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The Neck Posture of *Brachiosaurus brancai*

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With 3 Figures

Abstract

Compressive forces acting on the intervertebral discs along the neck of *Brachiosaurus brancai* from the Late Jurassic of Tendaguru are calculated for different neck postures. The distribution of compressive forces along the neck is compared to the distribution of the cross-sectional areas of the intervertebral discs. Neck postures in which the pattern of compressive forces does not match the pattern of cross-sectional areas of the intervertebral discs are rejected. The neck posture of *Brachiosaurus brancai* must have been nearly vertical. A more inclined neck posture can only occasionally have been kept. Therefore, *Brachiosaurus brancai* appears to have been an extremely specialized high browser. In the same area, different sized individuals fed in different heights instead of each individual exploiting an extended vertical feeding range.

Key words: Dinosauria, *Brachiosaurus*, reconstruction, biomechanics, functional morphology, feeding behaviour

Zusammenfassung

Die Halsstellung von *Brachiosaurus brancai* aus dem Oberjura von Tendaguru in Ostafrika wird untersucht. Die auf die Bandscheiben wirkenden Druckkräfte entlang des Halses werden für verschiedene Halsstellungen berechnet. Die Verteilung dieser Druckkräfte entlang des Halses wird mit der Verteilung der Querschnittsflächen der Bandscheiben verglichen. Halsstellungen, bei denen die Form der Kurve für die Druckkräfte nicht mit der Form der Kurve für die Querschnittsflächen übereinstimmt, werden verworfen. Es zeigt sich, daß *Brachiosaurus brancai* seinen Hals nahezu senkrecht getragen haben muß. Eine deutlich gegen die Vertikale geneigte Halsstellung kann nur gelegentlich eingenommen worden sein. Daher scheint *Brachiosaurus brancai* hoch spezialisiert für eine Nahrungsaufnahme in extremen Höhen gewesen zu sein. Im selben Gebiet haben unterschiedlich große Individuen verschiedene, aber eng begrenzte Höhenbereiche der Vegetation ausgebeutet.

Schlüsselwörter: Dinosauria, *Brachiosaurus*, Rekonstruktion, Biomechanik, Funktionsmorphologie, Freßverhalten

Introduction

Many sauropod dinosaurs are characterized not only by a very large body size but also by very long necks (e.g. McIntosh 1990, 1997). Whereas the necks of cetiosaurids and camarasaurids are comparatively short, the necks of diplodocids like *Diplodocus* or *Barosaurus* reach extreme length (e.g. Bonaparte 1986, McIntosh 1990, 1997). In *Brachiosaurus*, the neck comprises about 2/3 of the presacral vertebral column (Janensch 1950a, b).

The cervical vertebrae might be arranged in different, yet reasonable ways, leading to considerable differences in the neck posture (Janensch 1950b, Bakker 1987, Paul 1988, Frey & Martin 1997). In many reconstructions of *Brachiosaurus*, the neck is inclined forward forming an angle of about 30° with the vertical similar to the neck posture often seen in giraffes (Janensch 1950b). In contrast, some workers favour the idea of a rather vertical, S-shaped neck posture (Bakker 1987, Paul 1988).

The posture of the neck reflects its utilization. The neck utilization in sauropods, however, is controversial. The neck of *Brachiosaurus* might have been used primarily for browsing high above the ground as in a giraffe (Dodson 1990) or, in a different model, a long neck could have provided a large volume of feeding space by sweeping both laterally and vertically (Martin 1987). While the first mechanism seems reasonable especially in forms like *Brachiosaurus* with long forelimbs; the second mechanism seems likely in forms like *Diplodocus* with short forelimbs and apparently more flexible necks.

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A very long neck, however, causes physical problems that might lead to constrictions in its use. The transversospinalis muscles of *Diplodocus carnegii* were barely able to lift the neck from a horizontal to a vertical position, as demonstrated by Alexander (1985). Even with the possible help of the longissimus and iliocostalis muscles, lifting the neck seems to have been a strenous activity for this dinosaur. Another serious problem concerns the blood pressure required to perfuse the brain of an animal with an elevated head (Hohnke 1973, Seymour 1976, Hargens et al. 1987, Pedley 1987, Dodson 1990, Fastovsky & Weishampel 1996).

