fig. 4), the total vertical force exerted on the shoulder joints could have been as high as 3,500 kN or between 17 and 18 times the weight of the mass m. Then, the acceleration a of the mass m could have been between 16 and 17 times the acceleration due to gravity g (equation (1)) without evoking undue stresses in the humeri. Therefore, the minimum radius of curvature r of the trajectory of the mass m could have been as short as 13 cm (equation (2), Fig. 4).

In cartilage, however, the maximum sustainable stress is much lower than in bones (Yamada 1970, Alexander 1985). In each shoulder joint, almost the entire compressive force must have passed through an area of about 50,000 mm² or less (see methods). Assuming a yield stress of the cartilage of 20 MPa or less (Yamada 1970) and a safety factor of 3 for regularly occurring activities, the maximum stress in the joint cartilage could not exceed 7 MPa (see also Alexander (1985)). Then, the maximum force acting on each shoulder joint of *Brachiosaurus* is expected to have been less than 350 kN. At the transition points between the arcs of the trajectory of the

mass m carried on the shoulders, the total force acting on both forelimbs could not have been much higher than about 600 kN, which is just three times the weight force of the mass m. The corresponding minimal radius r of curvature of the trajectory of the mass m is about one metre or approximately a quarter of forelimb length (equation (2)).

Due to the action of muscles spanning over the shoulder joint, the compressive force in the cartilage must have been considerably greater than in the simple model presented above (see e.g., Preuschoft 1989, Biewener 1989a), so that the trajectory of the mass m carried on the shoulders must have been even more level.

So far, the front part of the body has been regarded as an isolated unit. Forces, however, could have been transmitted to the hindlimbs via the trunk, thereby reducing peak forces on the shoulders and increasing the load on the hips. During the critical phase of the stride discussed here, when the load on the shoulders is shifted from one limb to the other, however, only one hindlimb was placed on the ground. In the Berlin specimen of *Brachiosaurus*, compared to the shoulder joint, the surface area of the hip joint appears somewhat larger (by a factor of roughly 1.5). Given the higher fraction of body mass carried on the hip joints (see methods), however, a shift of force from the shoulders to a single hip joint appears unlikely.

A second problem with a model of walking with limbs that are kept at a constant length during the support phase is the fluctuation of potential energy. In this model of a *Brachiosaurus* at maximum walking speed, the mass m carried on the shoulders rises approximately 0.4 m during the first 1.75 m of a step and drops by the same height difference during the second 1.75 m of each step. This is equivalent to carrying the mass m uphill and then downhill at an average slope of about 13° during each step. Although most of the external energy needed to accomplish these changes in height could be regained by shifting potential energy to kinetic energy and back, a certain fraction of this energy would be lost due to internal friction (Taylor 1977, Alexander 1982).

In any case, animals of the size of *Brachiosaurus* must have largely reduced peak forces and energy fluctuations during locomotion (Alexander 1985a, b, 1989, Biewener 1989, Preuschoft et al. 1994, 1998, Langman et al. 1995). Therefore, it can be assumed that the fractions of body mass carried on shoulders and hips, respectively,

moved along smooth trajectories with maximum shifts in height that probably were less than 0.1 m. Therefore, as in extant vertebrates, *Brachiosaurus* had to change the effective limb length during the support phase. With overlapping support phases of both limbs of a pair, one limb can shorten while the opposite limb extends when the load is shifted from one limb to the other resulting in a smooth transition between the arcs along which the shoulder and hip joints move (Fig. 4C). Alternatively, during the support phase, the centre of gravity of the fraction of body mass carried by a pair of limbs might have changed its position relative to the hip or shoulder joints, respectively, thereby reducing the peak forces transmitted to the limbs.

