

**THE VERTEBRAL COLUMN  
OF  
BRACHIOSAURUS BRANCAI**

**BY**

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**WITH PLATES I – V.  
136 FIGURES IN TEXT  
AND SOME 7 TEXT SUPPLEMENTS**

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## Foreword.

Although remains of *Brachiosaurus* are relatively abundant in the Tendaguru Beds, vertebrae of satisfactory preservation were frequently only found from the caudal region. Due to the delicacy of individual elements and their complicated architecture the conditions of preservation in the usually poorly consolidated easily friable Saurian marls in which the bones are embedded are not favourable. Useable presacral vertebrae were hardly to be had wherever the marls near the surface are subject to the influences of erosion. Numerous sites, at which more consolidated sediments occur, in contrast, yielded good vertebrae from the cervical and dorsal region as well. The material originates from the Middle and Upper Saurian Marls, and is assigned to the single species *Brachiosaurus brancai* JAN., since I do not believe I can uphold the second species erected by myself, *Br. fraasi*.

The gaps, which the description of the available material leave open, are not too significant; they could be bridged with considerable certainty through comparative and interpolative inferences from the morphological evidence. The description provides the foundation for a number of observations about the functions of the articulations, about ligaments and musculature, and further, permits the more precise comparison with other genera of sauropods. For the confirmation of the pneumatic character of the presacral vertebral column on the basis of external sculptural features as well as vertebral sections, sections through vertebrae of *Brachiosaurus* were also utilized in the paper on the pneumaticity of the vertebrae of sauropods and other saurischians (JANENSCH 1947), that preceded this study, and are also comprehensively discussed here within a broader framework.

The peculiarity of the cervical ribs that attain an unusual length is discussed in detail and an attempt is made to appraise their functional purpose; thereby a very noticeable differentiation in the morphology of the rib of the second cervical vertebra was confirmed, which might perhaps be interpreted as a sexual difference.

The results of this study of the vertebral column of *Brachiosaurus* could be utilized in the plastic reconstruction of the skeleton that has been erected in the atrium of the Berlin Museum of Natural History; they were made visible in the very careful modeling of presacral and sacral vertebrae, through which Senior Preparator E. SIEGERT has earned merit.

My colleague Prof. Dr. W. O. DIETRICH supported me in constant true helpfulness through challenging discussion and important suggestions.

The preparation of the described material was particularly difficult and time consuming in the exceedingly complexly constructed presacral vertebrae, and extended over a longer succession of years. This task, which demanded a high degree of ability and precision, was fulfilled above all with the best results by Senior Preparator G. BORCHERT (†), Senior Preparator E. SIEGERT and Preparator J. SCHOBERT (†).

I am again indebted to Mr. H. WOLFF-MAAGE (†) for the sympathetically executed illustrations of the vertebrae; a number of additional figures were carefully completed by Miss SCHMIDT and Miss. E. v. SCHLIEBEN.

The publication of this study has been greatly delayed – through the effects of war the entire text set, as well as the document sources for the photolithographic plates were destroyed.

## Presacral vertebrae.

### Material.

The excavation at Site S in the Middle Saurian Marl yielded presacral vertebrae from two animals of different sizes of *Brachiosaurus brancai*. A number of anterior cervical vertebrae of the smaller animal SI were found, in addition to the skull described by me (JANENSCH 1935). They comprise, with the exception of an unprepared disintegrated vertebra, the axis and 5 additional vertebrae that obviously present an articulated series from the 2nd to the 7th. All vertebrae are not severely compressed and are completely or nearly completely preserved. All vertebral material from Skeleton SII, the very large individual, obviously comprises with the exception of atlas and axis, all remaining presacral vertebrae, although for the most part incompletely preserved. The total number of the vertebrae is 22; the original total count may have been 24. The vertebrae from the 3rd to 15th presacrals lay in articulation in a consolidated lime sandstone lens; of them, the 3rd to 5th vertebrae are tolerably complete, the remaining 10 vertebrae were articulated with one another, with one interruption that arose when the 8th presacral vertebra rotated out of the series and was displaced. While this one was well preserved, the upper portion of the posterior series from the 9th to the 15th vertebra was removed in a plane by an external influence, presumably moving water, so that beyond the vertebral centrum little, in part the prezygapophyses, has been preserved. The 16th vertebra also still belongs to this series, was however, already disarticulated and possesses a large portion of the lower section of the neural arch. Eight additional presacral vertebrae lay apart and somewhat deeper than the consolidated sandstone layer in the marl, mixed together with other skeletal elements; they were all isolated except for the last two that were still articulated. These individually embedded vertebrae are far too large to have belonged to the smaller *Brachiosaurus* SI, of which only the skull and the anterior and middle cervical vertebrae were present. In size they completely match the articulated vertebral series and can thus be associated with Skeleton SII without hesitation. Five of these vertebrae are fairly completely preserved, are certainly missing the ends of the diapophyses. Among the isolated vertebrae are two that are only preserved as centra, a third, less complete and crushed centrum still bears the prezygapophysis. All of the vertebrae exhibit evidence of crushing from slight to quite considerable degrees.

Quarry Y in the Middle Saurian Marl yielded several isolated quite complete cervical vertebrae, among the remains of a mid-sized animal. Two of them, whose position in the sequence could not be precisely determined, are included in the table of measurements; one of them is illustrated.

Disarticulated presacral and caudal vertebrae of *Brachiosaurus* were found in the same stratum in Quarry dd at Kindope north of Tendaguru, where bones of a skeleton of *Elaphrosaurus bambergi* JAN., two skeletons of *Dicraeosaurus hansemanni* JAN., as well as remains of *Barosaurus africanus* (E. FRAAS) have been discovered. For the most part only the centra, separated from the neural arches, are present in the presacral vertebrae, which were only considered in the description to a small degree since their morphology is more or less distorted, the characteristic preservation for this site.

In the discovery locality of Makangaga in Kilwa District, Mr. E. HENNIG found an articulated cervical vertebral column (be) deposited on the surface. The 2nd to 4th and the 6th vertebrae, to some extent strongly eroded, could be prepared and utilized in the description and the measurements. The peculiarly low shape of these vertebrae could be attributed to compression.

The important Find t of the Middle Saurian Marl yielded the atlas and proatlas as well as the anterior half of the axis in articulation with the complete skull.

Among the isolated vertebrae, two posterior dorsal vertebrae are valuable, AR 1 (collected by Mr. H. RECK) from the Middle Saurian Marl, and no. I from the Upper Saurian Marl; a dorsal centrum (W 3) from the middle layer yielded information about the internal structure.

### **Description.**

The description of the presacral vertebrae is based mainly on the two series of Site S; the observations about the vertebrae of sites y [sic], dd, be, t and W are included and only particularly emphasized as far as necessary. The good posterior dorsal vertebrae AR 1 and no. 1 are, in contrast, presented independently. The vertebral series of SI and SII as well as the finds from y [sic], be and t inform us about the construction of the anterior and middle cervical vertebrae; Skeleton SII informs us about the anterior cervical vertebrae and the dorsal vertebrae. Since the vertebrae between the 5th and the 17th presacral vertebrae of SII are mainly preserved as centra, the neural arches with their processes can only be very incompletely described and had to be reconstructed for the skeletal mount. The 5 more or less completely preserved isolated vertebrae provide information about the vertebral section from the 17th presacral vertebra to the 24th, the final dorsal vertebra. Concerning the order of these 5 dorsal vertebrae, the articulated vertebral pair S 11, S 12 is safely confirmed as the 23rd and 24th presacral vertebrae by the exact fit of the facets of the diapophyses and parapophyses of their posterior with the easily recognized final dorsal rib; just as the dorsal vertebra S 27 can unhesitatingly be considered the 17th presacral vertebra due to the exact fit with the 4th dorsal rib, whereby the seat of the parapophysis would fit well on the neural arch. The shape of the neurapophysis of vertebra S 29 is so similar to the 23rd presacral vertebra that I would like to see the position of the 22nd as very likely for it. Vertebra S 21 stands between S 27 and S 29, its neurapophyses and diapophyses differ so markedly from the shape of those of S 27, the 17th presacral vertebra, that it presumably had a greater distance from it than 29, which is considered to be the 22nd [presacral vertebra]; I therefore assume for it – with reservation – the position of the 20th presacral vertebra. The 18th, 19th and 21st positions are left for the more or less completely preserved centra. A more exact assignment to these positions must be abandoned.

### **External architecture of the presacral vertebrae of the sauropods.**

(Fig. 1-5.)

The dominant features of the external architecture of the presacral vertebrae are the laminae. They lie in planes in which compression and tension stresses occurred, that were generated by the muscles and ligaments that moved the vertebrae against or held them apart from one another. The laminae thus connect and stiffen the areas subjected to compression and tension, namely the articular ends

**Laminar system on presacral vertebrae of sauropods.**

Fig. 1. Middle cervical vertebra of *Brachiosaurus brancai*; lateral view. Fig. 3. Posterior dorsal vertebra of *Dicraeosaurus hansemani*; lateral view.

Fig. 2. Anterior cervical vertebra of *Brachiosaurus brancai*; anterior view. Fig. 4. Posterior dorsal vertebra of *Dicraeosaurus hansemani*; posterior view.

cedi = centrodiaepophyseal lamina  
cedih = posterior centrodiaepophyseal lamina  
cediv = anterior centrodiaepophyseal lamina  
cepah = posterior centroparapophyseal lamina  
cepav = anterior centroparapophyseal lamina  
di = diapophysis  
hy = hyosphene  
ifhy = infrahyosphenal lamina

ifpo = infrapostzygapophyseal lamina  
ifpr = infraprezygapophyseal lamina  
itpr = intraprezygapophyseal lamina  
lasp = laterospinal lamina  
n = neurapophysis  
pa = parapophysis  
padi = paradiaepophyseal lamina  
pl = pleurocentral cavity (pleurocoel)

po = postzygapophysis  
podi = postzygodiaepophyseal lamina  
posp = postspinal lamina  
pr = prezygapophysis  
prdi = prezygodiaepophyseal lamina  
prsp = prespinal lamina  
sudi = supradiaepophyseal lamina  
supo = suprapostzygapophyseal lamina  
supr = supraprezygapophyseal lamina

of the centra, the diapophyses and parapophyses, the pre- and postzygapophyses and the neurapophyses with one another in diverse ways. The sharp delineation of the laminae is the result of the principle, realized to a high degree in *Brachiosaurus*, whereby bone substance is extensively spared where it is not required due to mechanical stress. The deeply excavated niches between the laminae arose as a result.

Fig. 5. 8th cervical vertebra of *Brachiosaurus brancai* JAN. (Skeleton SII). ak = external excavation pl = pleurocoel. 1/10 nat. size

Other morphological elements occur in addition to the negative shapes of the niches, namely cavities in the centrum or in individual sections of the neural canal; they cause the cavernous structure. Pleurocentral excavations (pleurocoels) invade the lateral sides of the centra. Hollows of more or less rounded or elliptical outline or even of multi-sided shape with rounded corners are found in the neural arch. They are shallow, particularly when they are located on the thin lamella-like laminae, and are designated as “external excavations” when they occur on the external surfaces (Fig. 5).

Additional laminae can develop on the excavated surfaces of the pleurocoels and external excavations that reinforce the weak points along specific lines of pressure. The depressions between these laminae can be reinforced again by laminae. All these second order laminae illustrate how compression stresses run along the hollowed surfaces. They are frequently oriented with the main alignment of the laminar system but can also provide reinforcement in other directions. Such second order laminae often occur in parallel repetition and thereby make their direction of influence obvious. In this way the complexity of the external architecture of the presacral vertebrae is increased; it attains its highest degree in the middle and posterior cervical vertebrae.

I use the nomenclature of the laminar systems that I gave and established in greater detail in the study on the vertebral column of the genus *Dicraeosaurus* (JANENSCH 1929) to designate the various laminae. Figures 1-4 elucidate the course of the laminae and their designations.

### Proatlas.

Find SII (Fig. 6). The left arch of the proatlas of Skeleton SII is nearly complete. The entire morphology of the bone plate is similar to a very obtusely angled triangle. The entire posterior side is noticeably convex; the anterior is depressed in the centre. The anterior end, the shortest side of the triangle, is up to 15 mm thick, rugose in parts of the upper surface. The anterior end surface is depressed and has the character of a facet for the attachment to the occiput. The back of the arch becomes thin and finally very narrow. Without the unpreserved outer tip the bone is 8.8 cm long, with a width of 3.2 cm.

Both arches of the proatlas were found with skull t 1. The left arch is preserved in its entire length (9 1/2 cm); it is missing the medial margin up to a short section of the posterior tip. The right arch is only a fragment of half the length. As far as poor preservation allows an opinion, the proatlas of t 1 differs from that of SII to the extent that the posterior end is shaped somewhat broader and flatter.

Fig. 6. Left arch of the proatlas (SII). 1/2 nat. size  
m = medial margin, l = lateral margin

Fig. 7. Atlas (Find t); anterior view. 1/3 nat. size

Fig. 8. The same; left lateral side. 1/3 nat. size

### 1st presacral vertebra, atlas.

Find t (Fig. 7, 8). The intercentrum is a body with a trapezoidal cross section with a broader upper side. The depression for the condyle fills the entire anterior surface and the lower margin is extraordinarily rugose. The dorsal notch for the odontoid process is shallow. The broad ventral surface is clearly depressed concavely. The indistinctly defined suture surfaces of the upper arches truncate the upper lateral edges of the intercentrum obliquely. The maximum length (ventral) measures 5.0 cm, the maximum width (dorsal) 11.1 cm, the maximum height 5.3 cm. It is emphasized that a facet for a cervical rib cannot be recognized on the intercentrum.

Both complete halves of the neural arch are complete and hardly compressed, with the exception of eroded margins and encrusted surfaces. The basal portion has the shape of a low medially flattened cone. The dorsal, elongated, triangular, strongly vaulted lamella projects out of the lateral wall

and extends posteriorly into a reinforced medially curved tip, which is 13 1/2 cm long on the left and 8 cm wide. The anterior portion of the lamella forms the roof of the neural canal on both sides; behind it on the ventral side sits the elliptical, strongly concavely vaulted facet for the prezygapophysis of the axis. The lateral margin of the lamella develops in the shape of a narrow trochanter at the site where it is freed from the basal portion.

### **2nd presacral vertebra, axis.**

Find SI (Fig. 9, 10, 14-16). The vertebra is nearly complete, somewhat compressed laterally; the posterior portion of the neural arch appears to have become somewhat too tall as a consequence. The elongated centrum is narrowed on both sides of its middle portion to such a high degree by an extended pleurocentral excavation that bends inward, pocket-like, fore and aft, that in places only a 1-mm-thick septum remains between the two excavations, and which is positioned somewhat asymmetrically to the right of the median plane. The intercentrum and the atlas centrum as well as the odontoid process are fused with the anterior end. The approximately 4-cm-wide odontoid process projects strongly dorsally and possesses a strongly defined, broad longitudinal groove on its dorsal side; in other respects the end surface is clearly concave. The posterior end surface is deeply and evenly concave. The facet of the parapophysis, clearly visible on the left, rounded, very shallowly concave, and 18 cm wide, is positioned 2 1/2 cm behind the anterior end surface [of the odontoid process], slightly below the mid-height level [of the vertebra]. A horizontal lamella, which is short and thin on the right side but on the left borders the pleurocentral excavation along its entire length as a stronger spar (posterior centroparapophyseal lamina), extends posteriorly. The centrum is narrow and exhibits a ventral ridge.

Fig. 9. Axis (SII); ventral view. 1/5 nat. size

Fig. 10. Same vertebra; anterior section of the ventral side.  
2/5 nat. size. ic = intercentrum.

Fig. 11. Axis. (Find t); anterior view. 1/3 nat. size

d = odontoid process, di = diapophysis  
ic = intercentrum; pr = prezygapophysis

Fig. 12. Axis. (Find be 1); left lateral view.  
1/6 nat. size

Fig. 13. Same vertebra; anterior view. 1/6 nat. size

The prezygapophysis sits on top of and immediately next to the anterior opening of the neural canal as a knob with a shallowly vaulted, elliptical facet, 30 mm long and 18 mm wide on the right, that slopes sharply laterally. The diapophysis hangs down as a narrow tapering cone. The neuropophysis over the anterior half of the vertebra consists of a sharp, high, posteriorly ascending ridge that projects as an anterior point but becomes a broader roof posteriorly, ending in a thick, rugose, 6 1/2-cm-wide tuberosity, which covers a deeply invasive, extensive niche between the postzygapophyses. Its facet bends in a strong arc from outside to inside and down, and has a width of almost 5 cm in cranial-caudal orientation. The suprapostzygapophyseal lamina is thick and short; the postzygodiapophyseal lamina is initially thin and roofs a deeply invasive niche, then proceeds, truncated, in an arc downwards towards the diapophysis.

Dimensions of the presacral vertebrae from Finds SI, Y, be, no, AR in cm.

Catalogue Number	Position	Total length of the vertebra from the anterior end of the prezygapophysis to the posterior upper edge of the centrum	Total height of the vertebra	Total length of the centrum measured at mid-height	Length of the centrum minus condyle at mid-height	Height of the anterior end of the centrum	Length of the anterior end of the centrum	Height of the posterior end of the centrum	Length of the posterior end of the centrum
S 71	2		25.4	23.2 <sup>1)</sup>	–	9.8 (±)	9.0 (±)	10.0(±)	8.2 +
S 51	3	35.2	27.0	30.6	27.1	8.3	9.5	11.6	12.3(+)
S 70	4	51.0	32.5	45.7	42.2	10.0(±)	9.3 +	13.8	13.2(+)
S 58	5	65.9	34.8	56.0	51.8	12.5 ±	14.5 ±	15.2 ±	17.8(±)
S 65	6	71.0 +	34.7	69.1	61.8	12.3 +	17.3	15.0 +	22.1
S 43	7	75.7 +	49.2	70.5	63.0	–	17.8 ±	22.5	19.8
Y 3		66.4	36.0	59.7	51.5	11.5(+)	14.3(+)	15.4	16.1 +
Y 4		76.5	–	65.6 (+)	51.7(+)	15.1	17.5	18.6 +	21.2(+)
be 1	2		20.8	25.5 <sup>1)</sup>	22.9(+)	8.6	10.3	9.2	9.9 +
be 2	3	43.4	25.2	40.2	34.3	7.7	9.8	12.1(±)	13.7(±)
be 3	4	62.6	25.3 +	58.3	52.1	9.3	12.2	–	–
be 5	6	87.2	–	78.9	72.5	13.1	20.1	19.4	22.7
no 8			82.8	34.6	23.2	32.7	45.6(–)	38.1	44.7
AR 1			76.5 +	24.3			29.6 +	28.4	24.0

<sup>1)</sup> Length including odontoid process.