To avoid dangerous permanent stress on the cardiovascular system it has been suggested that sauropods might have fed habitually at moderate levels browsing very high above the ground only during short periods (Dodson 1990). Yet, we cannot exclude the possibility of mechanisms that might have allowed sauropods to cope with physiological problems associated with a highly elevated head (for giraffes see: Dagg & Foster 1976, Hargens et al. 1987, Pedley 1987). In order to decide which neck posture was habitual in a sauropod we had to conduct a biomechanical analysis.

Different neck, limb, and body postures evoke different patterns of stress in the skeleton (Kummer 1959, Pauwels 1965, Preuschoft 1969, 1970, 1971, 1976, Alexander 1985, 1989, Christian & Preuschoft 1996). If the skeletal remains of an extinct vertebrate are analysed with regard to the forces and torques that could have been sustained, we can obtain important evidence on the possible postures (and gaits) of this animal (Preuschoft 1976, Alexander 1985, 1989, Christian & Preuschoft 1996).

In this study the predominant neck posture of *Brachiosaurus brancai* is deduced from the shape of the vertebral column applying the method developed by Preuschoft (1976) to deduce the patterns of bending moments and compressive forces in the vertebral column along the long body axis (see below, see also Alexander 1985, Christian & Preuschoft 1996).

Palaeontological setting

The interpretation is based on a skeleton of *Brachiosaurus brancai* mounted for display at the Berlin Museum of Natural History. The skeleton is a composite of original bones, copies of bones, and plaster reconstructions of the missing parts (Janensch 1938, 1950b). The skeletal remains of *Brachiosaurus brancai* were excavated during the German Tendaguru Expedition between 1909 and 1912 (Janensch 1914a). They have been recovered from the Upper Jurassic Middle and Upper Saurian Beds of the Tendaguru Series exposed at different sites in the surroundings of the Tendaguru Hill in southeastern Tanzania, East Africa. The age of the Middle and Upper Saurian Beds has been much disputed. Today the age of both dinosaur-bearing beds is commonly considered as Kimmeridgian to Tithonian (e.g. Aitken 1961, Russell et al. 1980), however, the precise age determination requires further investigation. The mounting was directed by W. Janensch and finished in 1937. The skeleton was disassembled during World War II and remounted in 1952.

The major part of the composite skeleton belongs to one single individual of *Brachiosaurus brancai*, the so-called specimen S II. It is an incomplete skeleton which was recovered from the Middle Saurian Bed at site S, located about 1 km south of the Tendaguru Hill (Janensch 1914a, b). Skeleton S II, excavated between 1909 and 1911 (Janensch 1914a), supplied parts of the skull, the fairly complete presacral vertebral column (11 cervicals, 11 dorsals), cervical and trunk ribs, most of the anterior appendicular skeleton (e.g. both sternal plates and coracoids, left shoulder blade, right anterior limb, left humerus, ulna and radius), parts of the pelvis (e.g. both pubes), and incompletely preserved hind limbs, among them the fragmentary right femur, tibia, fibula, and badly preserved hind foot bones (Janensch 1929). Most of the preserved cervical series was originally found in natural articulation, except for cervical 8 and some cervical ribs recovered as separate elements (Janensch 1914b). The majority of dorsal vertebrae were disarticulated. The tail was already missing when the specimen was discovered, possibly due to erosion (Janensch 1914b). The taphonomic evidence suggests maceration and decay of the carcass prior to burial. With only few exceptions, the bones were disarticulated, but associated. Not all parts of skeleton S II are well preserved, however, the shape of most bones has not been substantially changed by taphonomic or diagenetic processes.

A second specimen of *Brachiosaurus brancai* (S I) which was also recovered from the Middle Saurian Bed at Tendaguru site S yielded additional material not represented in specimen S II (e.g. braincase, axis).