Forelimb posture in a walking *Brachiosaurus*

In the hindlimbs of *Brachiosaurus*, during the support phase, the effective limb length probably changed by moderate flexion and extension of the ankle joints possibly together with compression and extension of soft pads under the feet, as in elephants. In the forelimbs, however, the metacarpals were nearly vertical and thick pads of soft tissue under the feet were not present (Christiansen 1997). Consequently, without flexion and extension at the elbows, effective limb length would have remained nearly constant during the support phase. Assuming a height change of not more than 0.1 m in the trajectory of the centre of gravity of the mass m carried on the shoulder joints (see above), flexion and extension at the elbows must have resulted in a change in limb length of 0.2−0.3 m during each support phase. To cover this height difference, the angle formed between the upper arm and the forearm would have been 145° or less at the middle of the support phase if the limb was fully extended at maximum excursions. The change in effective limb length depends on the cosine-function of the angle between upper and lower limb (and to a lesser degree on the angle formed between the lower limb and the foot), whereas the lever arms of external forces increase approximately with the sine-function of this angle. At angles close to 180°, the sine-function changes much more rapidly than the cosine-function (see also Preuschoft & Demes 1985). Therefore, moderate flexion of straight or nearly straight limbs has little effect on limb length but leads to a considerable increase in the lever arms of external forces (Fig. 5). With the ground-reaction-force di-

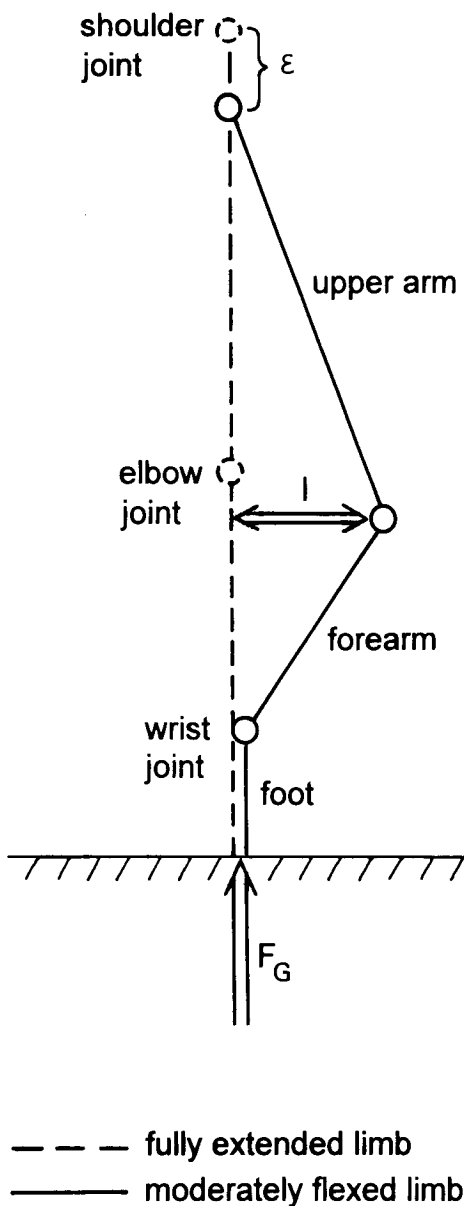— — — fully extended limb

———— moderately flexed limb

Fig. 5. Moderate flexion in the elbow joint results in little change of the effective limb length, but in considerable increase of the lever arms of the ground reaction force. F_G, ground-reaction-force (for simplicity F_G is assumed to point exactly upwards so that only the lever arm at the elbow joint is of importance). ε, maximum change in limb length during extension

rected toward the shoulder joint, an angle of 145° between upper arm and forearm would have increased the lever arm of the ground-reaction-force at the elbow by at least 0.3 m (depending on the angle formed between the lower limb and the foot) which is about half the maximum lever arm of the extensors of the elbow. An angle of 160° between upper arm and forearm would have resulted in only a small increase in the external torques at the joints, the maximum length change of the forelimbs, however, would have been less than 0.07 m. Therefore, it is doubtful whether *Brachiosaurus* used flexion

at the elbow during the middle of the support phase in order to accomplish the changes in limb length necessary to reduce peak forces on the limbs.

The CT-analyses of the humeri of several Tendaguru-sauropods conducted by Golder & Christian (1999) showed that in all of these dinosaurs forces were transmitted mainly through the broadened middle fractions of the proximal epiphyses of the humeri. The overall dimensions of the long forelimb bones (Christiansen 1997) and the thick walls of the shaft (see above) indicate an approximately axial loading of the long forelimb bones. These results are in accordance to the assumption of a fully extended limb posture with the humerus in line with ulna and radius.