Explanation of the symbols in the table.

+ Total too low due to incomplete preservation or due to distortion.

(+) Total somewhat too low due to incomplete preservation or due to distortion.

– Total too high due to distortion.

(–) Total somewhat too high due to distortion.

± Total uncertain, too low or too high.

(±) Total somewhat uncertain, too low or too high.

Find t (Fig.11). Only the anterior half of the vertebra is present, the neurapophysis of which is not preserved. The surface is largely interspersed mosaic-like with slightly open fractures; the volume may be somewhat increased as a result, while crushing may have reduced the height somewhat.

The atlas body with the odontoid process and the intercentrum are not ossified with the centrum. The sutures of both of these elements as well as the anterior end surface of the centrum have a rugose surface. The left pleurocentral excavation is deeper than the right. The postzygodiapophyseal lamina projects downwards as a short lobe. In addition to the diapophysis, the prezygapophysis differs from SI in that the columnar anterior margin of the neural arch that carries it is obviously much lower; possible crushing could hardly make up the difference.

A strongly pronounced step on the isolated atlas body laterally and ventrally separates the broadly extending, quarter-spherical, condyle-like true odontoid process from the broad conical socket. Close under its upper margin the odontoid process exhibits the deeply sunken, narrow, lengthy groove for the ligament leading to the condyle.

Find be I (Fig. 12, 13, Plate I Ill. 1, 4). The anterior section of the neural arch with the prezygapophyses, the right diapophysis, and part of the left diapophysis, are missing. The axis of be I considerably exceeds the axis of SI in length. In total aspect it differs noticeably from it [SI] in its low height. The facets of the postzygapophyses with their lateral margins are about 9 cm high, thus, despite the significant total size, not higher than in axis SI. The neurapophysis, only preserved in its posterior half, is much lower; it extends 12 cm above the base of the neural canal, compared with about 15 1/2 cm in SI.

The atlas body with the odontoid process and the intercentrum ossified and co-ossified without obvious sutures, sits on the centrum, which at most could be slightly crushed in a vertical orientation in its anteriormost section. The broad flattening of the middle section of the ventral surface of the body differs substantially from the asymmetrical keel formation in the axis of SI.

### **3rd – 24th presacral vertebra.**

(Fig. 17-66. Plate I, Ill. 2-3, 5-8)

Centrum. The extended vertebral centrum of the cervical vertebrae from the 3rd onwards is comprised of three sections: the anterior end with the spherical condyle, the more or less cylindrical posterior end that includes the cotyle, and a long central section that lies between the two end sections and that essentially only consists of a ventral plate and a medial or nearly medially positioned thin septum that ascends from it. The space on either side of this septum, the pleurocentral excavation (“pleurocoel”), extends backward into the posterior end of the centrum as a deep cavity. Anteriorly, the pleurocentral excavation does not invade the condylar section deeply or to a far lesser extent than in the posterior end, and is also generally not sharply defined here but rather mostly extends more or less into the lateral surface of the centrum. Normally the lateral border of the excavation ends at a very acute angle in the posterior portion. In contrast the pleurocentral excavation of the 3rd presacral vertebra of SII ends without a sharp border at the posterior end.

The condyle constantly increases in size in the series of cervical vertebrae. When uncrushed, it is always nearly hemispherical. It is impossible to clarify, whether the condyle of the last large vertebra had a circular outline or perhaps was somewhat broader than tall, because of the crushing in SII.

41

2nd – 7th cervical vertebra (SI). 1/10 nat. size  
Fig. 14, 17, 20, 23, 26, 29 Right lateral views,  
15, 18, 21, 24, 27, 30 Anterior views.  
16, 19, 22, 25, 28, 31 Posterior views.

42

3rd – 7th cervical vertebra (SII) 1/10 nat. size  
Fig. 32, 34, 37, 39, 41 Lateral views,  
33, 35, 38, 40, 42 Ventral views,  
36 Posterior view of the 4th cervical vertebra.

43

8th – 9th cervical vertebra (SII), 1/10 nat. size  
Fig. 43, 47 Lateral views,  
Fig. 44, 48 Ventral views,  
Fig. 45 Anterior view of the 8th cervical vertebra,  
Fig. 46 Posterior view of the 8th cervical vertebra.

The anterior broad section of the ventral surface of the centrum dips downward considerably on both sides. A pronounced, elongated depression is located ventrally between the parapophyses, which in the middle cervical vertebrae, for example the 6th and 7th presacral vertebrae, sinks separately into a sharply defined, narrow, lengthy cavity. With the transition to the trunk in the 13th presacral vertebra, and increasingly in the two subsequent first dorsal vertebrae, the flatness of the ventral surface behind the parapophyses gives way to vaulting; in the 15th presacral vertebra the middle section is completely cylindrical ventrally.

The changes in relation to the length and width of the centrum in the cervical and posteriormost dorsal vertebrae are obvious in the ventral views and outlines of the ventral surfaces, as well as in the dimensions in the table. In SII, length increases most strongly from the 39-cm-long (excluding condyle)

Dimensions of the presacral vertebrae of Skeleton SII in cm.

Position	Total length of the vertebra from the anterior end of the prezygapophysis	Total height of the vertebra	Total length of the centrum at mid-height	Length of the vertebral centrum minus condyle at mid-height	Height of the anterior end of the centrum	Width of the anterior end of the centrum	Height of the posterior end of the centrum	Width of the posterior end of the centrum
3	43 (±)	29 +		39	9.4 ±	11.0 ±	14.2	16.3
4	73	34 +		58	12.8 (±)	15.3		20.4
5			81	72				
6			90	78		24 (-?)		29.0 -
7			93	82		27.9 -		29.4 (±)
8	113		98	86 (±)	19.9 ±	21.9 +	24.4 +	24.7 (±)
9	123		98	85		32.6 (+)		35.2
10			100	87		36.0 (+)		40.6 (±)
11				87		41.0 -		43.8 (-)
12				81		43.0 (±)		47.2
13				67		46.3 ±		46.0 +)
14				46		42.6 +		43.0
15				36		41.2 (+)		
16								
17		107	36.0 (+)	28.5 +			26 ±	
18								
19								
20		77 +	33.0 (±)	29.4 (±)				
21								
22								
23		76 +						
24		79 +						

3rd to 4th, indeed almost by half; the increase to the 5th presacral vertebra amounts to barely a quarter that of the 4th presacral vertebra, then the increase in length becomes noticeably smaller up to the 8th presacral vertebra. From the 8th to the 11th presacral vertebra, length attains its maximum and thereby noticeably constant total of 88 to 89 cm. From the 11th to 14th presacral vertebra, the length is reduced to 48 cm in increasing leaps, and at 36 cm in the 15th presacral vertebra, already closely approaches the average length of the typical dorsal vertebra of approximately 30 cm.

Fig. 49. 10th–13th presacral vertebrae (10-13 cervical vertebrae) and 1st-2nd dorsal vertebrae in articulation (SII). Left lateral view.

1/10 nat. size

Fig. 50. The same vertebrae; ventral view. 1/10 nat.size

Fig. 51. 16th presacral vertebra (SII); right lateral view, 1/10 nat. size.

Fig. 52. The same vertebra, anterior view, 1/10 nat. size.

Fig. 53. 17th presacral vertebra (SII); left lateral view, somewhat more than 1/10 nat. size.

Fig. 54. The same vertebra. Anterior view, somewhat more than 1/10 nat. size.

Fig. 55. Isolated left diapophysis (SII); 1/10 nat. size.

The condyle becomes flatter in the transition to the trunk, nevertheless it retains a pronounced curvature as far back as the sacrum, as the 23rd presacral vertebra illustrates; the posterior end of the centrum retains a correspondingly strong excavation. The outline of the condyle and cotyle, which is lowered throughout the better preserved dorsal vertebrae of SII by crushing must, as made evident by the vertebrae from other sites (no, dd), have been almost perfectly circular.

The centrum of the 15th to 17th presacral vertebrae exhibits a somewhat depressed ventral field bordered by two rounded margins; in the remaining dorsal vertebrae in contrast, as in the three SII 121-123 (essentially preserved only as centra), they exhibit a median ventral ridge, which distinguishes the vertebrae of the larger posterior dorsal section of *Brachiosaurus* [sic].

The pleurocentral excavation is also shortened naturally in the transition to the trunk; in the 15th presacral vertebra it only consists of an approximately 7-cm-long oval hole behind the parapophysis. The pleurocentral excavation in the 17th presacral vertebra is shaped very differently on either side; on the right it has the outline of a semicircle about 14 cm long and 8 cm high, on the left, in contrast, it extends so far upwards anteriorly that an orthogonal isosceles triangle is formed. In vertebra S 21, the 20th presacral vertebra, the actual depression, which on the right side comprises a narrow, 11 1/2-cm-long and 5-cm-high oval, cuts into a wall with its upper rim, a wall which itself again recedes medially opposite the lateral wall of the neural arch. The pleurocentral excavation on the left side of the 23rd presacral vertebra consists of a deep excavation with a semicircular, sharp upper margin, from under which the centrum extends laterally, thick, and cylindrical.

Neural arch. In the cervical vertebrae, the actual basal portion of the neural arch, which encloses the neural canal, does not extend particularly far above the height of the canal; to a considerable degree, in contrast, in the dorsal vertebrae. In these, the massive, cubic, basal portion of the neural arch is built up upon the centrum, far above the height of the neural canal. A niche develops in its anterior side, close up under the level of the horizontal facets of the prezygapophyses; it is only hinted at in the 16th vertebra, but is very clear and 5 cm deep in the 20th vertebra; the neural canal sits at its base. A shallow niche on the posterior side of the neural arch of the 17th vertebra is only indistinctly preserved, in the 24th vertebra such a niche is not developed, as can be clearly seen.

Neural canal. The neural canal itself appears extraordinarily narrow in relation to the dimensions of the vertebrae, with the exception of the first cervical vertebrae. In the 3rd cervical vertebra of SII the anterior opening of the canal is approximately 2.7 cm wide, in the 4th vertebra the noticeably downwardly crushed posterior opening is about 3 cm high, 4 cm wide, in the 8th cervical vertebra the anterior opening cannot be precisely measured, about 3 cm high and wide, the posterior opening 3.5 cm high and 3.4 cm wide. In the dorsal vertebrae the anterior opening of the neural canal, crushed in every example, would not have been more than 5 cm high.

Prezygapophysis. The prezygapophysis of the cervical vertebrae from the 3rd onward are very strong, anteriorly tapering projections that extend considerably over the anterior end of the condyle; they are constructed of three laminae, namely the infraprezygapophyseal lamina, the supraprezygapophyseal lamina, and the prezygodiapophyseal lamina. Accordingly, the cross section of the prezygapophysis has three radii. The facet of the 4th cervical vertebra of SII is 7 1/2 cm long on the right and about 8 cm wide. The longer axis of the facet from the front upper surface proceeds laterally, then down medially towards the rear; its surface is strongly inclined medially, shallowly convex; in the very much larger 8th cervical vertebra it is about 10 cm long

Fig. 56. 20th (?) presacral vertebra (SII); right lateral view,  
1/10 nat. size.

Fig. 57. The same vertebra; anterior view, 1/10 nat. size.

Fig. 58, 59. Isolated centrum (SII), right lateral views,  
1/10 nat. size.

Fig. 60. 22nd (?) presacral vertebra (SII); lateral view,  
1/10 nat. size.

Fig. 61. The same vertebra, posterior view, 1/10 nat. size.

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and 8 1/2 cm wide. The surface of the facet does not increase in size in the same proportion as the vertebrae increase in size. The preserved left prezygapophysis of the 9th vertebra has a roughly triangular-shaped facet that is 13 1/2 cm long and 9 cm wide, and is slightly concave in the broader section, convex in the narrower section.

The prezygapophysis is shorter in the dorsal vertebrae than in the cervical vertebrae, it also sits higher and extends out of the raised, thick, lateral wall of the neural arch. The far larger anterior portion of the dorsal vertebral column is characterized by the development of a hyposphene on the postzygapophyses, unique to the sauropods. The nearly sagittally placed facets of the hyposphene correspond with identically positioned facets that are situated on the medial surfaces of the articular processes of the prezygapophyses. The distance between them totals about 8 cm in the 16th presacral vertebra, but only about 4 1/2 cm in the 20th and 23rd presacral vertebra.

**Postzygapophysis.** The postzygapophyses of the cervical vertebrae consist essentially of more or less sagittally situated walls that are reinforced at the upper rear and carry the lateral facing articular facets here. The articular facet has an oval outline, it is curved strongly concave and forms a column on a section of the surface that is strongly sloped toward the front. The postzygapophysis bears a highly rugose longitudinal tuberosity above and in front of the facet, the *processus dorsalis*. The strongly medially oriented right facet in presacral vertebra 4 of SII is about 8 cm long, 11 1/2 cm wide. The well preserved facets in presacral vertebra 8 of SII are informative, especially the left; it is oval, 12 1/2 cm long, 7 cm wide, steeply anteromedially shaped; the long axis of the oval proceeds obliquely posteromedially. The anterior portion of the facet is slightly convex; the rear is narrow, clearly concave, and extended forward laterally. This incline of the posterior section of the facet prevents the vertebra from bending laterally against the following vertebra.

In typical dorsal vertebrae the postzygapophyses extend out of the posterior side of the neuropophyses. The articular facets have the corresponding shape of the prezygapophyses, a horizontally (frontal) oriented and branching, vertically oriented sagittal section; both sagittal sections of the facets form the lateral walls of a pretty thin, wedge-shaped median zygosphene; the walls are somewhat more robust dorsally. The zygosphene of the 17th presacral vertebra is clearly thickened dorsally, wedge-shaped and about 10 cm high. In the last presacral vertebrae the horizontal section is much longer than the vertical section is high. The 22nd presacral vertebra SII 29 illustrates a particularly well preserved postzygapophysis. The slightly concave, narrowly elliptical horizontal facet is about 12 cm long, 6 cm wide. In contrast, the zygosphene is only about 5 cm high, but curves out widely backward with a rounded contour, and from the rear is deeply grooved along the median.

**Diapophysis.** In the cervical vertebrae the diapophysis extends steeply downward out of the extensive lamellae that together form the prezygodiapophyseal lamina and the posterior centrodiapophyseal lamina. In the cervical vertebrae of SII, in which the tuberculum is co-ossified with the diapophysis, the ossification site is recognizable as a rugose zone. In the 3rd cervical vertebra the diapophysis forms an almost rectangular thin flange; in the succeeding vertebra, one that has a triangular outline truncated by the facet.

The diapophysis of the 17th presacral vertebra extends far out laterally, giving the vertebra a total width of 110 cm, is a baulk that ascends somewhat laterally, and has an approximately cruciform cross section, in that the quite weakly developed supradiapophyseal lamina and the very large surfaced posterior centrodiapophyseal lamina form the perpendicular beam of the cruciform cross section, while

Fig. 62. 23rd and 24th presacral vertebra (SII); left lateral view.  
1/10 nat. size

Fig. 63. 23rd presacral vertebra (SII); anterior view. 1/10 nat. size

Fig. 64. 24 th presacral vertebra (SII); posterior view. 1/10 nat. size

Fig. 65. Posterior sacral vertebra (Find no 8); lateral view.  
1/10 nat. size

Fig. 66. The same vertebra; posterior view. 1/10 nat. size

the completely insignificant prezygapophyseal lamina and the paradiapophyseal lamina form the other baulk. An isolated right diapophysis (Fig. 55) differs somewhat in the low height of the distal end; with a length of about 43 cm the total width of the vertebra can be calculated at over one metre. The diapophysis must have belonged to a vertebra that followed the 17th vertebra. The diapophysis of presacral vertebra 20 (Å), of which a large distal portion as well as the parapophysis is missing, differs from that of presacral vertebra 17 in its medial section by the more significant width of the horizontal lamella. Two lamellae carry the diapophysis from below; the upright centrodiaepophyseal lamina, which crosses the anterior centropostzygapophyseal lamina at an acute angle, and the centroparapophyseal lamina. The diapophysis of the 23rd presacral vertebra is also a medially broad lamella; in presacral vertebra 24, in contrast, it is much narrower.

**Parapophysis.** The parapophysis of the cervical vertebrae issues laterally and flange-like from the ventral wall of the centrum, without a suture. In presacral vertebrae 3-12 the accompanying rib is co-ossified, the suture characterized as a rugose strip. However, in presacral vertebra 14, the first dorsal vertebra, the parapophysis forms a massive cone that carries a rugose facet; in the 15th vertebra it only protrudes slightly from the side wall of the centrum, in presacral vertebra 17 it sits with its upper end at approximately the same height as the upper margin of the prezygapophysis. In the 24th presacral vertebra the small parapophyseal facet is located about 14 cm before the lateral end of the diapophysis.

**Neurapophysis.** The neurapophysis of the cervical vertebrae is, as far as can be compared, formed completely identically in SI and SII. In the 3rd cervical vertebra (SI) the neurapophysis consists mainly of a rugose, rectangular knob, thick at the back and narrowing at the front. In the following vertebrae the terminal head becomes more lath-like, in part irregularly thickened and obliquely bordered, as in the 8th presacral vertebra of SII. In this vertebra it is about 20 cm long and 8 cm wide. The terminal knob exhibits a fine, fibrous, longitudinal structure, which is very obvious at the sides, but which also extends posteriorly. This illustrates that the dorsal elastic ligament was attached over quite a large surface and was certainly very strongly constructed. The niches, laterally enclosed on one side by the suprapre- and on the other side by the suprapostzygapophyseal laminae, approach one another in the median plane to within a small distance, which measures only 10 cm in the large vertebra presacral 8 (SII); between them runs a very thin median septum upon which the terminal knob sits.