Skeleton S II provided the bulk of the bones, however, only some of them could be included in the mount. The skull, the cervical and dorsal vertebrae had to be replaced by plaster reconstructions due to their extreme fragility (Janensch 1950b). The right shoulder blade, some bones of the left manus, four trunk ribs, and the left ischium are also plaster reconstructions. They have been modelled from existing counterparts of the other body side (Janensch 1950b).

Some missing elements of skeleton S II either have been substituted by bones of other specimens of the same species and size or by plaster reconstructions. Other missing items have been replaced by bones or copies of bones from different-sized specimens, also of the same species.

Most important for this study is the preservation of the vertebral centra and the spinal processes of the cervical vertebrae of skeleton S II. According to Janensch (1950a), there are 13 cervicals in *Brachiosaurus brancai.* Centra and spinal processes are preserved in the cervicals 3 to 5 and 8. The spinal processes of all other cervicals are reconstructed. The centra of cervicals 9 to 13 are preserved. The axis is well preserved in skeleton S I but completely reconstructed in skeleton S II.

A fairly complete caudal series of 50 vertebrae recovered from the Upper Saurian Bed at Tendaguru site "no" has been installed as the tail of the skeleton (Janensch 1950a, b). Its size seems to correspond well to main skeleton S II (Janensch 1950 b). The missing first caudal vertebra and most of the haemapophyses are plaster reconstructions. At the end of the tail a few small pieces also modelled in plaster were added.

In addition, a left femur and a left zygopodium (tibia, fibula) have been included in the skeleton reconstruction. They have been obtained from the Middle Saurian Bed exposed at Tendaguru localities "Ni" and "Bo". The left tibia and fibula from site "Bo" are of the same size as the installed right tibia and fibula of specimen S II (Janensch 1950b). In contrast to that, the involved left femur from locality "Ni" is slightly shorter than the installed right thigh bone of specimen S II. The pelvis of specimen S II has suffered damage, particularly to the ilia and ischia. Therefore, a right ilium from the Middle Saurian Bed (site "Ma") as well as an incomplete right ischium obtained from the Upper Saurian Bed (site "L") have been included in the skeleton reconstruction (Janensch 1950b). Both pubes are originals of specimen S II. The sacrum was modelled in plaster after partial skeleton "Aa" from the Middle Saurian Bed and partial skeleton "T" recovered from the Upper Saurian Bed (Janensch 1950b).

The right forefoot is a fairly complete original of skeleton S II (Janensch 1922, 1950b, 1961), the left modelled in plaster. Like the left forefoot, most hind foot elements are plaster reconstructions. The reconstruction of the hind foot skeleton is mainly based on bones from Tendaguru site "Bo" as well as badly preserved metatarsals and phalanges from specimen S II (Janensch 1950b). Only a few pes phalanges have been reconstructed without Tendaguru counterparts.

Method

Neck, trunk, and tail of an animal experience forces and torques (bending moments) depending on its posture and the distribution of body mass. Bending moments along the longitudinal body axis act primarily in a sagittal plane unless parts of the body, e.g. the tail, are accelerated quickly sidewards. The pattern of bending moments along the vertebral column depends on mass distribution, posture, and forces exchanged between the animal and the substrate (ground-reaction-forces).

In the neck, bending moments are usually highest at the base and drop towards the head. However, the neck experiences very little bending moments or no bending moments at all with a more or less vertical neck posture. The bending moments M can be calculated according to the rules of statics (Pauwels 1965). In this study, the calculations of bending moments along the neck of *Brachiosaurus brancai* are based on the mass distribution determined by Gunga et al. (1995). These data allow to calculate the bending moments and the weight forces at 10 locations along the neck which do not match the positions of the intervertebral discs. The bending moments and weight forces at the locations of the intervertebral discs were obtained from these data by linear interpolation.

As long as the neck is not orientated backwards, bending moments along the neck must be counteracted at the intervertebral junctions by tension in epaxial muscles, tendons, or ligaments that are located dorsally to the vertebral centra (Preuschoft 1976, Alexander 1985, 1989, Christian & Preuschoft 1996).