As argued above, with little compliance in the forelimbs and a straight alignment of the long forelimb bones throughout the support phase, the shoulder joints must have changed by a vertical distance of 0.2—0.3 m relative to the centre of gravity of the fraction of body mass m carried on the shoulder joints during each step. If and how this might have been possible will be the subject of a further study.

Activities different from straight forward locomotion at constant speed

Any animal has to fulfil tasks other than walking forwards at constant speed. From time to time changes in speed and direction of locomotion are inevitable. In addition, reproduction, feeding, defence, and other activities might induce stresses in some parts of the locomotor system in excess of those that occur during locomotion. During such activities bones might have to sustain bending moments that induce stresses that are much higher than during regular locomotion.

The long limb bones of *Brachiosaurus* are strong enough for sustaining some additional stress (see above). Compared to other vertebrates, however, especially in the forelimb there was little potential for strenuous activities. The overall construction of *Brachiosaurus* with its very long and vertical neck and relatively long forelimbs is related to an extreme task: browsing high above the ground (Christian & Heinrich 1998). Probably in contrast to many other sauropods, the neck was regularly kept in a vertical position and did not move much from side to side (Christian & Heinrich 1998), so that only moderate torques were transmitted to the trunk. Therefore, there was no need for a very long tail

that could have counteracted such neck movements, as in many other sauropods, and the forelimbs did not have to exert ground reaction forces with high horizontal components which occur if neck and tail are shifted to the side. Indeed, compared to sauropods that are likely to have had a less vertical neck posture, the forelimbs of *Brachiosaurus* are less compact (Christiansen 1997).

Even with some flexibility in the pectoral girdle, the forelimbs of *Brachiosaurus* are not suited for producing high impulses since the maximum change in length under heavy loads was short. Not only forward and backward accelerations (Christiansen 1997) but also torques necessary to turn the body to the side must have been produced mostly by the hindlimbs. Turning was less of a problem than in sauropods with a more horizontal neck posture and a very long tail, such as *Diplodocus*, because in *Brachiosaurus* the body mass was concentrated closer to the centre of gravity resulting in a reduced moment of inertia about the vertical axis through the centre of gravity. Therefore, with one hindlimb pushing forward and the other hindlimb pushing backward the torque necessary to turn the body to the side could have been produced, possibly with the addition of sideways movement of the tail. The forelimbs probably have been involved in turning by producing some sideways forces. However, with straight and rather rigid forelimbs and fully extended hindlimbs, *Brachiosaurus* was not capable of high acceleration or swift turns. Even lying down with the trunk resting on the substrate and rising again must have pushed *Brachiosaurus* to its limits — if this was ever done — as will be demonstrated in the following.

Assuming a more or less vertical ground reaction force, during lying down and standing up, the outlever/inlever ratio (ratio between the lever arm of the external force and the lever arm of the muscles) at the elbow joints would have been at least 2.5. Thus, the compressive force acting on each elbow joint would have been more than 350 kN. In flexed posture, the surface of articulation in the elbow joint was 50,000 mm^2 or less, so that the stress in the joint cartilage was at least 7 MPa which is rather high for cartilage (Yamada 1973, Alexander 1985, see above). The energy needed to lift the centre of mass over a height difference of about 3 m is approximately 1,850 kJ. With the maximum performance of striated vertebrate muscle contracting slowly through its entire range being 0.22 kJ/kg muscle

(Alexander & Bennet-Clark 1977), at least 8,400 kg of muscle mass or one seventh of the total body mass was necessary to lift the body of *Brachiosaurus* from a lying to a standing position. The same result, the mass of active muscle being at least one seventh of the total body mass, calculated for an average sized human (70—75 kg) would be equivalent to rising from a prone to a standing position carrying a backpack of 150 kg mass. If *Brachiosaurus* ever lay down fully, rising must have been a strenuous activity. A special technique might have been used in order to reduce peak forces. The hindlimbs might have been flexed first during lying down and the forelimbs were extended first during rising, so that the load on the flexed forelimbs was reduced. The tail might have served as a fifth limb. In the light of these considerations it appears doubtful whether *Brachiosaurus* ever reared up on its hindlimbs.

Conclusions

The analysis presented above is inevitably based on many assumptions. However, even with considerable errors in some of the estimates used for the calculations, the general conclusions are not significantly affected.