The neurapophyses are missing from the 9th to the 16th presacral vertebrae inclusive; more or less completely preserved in the 17th vertebra, in the 23rd and 24th, as well as in those vertebrae that are considered to be the 20th and 22nd presacrals. The neurapophysis of the 17th presents quite a tall rod that is about 7 cm thick and is only supported by weakly developed lateral laminae. Its dorsal end broadens quickly to about 24 cm toward the rounded profile terminal section.

In the 23rd and 24th presacral vertebrae the neurapophysis is much broader than in the 17th vertebra, but at the same time much lower; it has the pronounced cross section of a cross, which is formed by the anterior, posterior and the two lateral longitudinal laminae. The prespinal lamina projects about 6 cm on average in both vertebrae; the supraprezygapophyseal lamina, quite massive in the 23rd vertebra and thinner in the 24th vertebra, is attached laterally to its anterior margin, faces obliquely outward, and simultaneously thereby broadens the prespinal lamina considerably; [the prespinal] lamina marks its actual area between the supraprezygapophyseal laminae in the anterior view, by a narrow, rugose median zone. Noticeable in the 24th vertebra is a thick, extraordinarily rugose, arch-like projecting outgrowth of the prespinal lamina in its upper section.

The postspinal lamina in the 23rd vertebra projects arch-like as a thick wall on the lower three quarters of the height of the neurapophysis. The entire contour corresponds to that of the prespinal lamina of the 24th vertebra so that they articulate exactly. Presumably both vertebrae almost touched each other at the thick, strongly rugose margins of the laminae and were connected by ligaments. The present distance is obviously the result of displacement caused by crushing. The broad terminal section of the neurapophysis of the two last vertebrae has a semicircular contour; it bears a bone lamella of semicircular wheel shape, which is about 11 1/2 cm wide in both vertebrae.

The neurapophysis of vertebra S 29, presumably the 22nd presacral vertebra, connects to that of the last two vertebrae through a broad outline. The neurapophysis of vertebra S 21 (? 20th presacral vertebra), which has perhaps been mounted too low, stands between the 17th and the final presacral vertebrae according to its morphology.

The most severely felt deficiency in preservation and thus also in the description in the presacral vertebral column is the lack of neurapophyses in the vertebrae from the 9th to the 16th. It may be asked whether the missing neurapophyses of these vertebrae were bifurcated like those in the previous cervical and following dorsal vertebrae, or whether they were partly or completely bifurcated as in *Diplodocus*, *Dicraeosaurus*, *Camarasaurus* and *Apatosaurus*. In all these genera the bifidity is already obvious before the 9th and even after the 16th presacral vertebra. It can be assumed that the neurapophyses in *Br. brancai* were undivided throughout, since no indication of bifidity can be found in either the 8th or in the 17th, or even only any indication of metapophyses.

Posterior dorsal vertebra AR 1 from the Middle Saurian Marl (Plate I, Ill. 9-11). The vertebra exhibits little crushing, the diapophyses and the greater portion of the neurapophysis are missing. The apparently uncrushed centrum is remarkably short; the pleurocentral excavation sits high, which, among the vertebrae of comparable grade in SII, only the 24th presacral vertebra illustrates. The anterior end surface is large, strongly vaulted in its mid-section. The posterior end surface is significantly wider than high, slightly concave. The postzygapophyses possess very large facets. The horizontal portion of the left extends 11 1/2 cm laterally. The zygosphenes, a 24 –37-mm-strong, almost parallel-surfaced wall, has the noticeably great height of almost 13 cm. The neurapophysis is missing most of the attached laminae; its low elevation above the horizontal facets of the postzygapophyses, like the morphology of the centrum, indicates a position for the vertebra at the end of the sequence.

Posterior dorsal vertebra no 1 from the Upper Saurian Marl (Fig. 65, 66). The lateral sections of both diapophyses are missing. The centrum is slightly shortened in the direction of the long axis, the anterior and particularly the posterior end surface is thereby crushed broader out of its original shape. The anterior end is quite convex; it is, like the rear, considerably wider than tall. The middle section of the centrum appears to be too strongly compressed ventrally due to crushing. The pleurocentral excavation sits in about the upper third of the lateral wall of the centrum, and is low, considerably shorter on the right than on the left. The neurapophysis is broad and low, in any case likely lowered somewhat because of compression.

Vertebra no 1 exhibits major correspondence to presacral vertebra 23 of SII and may be the 23rd or perhaps one of the immediately preceding vertebrae.

### Surface sculpture.

In the preceding description of the main architectural elements of the presacral vertebrae the morphology of the neural arch, the shape of the apophyses as well as the course and position of the laminae that form them, were presented in their essential character. The cervical vertebrae are, beyond this, distinguished to a high degree by the extremely developed surface sculpture. Extensive excavations, depressions in the surfaces of the laminae, further reduce the already weak lamellae. The outline of these "external cavities" is usually more or less rounded, circular, elliptical, egg-shaped, but also three and more sided with rounded corners. Laminae of a second order occur on the depressed surface areas of the external cavities, especially when these are of a greater expanse, and run in the direction of stress forces. Such laminae also occur on the surfaces that delineate the pleurocentral cavities medially. External cavities appear on the lateral surfaces of the neural arch, on the dorsal side of the parapophyses, here most often very strongly developed on the supraprezygapophyseal lamina, on the posterior centrodiapophyseal lamina, on the postzygodiapophyseal lamina, on the posterior centrodiapophyseal lamina, on the lateral laminae of the neurapophysis and attached farther ventrally. Almost all laterally and dorsally oriented surfaces of the neural arch and the apophyses are occupied by such external cavities; only the diapophysis is quite free of them.

It can be clearly recognized that the complexity of this external sculpture increases in the series of cervical vertebrae that increase in size. In the 8th cervical vertebra (Fig. 1, 43) the surfaces of the individual architectural portions are absolutely pitted by the numerous incised external cavities. The picture becomes diverse and turbulent to an increasing degree with the appearance of laminae of the second order. It can be assumed with certainty, though it cannot be confirmed in the available material, that the external sculpture became more complicated after youth, with increasing size.

The support and motion of a neck as long and heavy as in *Brachiosaurus* subjects it to such significant stresses that it had to be extensively lightened by a hollow construction and, as I believe I must accept, through the development of a system of pneumatic spaces. Since these stresses do not occur in the same way and to the same degree in the dorsal vertebrae, their external sculpture was not modified as strongly as occurred in the cervical vertebrae. Yet in these, the hollow construction of the dorsal end of the neurapophyses, the terminal knob of the diapophyses, as well as, sporadically, the parapophysis (17th presacral vertebra), is noteworthy. Invasive cavities are found at these sites under the terminal ends and under the articular facets respectively. The anterior wall of the anterior centrodiapophyseal lamina can also exhibit depressions, which in their character resemble external cavities.

### Structure of the centrum.

The overall extensive hollowing out of the centrum by the deeply invasive pleurocoels is illustrated by a transverse fracture through a dorsal centrum from Quarry dd (Fig. 67). Appropriate to the exceptional preservation in this quarry, the shapes are somewhat distorted or compressed, but asymmetry is likely not caused thereby, if somewhat increased. The transverse fracture illustrates how extremely thin the partly restored median septum between the pleurocoels is; in places it is only millimeters thick. The pleurocoels are extraordinarily widely opened; the cavities also particularly invade the ventral wall of the centrum.

A very similar view is illustrated by the cross section of a dorsal centrum of *Camarasaurus* (= *Morosaurus*) *grandis* figured by Marsh (1896 p. 181, Fig. 33), as well as the cross section through a small posterior centrum of *Camarasaurus lentus* (Marsh 1896, Plate 32, Ill. 2a). The two dorsal centra possess equally deeply invasive pleurocoels and a thin median septum; one is from a juvenile that J. W. HULKE (1879) describes and figures with the genus name *Ornithopsis* from the English Wealden, furthermore a dorsal vertebra of *Bothryospondylus madagascariensis* [sic] THEVENIN (1907, Fig. 5). All of the cited cross sections exhibit a similar degree of specialization as *Brachiosaurus*, in relation to the degree of excavation of the centra by the pleurocoels.

Fig. 67. Cross section through a dorsal centrum  
(Quarry dd). 1/4 nat. size

Fig. 68-70. Transverse section through the condyle of a  
cervical vertebra (Find Aa). 1/3 nat. size  
Fig. 68. Anterior section. Fig. 69. Same vertebra reconstructed.  
Fig. 70. Posterior section.

To understand the interior structure of the condyle of the cervical vertebrae, sections were prepared from two specimens. The condyle of a large posterior cervical vertebra from Find Aa was transversely sectioned twice at 3 1/2 cm intervals. Like the external morphology, the cross section also exhibits the characteristics of considerable compression, which lowers the outline dorsoventrally, compresses the ventral wall, and has disturbed the interior lamellar structure. Figures no. 68 and 70 reproduce views of both sections, details enhanced by combining the views of both sides of each section, which are not completely congruent due to the thickness of the section. Fig. 69 is a reconstruction of the anterior cross section, in which it was attempted to graphically illustrate the crushing and the fractures of the interior lamellae. The interior of the condyle exhibits a highly cancellous structure; the anterior transverse section exhibits only five

Fig. 71  
Sagittal section through the condyle  
of a cervical vertebra (SI).  
1/3 nat. size

Fig. 72  
Sagittal section through the anterior end  
of a dorsal vertebra (Find W).  
1/3 nat. size

Fig. 73  
Half transverse section through the  
centrum of the same vertebra  
as Fig. 72. 1/3 nat. size

large cavities; the number is higher in the posterior section where smaller lateral cells occur in addition to the large central cells. The walls of the cells are for the most part very thin, often no thicker than 1 mm. In thinner areas the structure is much more compact than in the thicker areas and outer wall. A sagittal section near the median plane of the moderately dorsoventrally compressed condyle of a fragmented middle cervical vertebra from Find SI is illustrated in Fig. 71, and indeed without any noteworthy corrections of the section illustration. The figure illustrates a wreath of small short cells sectioned; while caudally a few extensive elongated cavities running quite parallel were caught. Their lack of a posterior termination can be confirmed in the vertebrae themselves, while the section illustration does not extend sufficiently caudally, and only displays the free end of a cell wall at one site. The separating walls appear very robust in places, a consequence that the

section falls in the plane of these lamella-like septa here. The sections through the cervical vertebrae of SI and Aa illustrate that the external wall of the condyle is much more robust dorsally than ventrally. This may be related to the fact that the dorsal side of the condyle was burdened by the weight of the preceding section of the neck. The difference in the strength is also recognizable in the sagittal section, however, not as clearly since the dorsal wall is not preserved for the most part.

A large dorsal centrum from Site W in the Middle Saurian Marl, broken into numerous fragments, furnishes particularly valuable information about the interior structure. The lamellae and septa that run through the interior of the centrum are excellently preserved and strengthened by a calcareous hardened crust, so that the cavities could be exposed by removing the soft marl, and their morphology becomes extremely clear. A sagittal section was made through the anterior end of the centrum almost exactly in the median plane; the right half was then sectioned in a transverse plane at a distance of 8 cm from the site at which the condyle projects the farthest. The overall character of the interior structure of the centrum is distinguished in that it is interwoven by large cells, whose septa are quite robust, usually 4-8 mm thick. All outer walls are particularly thick. The excavation of the centrum is by far not as extreme as, for example, in *Barosaurus*, in the dorsal centrum of which only a very thin outer wall has remained. The inner median septum, characteristic of the excavated presacral vertebrae of many sauropods, unusually does not separate the entire inner space of the centrum, but rather only the upper half; in the middle section it is fused at a right angle with the floor of the left pleurocoel, while it is not filled on the right.

The sagittal section (Fig. 72) illustrates that the anterior end of the centrum in the region of the condyle is filled by large cells that clearly diverge anteriorly. The second lowest of these cells is connected with an extensive low chamber that passes through the entire vertebra in a frontal plane. This chamber is also roofed by a frontally situated plate that simultaneously forms the floor of the pleurocentral excavations in the middle section of the vertebra, as can be clearly recognized in the transverse section (Fig. 73). Ventrally the chamber and associated spaces are in widely open communication. A low extensive cavity is also visible above the plate, which, however, narrows and closes posteriorly. Above this are situated the smaller, rounded or elongated, partly coalescing cross sections of the cells that invade the condyle. Bone tissue, usually more than 3 cm thick in the dorsal, ventral and anterior septum formed by the condyle, is predominantly cancellous.

An extensive chamber is found in the posterior section of the centrum (which is not exposed in the sections) as an extension of the aforementioned large, frontally expanded cavity, but which is separated from the cavity posteriorly by a transverse wall, and which is enclosed by the wall of the cotyle that is 3 1/2 cm thick on average, and ventrally by the 1 1/2- to 2-cm-thick ventral septum. The pleurocoels expand dorsally against the floor of the neural canal; in addition, on the right, three visible cells extend dorsally from the canal into the lateral walls of the canal, and make it decidedly hollow. The septa of the cells and chambers are interrupted in numerous places by openings so it is unquestionable that the cavities all communicate with one another and furthermore with the pleurocoels.

The structure of the dorsal vertebra from the Wealden of the Isle of Wight, which R. OWEN (1875 Plate 9, Ill. I) figures as *Bothryospondylus magnus* [sic], is much smaller-celled.

If one accepts that in sauropods, as in birds, air sacs invaded the vertebrae and indeed through the pleurocentral openings, then one can further conclude with considerable probability, that the large cells in the vertebral condyles that were connected to pleurocoels were pneumatic.

### **Sacrum.**

Sacrum of the Quarry Aa (Fig. 74, 75). The sacrum lay on its right side and was so extensively eroded, that of the sacral vertebrae, only the upper right half of the fifth, further the neurapophyses, the right diapophyses and transverse processes are preserved. The latter too, are incomplete to a degree, particularly the second and third in their lamellar sections.

The incomplete fifth centrum possesses a nearly flat end surface with a tuberos thickened margin. The posterior entrance of the sacral neural canal has a triangular outline; it is 7 cm high and about 8 cm wide. The transformation of the neural canal is only preserved in the fifth sacral vertebra; the height remains approximately the same in its passage here.

The two final neurapophyses are separated; the three anterior ones are fused. The final one presents a plate of very rectangular outline. A short, thick supradiapophyseal lamina sits low on the side. The upper margin of the neurapophysis is hardly thickened; its free height above the diapophysis measures 22 1/2 cm. The neurapophysis of the fourth sacral vertebra is similar to the preceding one; it is somewhat longer, on average 15 cm long in its upper section. The greatest difference is that the thicker, thickly reinforced dorsal end of the neurapophysis extends laterally and roofs, with a sharp margin, two successive excavations; posteriorly this thickening is further reduced on both sides and proceeds to the suprapostzygapophyseal lamina. The outline of the neurapophysis of the 4th vertebra is fused with the preceding neurapophysis for about one third of its height. The neurapophysis of the first three sacral vertebrae is fused into an undivided thin plate; its dorsal end is increasingly thickened in the 3rd and in the 2nd vertebra. Descending remnants of thin lamellae on the neurapophyses are interpreted as supradapophyseal [sic] laminae. Rounded cavities (external excavations) deeply invade the three neurapophyses underneath the terminal surfaces. Of the 48 cm total length of the terminal neurapophyses, about 17, 17 and 14 cm grow over the individual vertebrae from posterior to anterior.

The lateral processes are composed of the diapophysis, the parapophysis and the sacral rib, which constitutes by far the majority. Sutures between parapophysis [sic] and sacral rib cannot be confirmed; between the diapophysis and the sacral rib in contrast, they are generally clearly recognizable. The lateral process of the 5th vertebra is a large plate, quite thin in the middle, about 29 cm high medially, approximately 36 cm laterally. The diapophysis may be seen in the anteriorly extending dorsal margin of the middle section. In the lateral half, the upper margin is repositioned far to the rear in a ridge. As in all four posterior sacral ribs, the robust lower margin is thickened laterally to a massive cone. The greatest distance of this surface from the median plane measures about 40 cm. The 4th lateral process is more upright than the 5th and about 31 cm high; it is only a few mm thick over much of its area. The diapophysis is revealed as a laterally narrowing plate. The diapophysis is significantly broader in the 3rd transverse process than in the 4th. About the very incompletely preserved sacral rib it can be said that it

Fig. 74. Sacrum (Find Aa); right lateral view. 1/10 nat. size

Fig. 75. The same sacrum; view obliquely from above and behind.  
1/10 nat. size

Fig. 76. Sacrum (Find T); ventral view. 1/10 nat. size

was very thinly lamellar other than in the very robust, conical lower section, and that the lateral margin did not extend continuously over this as far as the ilium, but rather left an extensive opening. The height was greater, medially and laterally, than in the 4th transverse process. The 2nd transverse process must have been similar to but higher than the 3rd. The diapophysis, which roofs a deep niche open at the posterior end, is about 14 cm wide laterally. With the exception of the posterior sacral ribs, the incompletely preserved conical thickening sends up a thin anterior and posterior septum, both of which, however, are only preserved in a small area; they enclose a wide chamber. The diapophysis is narrower in the first transverse process; thereby it differs considerably from the posterior ones in that it has a triangular outline and is pronouncedly convex anteriorly. The lower margin that descends steeply dorsolaterally, becomes only very slightly more robust laterally, and although the lower lateral section is not preserved, it can clearly be recognized that a similarly massive reinforcement like that in the other ribs was not developed. The lateral margin of the thin plate that is preserved in the dorsal section is very thin and did not extend here up to the ilium. A rounded expansion is only found dorsally, which indicates an attachment site for the ilium. The first transverse process considerably exceeds the others in extent; the preserved three sided plate has a length of about 50 cm on each side.

Sacrum from Quarry T (Fig. 76). Quarry T in the Upper Saurian Marl has yielded the remains of a juvenile *Brachiosaurus*, among which was a sacrum in addition to dorsal vertebrae. The preservation is poor in that the external morphology is often distorted as a result of internal crystallization processes. The walls of the neural arches are incomplete; the diapophyses are almost completely missing.