A muscle force F_m acting in a sagittal plane at a distance h above the transverse axis of an intervertebral joint produces a torque $F_m h$ about that joint. h is the lever arm of the force F_m. The lever arm is the distance between the line of action of the force and the axis of the joint. The transverse axis of an intervertebral joint can be assumed to pass through the center of the intervertebral disc (Preuschoft 1976, Alexander 1985). The lever arms of the epaxial muscles can be estimated to be equal to the vertical distances between the centers of the intervertebral discs and either the centers of the epaxial muscles (Preuschoft 1976) or the line that connects the tips of the neural spines (Alexander 1985). Both methods lead to similar results if the general pattern of torques along the vertebral column is of interest (Christian & Preuschoft 1996). In any case, as long as the general construction of the examined vertebrae is similar, the mean lever arm of all muscles, tendons, and ligaments being effective at a given intervertebral joint must be a constant fraction of the distance between the center of the intervertebral disc and the line connecting the tips of the neural spines.

In this study, we use the distance between the center of an intervertebral disc and the line connecting the tips of the neural spines as measure for the lever arm h. The measurements were taken from the scaled reconstruction of *Brachiosaurus brancai* presented by Janensch (1950b). Difficulties in estimating h arise if epaxial muscles or their tendons are located far above the spinal processes. This is quite common in the necks of mammals (Preuschoft & Fritz 1977, Preuschoft & Günther 1994) but unlikely in most parts of the necks of *Brachiosaurus* and other sauropods because neither the shape of the neural spines nor the rather moderate length of the neural spines in the shoulder region indicate the existence of muscles, tendons, or ligaments that were located considerably above the tips of the neural spines, with the possible exception at the base of the neck (see below, see also Paul 1988).

The maximum muscle force F_m at a given position in the vertebral column is difficult to obtain, because the functional cross-sections of the muscles cannot be deduced from skeletal remains. However, with the bending moment M and the mean lever arm h the muscle force F_m can be calculated by $F_m = M/h$.

The pulling force F_m of the epaxial muscles evokes a compressive force of the same magnitude between the vertebral centra (Preuschoft 1976). The total compressive force F acting on an intervertebral disc is the sum of two components: first, the muscle force F_m due to the bending moment M, as described above, and second, the weight force F_g of the fraction of the neck cranial to the regarded position multiplied by the cosine of the angle φ between the plane of the intervertebral disc and the horizontal plane (see Preuschoft 1976):

$$F = F_m + F_g \cdot \cos \varphi .$$

The highest regularly occuring compressive forces F along the neck should be proportional to the transversal cross-sections of the centra or of the intervertebral discs, under the assumption of equal safety-factors (the thin and elongated cervical ribs are not suitable for transmitting high compressive forces onto the vertebral centra). The transversal cross-sections A of the intervertebral discs may be the better measure for the compressive forces and can be estimated from the diameters of the surfaces of the adjacent vertebral centra (Preuschoft 1976). The transversal cross-section A of each intervertebral disc was calculated by assuming an elliptic shape with the lateral and the dorsoventral diameters of the caudal surface of the adjacent vertebral centrum as major axes (Preuschoft 1976, Christian & Preuschoft 1996). The measurements were taken from the scaled illustrations of the vertebrae by Janensch (1950a). In the case of obvious and critical deformations, however, the surface was reconstructed. The relative error in determining the cross-sectional areas of the intervertebral discs was estimated to be about 10%. The distances of the intervertebral discs from the occipital condylus were measured along the vertebral centra. The measurements were taken from the scaled illustration of the completely reconstructed skeleton by Janensch (1950b).

To decide which neck posture was habitual in *Brachiosaurus brancai*, the distribution of the compressive force F was calculated for three different hypothetical neck postures (see below). For each posture, the distribution of compressive forces along the neck was compared with the distribution of cross-sectional areas A of the intervertebral discs. The neck posture was rejected if both distributions did not match.