The locomotor capability of *Brachiosaurus* was very restricted. Its overall construction was related to an extreme task, browsing high above the ground. Tasks different from standing and straight forward locomotion must have been very strenuous for *Brachiosaurus*. Sharp changes of direction were impossible not only for the whole animal but for large body parts like the limbs or the neck, as well. All movements of *Brachiosaurus* that involved considerable fractions of the total body mass must have been slow and smooth, giving the moving animal a somewhat fluid appearance. However, even in an animal the size of *Brachiosaurus*, some mobility in both pairs of limbs is necessary in order to fulfil basic tasks like accelerating or turning to the side. During forward walking at constant speed, either the forelimbs had to be flexed to some degree during the support phase, or the shoulder girdle was mobile enough to allow marked movements of the shoulder joints relative to the chest so that peak forces acting on the limbs were reduced. Additional work on the mechanics of the pectoral girdle is necessary for a better understanding of the dynamics of *Brachiosaurus*.

Acknowledgements

References

Alexander, R. McN. 1976. Estimates of speeds of dinosaurs. — Nature **261**: 129–130.
– 1980. Optimum walking techniques for quadrupeds and bipeds. — Journal of Zoology, London **192**: 97–117.
– 1982. Locomotion of Animals. 163 pp., Blackie, Glasgow and London, UK.
– 1985a. Mechanics of posture and gait of some large dinosaurs. — Zoological Journal of the Linnean Society **83**: 1–25.
– 1985b. Body Support, Scaling and Allometry. *In* Hildebrand, M., Bramble, D. M., Liem, K. F. and Wake, D. B. (eds.). Functional Vertebrate Morphology: 26–37, Harward University Press, Cambridge, USA.
– 1989. Dynamics of Dinosaurs and Other Extinct Giants. 167 pp., Columbia University Press, New York.
Alexander, R. McN. & Bennet-Clark, H. C. 1977. Storage of elastic strain energy in muscle and other tissues. — Nature **265**: 114–117.
Alexander, R. McN., Ker, R. F. & Bennett, M. B. 1990. Optimum stiffness for leg bones. — Journal of Zoology, London **222**: 471–478.
Bakker, R. 1975. Dinosaur renaissance. — Scientific American **232** (4): 58–78.
– 1986. The Dinosaur Heresies: New Theories Unlocking the Mystery of the Dinosaurs and Their Extinction. 482 pp., William Morrow, New York.
Biewener, A. A. 1982. Bone strength in small mammals and birds: Do safety factors change with body size? — Journal of experimental Biology **98**: 289–301.
– 1989a. Scaling body support in mammals: limb posture and muscle mechanics. — Science **245**: 45–48.
– 1989b. Mammalian terrestrial locomotion and size. — Bioscience **39** (11): 776–783.
– 1990. Biomechanics of mammalian terrestrial locomotion. — Science **250**: 1097–1103.
Charig, A. J. 1979. A New Look at the Dinosaurs. 160 pp., Heinemann, London.
Christian, A. & Garland, T. 1996. Scaling of limb proportions in monitor lizards (squamata: varanidae). — Journal of Herpetology **30** (2): 219–230.
Christian, A. & Heinrich, W.-D. 1998. The neck posture of *Brachiosaurus*. — Mitteilungen des Museums für Naturkunde, Berlin, Geowissenschaftliche Reihe **1**: 73–80.
Christian, A., Müller, H. G., Christian, G. & Preuschoft, H. 1999. Limb swinging in elephants and giraffes and implications for the reconstruction of limb movements and speed estimates in large dinosaurs. — Mitteilungen des Museums für Naturkunde, Berlin, Geowissenschaftliche Reihe **2**: 81–90.
Christiansen, P. 1997. Locomotion in sauropod dinosaurs. — Gaia **14**: 45–75.
Coombs, W. P., Jr. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. — The Quarterly Review of Biology **53**: 393–418.
Fastovsky, D. E. & Weishampel, D. B. 1996. The Evolution and Extinction of the Dinosaurs. 460 pp., Cambridge University Press, Cambridge, USA.