Four sacral centra are present; the two middle vertebrae are articulated while the last two are separated; the anterior half of the last vertebra is missing; the rugose surface of its posterior shallowly concave end surface illustrates that a final 5th centrum bordered it. The first centrum very strongly resembles that of a posterior dorsal vertebra; its anterior end surface is strongly convex, about 25 cm wide. The incomplete height, a result of poor preservation of the ventral margin, can be estimated as 18 cm. Extensive pleurocentral excavations invade so deeply that it appears that only a very thin median lamella separates them.

The anterior opening of the sacral neural canal is laterally enclosed by a robust wall that grows out over the posterior end surface, about 9 cm upward and far out laterally. Between both of the broadened end surfaces, the flattened ventral side of the centrum is strongly waisted, up to about 20 cm; a shallowly rounded ridge proceeds along the median. The anterior section of the quite quadratic ventral side of the second centrum is, similar to the first, flat with a low, rounded median ridge. The third centrum is distinguished in that its ventral section very rapidly narrows to a cylinder that originally is not more than 4 cm wide in the middle. The 4th centrum, of which the anterior portion is missing, is once again greatly narrowed ventrally to almost 5 1/2 cm in its linear centre. The rugose posterior end surface is elliptical, about 17 1/2 cm high and 14 1/2 cm wide.

The transverse processes are missing the diapophyses. The ascending, dorsally thinner, largely sheet-like sections could not be reassembled from the numerous fragments into which they had fallen. The ventral cross members, most of which are compressed and therefore shortened, are common in the three middle sacral ribs, in that they are slender in their middle section, are greatly thickened medially, but particularly, become massive block-like heads laterally, which exhibit the extensive sutures for the ilium.

The dorsal view of the centrum illustrates that the neural canal is about 6-7 cm wide between the lateral sections of the walls that are present dorsal to the neurocentral suture. A small, approximately 2-cm-long depression is found in the first centrum, about 4 cm before the anterior end surface of the centrum, median in the floor of the neural canal. In the second vertebra, a noticeably large, about 5-cm-long excavation with perpendicular walls is sunk into the centrum; in the third it is equally long, but wider and thereby even more extensive; its posterior wall, however, descends obliquely forward. The isolated posterior half of the floor of the neural canal of the fourth vertebra is completely level.

The total length of the three anterior sacral vertebrae measures about 48 cm in the median plane, of which about 14 cm comprise the first; the restored fourth vertebra may have increased the length to 66 cm. In the second vertebra the lateral displacement of the lateral sutures of the ilium on the ventral margin can be estimated at about 60 cm.

The preserved portion of the right side of the neural arch permits few statements about the sacral neural canal. The intervertebral section of the neural canal between the second and third sacral vertebra is expanded to an extraordinarily spacious, approximately 20-cm-high and 13-cm-long chamber, from which a canal ascends dorsally. In the region of the third sacral vertebra, the roof of the neural canal sinks downwards perhaps 5 cm. This intervertebral constriction of the neural canal is broad and flat, thus does not have the character of an invasive thin lamella, as I have found them in *Dicraeosaurus sattleri* (JANENSCH 1933).

The neurapophyses of the four anterior sacral vertebrae are preserved, of them the second and third are tightly fused without recognizable suture; the first is still unfused, and the neighbouring surfaces on it and the second neurapophysis match so precisely that the cartilage suture could only have been narrow. The fourth neurapophysis, whose articulation with the neural arch is preserved, is unfused throughout its entire length. The neurapophyses, considered as a whole, present a thin bone wall on which lateral vertical laminae are slightly developed. The dorsal margin is thickened to a rounded axial swelling to a moderate degree. The low height of the neurapophyses is apparent in the unfused height of the fourth neurapophysis, which only measures about 23 cm. The cranio-caudal length of the dorsal margin measures approximately 13 1/2 cm in the first neurapophysis, for the two succeeding fused neurapophyses after the deduction of two gaping transverse fractures, 30 cm, and for the 4th, 11 1/2 cm.

The comparison of the sacra of Finds Aa and T must be limited to few points due to the varied incompleteness of both. It must be taken into consideration that Find T comes from a much younger animal, and that the age difference can also have caused morphological differences. That could have been the reason that the pyramidal lateral lower enlargement of the sacral ribs of Aa is more massive throughout than in T. The difference in robustness is particularly noticeable in the fourth sacral rib. The neurapophyses of both sacra are very alike. The somewhat lesser degree of fusion of the neurapophyses in sacrum T in contrast to sacrum Aa is certainly due to a lower age.

## **Caudal vertebrae.**

### **Material.**

From the Middle Saurian Marl:

Find Aa: Articulated vertebral column, including the anterior 18 vertebrae and haemapophyses.

Find p: 11 anterior caudal vertebrae, not completely articulated.

Find dd: 14 isolated vertebrae from the anterior, middle and posterior sections.

Find Gl: 16 isolated centra from the anterior, middle and posterior sections.

Find St: 4 anterior vertebrae.

Find Y: 2 vertebrae from the middle section.

From the Upper Saurian Marl:

Find D: 29 vertebrae, of which 23 are articulated behind the sacrum.

Find no: 50 caudal vertebrae in original sequence, from the second onward.

Isolated finds.

### **Description.**

The best preserved caudal vertebral sequence from Find Aa is placed in the foreground of the description, which comprises the anterior and a portion of the middle section. Find D informs us about the posterior section of the middle section. Finally, Find no elucidates the posterior section. The remaining finds listed are only briefly considered. Several isolated finds of caudal vertebrae are not considered, with the exception of vertebra J 40.

Caudal vertebral sequence Find Aa (Plate II). The caudal vertebral sequence of Find Aa lay in unbroken articulation behind the last sacral vertebra and comprises the anterior 18 vertebrae (catalogue number Aa 17-34). Since the sediment in which the vertebral sequence was embedded was highly consolidated, fine grained lime sandstone, the vertebrae exhibit only insignificant compression. The left transverse processes are missing up to the 7th vertebra. In other respects the vertebrae are completely preserved except for the right transverse processes of the 3rd and 5th vertebrae, both prezygapophyses of the first, the right of the 3rd and several missing elements, mostly on the margins of the end surfaces of the centra.

The centrum of the first three vertebrae has the form of a thick circular plate. The length of the centrum hardly changes at all in the following vertebrae. However, height and width are steadily reduced from the 2nd vertebra onward, initially strongly, later less so. The thick-plated morphology of the centrum then transitions to a more short-columnar shape. Since the height is reduced noticeably more sharply than the width from the 4th vertebra onward, the circular outline of the end surfaces of the first vertebrae changes to a short-elliptical outline in the following vertebrae.

The margin of the anterior end surface of the 3rd to 15th vertebra extends slightly forward dorsally. The dorsal half of the anterior end surface of the first caudal vertebra extends strongly forward, certainly in accordance with a corresponding retraction of the ventral half of the posterior end surface of the last sacral vertebra.

The anterior end surface is sunk concavely to a small but not equal degree in all vertebrae. In most vertebrae, particularly strongly in the first, a field in the middle, under the

upper margin, is clearly swollen convexly out of the concavity. The posterior end surfaces are, like the anterior ones, clearly but usually not strongly concave; from the 8th to the 11th vertebrae they are noticeably more concave than the anterior vertebrae. An encircling facet up to 2 cm wide is obliquely beveled on the margins of the posterior and anterior end surfaces, upon which, certainly, the ligament connecting the neighbouring vertebra was attached. The centrum is strongly waisted between the end surfaces; the kind and degree of narrowing here determines the shape of the transverse section. In the first caudal vertebra the waisted lateral surfaces clearly converge ventrally, whereby the ventral surface becomes constricted. In the 2nd vertebra in contrast, the ventral surface is much broader, to once again become increasingly narrow in the following vertebrae.

Dimensions of the caudal vertebrae from Find Aa in cm.

Position in the caudal vertebral sequence	Length of the centrum at mid-height	Anterior end of the centrum Height	Anterior end of the centrum Width	Posterior end of the centrum Height	Posterior end of the centrum Width	Total height of the vertebra	Total width of the vertebra
1	14.5 +	23.0 (+)	22.3 +	23.9	23.4 (+)	51.9	
2	14.3	23.6	23.9 (+)	22.0	22.5	47.6	
3	14.5	22.4	23.4	20.9 (+)	22.5	44.3	
4	14.3	20.8	22.9	19.5	21.5	41.1	
5	14.6	19.1	22.1	18.7	21.2	38.0 (±)	
6	14.2	17.9	21.3	18.2	20.1	35.6	
7	15.0	17.2	20.4	18.0	20.2	34.3	
8	14.9	16.3	20.7	17.3	20.8	32.3	29.1
9	14.6	15.1	20.0	15.4	19.3	30.2	
10	14.5	14.2	20.1	15.3	19.2	28.8 (±)	23.3
11	14.6	13.6	19.4	14.5	18.5	28.1	20.5
12	13.9	13.5	18.7	13.6	18.0	26.8	18.2
13	14.2	13.2	17.6	14.4	16.6	25.9	16.4 (+)
14	13.9	12.9	16.9	13.5	16.2	24.2	14.9
15	14.2	12.2	16.1	13.2	15.3	23.5	13.4
16	14.1	11.5	15.6	12.3	14.6	22.3	12.3
17	14.0	11.4	14.9	11.0	14.1	21.2	11.6
18	13.8	10.7	14.2	10.1	13.3	20.1	10.5

The facets for the haemapophyses are not clear on the posterior end surface of the 2nd to the 4th vertebra, but become clear from the 5th vertebra onward. Pleurocentral excavations are absent; only under the root of the transverse process of the 2nd is an elongated, about 4-cm-long depression clearly developed, particularly on the right.

Since the neural canal descends strongly posteriorly in the first vertebra the posterior end surface sits considerably deeper than the anterior; this already diminishes in the 2nd vertebra and from the 6th vertebra onward the neural canal proceeds nearly parallel to the longitudinal axis.

In general the neural arch is quite simply constructed; it encircles the neural canal roof-like with thick walls. The cross section of the neural canal in the 2nd vertebra is about 44 mm high, 38 mm wide slightly behind its anterior opening; by the 18th vertebra these figures have been reduced to 20 and 25 mm;

the neural canal is thus taller than wide in the anterior vertebrae; in the course of the vertebral column it becomes wider than tall.

The transverse process is predominantly formed from the caudal rib; the suture of these vertebrae is not recognizable. In the anterior vertebrae it is also of smaller size and simple construction, compared with other sauropods. A laminar formation is recognizable to a slight degree in the first vertebra. The distal portion is flat, about 9 1/2 cm wide, bent posteriorly in a hook shape; out of its anterior a thin lamella descends outward against the centrum; a second thin anterior lamella ascends obliquely to the prezygapophysis. In the following vertebrae the transverse process becomes a simple, flat, weakly posteriorly directed peg without laminae, and is constantly reduced in length, width and robustness; from the 6th vertebra onward an elongated rugose swelling that ascends obliquely anteriorly forms over the anterior end of the peg, which may have served as the insertion point of a muscle or tendon. The transverse process is only a short point from the 11th vertebra onward, from the 15th, an insignificant knob.

In all vertebrae at hand the neurapophysis presents a simple, rectangular, plate-like, posterior leaning process, the height of which decreases constantly, and which in the posterior vertebrae is noticeably lower than tall. Anterior and posterior margins are rough and rugose; the interspinal ligament attached to them. The profile of the dorsal margin of the neurapophysis is straight or forms a slight wave.

In the first vertebrae the prezygapophyses are broad processes that strongly ascend anteriorly. From the 4th vertebra onward the prezygapophysis becomes narrower, furthermore finger shaped and peg shaped in the final vertebrae. The articular facet of the 2nd vertebra is level and the angle measures 70°. In the 5th to 6th vertebra the vertical positioning is also about 10° less; the outline broadly elliptical. The posterior vertebrae on the other hand exhibit a somewhat more vertical placement of the facets; their outline in these vertebrae is more or less narrowly elliptical to egg shaped. The distance between both facets of one vertebra, measured between the mid-points, is noticeably the same in the entire vertebral sequence.

In most vertebrae the postzygapophyses extend as short processes over the posterior contour of the neurapophysis, longer only in the last vertebrae; laterally only their dorsal margin extends over the lateral wall of the neurapophysis. A small depression is found between the posterior margins in the first vertebrae, which becomes unclear in the succeeding vertebrae. The postzygapophyses fuse ventrally in the first vertebrae, and form a solid wedge that one could compare to a zygosphenon.

Caudal vertebral series Find D (Plate III). The vertebral column of skeleton D comprises 31 vertebrae, according to the Find Catalogue, that lay attached to the very poorly preserved sacrum in original sequence in the sediment. In any case, only 29 vertebrae are present; a gap is obvious behind the 23rd vertebra and also again after the following similarly sized vertebra (D 30). The five smallest (D 26-29, D 31) again appear to constitute an articulated series, even if somewhat different from the catalogue numbers. The dorsally directed upper arches are completely preserved in only a few vertebrae; they are also for the most part somewhat reduced in height by compression. The centra of the anteriormost four vertebrae are also somewhat compressed dorsoventrally, perhaps as a consequence of this compression.

The centra of the anterior vertebrae, as in tail Aa, exhibit parallel anterior and posterior margins, but none are wedge shaped.

Dimensions of the caudal vertebrae from Find D in cm.

Position in the caudal vertebral sequence	Length of the centrum at mid-height	Anterior end of the centrum Height	Anterior end of the centrum Width	Posterior end of the centrum Height	Posterior end of the centrum Width	Total height of the vertebra	Total width of the vertebra
1	12.3 +	21.0 (+)	24.7	22.2 (±)	25.0		
2	12.6	20.5 (+)	25.5 (±)	21.7 (±)	24.4	39.7 (+)	45.0
3	12.2	21.1 (+)	25.0 (-)	19.9 (+)	23.1	39.3 (+)	
4	12.6		23.5	19.1 (+)	22.2		
5	13.1		22.4 (±)	17.9 (±)	21.3 (±)	33.04 +)	
6	13.0	17.3 +	20.5	17.1 (±)	20.3 (±)		
7	12.8 (+)	17.6	18.3	17.4 (±)			
8	12.7	15.3 (+)	16.1 (+)	15.5	18.5	30.4	
9	12.8	15.2	17.2	15.5	17.5 (±)		25.2 +
10	13.0	14.7		15.1	16.5		
11	13.0 (±)	14.4 (±)		14.7	15.7		
12	12.8 (±)	13.4		13.9	15.6		
13	13.1	13.3	15.7	13.6	15.2		
14	12.8	13.2	14.4	12.8 ±	14.6		
15	12.5	12.2 (+)	13.9 (±)	12.3 ±	13.3		
16	12.8	12.4 (±)	13.6 (±)	11.3 (+)	12.8		
17	12.3	11.8	12.3	10.5	12.3		
18	12.5			10.4	11.7		
19	12.0	10.0		9.8	11.4		
20	12.2	9.6	11.3	9.2	11.1	17.5	
21	12.4	9.3	10.7	8.9	11.1		
22	12.7	8.3	11.0	9.0 a)	11.2	19.5	
23	10.9 b)	8.8	10.9	8.1	11.0		
Gap							
?		7.4 (+)	9.8				6.2
Gap							
?	11.2	7.2	9.3 c)				
?	11.3 d)	6.5 ±	8.0	6.7	7.6		4.6
?	10.7	6.9	7.7	6.1	7.5	11.1	4.5
?	10.2	6.7	7.5	6.3	7.5	11.0	5.1
?	9.6			5.9	7.0		4.3

a) Abnormally high. b) Abnormally short. c) Broadened by pachyostosis. d) Abnormally oblique.

The centrum of the first vertebra from D has a very much broader ventral surface than the first from Aa; nevertheless, that of the second is still considerably wider; in the following vertebrae it again becomes narrower. As in Aa, a short and narrow cavity is present below the transverse process of only the second vertebra. The resemblance in morphology and size of the transverse process of the first caudal vertebra is complete in both tails, while in the following vertebrae the transverse processes in D are relatively less robust and narrower than in Aa. The neuropophyses of both series are very similar in height, morphology and orientation; only in the anterior vertebrae are they somewhat thicker than in Aa.

The posterior vertebrae of series D attain an increasingly cylindrical shape. The neurapophysis in the 20th vertebra is a low plate; in the 22nd vertebra the posterior section of the neural arch is an obliquely ascending process with a roof-like dorsal side. Furthermore, the neurapophysis disappears around the 30th vertebra; the posterior section of the neural arch has become a posteriorly oriented spike on which the postzygapophyses are hardly still noticeable; it exceeds the robustness of the prezygapophyses only a little, which have maintained the character of half-round rods.

Caudal vertebral column Find no (Plate IV). The 50 vertebrae were not articulated, with the exception of a few at the end, but altogether relatively in sequence. For the most part the bones are compressed, frankly distorted and in places distended by calcite filled fractures. The upper arches in the larger vertebrae are frequently somewhat dorsoventrally compressed. In most cases the volume of the vertebrae has been decreased by the distortions. The neurapophyses are missing in a number of the anterior vertebrae; the preserved neurapophysis of the second vertebra is thick, block-like, that is, somewhat different from Aa. In other respects, despite the poor preservation of the anterior 30 vertebrae it can be recognized that these do not differ from those in the other two vertebral sequences in any noteworthy manner. Their dimensions provide values that are uncertain in large part. The size relationship of Aa and no proves to be approximately 4:5 from the comparison of the caudal vertebrae. It can be said about the overall morphology of the centra, that the end surfaces of the centra are wider than tall up to the 30th vertebra. The first caudal vertebra is missing.

The vertebrae of the posterior tail section of no permit the description of the anterior and middle tail section based on Finds Aa and D to be supplemented. The anterior caudal vertebrae of no from the 32nd vertebra onward are not or not significantly crushed. Certainly the upper arches are missing the projecting zygapophyses throughout and the spine-like posterior processes that correspond to the postzygapophyses are often completely or for the most part missing.