The following three hypothetical neck postures were analysed: In the first model, the neck was assumed to be fully stretched out in a horizontal plane with the head pointing forward (in the following refered to as "horizontal neck posture"). In the second model, the neck was posi-

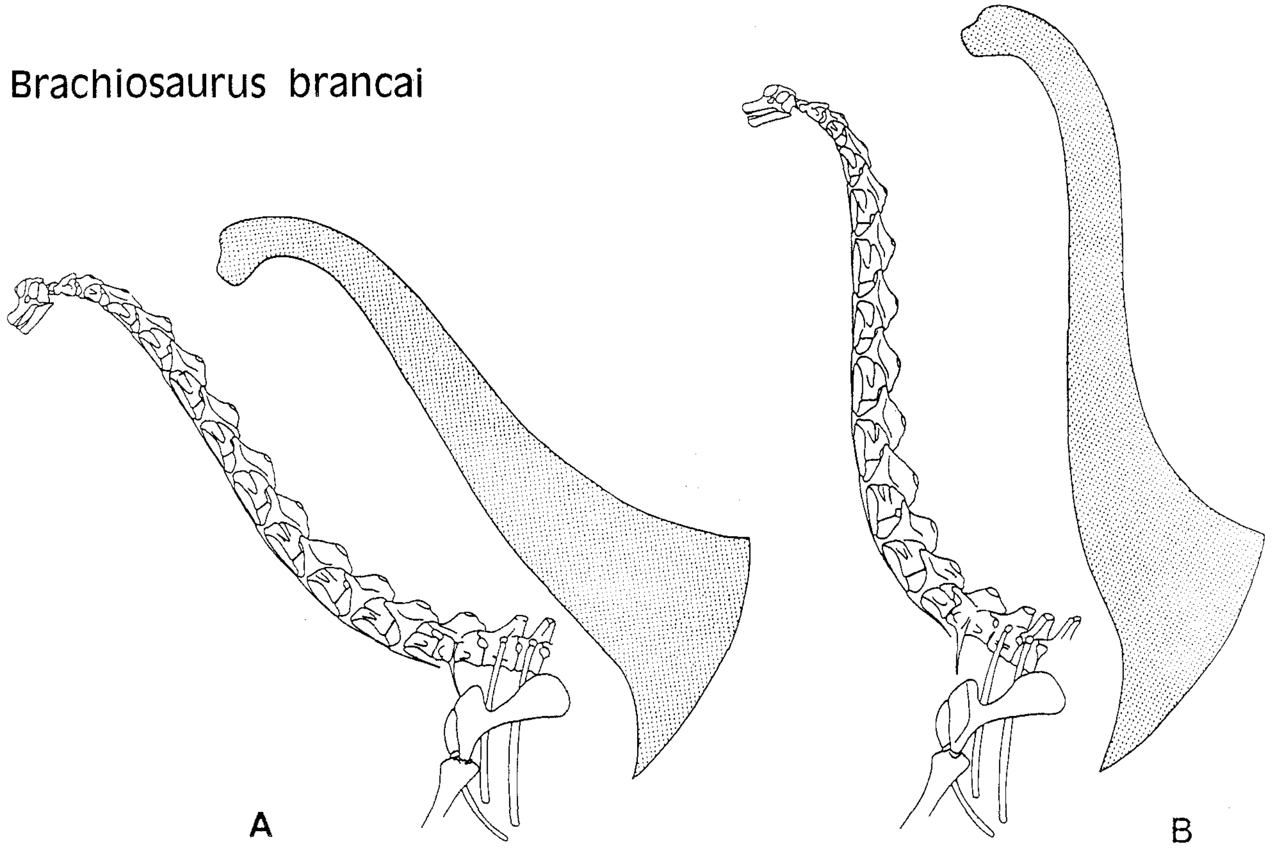

Fig. 1. Hypothetical neck postures of *Brachiosaurus brancai*. **A**: after Janensch (1950b), **B**: "vertical" posture

tioned as in the reconstruction by Janensch (1950b) with the middle fraction of the neck forming an angle of about 30° with the vertical ("mounted neck posture", Fig. 1A). In the third model, the same shape of the most cranial three quarters of the neck was used as in the reconstruction by Janensch (1950b) but the neck was rotated around its base so that the straight middle part of the neck is fully vertical ("vertical neck posture", Fig. 1B).