Golder, W. & Christian, A. 1999. CT findings in extremity bones of Tendaguru saurians. — Investigative Radiology, in review.
Gambaryan, P. P. 1974. How mammals run. 367 pp., John Wiley & Sons, New York.
Haynes, G. 1991. Mammoths, Mastodonts and Elephants. Biology, Behavior, and the Fossil Record. 413 pp., Cambridge University Press, Cambridge.
Janensch, W. 1935. Die Schädel der Sauropoden *Brachiosaurus, Barosaurus* und *Dicraeosaurus* aus den Tendaguru-Schichten Deutsch-Ostafrikas. — Palaeontographica, Supplement **VII**, 1 Reihe, Teil 2, Lieferung 1: 145–248.
– 1950. Die Skelettrekonstruktion von *Brachiosaurus brancai*. — Palaeontographica, Supplement **7** (1), 3, 2: 95–103.
– 1961. Die Gliedmaßen und Gliedmaßengürtel der Sauropoden der Tendaguru-Schichten. — Palaeontographica, Supplement **7** (1), 3: 177–235.
Langman, V. A., Roberts, T. J., Black, J., Maloiy, G. M. O., Heglund, N. C., Weber, J.-M., Kram, R. & Taylor, C. R. 1995. Moving cheaply: energetics of walking in the African Elephant. — Journal of Experimental Biology **198**: 629–632.
Lockley, M. G. 1991. Tracking Dinosaurs: A New Look at an Ancient World. 238 pp., Cambridge University Press, Cambridge, United Kingdom.
Lockley, M. G. & Hunt, A. P. 1995. Dinosaur Tracks and Other Fossil Footprints of the Western United States. 338 pp., Columbia University Press, New York.
McMahon, T. A. & Bonner, J. T. 1983. On Size and Life. 255 pp., Scientific American Books, W. H. Freeman, New York.
Mochon, S. & McMahon, T. A. 1980a. Ballistic walking. — Journal of Biomechanics **3**: 49–57.
– 1980b. Ballistic walking: an improved model. — Mathematical Biosciences **52**: 241–260.
Paul, G. S. 1987. The science and art of restoring the life appearance of dinosaurs and their relatives. *In* Czerkas, S. & Olsen, E. (eds.). Dinosaurs Past and Present: 4–49, Natural History Museum of Los Angeles County, Los Angeles, USA.
– 1988. The brachiosaur giants of the Morrison and Tendaguru with a description of a new subgenus, *Giraffatitan*, and a comparison of the word's largest dinosaurs. — Hunteria **2** (3): 1–14.
Preuschoft, H. 1989. The external forces and internal stresses in the feet of dressage and jumping horses. — Zeitschrift für Säugetierkunde **54**: 172–190.
Preuschoft, H. & Demes, B. 1985. Influence of size and proportions on the biomechanics of brachiation. *In* Jungers, W. L. (ed.). Size and scaling in primate biology: 383–399, Plenum Press, New York.
Preuschoft, H., Witte, H. Christian, A. & Recknagel, S. 1994. Körpergestalt und Lokomotion bei großen Säugetieren. — Verhandlungen der Deutschen Zoologischen Gesellschaft **87** (2): 147–163.
Preuschoft, H., Günther, M. M. & Christian, A. 1998. Size dependence in prosimian locomotion and its implications for the distribution of body mass. — Folia primatologica **69** (suppl.1): 60–81.
Schmidt-Nielsen, K. 1984. Scaling: Why is Animal Size so Important? 241 pp., Cambridge University Press, Cambridge, United Kingdom.
Taylor, C. R. 1977. The energetics of terrestrial locomotion and body size in vertebrates. *In* Pedley, T. J. (ed.). Scale Effects in Animal Locomotion: 127–141, Academic Press, London.
Thulborn, R. A. 1990. Dinosaur Tracks. 410 pp., Chapman and Hall, London.
Steudel, K. & Beattie, J. 1993. Scaling of Cursoriality in Mammals. — Journal of Morphology **217**: 55–63.
Weishampel, D. B., Dodson, P. & Osmólska, H. (eds.) 1990. The Dinosauria. 733 pp., USA, University of California Press, Berkeley.
Yamada, H. 1973. Strength of Biological Materials. 297 pp., R. Krieger Publishing Company, New York, USA.