The well preserved centra from the 32nd vertebra onward exhibit an elongated columnar shape with rounded cross section, which is usually somewhat shorter than wide; but also in part equally tall as wide in the anterior vertebrae. The cross section increases significantly to the anterior and posterior end of the centrum. The end surfaces of the centra are approximately circular in the anteriormost vertebrae of this end series; in part slightly lower than tall, and with indication of quadratic outline; in the 31st and 32nd vertebrae they are slightly concave, in the following vertebrae, are formed variably and irregularly; the anterior end surface of the 33rd vertebra is planar, the posterior strongly convex, and such irregularities are to be found in manifold modes up to the final vertebrae.

The neural arch becomes increasingly shorter in the posterior vertebrae and inclines forward; it has a roof-shaped, dorsally broadly rounded cross section and forms a weakly dorsally curved, rod-shaped process at the back, on which nothing of the postzygapophyseal facet can be distinguished. The neural arch and its attachment surface become steadily shorter in the following vertebrae. A neural arch is not preserved on the posteriormost rod-like vertebrae, of which the 45th and 49th are only present in their anterior half.

The attached table of dimensions of the caudal vertebrae includes only a selection of vertebrae from the anterior 30 vertebrae, the preservation of which permitted useful values to be obtained.

Caudal vertebral column Find p. A series of 11 unprepared caudal vertebrae from the base of the Middle Saurian Marl, from a juvenile animal, of which one of the anteriormost,

Dimensions of the caudal vertebral column from Find no in cm.

Position in the caudal vertebral column	Length of the centrum dorsally	Anterior end of the centrum Height	Anterior end of the centrum Width	Posterior end of the centrum Height	Posterior end of the centrum Width	Total height of the vertebra	Total width of the vertebra
2	15.0 (±)	32.0 ±	35.9 ±	31.0 (±)	31.7 +	59.9	52.2
5	17.5	24.5	27.9	22.8 (±)	25.0 (±)		
7	17.7	21.8	26.6	20.8 ±	25.0 (±)	40.6 ±	40.2
8	16.5	20.0	24.3	20.8 (±)	22.8		35.5 (+)
10	16.6 (±)	18.0	17.7 (±)	21.2	21.5		
12	17.5 ±	17.5 +	21.7 -	17.2	20.6		
13		17.2				32.9	
15	16.9 (±)	15.8	19.1	17.3	20.6 -	27.8 +	18.0 (±)
19	18.3 ±	15.0	18.3 ±	18.8 ±	18.9 (±)	25.0	13.2 (±)
25	15.7	12.1 (±)	13.4 (±)	11.4	13.6	16.6 +	
27	16.3	11.4 (±)	12.6	10.9 (+)	11.9 (±)	17.3	
30	14.0 ±	9.6 ±		8.4 ±	9.9 (-)		
31				7.8	8.8	12.3 (±)	
32	12.2	8.0	8.5	7.3 ±	8.3	11.7	
33	11.4	7.5	8.5	6.6	7.3		
34	11.7	6.8	7.4	6.1	6.8	9.5	
35	10.9	6.0	6.5	5.9	6.5		
36	10.1	5.9	6.2	5.4	6.3	8.4 (+)	
37	10.6	5.4	6.0	6.1 (-)	6.1		
38	10.2	5.4	6.6 (+)	5.0	5.5		
39	9.8	5.3	5.5	5.1	5.7		
40	9.0	4.7	5.0	4.8			
41	8.6	4.7	4.2	4.0	4.3		
42		4.6	3.9				
43	7.8	4.4	4.2	4.1	4.1		
44	7.4 ±	3.7	3.9		4.2 ±		
45		4.3	3.9				
46	6.8	3.8	3.9	3.9	3.9		
47	7.4 ±	3.9	3.7	3.7	3.8		
48	6.9	3.6	3.4	3.5 ±	3.4		
49		3.1 (±)	2.9 (±)				
50	6.8	3.0	3.1	3.0	2.8		
51	6.2	2.9	2.8	2.7	2.7		

perhaps the second, has an anterior end surface of about 22 cm wide and 19 cm high, and 1.6 cm long, is distinguished by a quite strong concavity of the anterior end surface. Another vertebra has an equally strong concave anterior centrum that is 14 cm high anteriorly and 17 cm wide and 13 cm long. This length permits the assumption of a not fully grown animal.

Caudal vertebrae from Quarry St. The four caudal vertebrae at hand originate from a large animal, probably from the same for which a rear extremity with a 183-mm-long femur (St 291) is present. The vertebrae are uncrushed. The neuropophyses are missing up to the second largest (St 272) or are incomplete; the prezygapophyses in part as well.

The two large and the two small [vertebrae] must have once been positioned close to one another, and perhaps had even been neighbours.

All vertebrae are very similar to those of tail Aa, but a little larger, their end surfaces relatively wider. A horizontal ridge on the left wall of the centrum, 3-4 cm below the short, hook-shaped transverse process is noticeably robust on the two smaller vertebrae; on the right, such a ridge is only indicated. The neurapophysis that is preserved on one vertebra is a little longer and taller than in the corresponding vertebra of Aa. Based on a comparison of the transverse processes with those of Aa, the vertebrae may be regarded as the 8th, 9th, 11th and 12th caudal vertebrae.

Caudal vertebrae from Quarry dd. In addition to dorsal vertebrae, the quarry also yielded 14 caudal vertebrae, poorly preserved due to distortion. According to their dimensions, they belong to a subadult animal and originate from the anterior, middle and posterior region of the tail, though those from the anteriormost and posteriormost section are missing. The transverse processes of the three largest vertebrae are disarticulated, and exposed deeply invasive sutures with coarse ray-like sculpture. The entire neural arch has also been disarticulated in three large vertebrae. The medium size of the animal is related to the length of the anterior centra, about 13 1/2 cm on average. The end surfaces of the anterior vertebrae have quite a high outline while strongly broad-elliptical end surfaces appear on the middle vertebrae, also in quite small vertebrae. The neural arches and the neurapophyses match those of Aa well.

Caudal vertebra Find Y. A 121-mm-long caudal vertebra with incomplete neural arch from the Middle Saurian Marl of Kindope has a 10.6-cm-wide and 8.7-cm-high anterior end surface; its outline is thus relatively wide and low. Another 7.8-cm-long caudal vertebra has a 4.7-cm-wide and 4.0-cm-high posterior end surface; the outline is thus relatively higher.

Caudal vertebra from G1. The site G1 in the Middle Saurian Marl has yielded weathered remains of *Brachiosaurus*, portions of extremity bones, and centra from various regions of the tail. Among 15 complete and 6 half centra, one (G1 4), with ample 25-cm-high posterior end surfaces, distinguishes itself as the second caudal vertebra by its extraordinarily wide ventral surface. It possesses, in accordance with tails Aa and D, a small lateral depression that is, however, much more clearly formed. The end surfaces are noticeably wider than tall, which can be confirmed despite incomplete preservation. Another anterior centrum attains a width of 28 cm anteriorly and posteriorly, with an anterior height of about 23 cm and a length of about 16 cm. The vertebrae from the middle and anterior section of the tail are distinguished by the particularly low, broad outline of the end surfaces. Thus in one centrum the anterior end surface is about 16 cm wide and 11 cm high, in another the posterior end surface is 12.7 cm wide and 9 cm high, another end surface 7.2 cm wide and only 5.2 cm high.

### **Comparison of the various finds of caudal vertebrae.**

The dimensions given in the tables illustrate that, apart from the anteriormost caudal vertebrae, the length of the centrum remains nearly identical to about the 22nd or 27th vertebra. It measures 16 cm on average in Aa, 12.7 cm in D, in no the relatively reliable measurements indicate

an average value of 17 1/4 to 17 1/2 cm; among the short series of caudal vertebrae was found one of 13.5 cm in dd, of 15.5 cm in St, of 15.9 cm in Gl; in p about 13.5 cm can be assigned. Placing these average lengths relative to the length of an associated extremity bone is only possible in D and Aa; of those in which the length of the humerus is compared, we have at our disposal 160 cm for D, 172 cm for Aa. The proportion figures for both cases vary considerably; in Aa centrum length relates to humerus length as 1:10.8, in D as 1:12.6. Measurements on more material would be necessary to determine whether perhaps in smaller, younger animals the vertebrae are relatively shorter than in larger, older animals.

In a comparison of the size relationships of the centra of the various caudal vertebral columns, those of the anterior half of the tail of no are not considered because of their morphological distortion. The anterior centra of Aa, D and Gl have quite similar outlines that do not deviate from the circular, when it is considered that they are obviously somewhat dorsoventrally compressed in D. The first vertebra of D is much wider ventrally than Aa. The outlines of the end surface in Aa become much broader in a larger section of tail, from about the 10th vertebra onward, whereas in D this obvious later, mainly only after the 20th vertebra, and then also to a minor degree. The few centra of the middle caudal vertebrae of Gl exhibit particularly broad end surfaces. The end surfaces of the centra of the posterior caudal section have outlines that again mostly approach circularity, though great irregularities also occur, particularly among them. It could well be that the greater relative width of the centra is connected with greater age, and does not merely indicate individual variation. The relative length of the anterior caudal vertebrae is also noticeably variable. The undescribed vertebra J 40 from the Upper Saurian Marl, which may be considered the second or third, is not quite 13 cm long at about mid-centrum height, while Gl 4, a second caudal vertebra, is about 16 cm long, even though the size of the end surfaces of the centrum does not greatly differ in both. The anteriormost vertebrae of D, with considerably smaller centrum end surfaces, are almost as long as in J 40, even longer ventrally. In Aa the first caudal vertebrae are again absolutely and relatively somewhat longer than in D, with end surfaces of very similar size. That the animals from the Upper Saurian Marl (D, J, no) are distinguished from those of the Middle Saurian Marl (Gl, Aa, p) by the shortness of the anteriormost caudal vertebrae, and the conclusion that variability of the vertebral length indicates two different species of *Brachiosaurus* in the two horizons, is in no way made probable by the measurements. Not only do the external size ratios of the centra vary, but the degree of concavity of the end surfaces varies somewhat. Variations in the neurapophysis are also quite noteworthy; it can be plate-like throughout in anterior caudal vertebrae, or it can become dorsally thickened to a greater or lesser degree. The latter difference appears connected with varying age; the neurapophyses become thicker with age. As mentioned previously, the transverse processes in D, apart from the first caudal vertebrae, are considerably more delicate than in Aa.

It does not seem out of the question that among the morphological variations presented, in addition to individual variations, others occur, which indicate sexual characteristics, an interpretation that may perhaps be considered particularly for the variability of the relative length and outline of the anteriormost centra.

The important isolated find of a large sauropod caudal centrum, that E. HENNIG collected from the slope of Kikomela at the outlet of the Namgaru in the Cretaceous plateau during his last expedition

and kindly forwarded to the Berlin Tendaguru Collection is to be cited here in particular, as it could belong to a titanosaur according to Frh. v. HEUNE (E. HENNIG 1937, p. 119). This interpretation has not been confirmed. The centrum, which possesses end surfaces about 22 cm wide and almost identically high and is about 14 cm long, matches completely with anteriormost caudal vertebrae of *Brachiosaurus brancai*; the considerable concavity of the end surface does not exceed the observed morphological variations.

### **Length of the individual sections of the vertebral column.**

The lengths of the various sections of the vertebral column can be given with the totals produced from the skeletal reconstruction; during the mounting of the presacral and sacral vertebrae, modeled with great accuracy by Senior Preparator E. SIEGERT, as well as the caudal vertebral column no. The totals are somewhat greater than the sum of the lengths of the individual vertebrae would produce, because small intervals that corresponded to the probable thickness of the intervertebral discs were inserted between them. The length along the neural canal is 878 cm in the neck, 392 cm in the trunk, 107 cm in the sacrum, and 736 in the tail excluding the four final modeled rod like vertebrae with a total length of 26 cm. A total length of 2113 cm results. A measurement of the skeleton along the ends of the neurapophyses yielded a noticeably higher value, namely 2137 cm. The stronger curves of this line suffice to explain the difference.

### **Characterization of the vertebral column of *Brachiosaurus*.**

The comparison with other sauropods allows the characteristic features of the vertebral column of *Brachiosaurus* to stand out. The presacral vertebrae are of extremely cavernous construction. They possess deeply invasive niches (external excavations), multitudinous lamellae formation of the second order, thus a very complicated architecture. The pleurocoels are extensive and deep. The cervical vertebrae are, apart from the first and last, very greatly elongated. The most probably entirely unbifurcated neurapophyses are quite low in the posterior trunk and increase in height from the sacrum to just before the mid-trunk. With them, the diapophyses simultaneously increase in length to a significant length up to the 17th presacral vertebra. It is characteristic that the lateral processes of the sacrum extend relatively far laterally, the first is particularly extensive; the neurapophyses are low, as in the preceding dorsal vertebrae. The caudal vertebrae are simply constructed compared to the presacral vertebrae; their centra more or less clearly biconcave, relatively short, not elongated in the middle tail section, without or at most with only very subordinately appearing lateral longitudinal ridges. A pleurocoel-like hollow is indicated in the second caudal vertebra. The lateral processes are also weakly developed in the first vertebrae. The neurapophyses are quite low, plate-like, also in the anterior caudal vertebrae; in these they appear to become somewhat thickened with age.

## Function of the articulations.

The flexibility of the cervical vertebral column of *Brachiosaurus* cannot be fully judged from the examined material because the zygapophyses are not preserved in the posterior cervical and anteriormost dorsal vertebrae.

The motion between occipital condyle and atlas and between atlas and axis was certainly versatile; as in the extant reptiles and birds, certainly rotation was possible in addition to lateral and sagittal bending. The degree to which each of these motions were performed at each of the two articulation sites cannot be determined in the fossil vertebrae. The morphological configuration allows such extensive and manifold possibilities of motion at these two sites as unquestionably never occurred in life; the limitation and alignment of this mobility by ligament and muscle connections cannot be reconstructed.

The zygapophyseal connection that exists between the atlas and axis exhibits articular facets that fall quite precisely in a spherical surface and thereby, in contrast to the articular apophyses of all other vertebrae, permits the most versatile joint movements. That these, according to the morphological evidence, were truly strongly used in life to the inferred versatility, appears in no way certain, considering the fact that, according to the description by C. W. GILMORE (1936, Fig. 6), the atlas and axis of *Apatosaurus louisae* in the Carnegie Museum were immovably fused.

The vertically oriented facets of the zygapophyses on cervical vertebrae following the axis permitted only sagittal bending; a lateral bending between neighbouring vertebrae of the middle neck section is, in addition, excluded by the aforementioned peculiar curvature of the facets. In the vertebrae of the transitional region from neck to trunk where zygapophyses are not preserved, a certain lateral bending ability is assumed, analogous to other sauropods, since it is highly unlikely that a lateral bending of the neck was completely impossible.

The classification of the neck in three sections according to their flexibility, as I. BOAS (1929) could confirm for the majority of extant birds, cannot be made probable for sauropods from the morphology of the articulations of the cervical vertebrae. The type of motion of the neck of the African ostrich does not prove the tripartite classification; on the contrary, an identical, ventrally and dorsally oriented bending is possible in the entire course of the neck.

The neck of *Brachiosaurus* was certainly much less movable and bendable than that of the ostrich; the head must also have been lowered and raised differently. In the ostrich the head is carried in a very characteristic manner; in a constant position up and down, the latter to a specific distance from the ground. In lowering the head, first the lower neck section is curved downward and this curvature continues ever farther cranially; correspondingly, the extended upright upper section of the neck shortens. This style of head movement requires a strong flexibility at every part of the neck and a large number of vertebrae and flexible articulation points. In the neck of *Brachiosaurus* that was stiffened by long cervical ribs, a similar style of head motion can at best have been suggested; in the main, the head would have been lifted and lowered much more by the up and down traversing of the entire neck.

The zygapophyseal articulation in the middle and posterior dorsal vertebrae from the 16th onward is characterized in *Brachiosaurus*, as in other sauropods, by the formation of a zygosphene that prevented lateral bending and permitted only sagittal bending. The prezygapophyses are a considerable distance apart in the 16th presacral vertebra of the anterior trunk, and if one thus cannot assume a typical narrow zygosphene for the preceding vertebra, then one can conclude from the angled facet on the prezygapophyses of the 16th presacral vertebra that it adapted to a zygosphene, that a true lateral bending was also hardly possible between the 15th and 16th vertebra.

Only sagittal bending was possible in the first two caudal vertebrae as well, since the extensive, very vertically oriented facets of the zygapophyses did not permit lateral bending. An insignificant lateral flexibility may have been present after all with the quite small zygapophyseal facets of the later, following vertebrae – already from the 5th caudal vertebra (Skeleton Aa) onward, they are noticeably reduced. In any case, up to the middle of the tail the vertebral column was essentially only sagittally flexible. In contrast lateral bending in the posterior vertebrae was only restricted to a small degree or not at all by the zygapophyses.

### **Ligament connections between the vertebrae.**

The neurapophyses of the cervical vertebrae end, as has been confirmed in the series of vertebrae from the 3rd to the 8th, in a more or less knob-like thickening. This is so robustly constructed that it can be assumed that it served as the contact for a strongly developed supraspinal ligament, which connected the individual vertebrae and likely extended as far as the sacrum, to continue farther over the caudal vertebrae. This ligament would have had the task to hold and carry the neck in its normal, vertically oriented position and thereby to relieve the neck musculature. Simultaneously such a ligament would have braked and impeded the bending of the neck in a sagittal direction to a certain degree since the musculature to bend the neck had to overcome the resistance of the ligament to stretching. As a consequence of incomplete preservation it cannot be confirmed if the connection of the neurapophyses by the supraspinal ligament in the posteriormost neck section and in the anterior portion of the trunk was weaker than in the remaining sections of the presacral vertebral column, thereby increasing the flexibility; this in no way appears impossible. The construction of the neurapophysis and the supraspinal ligament differs considerably from the conditions in the sauropods with bifurcated neurapophyses, particularly in *Dicraeosaurus*, the most extensively specialized in this regard, for which I (JANENSCH 1929) attempted to reconstruct the ligament connections between the presacral vertebrae. I arrived at the concept that in the region of vertebrae with bifurcated neurapophyses a neck ligament ran between the forked branches, from which special entrances to individual vertebrae divided ventrally and fundamentally attached between the bifurcations. A neck ligament constructed in this manner cannot be reconstructed for the sauropods with undivided neurapophyses, therefore also not for *Brachiosaurus*. It is obvious that a traversing supraspinal ligament that ran at a considerable internal distance above the pivot points found in the centrum condyles, limited the flexibility of the cervical vertebral column to a far greater degree

than a neck ligament that attached itself closely over the neural canal by means of its entrances deep between the branches of the neurapophyses.