Results

The calculated compressive forces acting on the intervertebral discs for all three hypothetical neck postures are given in Table 1. The accuracy of these data depends on the precision of the estimates of segment masses provided by Gunga et al. (1995). A systematic error in these data would not affect our conclusions (see below).

The results are illustrated in Fig. 2. The compressive forces increase towards the base of the neck in all three examined neck postures. The forces are increasingly higher in more inclined neck postures due to higher bending moments, except in the most cranial part of the neck.

The pattern of compressive forces is very different from the pattern of cross-sectional areas of the intervertebral discs in both horizontal and mounted neck posture. The forces increase much quicker towards the base of the neck than the cross-sectional areas do in these postures.

The distribution of the cross-sectional areas of the intervertebral discs fits very well the distribution of compressive forces at most parts of the neck in the "vertical" posture (Fig. 2). However,

Table 1

Estimates of the cross-sectional areas A and calculations of the compressive forces F acting on the intervertebral discs at different locations along the neck of *Brachiosaurus brancai* for three different hypothetical neck postures. x: distance from the occipital condyle.

x [m]	[10^{-4}m^2]	F [N]		
		horizontal	*mounted*	*vertical*
0.82	151 ± 15	8.560	7.790	9.660
1.42	250 ± 25	14.800	13.600	13.900
2.14	253 ± 25	26.000	22.500	17.500
2.98	377 ± 34	52.400	38.200	23.100
3.82	377 ± 38	79.800	54.400	28.700
4.76	471 ± 47	110.200	77.800	36.500
5.67	658 ± 66	160.500	106.000	44.700
6.55	660 ± 66	219.900	146.000	68.900
7.41	709 ± 71	315.000	216.000	119.000
8.20	939 ± 94	409.800	293.000	256.000

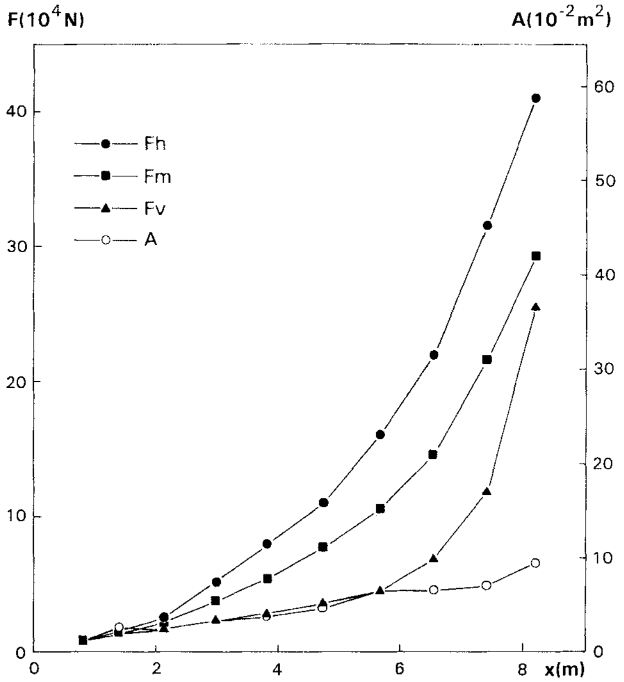

Fig. 2. Cross-sectional areas of the intervertebral discs A along the neck of *Brachiosaurus brancai* and compressive forces $\mathbf{F}_h$, $\mathbf{F}_m$, and $\mathbf{F}_v$ acting on the intervertebral discs in a fully horizontal (**h**) neck posture,in the mounted neck posture (**m**), and in a vertical (**v**) neck posture, respectively, plotted against distance x from the occipital condyle

even in this posture considerable deviations between the curves of cross-sectional areas and compressive forces, respectively, occur at the base of the neck. This might indicate that the middle fraction of the neck was slightly inclined backwards giving the neck a S-like shape (Fig. 3) as suggested by Paul (1988). Such a change of the neck posture would barely affect the pattern of compressive forces in the cranial two thirds of the neck but with the neck's center of mass being located more or less directly above its base, bending moments and compressive forces would be considerably reduced in this region. In addition, the calculated forces close to the base of the neck should be regarded with caution. The neural spines of the cervical vertebrae 9 to 13 are not preserved (see above) and might have been somewhat higher than reconstructed. Furthermore, it cannot be excluded that some ligaments were located above the spinal processes at the base of the neck where it was curved backwards. Therefore, the lever arms of the epaxial muscles might be underestimated at the base of the neck, starting at a distance of about 6 m from the occipital condylus. Longer lever arms would lead to lower compressive forces in this region making fit better the curves.