In addition to the supraspinal ligament, an interspinal ligament certainly connected the neurapophyses of the dorsal vertebrae, that stretched between the prespinal lamina of the vertebra and the postspinal lamina of the preceding vertebra, and thereby was divided in separate intervertebral sections. This interspinal ligament could almost completely ossify, as the case of the last two presacral vertebrae of Skeleton SII illustrates.

### **About the muscles of the vertebral column.**

The attachment of muscles or tendons on the presacral vertebrae is only noticeable to a slight degree. The always very difficult attempt to reconstruct the vertebral musculature therefore only allows the expectation of few trustworthy results for *Brachiosaurus* and likely for the sauropods in general. Therefore only a few additional points will be alluded to here, in addition to those which are presented in the chapter about the functional significance of the cervical ribs and about the muscles that were connected with them. The truly obvious insertion points that are displayed by the processus dorsalis over the postzygapophyses serve as insertion points, as BOAS (1929) explains, for important dorsally running muscles in birds; these are the m. spinalis, which forms a united group with mm. biventer, pygmaei and splenii that insert on the spinal processes, and the mm. ascendentes cervicis, dorsal flexors that insert on the so-called knob processes that sit next to the prezygapophyses, but do not exist in the sauropods. On the absence of such knob processes or corresponding, differently developed insertion points, it can likely be concluded that such neck flexing muscles, if even present, were much more weakly developed than in birds.

If one asks, what filled the space between the vertebrae neighbouring the ansae and the spaces within the individual ansa, the fo. transversaria, the description by BOAS also gives us a perception of the presumed musculature. Here he lists the mm. intertransversarii that insert on the anterior margin of the ansa and attach to the external side of the ansa of the preceding vertebra; also the mm. inclusi, specially constructed portions of the mm. intertransversarii that insert on the anterior and ventral margin and attach to the sides of the neural arch of the preceding vertebra. One can conjecture that the spaces between and within the ansae of sauropods housed, in addition to the arteria vertebralis and possibly other vessels like nerves, muscles such as the aforementioned. It is, however, difficult to imagine that very extensive spaces such as the fo. transversaria in *Brachiosaurus* and especially *Apatosaurus* were completely filled; an extraordinarily massive musculature would have been necessary, that would have made the neck excessively heavy. Since I consider the presacral vertebrae of the sauropods to be pneumatized with pleurocoels, I consider it far more likely that the extensive spaces within and between the ansae, as in birds, also contained air sacs, which could perhaps be very extensive.

## **Comparison of the vertebral column of *Brachiosaurus brancai* with that of other sauropods.**

The dorsal vertebrae of the African *Brachiosaurus brancai* correspond extensively to those of *Brachiosaurus altithorax*, of which the seven posterior vertebrae were described by RIGGS (1904) from the Morrison Formation of North America. The vertebrae in the two species exhibit extensive pleurocentral excavations and undivided, dorsally widened neurapophyses, which are relatively low in the anterior dorsal vertebrae, but which become taller from the sacrum up to just before the mid-trunk; in addition there are horizontally or almost horizontally oriented diapophyses that are of considerable size prior to the mid-trunk. The considerable increase in the height of the neurapophysis from the sacrum to just before mid-trunk is a characteristic that is found in no other sauropod genus in the same manner; it is also particularly characteristic for *Brachiosaurus*. However, other differences between both species can be confirmed, that concern the overall morphology. Thus the centra of the dorsal vertebrae of *B. altithorax* are noticeably longer. In *B. brancai* the neurapophysis and the entire vertebra of what is probably the eighth-last presacral vertebra is taller and the diapophyses longer than in the seventh-last presacral vertebra of *B. altithorax*. In any case, these differences could prove to be less or perhaps even disappear if vertebrae from the same position could be compared. As the vertebral column of the American species was embedded in sediments with centra that were oriented upward, it could perhaps also be possible that the height of the vertebrae has been reduced by rock pressure. The specified differences are, however, under no circumstances so large that they would exclude the generic affiliation of the two species.

If we compare the presacral vertebrae of *Brachiosaurus* with those of other sauropod genera, it is obvious in all the variation that in the construction of the neural arch and its processes the character of the laminar system, conditioned by the similarity in mechanical function, has resulted in a great deal of similarity. This is particularly valid for the cervical vertebrae when they exhibit similar size relationships, above all a similar degree of elongation in the genera compared. In addition to the overall size relationships it is above all the morphology of the neurapophysis, especially the presence or absence of bifidie that is characteristic. The extent and depth of the pleurocentral excavations furthermore yield differences that are to be considered.

First, genera will be compared that do not possess bifurcated neurapophyses, as they are to be assumed in *Brachiosaurus*.

As a quite well known genus with undivided neurapophyses, *Haplacanthosaurus* [sic] merits a more exact consideration. HATCHER (1903) described two finds that included the vertebral column, as two species, though a specific separation does not seem justified to me. In the centrum the dorsal vertebrae differ from those of *Brachiosaurus* practically only in the almost total absence of an anterior condyle and usually smaller pleurocoentral cavities. The neurapophysis is no taller in the middle trunk section than in the posterior section; the cervical vertebrae are much less elongated; in all presacral vertebrae the bone reduction, the elaboration of secondary laminae and the cavernosity is obviously much weaker, for which, however, the significantly smaller size range could also be responsible. Furthermore, RIGGS already alluded that *Brachiosaurus* is characterized by more robustly developed hyposphene articulation, greater thinness of the septa, and greater length of the dorsal centra, whereas in *Haplacanthosaurus* [sic] the pedestal of the neural arch ("vertebral pedicles") are more strongly elevated

and the diapophyses are more vertically oriented. Another variation from *Brachiosaurus* is the number of presacral vertebrae, which was higher in *Haplacanthosaurus* [sic]. In any case I, like Frhr. v. HUENE, consider the count of 29 presacral vertebrae assumed by HATCHER as too high; in the interpolation of non-preserved vertebrae he certainly reckoned with too gradual a change in morphology and size change within the vertebral gap. The formula assumed by Frhr. v. HUENE (1927-1929) of 13 cervical and 12 dorsal vertebrae appears to me to be the lowest possible number that one could infer from the illustrations of HATCHER. *Helopus* from Shantung, for which C. WIMAN (1929) assumes 32 presacral vertebrae, though only 3 sacral vertebrae, is proof that even higher numbers of presacral vertebrae can occur in sauropods; if one deducts one dorsal-sacral vertebra, 31 true presacral vertebrae remain. As a consequence of the reduced length of the cervical vertebrae, *Haplacanthosaurus* [sic] possessed a relatively short neck that caused a substantially divergent external appearance of the entire animal. The specified differences indicate a highly dissimilar specialization that for the most part refutes a direct close relationship of both genera.

Known very incompletely from only a few fragments, the vertebral column of the genus *Elosaurus* (PETERSON and GILMORE 1902) from the Morrison Formation, exhibits undivided neuropophyses in the cervical and dorsal vertebrae. However, we are dealing with such a juvenile animal that a comparison with mature individuals of the genera is only inadequately practical.

Among the English sauropods *Cetiosaurus oxoniensis* PHILLIPS from the Great Oolite of Oxford is the first to be compared; according to the illustrations provided by Frhr. v. HUENE (1927) it differs from *Brachiosaurus* in the construction of the dorsal vertebrae in that the diapophyses stand quite steeply laterally. The low, unbifurcated morphology of the neuropophysis is comparable to that of *Brachiosaurus*. If the considerably larger anterior caudal vertebrae illustrated by Frhr. v. HUENE also belong to the same genus, they would be considerably different by the extensive, tall transverse processes (caudal ribs). In contrast the vertebrae designated as middle caudal vertebrae are very similar to those of *Brachiosaurus* according to the overall morphology and kind of the transverse processes. The characters cited by Frhr. v. HUENE (1932), the non-cavernous, only weakly pleurocentral depressions in the centra of the dorsal vertebrae, the thick reinforcing struts, are weighty variations from *Brachiosaurus*. Also considered here to be in agreement is *C. leedsii* (HULKE) (A. S. WOODWARD 1905) from the Oxford Clay of Peterborough, previously also placed with *Cetiosaurus* and later named to the special genus *Cetiosauriscus*. Of the presacral vertebrae indeed only the posteriormost dorsal vertebra is incompletely known. Even if one were to assume that the noticeable shortness of the centrum is due to compression, it already differs so greatly from *Brachiosaurus* by the high-placed, small, round pleurocoels that closer relationships between the two genera are not to be accepted.

Of the species that OWEN (1875) introduced under the generic designation *Bothriospondylus* from the Kimmeridge of England, those centra described from the dorsal and sacral region and illustrated as *B. suffosus* cannot be judged in relation to their affinity; in part they are not those of sauropods. The same is likely true of the much larger dorsal centrum from the Forest Marble of Bradford. The dorsal centra from the Wealden, which R. OWEN (1875) named as *Bothriospondylus elongatus* and *magnus*, are undoubtedly those of sauropods; it is not evident that they belong to forms that have an affinity to *Brachiosaurus*, also due to the incompleteness of the specimens.

More valuable for comparison in contrast, are the presacral vertebrae, also originating from the English Wealden, that J. W. HULKE (1880) illustrated with the SEELEY generic name *Ornithopsis*, and which, according to Frhr. v. HUENE, are to be designated as *Pelorosaurus hulkei* SEELEY. Two of the three cervical vertebrae are built quite short and quite tall, their zygapophyses are more robust, the entire external sculpture much coarser than in *Brachiosaurus*. The neurapophysis, not completely preserved in any of these vertebrae, is in any case not deeply bifid; whether they were completely unbifurcated cannot be judged with certainty. The third, incomplete cervical vertebra that is much more elongated, and in case it belongs to the same species as the other two, must have had another position in the neck, does not exhibit the strong constriction of the ventral surface of the middle section as *Brachiosaurus*. All three cervical vertebrae differ considerably from those of *Brachiosaurus*, so that closer affinities to this genus are difficult to accept. The dorsal vertebra that J. W. HULKE (1880 Table 4, Fig. 5 to 7) illustrates, on the other hand, exhibits quite significant similarity to the posterior dorsal vertebrae of *Brachiosaurus*. This is valid for the development of the laminar system, but also particularly for the morphology of the neurapophysis; the median longitudinal margin on the ventral side of the centrum is also mentioned by HULKE. The only noteworthy difference to be cited is that the diapophyses extend less laterally; this does not appear to me to weigh very heavily. The similarity is so great otherwise that a generic association does not appear to be excluded. If the cited cervical vertebrae, described by HULKE, belong to the same species as the dorsal vertebrae, an affinity to the same genus would be less probable.

Additional isolated vertebrae from other regions are cited that have also become familiar under English generic names. Among the sauropod remains from the Lower *Virgula* Beds of Moutier (Switzerland) that Frhr. v. HUENE (1922) described in detail as *Ornithopsis? greppini*, later (1932, p. 255) referred questionably to *Cetiosauriscus*, there are no presacral vertebrae, but likely in the material of *Bothriospondylus madagascariensis* LYDEKKER from the Middle Jurassic of Madagascar. A. THEVENIN (1907) illustrates a cervical vertebra and one anterior and one posterior dorsal vertebra, of which the last two originate from two individuals of different size from the same species, if not indeed from different species or even genera. The neural arch is completely or mostly missing in these vertebrae. The anterior dorsal vertebra obviously has a very extensive pleurocentral depression, whereas this is very small and positioned high in the posterior dorsal vertebrae, completely different from *Brachiosaurus*. However, the incompleteness of the cervical vertebrae and anterior dorsal vertebrae too, does not permit similarities and affinities to *Brachiosaurus* to be confirmed.

The genus *Torniera* [sic] (= *Gigantosaurus* E. FRAAS) from the Tendaguru Beds obviously does not possess bifid neurapophyses. The very short anterior dorsal vertebrae with their reduced neurapophysis and the robust diapophyses that recall those of the titanosaurs in their strongly concave-convex caudal vertebrae, exhibit entirely different specializations in contrast to *Brachiosaurus*.

Frhr. v. HUENE (1929) could not confirm an entirely unbifurcated neurapophysis in the South American Late Cretaceous *Titanosaurus australis* LYDEKKER. Otherwise, however, these presacral vertebrae differ greatly from those of *Brachiosaurus* in that the cervical vertebrae are built tall, and are relatively short in comparison with the dorsal vertebrae, the dorsal vertebrae have a strongly extending condyle, and the entire architecture exhibits far fewer deeply developed struts and excavations. That no closer taxonomic affinities could exist between *Titanosaurus* and related [sauropods] like *Antarctosaurus*

is confirmed by the highly different, extremely rod-like dentition of the titanosaurs; the extremely concave-convex construction of the anterior and middle caudal vertebrae of *Titanosaurus* also speaks against this.

In a comparative consideration among genera with bifid neurapophyses, the genus *Camarasaurus* is thus particularly important because it is so similar to *Brachiosaurus* in the construction of the skull that it can be considered closely related. As OSBORN and MOOK's large monograph (1921) teaches, *Camarasaurus* exhibits pronounced bifidie in the neck and anterior trunk; the notch extends very deeply between the two branches of the neurapophysis, particularly in the posterior cervical and anterior dorsal vertebrae. The undivided neurapophyses in the posterior dorsal half are narrow and wide; the middle dorsal vertebrae differ in this from those of *Brachiosaurus* more than the posterior vertebrae do from the corresponding vertebrae of this genus [*Brachiosaurus*]. A considerable similarity nevertheless exists between the posterior dorsal vertebrae. The development of a pleurocoel in the cervical and dorsal vertebrae is quite conformable. The number of presacral vertebrae is the same in both genera, though they are divided differently between the neck and trunk. *Brachiosaurus*, in which 13 of the 24 presacral vertebrae are included in the length of the neck, is more advanced than *Camarasaurus*, in which both regions include 12 vertebrae. The genus *Uintasaurus* (HOLLAND 1919) is obviously closely related to *Camarasaurus*, with a greater elongation of the cervical vertebrae; can likely be assessed as similar to *Camarasaurus*.

The genus *Helopus* is to be considered in connection with *Camarasaurus*; in its skull construction and tooth morphology I believe, in contrast to Baron NOPSCA [sic], that similarity and relatedness with *Brachiosaurus* must be seen, about which I have previously alluded (JANENSCH 1935). The posterior cervical vertebrae and the anterior dorsal vertebrae in *Helopus* are indeed not actually bifid, but they do exhibit low metapophyses ("processus pseudospinosi" of WIMAN), between which the equally low neurapophysis sits. The architecture of the vertebrae is in particular simple, less strongly secondarily dissected, perhaps in part a consequence of the much smaller size. The pleurocoels in the cervical vertebrae are incompletely bordered; in the dorsal vertebrae generally somewhat less extensive. The elongation of the cervical vertebrae compared to the dorsal vertebrae is less than that in *Brachiosaurus*; in contrast, *Helopus* proves to be more specialized since the number of presacral vertebrae totals seven more than in *Brachiosaurus*, that is 31 (without dorso-sacral vertebrae), of which 17 (or 18) comprise the neck and 14 (or 13) the trunk.

Among the genera equipped with bifurcated neurapophyses, *Diplodocus* and *Barosaurus* are characterized by greatly elongated cervical vertebrae. In the North American *Barosaurus lentus* MARSH the elongation attains an even greater degree than in *Brachiosaurus brancai*. Since the significant elongation of the cervical vertebrae is connected with a highly specialized lamellar architecture and cavernosity, the cervical vertebrae appeared, with the exception of the bifurcated neurapophyses, to be relatively similar externally to those of *Brachiosaurus*. This is particularly valid for the long cervical vertebrae of *Barosaurus*, the metapophyses of which are very low and not very noticeable, which *Barosaurus africanus* (E. FRAAS) from the Tendaguru Beds also shows. The dorsal vertebrae of *Barosaurus* and *Diplodocus* differ considerably from *Brachiosaurus* as a result of the strongly pronounced bifidie and the less widely constructed, in *Diplodocus* also very much higher neurapophysis of the posterior vertebrae. In *Barosaurus* in addition, I could demonstrate that the centra are excavated by air cells to an even greater degree than in *Brachiosaurus*.

*Apatosaurus* and *Dicraeosaurus*, which are characterized by deep bifurcation of the neurapophyses far back in the neural arch of most cervical and anterior dorsal vertebrae, also differ significantly from *Brachiosaurus* in external dimensions due to the minimal elongation of their cervical vertebrae. *Apatosaurus* possesses a character in the exceedingly long branches of the rib head that span an extraordinarily wide foramen transversarium, which indicates a particular specialization in contrast to *Dicraeosaurus* and also in contrast to *Brachiosaurus*. The differing type of the skull of *Dicraeosaurus*, as in *Diplodocus* and *Barosaurus*, militates completely against a closer affinity with *Brachiosaurus*. The construction of the caudal vertebrae too, is considerably different than in *Brachiosaurus*, particularly the anterior [vertebrae] with their specialized architecture.

The comparative study has shown that, apart from the North American *Brachiosaurus*, among the genera considered with presacral vertebrae of unbifurcated neurapophysis, only the dorsal vertebra from the English Wealden that HULKE illustrated with the designation *Ornithopsis*, is so similar to *Brachiosaurus* that closer affinity is certainly possible. However, this assumption will only be positively confirmed when the skull of the sauropod to which that vertebra belongs is known and its type is found to be conformable to that of *Brachiosaurus*. As has been demonstrated, the posterior dorsal vertebrae and the caudal vertebrae of *Camarasaurus*, proved to be a relative to *Brachiosaurus* by its skull morphology, are quite similar to those of *Brachiosaurus*. Characteristics of the presacral vertebral column of *Camarasaurus*, such as the bifurcated spinal processes of most cervical and the anterior dorsal vertebrae, and the greatly reduced elongation of the cervical vertebrae, indicate divergent traits. Thus *Camarasaurus* and *Brachiosaurus* illustrate that in sauropods of closer affinity similarities and considerable differences can be manifested in the vertebral column simultaneously.