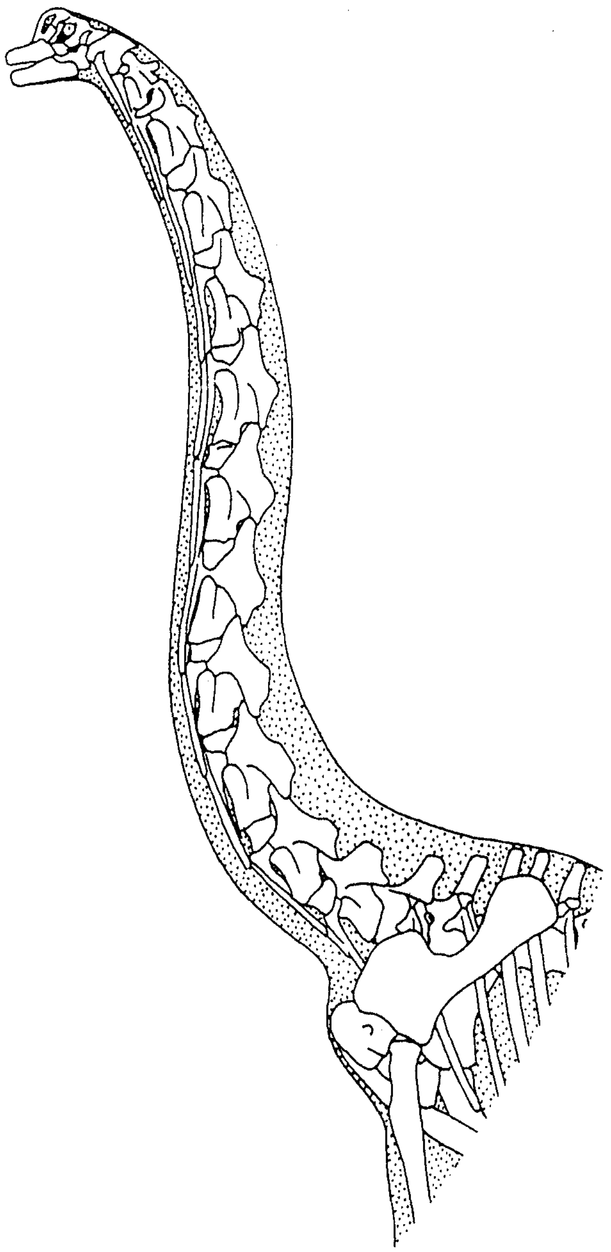

Fig. 3. *Brachiosaurus brancai* habitually kept the neck in a vertical posture. Drawn after Paul (1988) with some slight alterations in the outlines

Discussion

The comparison between the distribution of cross-sectional areas of the intervertebral discs and compressive forces along the neck conclusively proves, that the neck of *Brachiosaurus brancai* was habitually kept in a nearly vertical posture with its center of mass located closely above its base. The neck was probably slightly S-shaped most of the time. The reconstructions of Bakker (1987) and Paul (1988) fit well to this result (Fig. 3). The conspicuous cervical ribs are not strong enough for transmitting high forces onto the vertebral centra. Due to the short distance between the cervical ribs and the intervertebral joints, the resulting torques about the intervertebral joints cannot have been sufficiently high for supporting a more horizontal neck posture as suggested by Frey & Martin (1997). However, tensile forces transmitted by the cervical ribs might have been effective in stabilizing the neck when it was occasionally slightly bent backward or in braking backward movements of the neck.

It should be pointed out, that the method used in this study does not rely on absolute data on the mass distribution in the neck. Only marked relative differences between the masses of different neck segments would considerably change the calculated pattern of forces along the neck. Therefore, the same results would have been obtained with an overall heavier or lighter neck.

The curves of compressive forces and cross-sectional areas of the intervertebral discs along the neck differ already much if the more or less straight middle part of the neck forms an angle of about 30° relative to the vertical. These differences are tremendous in a horizontal posture. Similar results would have been obtained if the neck was orientated backwards or towards the side. Therefore, it is very unlikely that the middle part of the neck of *Brachiosaurus brancai* frequently formed angles of more than about 15° or 20° with the vertical in any direction. *Brachiosaurus* might have been able to hold the neck in a very inclined or even in a fully horizontal posture, but regardless of how flexible the neck was (see e.g. Paul (1988) vs. Martin (1987)) this could have been done only occasionally. Because of the much higher compressive forces acting along the cervical spine in more horizontal postures, a frequent utilization of a neck posture outside the range suggested above would be reflected in the distribution of cross-sectional areas of the intervertebral discs even if it was less often assumed than a vertical posture.

The results throw new light on the discussion about the feeding range of *Brachiosaurus.* The average height of the head of the Berlin specimen S II was about 14 m above the ground than 12 m as in the reconstruction by Janensch (1950b). Janensch (1950b) did not reconstruct the forelimbs in a fully erect posture. With a fully erect forelimb posture the position of the head would be even higher depending on the reconstruction of the shoulder girdle.

Whereas *Brachiosaurus* was able to exploit resources in extreme heights, its feeding range was rather limited. The neck posture must have been nearly vertical during most of the feeding time, provided that *Brachiosaurus* spent much time on feeding. Therefore, *Brachiosaurus* could not exploit a large volume of feeding space as it was suggested for the use of a long neck by Martin (1987). An upper limit of the space that was usually exploited by *Brachiosaurs* without moving its trunk might be calculated with a maximum inclination of the neck of about 20° relative to its mean position. If the distance between the head and the base of the neck was about 9 m, the head would have swept over a spherical calotte with the surface area A given by

$$A = 2 \cdot \pi \cdot 9^2 \cdot (1 - \cos 20°)\ \mathrm{m}^2 \approx 31\ \mathrm{m}^2 .$$

The neck probably was shortened or extended during feeding to some degree by assuming a more or less curved posture. However, the neck could not have been frequently curved much more than shown in Fig. 1B or in Fig. 3. A much more curved neck posture would be reflected in the distribution of compressive forces and therefore in the distribution of cross-sectional areas of the intervertebral discs along the neck. For example, in the first third of the neck the compressive forces acting on the intervertebral discs would increase much quicker towards the caudal than they do in the "vertical" neck posture illustrated in Fig. 1B. The distance between head and base of the neck might have been varied by about $\Delta l = 1$ m during feeding, so that the volume V of the space that was exploited was about

$$V \approx A \cdot \Delta l \approx 31\ \mathrm{m}^3 .$$

This estimate is very rough. The volume V might be overestimated rather than underestimated, even if we take moderate movements of the base of the neck into account that could have slightly increased the feeding range of a resting *Brachiosaurus.* Therefore, we might conclude that a specimen of *Brachiosaurus brancai* of the size of the Berlin specimen S II regularly exploited a feeding space of 20–30 m^3 volume or less before moving the body to a different location. The usual variation in feeding height probably was just about 2 m.

It might cause difficulties to physiologists to explain how a giant like *Brachiosaurus* was able to gather sufficient food with a rather restricted vertical feeding range. However, different sized specimens living in the same area browsed in different heights, so that intraspecific competition was reduced. Yet it has to be shown that smaller (younger) specimens were similarily restricted in the feeding range as the Berlin specimen S II.

A reduction of fluctuations in the blood pressure in the head might be an important advantage of reduced changes in head height.

The results presented here cannot be applied to other sauropods without specific examination. Body proportions differ considerably among sauropods (McIntosh 1990, 1997), important morphological features of *Brachiosaurus*, like the relative forelimb length, are not typical of sauropods (Dodson 1990), and the neck posture might have been very different in other forms (see e.g. Borsuk-Bialynicka 1977).

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