The comparison of the sacrum of *Brachiosaurus brancai* with that of *B. altithorax* shows important agreement. The extensive, triangular first sacral rib is completely similar in both species. The long extension by which the sacral rib of the second sacral vertebrae attaches to the first and second centrum is also to be found in the American forms and indeed apparently somewhat more so. The characteristically great length of the transverse processes, that confers the sacrum its significant width in comparison to other genera, is again conformable. The neurapophyses, as relatively low bone plates, have exactly the same character. That the first three neurapophyses are fused in sacrum Aa of *Brachiosaurus* from Tendaguru, but in the juvenile sacrum T as in *B. altithorax* only the second and third, signifies a variation in the kind of fusion, just as in *Diplodocus* and *Apatosaurus*, according to the presentation of E. S. RIGGS (1903, Fig. 10-17), the same neurapophyses in each of these genera are not always fused. The conforming characters of the sacra also advocate for the affinity of the African sauropod to the genus *Brachiosaurus*, in the same way as many other morphological traits of the vertebral column, the ilium and the large extremity bones.

The assumption that the different fusion styles of the neurapophyses in sacrum Aa from the Middle and of Find T from the Upper Saurian Marl indicates different species or temporal mutants, is indeed not to be refuted, but is also not supported by other observations.

In its construction the second caudal vertebra of *B. altithorax* [sic] that RIGGS (1904) illustrated resembles the corresponding vertebra of *Br. brancai* extraordinarily; it falls out of the range of variability of the grouping of the various caudal vertebral series that have been found, in only a few, not significant points.

It should be mentioned that a lateral depression is not indicated, that the neurapophysis is particularly thickened block-like dorsally, and that the wedge at the ventral end of the postzygapophyses has a stronger zygosphenal character, so that laterally it extends somewhat process-like.

Only a few other genera are considered for comparison due to similar, simple morphology. The caudal vertebrae of *Camerasaurus supremus* [sic] are quite similar to those of *Brachiosaurus* judging from the illustrations of OSBORN and MOOK (1921). The transverse processes are somewhat more extensive in the anteriormost vertebrae; the neurapophysis up to about the 10th vertebra is thicker, more club-shaped than is usual in *Brachiosaurus brancai*, but like *B. altithorax*; its height is reduced much slower in the course of the series. The very similar centrum only displays lateral longitudinal ridges in a few figures. The caudal vertebrae of the juvenile skeleton of *Camerasaurus lentus* described by C. W. GILMORE (1925) are obviously quite similar to those of *C. supremus*; that is, also simply formed. GILMORE does not mention lateral ridges on the centra; the presentations of the skeleton on Plate 13 and 14 also show nothing of this. However, lateral ridges appear to be indicated on a number of vertebrae in the reconstruction illustration Plate 17.

The caudal vertebrae of *Haplacanthosaurus* [sic] have in common with *Brachiosaurus* the simple overall morphology and the negative character of the absence of sculpture on the walls of the centrum. Apart from the shorter shape of the centrum the anterior caudal vertebrae are characterized by greater surface extension of the transverse processes than those of *Brachiosaurus*; the cross section of the centrum in the caudal section behind the anteriormost vertebrae is strongly laterally crushed.

The caudal vertebrae of *Bothriospondylus madagascariensis*, the sauropod from the Middle Jurassic of Madagascar named by A. THEVENIN (1907), are quite similar. The similarity could indicate points of affinity. Since, however, an illustrated centrum is much more primitive than in *Brachiosaurus* and only exhibits an insignificant pleurocoel, only a distant affinity could be considered that could be a condition of the difference in geological age. The short, wide tooth crown, which is assigned to the same species, differs considerably from the teeth of *Brachiosaurus*, and even a great deal more from the rod teeth of *Diplodocus* or *Dicraeosaurus*. That which is illustrated of the cervical vertebrae, which cannot be clearly assessed due to incompleteness, does not preclude a distant affinity. The unspecialized form of the caudal vertebrae, as befits *Brachiosaurus*, is in itself not particularly suited to the recognition of points of affinity.

The vertebral length in the caudal vertebral series in sauropods is noticeably variable. While the length of the centrum in the anterior tail section of *Brachiosaurus brancai* remains nearly the same until about the region of the 25th vertebra, it increases considerably in *Diplodocus longus* from about the 20th onward, according to measurements provided by C. W. GILMORE (1932), to again be reduced from about the 20th vertebra. [Literal translation of the sentence – putative error or ambiguity exists in specifying the transition from increasing to decreasing centrum length]. In *Apatosaurus excelsus* (GILMORE 1936) too, a very strong increase in length manifests itself, but is later reduced, similar to an indeterminate *Apatosaurus* species measured by GILMORE, while in *A. louisae* this condition is hardly indicated. In *Dicraeosaurus hansemanni* too, the centra from about the 13th caudal vertebra onward became obviously longer (JANENSCH 1929, p. 79). *Diplodocus*, *Apatosaurus* and *Dicraeosaurus* [sic] are genera with a very long tail. The tendency to develop a very long tail thus also expresses itself in the obvious elongation of the caudal centra in the section behind the 10th vertebra.

## **Ribs of the cervical vertebrae (2nd – 13th presacral vertebrae).**

### **Material. Fusion.**

The large skeleton SII provides extensive information about the cervical ribs. The description is thus based primarily on the material of the cervical ribs that this skeleton has yielded. Among these were the two ribs of the second cervical vertebra that were not fused with their vertebra, the vertebra which did not appear during the excavation, and which was obviously removed or destroyed prior to the final burial of the neck and the remaining skeletal elements; their heads are free. In contrast, the rib heads are tightly fused with their vertebrae in the 3rd to 12th cervical vertebrae. The ribs of the 13th presacral vertebra are again unfused and in this characteristic, indicate the transition to the dorsal ribs.

The extraordinarily long, thin shafts of the ribs of the cervical vertebrae had for the most part still nearly retained their original position in the sediment. Since the neck was recovered in individual, mostly large blocks, it could not be avoided that in those places where the fragile, thin shafts of the cervical ribs were separated by the fracture planes, slivers and fragments were lost. Despite this the cervical ribs could subsequently often be reassembled into long sections. Moreover, often even if pieces were missing, matching sections could be recognized on the basis of the similarity of cross section. In the region of the 3rd to 12th cervical vertebra the thin shafts of the ribs at times extended past the ventral surface of the rib heads of the succeeding rib. On the rib heads of three vertebrae, fragments of the ribs of preceding cervical vertebrae are present that pass over them. A portion of the third cervical rib lies on the ventral side of the right rib head of the 4th cervical vertebra, and lateral to this a very thin section of the cervical rib of the axis. A thin piece of the fourth cervical rib lies on the left rib head of the 7th vertebra, medial to the depression for the rib of the 6th vertebra. Fragments of the 7th, 9th and 8th ribs counted from the side lie immediately next to one another, on the left rib head of the 10th cervical vertebra, displaced somewhat medially and simultaneously obliquely oriented.

Apart from the specially treated, remarkably differentiated ribs of the axis, the ribs of the succeeding vertebrae from the finds SI and be are not described more exactly, since they are very similar to those of SII. It suffices to say that the proximal sections of the cervical ribs of the smaller SI are more delicate and in general delicately edged than those of the other larger animals. The ribs of the axis, the right rib of the third cervical vertebra, both ribs of the 3rd, 4th, 5th and 6th as well as the left rib of the 7th cervical vertebra of SII are present. The proximal sections are completely or nearly completely preserved and not or slightly compressed. The thin distal sections are absent in all to a greater or lesser degree. The ribs inclusive to that of the 5th vertebra were not co-ossified at the sutures with the diapophysis and parapophysis, and were separated from the associated vertebrae or at least displaced. They are tightly attached to the 6th and 7th vertebra. From this it follows that in the course of their growth the ribs of the middle cervical vertebrae co-ossified earlier than in the anterior [cervical vertebrae]. The same advanced stage of co-ossification is reached in the considerably larger cervical vertebrae of Find be as in the large SII. This is evident in the preserved proximal sections of the left cervical ribs, which are tightly fused in the 6th, 4th and 3rd vertebra, whereas the short proximal section of the atlas rib lies adjacent to the vertebra; indeed, in an undisturbed position, but was clearly separated from it by a sediment filled gap, thus was not fused.

## Rib of the axis.

### Description.

The noteworthy differentiation that the ribs of the axis of *Brachiosaurus brancai* exhibit demands a separate, detailed presentation of the three existing finds from SI, SII and t. The description of the rib of the axis of SII, which has the most strongly pronounced unusual morphology, is placed in the foreground. The approximately 4-cm-long and 3-cm-wide anterior end of the rib that sits on the axis of Find be is too insignificant to be described.

Find SII (Fig. 77, 78, 83). The right rib is present in a length of 99 cm, the final section of which attaches to the ventral side of the rib head of the 4th cervical vertebra; an unconnected, very thin end piece of 1.2 cm probably belongs with it. Of the left rib, there exist an approximately 21-cm-long anterior end without head and a fragment that is 27 cm long and follows immediately, but is separated by a small gap; displaced by buckling, two fragments of about 10 cm and 2 1/2 cm are associated with it; a somewhat thinner, almost 5-cm-long fragment could also belong to this rib.

The rib is characterized by the remarkable robustness of the proximal section and by an s-shaped curvature. The head extends strongly upward and downward; its very rugose, 2.9-cm-long (in the direction of the long axis of the rib) and 4.7-cm-wide facet sits at a very oblique angle. The cross section of the rib is compressed immediately behind the head. A long, robust enlargement extends dorsally out of the convex medial side of the proximal bend of the s-curve. The medial enlargement disappears in the transition to the posterior shallow curve of the s-curve, the medial surface becomes flat, the upper margin of the blade thins to a few millimeter-thick lamella. As the left rib presents particularly clearly, the upper lamella-like margin lowers suddenly with a pronounced step and then disappears altogether about 10 cm later.

Find SI (Fig. 79, 80, 83). Both ribs are present, the right preserved in a length of 34 cm, the left in 24 1/2 cm. The rib is significantly more delicate than that of SII; in contrast to SII the shaft exhibits a very weakly s-shaped curvature and a much smaller, enlarged reinforcement on the medial side, as the comparison with the cross section outlines (Fig. 83) explains. In contrast the attached lamella, which in the same manner discontinues posteriorly in a step, is very pronounced.

Find t (Fig. 81, 83). Only short, proximal sections of the two ribs are preserved; the right in a 6 cm length, the left in a 10 cm length. The rib shaft of both ribs conforms; it is a flat blade, sharpened dorsally; the outer side is shallowly arched, the inner side flat to gently depressed. The rib head is constructed very differently. In the left rib it is two-headed. The lower, stronger branch, the capitulum, carries an elliptical, strongly rugose facet that is attached very obliquely. The tuberculum extends out of the sharp upper margin and carries a small, upwardly oriented concave facet. The right rib conspicuously, only has the facet of the capitulum. A tuberculum is not present. The upper sharp margin is slightly crumbled away, but from its contour and robustness it can be concluded that a tubercular branch and a facet truly could not have been present.

## Ribs of the axis.

- Fig. 77. Left rib (SII); View from above. 1/3 nat. size  
Fig. 78. Right rib (SII); Medial view. 1/3 nat. size  
Fig. 79. Left rib (SI); Medial view. 1/3 nat. size  
Fig. 80. Right rib (SI); View from above. 1/3 nat. size  
Fig. 81. Left rib (t); Medial view. 1/3 nat. size  
Fig. 82. Right rib (t); Medial view. 1/3 nat. size  
Fig. 83. Cross sections through the ribs of the second cervical vertebra of Finds  
SII, SI and t. Nat. size. l = lateral. m = medial.  
The numbers present the distance from the proximal end in cm.

### Question of association.

The question, to which of the first cervical vertebrae the described ribs from SII and SI belong, and the question, whether the differences of these ribs from the axis ribs of t was due to the fact that the former are atlas ribs, leads to the following considerations:

1. The axis of SII was no longer present in the sediments; rather, like the atlas and the skull case, was removed from the slope by abrasion before the deposition of the sediments. Of the two described ribs that were not affected by abrasion, at least the right one retained its original position in the cervical vertebral column, since it attaches in normal fashion to the ventral side of the fourth cervical vertebra with the corresponding section of the thin distal end. Since a considerably more robust fragment of the rib belonging to the third cervical vertebra sits next to it, the former rib must belong to the atlas or axis; to which of the first two vertebrae [it belongs] can in any case not be decided in this find; it could indeed be possible that the rib of the axis was shorter than that of the atlas, as I could confirm in the skeleton of the Nile crocodile, and that the rib of the atlas extended to the rib head of the fourth vertebra, but not that of the axis.

2. In Find t only the two associated cervical ribs of the axis were present. Since the Skull t 1 and the first two cervical vertebrae lay together in natural association, atlas ribs would unquestionably have to have been visible while being exposed, if they were present.

3. In cases in which the atlas is furnished with a rib, a distinct facet is developed for it on the intercentrum of the atlas. Thus C. W. GILMORE (1907, Plate 12) found a distinctly developed facet for a rib on the intercentrum of the atlas of MARSH's type specimen of *Camarasaurus* (= *Morosaurus*) *agilis*, which comprised the posterior skull section and the first three cervical vertebrae. Such a facet is also shown in the illustration of the atlas of *Diplodocus longus* in MARSH (1896, Plate 27, Fig. 1); it is also very distinctly developed in an intercentrum from the Tendaguru Beds, which I would like to assign to the genus *Barosaurus*. GILMORE (1936) also figures a very strongly developed facet for a rib on the intercentrum of the atlas of *Apatosaurus louisae*.

Since in contrast to these cases it is to be concluded that *Brachiosaurus* did not possess an atlas rib due to the absence of a facet for the rib on the atlas of Find t, and since in this find an atlas rib also quite obviously was not present, then it must be deduced that the unusually robust and uniquely s-shape curved ribs in SII and also the similar, but less pronouncedly shaped cervical ribs of SI are to be considered as ribs of the axis, although in Find t these are shaped normally and are thus shaped completely differently from those of the former.

### Differentiation of the rib of the axis and attempt at interpretation as a secondary sexual difference.

A comparison of the cross sections of the individual finds, as the grouping (Fig. 83) illustrates, clearly shows the great differences between the axis rib of Find t and that of SII. While the rib of t presents a laterally compressed straight blade with flat or even somewhat depressed medial side, it is curved into an s-shape in the rib of SII and thickly enlarged on the medial side. The rib of SI shows the character of the rib of SII to a reduced degree; the lateral curvature is weaker and the thick enlargement is less; the facet on the anterior end is also much smaller.

The interpretation of the unique difference in the morphology of the axis rib of the three finds that in no way can be viewed as only variability, is made more difficult by the fact that, as far as I can see, a comparable example is known in neither living nor extant reptiles. Thus one can only attempt to derive an interpretation from the morphological evidence. The unusual reinforcement of the proximal rib section certainly indicates an increase in the functional ability. Since, as I will still present later, the extraordinarily long and in a long proximal section also very robust ribs of the cervical vertebrae of *Brachiosaurus* certainly functioned to stiffen the neck against too severe bending, one can imagine that the reinforced section of the ribs of the axis of SII restricted the bending between the axis and the third cervical vertebra. For this interpretation it would follow that the anterior large arc of the s-curve specially strengthened by a thickening must have been oriented in a nearly sagittal plane. One can probably assume that a ligamentous tissue was inserted onto the proximal section, that perhaps connected the axis rib with the 3rd vertebra, and that even increased the connection of both vertebrae. It is difficult to explain why this neck site was so stiffened in the large skeleton of SII, to a lesser degree in the small SI, while in t a stiffened reinforcement is obviously absent. Did the reinforced axis rib of SII have the significance of secondary sexual variation? One could imagine that the animal SII was an adult male, that performed bumping or pushing movements against rivals in competition over a female or even against the female before or during mating; perhaps it grasped it in its jaws as, for example, lacertilians do. The stiffening of the anteriormost neck section could be functionally related with such activities.

The smaller animal SI, in which the axis rib is strengthened to a small degree, could be regarded as a juvenile male in which the secondary sexual characteristic was not yet fully developed, and animal t, which greatly exceeds it in size, without a reinforced axis rib, as a female.

Due to the position of the ribs of the axis near the throat one could attempt still another interpretation, that is, to trace the reinforcement back to its connection with the formation of an organ found only in the male sex for producing calls or other sounds. The morphological evidence could, however, in no way suffice for a specific anatomical reconstruction of such an acoustic apparatus, as living vertebrates provide no example of this.

### **Ribs of the 3rd – 13th cervical vertebra.**

(Fig. 26-50, 84, 85, Plate I, Fig. 3, 5-7.)

#### **Description.**

The following description relates mainly to the cervical ribs of SII. The preserved cervical ribs of SI and be conform with those of SII so extensively that they do not need to be handled specially.

The two-headed proximal section in ribs of the 3rd to 12th cervical vertebra present a bone lamella that is bent at an angle in the orientation of the longitudinal axis of the vertebra. The tuberculum ascends dorsally as a plate-like, narrowing process that is fused with the diapophysis

of the vertebra. The articular surface of the capitulum, with which it is fused with the prezygapophysis, is significantly larger than that of the tuberculum. The anterior margin between capitulum and tuberculum is bent inward; ventrally it proceeds in an extension. The tuberculum and capitulum are reinforced against one another on the medial side by a laminar connection. (Fig. 84.) Through increased narrowing the proximal section changes toward the back into a long rod-shaped shaft. The expansion, length and width of the tubercular and capitular branches constantly increase in the proximal section of the vertebral series. The medial reinforcement between both forks increases simultaneously through multiplication or elevation of the supporting lamina.

Fig. 84. Right rib of the 5th cervical vertebra of SI; medial view. About 1/5 nat. size

Foramen transversarium. The fo. transversarium constantly increases in size in the course of the cervical vertebral series. As the anterior section of the centrum is excavated up to the median septum as a result of the deeply invasive pleurocoels, the area of the foramen expands to the septum. The considerable width of the foramen can be seen in the following size figures: In the 6th cervical vertebra its lumen has a lateral width, measured into the interior of the pleurocoel, of about 20 cm, a height of 14 cm; in the 7th cervical vertebra, a width of 23 cm, a height of 15 cm; in the 9th to 11th vertebra the width measures about 39, 40 and 43 cm, while the height cannot be reported in these vertebrae due to severe compression.

Shaft. As the two-headed proximal end from the 3rd vertebra onward constantly increases in expansiveness, so the connecting section of the shaft up to the 12th vertebra becomes increasingly broader, and the shaft overall becomes constantly more robust. The end always truncates in a point, so far as it is preserved. While the terminal section of the ribs of the 4th vertebra is very thin, it is increasingly robust in the following ribs, and thickly spear-shaped in the last one. The terminal section, which frequently has a somewhat triangular but also strongly compressed varying cross section even within the same rib in this sense, is characterized by an increasingly more strongly developed sculpture as the robustness of the rib increases, [sculpture] which is formed of longitudinal ridges and in frequently transverse, fine wrinkles that cover them. In the short rib of the 12th vertebra this extremely strongly sculptured terminal section even occupies the greater part of the entire length.

Cross sections of the 3rd to 12th cervical ribs, with the exception of the 8th, are assembled in Fig. 85 and 86 in such a manner that cross sections that are of identical distance from the beginning of the free shaft, that is, from the farthest cranially situated point of the sinuous caudal contour between capitulum and shaft, are at nearly the same height. This compilation should enable the easy comparison of the cross sections of every individual rib and thus the changes with increasing distance

from the cranial end of the shaft, as well as show the differences between the individual ribs.

The free shaft is so complete in the three shortest ribs of the 2nd, 11th and 12th cervical vertebra that their entire original length can be estimated approximately without any further issue. Approximate lengths for the three rib shafts of 104 cm, 125 cm and 82 cm are produced. The length of the ribs of the 7th and 8th cervical vertebra can be determined approximately with the assistance of the circumstance that a piece of their shaft lies close to the rib head of the 10th vertebra and indeed the rib of the 7th vertebra with the end piece [of the 10th vertebra]. The length to the point of adjacency in the rib of the 8th vertebra, also the end piece that extends beyond it, can be estimated approximately. A free shaft length of about 290 cm results for the rib of the 7th cervical vertebra; for that of the 8th vertebra, a length of about 240 cm.

13th cervical rib (Fig. 87, 88). The articular end of the capitulum is missing in both ribs, the end of the shaft of the right rib, and the largest part of the left, not to mention a larger central portion of the tuberculum of the left rib.

The 13th presacral rib clearly illustrates the transition to the dorsal ribs in its morphology. The proximal portion of the rib is a quite shallowly arched, thin, triangular plate. The capitulum is long, rod-shaped. A triangular, rough articular surface of approximately 11 cm width (left) is very shallowly beveled on the tubercular branch. An incompletely preserved thin flange extends forward from the lateral longitudinal lamina of the shaft. A large rounded depression lies on the lateral side of the capitular branch.

The shaft almost proceeds into the process of the capitulum that initially narrows strongly, further along more gradually. The shaft tapers to 2.5 cm at the broken end. The rib is restored to a length of about 100 cm to the end of the tuberculum.

Fig. 87

Right rib of the 13th cervical vertebra (SII);  
View from the front. 1/15 nat. size

Fig. 88

Left rib of the 13th cervical vertebra (SII);  
View from the front. 1/15 nat. size

### Comparison.

Related to *Brachiosaurus*, the genus *Camarasaurus* also possesses, as GILMORE's (1925) investigation of the skeleton of *C. lentus* (MARSH) in the Carnegie Museum of Pittsburg [sic] shows, relatively very long cervical ribs. The longest rib, which belongs to the 7th cervical vertebra, reaches to near the anterior end of the centrum of the 11th cervical vertebra, thus extends itself over the associated vertebrae almost over

Fig. 85. Cross section through the ribs of the 3rd – 7th cervical vertebra. Nat. size  
l = lateral. m = medial.  
The Arabic numerals give the distance from the proximal end.

Fig. 86. Cross section through the ribs of the 9th – 12th cervical vertebra. Nat. size  
l = lateral. m = medial.  
The Arabic numerals give the distance from the proximal end.

three additional vertebrae. The great length of the cervical ribs is connected with a not remarkable length of the cervical vertebrae, which moreover could still be particularly short in the former skeleton due to youth. The cervical ribs of *Uintasaurus* (W. J. HOLLAND 1924) are also long, in which those of the fifth-last cervical vertebra reach to the middle of the second following rib, and also in the Shantung sauropod *Helopus* (C. WIMAN 1929), in which the longest cervical ribs exhibit 2 1/2 times the vertebra length.

Greatly elongated cervical ribs are not, however, found in all sauropods. The cervical ribs of *Plateosaurus* also carry very long ribs, which in *Pl. quenstedti*, according to the assertions of Frhr. v. HUENE (1932), could attain four times the length of the centrum in the 3rd, 4th and 5th vertebra. In a Halberstadt *Plateosaurus* of the Geological-Palaeontological Museum in Berlin the rib of the 3rd cervical vertebra extended as far as the middle of the 5th vertebra. B. PEYER found long cervical ribs in *Thanyostrophaeus* [sic] (1931) and *Macrocnemus* (1937). In the latter genus, some cervical ribs attained lengths of more than two cervical vertebrae lengths and in *Thanyostrophaeus* [sic] the ribs of the 3rd and 4th cervical vertebra, the centra of which measure 25 and 31 mm, are 71 and 73 mm long. The South African thecodont genus *Chasmatosaurus* in which, according to BROILI and SCHRÖDER (1934) the rib of the atlas reaches up to the fourth cervical vertebra, and the incompletely preserved rib of the axis is also very long, shows that in comparison with *Brachiosaurus*, even moderately elongated cervical vertebrae can carry very long ribs.

### **Functional significance of the cervical ribs.**

To understand the purpose and function of such remarkably greatly elongated cervical ribs it appears to me the best method would be to comparatively assess the relationships in the neck of birds - with the necessary caution. The foundation for this is provided by the precise investigations of H. VIRCHOW and the extensive treatment of J. E. V. BOAS (1929) about the neck of birds. As BOAS shows, tendons of the m. longus colli (anticus) attach to the ends of the cervical ribs of, for example, *Struthio* and *Larus*, which issues from ventral projections of the anterior dorsal vertebrae and posterior cervical vertebrae, the hypapophyses or paired sublateral processes, as well as from the underside of the "ansae", the blades that are formed from the cervical rib, dia- and parapophysis, and which enclose the foramen transversarium. The first-mentioned processes are absent in the vertebrae of *Brachiosaurus*; the "ansae" would have offered plentiful surfaces for the origin of the m. longus colli and its tendons. One could well imagine that in the sauropods too, the individual portions of the m. longus colli with its tendons inserted on the ends of the cervical vertebrae. To include the various scapular muscles that are present and issue from the cervical ribs in crocodiles and lacertilians in this study appears to me to be of little advantage, since the neck musculature in the long-necked sauropods was certainly evolved very differently from that of the short-necked reptiles.

Apart from the relationships of the cervical ribs to musculature, the cervical ribs, in consequence of the extraordinary development of their shafts, must have had a specific mechanical functional significance. The curvature of the cervical vertebral column fulfills itself at the articular sites of the centra. How flexible the cervical ribs were – and presumably they were to a greater extent than other bones of similar strength – and to what extent they could participate in the flexion of the vertebral column at the articular ends of the centra through their own bending, we do not know. One does, however, obtain a certain understanding of the resistance they offer to bending when one examines the size of the rib cross sections in the region of articulation between two vertebrae. Thus

the rib of the third cervical vertebra has a narrow-oval cross section on its rear articular end that is about 15 mm long and 7 mm wide; the corresponding rib cross section in the 4th cervical vertebra measures 12 X 9, in the 5th 19 X 11, in the 6th 33 X 11, in the 7th 31 X 10, in the 9th 29 X 12, in the 10th 27 X 15, in the 11th 26 X 13, in the 12th 22 X 15 mm. These numbers show that the ribs at the bending points between the host and the following vertebra had the character of quite robust rods that offer considerable resistance to bending. They proceeded ventral of the rib heads, stiffened the neck in collaboration with the supraspinal ligament; even if they perhaps could yield to a degree within the musculature or other tissues in which they were embedded and did not have to fully participate in all the flexion of the cervical vertebral column, and relieved the extensor musculature in bearing the neck. The numbers also show, as does the compilation of the cross section illustrations, that corresponding to their stresses the cervical ribs become stronger up to the 10th vertebra. In the last two cervical vertebrae that are greatly shortened, the associated ribs also quickly become shorter and their cross sections are reduced caudally more rapidly, both likely in connection with the increased flexibility that is to be assumed for the sauropods in the transition to the trunk. The stiffening of the cervical vertebral column through the ribs is increased even more because the extraordinarily long shafts overlap caudally not only past the articulation with the following vertebra, but rather usually past two additional articulation sites. While the rib shaft at the 3rd articulation site is naturally very thin, in the second it is mostly of considerable robustness; thus the cross section here of the rib of the 7th vertebra is 19 mm long and 9 mm wide, in the rib of the 9th vertebra these measurements total 18 and 12 mm, in the following cervical rib 26 and 12 mm. This mostly very pronounced wide morphology of the cross sections at the articular points again permits the conclusion that the stiffening against lateral bending was particularly effective, that is in the same sense as the vertically oriented facets of the zygapophyses.

## **Ribs of the dorsal vertebrae.**

### **Description.**

Find SII (Fig. 89-106). During excavation it was evident that the orientation of the ribs in their original sequence could not be recognized. The ribs too, in their distal section, were affected by the erosion of the stream. Numerous fragments of them could be collected in the streambed and later used in large part for the reconstruction of the ribs. In the arrangement of the ribs there were eleven different ribs, that is, 11 rib pairs. Of the 22 ribs, the right of the 1st, 7th and 11th and the left of the 5th pair could not be identified in the material. No indications were found that more than 11 pairs were present. It can be noted from the table how complete the individual ribs are, also how long the incomplete ribs were reconstructed for the skeletal reconstruction. Completely preserved are the 3rd and 4th left and the 8th right rib.

The extant dorsal ribs could easily be arranged in their correct sequence according to specific characteristics that changed successively. The morphology of the head portion that changed in stages, the curvature of the shafts and the large difference in the robustness is illustrated

Fig. 89–96. Right ribs of the 2nd – 6th and 8th – 10th dorsal vertebra,  
Views from the front. 1/15 nat. size

Fig. 97–106. Left ribs of the 1st – 4th and 6th – 11th dorsal vertebra;  
Views from the front. 1/15 nat. size

by the figures 89-106. The morphology is of the same character as in other genera of sauropods of which the ribs are described. The very large difference in the circumference of the proximal section and in the robustness of the shaft, the greatest width of which diminishes from 16.0 cm in the 3rd rib to 4.3 cm in the 10th, is to be emphasized. From the varying degree of curvature of the rib shafts it can be concluded that the dorsal cross section was narrower in the front than in the back.

Cavernous construction (Fig. 107, 108) can be confirmed in the head of the most robust dorsal ribs, particularly well developed in the second. In the right second rib a 9-cm-long, approximately egg-shaped pocket is deeply sunk into the anterior wall, immediately in front of the upper lateral corner of the extremely delicately built tubercular branch, and immediately next to it medially on the rear side is found a depression that invades deeply on top and becomes shallow toward the bottom. In the left second rib the pocket on the front side is not as sharply bordered at the bottom. I interpret these depressions as manifestations that developed through the formative pressure of air sacs. In *Brachiosaurus altithorax* (RIGGS 1904) a large foramen even sits in the upper section of the shaft, which leads to an internal cavity and is to be interpreted as pneumatic.

Fig. 107

Proximal section of the 2nd left dorsal rib  
with pneumatic cavity in the tuberculum;  
Front view. 1/10 nat. size

Fig. 108

Proximal section of the same rib with  
pneumatic cavity in the tuberculum;  
View from behind. 1/10 nat. size

Dimensions of the dorsal ribs of Find SII in cm.

Rib	Length over the curve: Tuberculum – distal end Preserved	Length over the curve: Tuberculum – distal end Restored	Length, straight line: Capitulum – distal end Preserved	Length, straight line: Capitulum – distal end Restored	Minimum width (Distal section)	Maximum width (Middle section)	Proximal width: Capitulum – tuberculum
1 right							
left		228		223		11.7 ±	
2 right	140 +	261		229		11.9	68
left	161 +	258		229		11.6	63
3 right	208 +	262		255		15.9	62
left	263		255		10.8	16.0	62
4 right		260		249	6.3	9.7	
left	260		249		5.9	10.0	46
5 right	235 +	254		240	6.5	7.8	40
left							
6 right		237		224			
left		239		226	4.2	6.9	
7 right							
left		227		211		5.0	32 +
8 right	204		192		3.0		34
left		210		197		5.0	32 (+)
9 right	88 +	188		175		5.2	29
left		194		179			
10 right	144 +	167		152	2.8	4.3	
left		172		157		4.4	
11 right							
left	87 +	92		95	2.8	5.0	

### Comparison.

The existing material from other finds of dorsal ribs of *Brachiosaurus brancai* is not significant, so that a comparative discussion is abandoned. On the other hand, several statements of RIGGS (1904) about the ribs of the American *Brachiosaurus altithorax* are of interest. The length of a middle, slender rib of this species amounts to 274.5 cm, thus exceeds the greatest measured length in *B. brancai*, 263 cm in the third rib, by 11.5 cm. Still more significant is the difference in the width of the shaft, which RIGGS gives as 20.4 cm from a rib, in comparison with 16 cm in as the greatest width in *B. brancai*. OSBORN and MOOK give a maximum length of 216 cm for the 5th rib of *Camarasaurus supremus* COPE. In the giant *Apatosaurus luisae* [sic] GILMORE (1936) measured a maximum length of 213 cm in the 5th rib, thus significantly less than in *Brachiosaurus*.

In no other sauropod genera in which they are well known, is the robustness of the ribs as strong and noticeable as in *Brachiosaurus*. The distribution of maximum strength with the rib cage of the various genera exhibits considerable and remarkable

differences. *Dicraeosaurus* differs particularly strongly from *Brachiosaurus* in that in the former the first two ribs are extraordinarily delicate; the 4th, 5th and 6th ribs are the strongest. *Apatosaurus* on the other hand, is more similar to *Brachiosaurus* because the 2nd to 4th ribs in *Ap. louisae* and the 2nd and 3rd ribs in *A. excelsus* (according to RIGGS 1903) are the strongest. *Diplodocus* differs again; in *D. longus* the 4th to 6th ribs are the most robust as in *Dicraeosaurus*. The genus *Camarasaurus*, which of the well known genera is most closely related to *Brachiosaurus*, has a much shorter neck, differs considerably from it in the distribution of rib strength. In *C. lentus* (according to GILMORE) the 5th rib is the most robust; in the rib series of *C. supremus* assembled by OSBORN and MOOK from the mass of COPE material, the greatest rib strength is found immediately before or in the middle of the rib cage.

### **Significance of the differences in rib strength.**

If one attempts to interpret the remarkable difference in the strength between the anteriormost and the rear dorsal ribs of *Brachiosaurus*, it is obvious that the relationship of rib strength in ungulates should be considered comparatively. A difference in the strength between posterior and anterior dorsal vertebrae is also frequently highly pronounced in them. It is particularly noticeable in the giraffe, in which the posteriormost ribs are exceptionally thin, which appears noteworthy in view of the analogy to the external appearance in *Brachiosaurus*. The broad true ribs of the ungulates have, as J. U. DUERST (1931) emphasizes, primarily a bearing function in the suspension apparatus of the forelimbs, a function in which the shoulder musculature participates. It must be considered that the connection between rib cage and forelimbs is more tightly constructed than in the ungulates, in that the pectoral girdle is directly connected with the chest by means of the coracoids. A suspension of the rib cage must thereby be less pronounced in the reptiles. The condition too, that within the sauropods, in contrast with the ungulates, very significant differences in the distribution of the various rib strengths occurs, as the comparison of *Brachiosaurus* and *Dicraeosaurus* shows particularly clearly, makes it probable that the differences in rib strength in ungulates and sauropods cannot be judged quite the same.

That in *Brachiosaurus* the first dorsal ribs are the strongest can likely be explained for the most part, by the fact that the weight of the enormous neck rested on them particularly, on the path over the anteriormost dorsal vertebrae. That must have been the case not only while standing or while walking but also especially while reclining, when the anterior trunk rested on the sternal plates. The neck of *Apatosaurus* was not similar in length to that of *Brachiosaurus*; the broadly spanned heads of the cervical ribs bestowed such a significant cross section that the weight of the neck, even if as I suspect, extensive air sacs were situated in it, must certainly have been very great, and the strength of the anterior dorsal vertebrae can be explained in the same way as in *Brachiosaurus*. The extremely long-necked *Helopus* from the Lower Cretaceous of Shantung (C. WIMAN 1929) has a particularly robust third dorsal rib, which is in complete agreement with the condition in *Brachiosaurus*.

That, apart from the mechanical compression stress, the width of the anterior dorsal ribs of *Brachiosaurus* also originally stood in association with a strong development and activation of the muscles that insert on the scapula and which come from the anterior ribs (m. serratus superficialis and m. serratus profundus), since in the long and heavy-necked genera

they probably had more to achieve than in the short-necked genera, does not seem to me to have been the main reason for the broadening of the ribs.

The circumstance that the anterior ribs of *Brachiosaurus altithorax* are even wider than those of *B. brancai* is to be considered. That may be related to the fact that the dorsal vertebrae of the American species are noticeably larger than those of the African. The greater the length of a dorsal vertebra, the longer the dorsal portion falls out on the associated rib, so the individual rib is more heavily loaded, in addition to the burden of the neck, than the rib of a short vertebra.

### Haemapophyses.

Haemapophyses of Find Aa (Fig. 109–136). The haemapophyses of 16 caudal vertebrae or parts of them are present. The assignment to the associated vertebrae could be completed with considerable certainty on the basis of the position in which they were discovered on the centrum, or through placing them in sequence according to the changes in their morphology and size. The haemapophyses are distributed on the vertebrae from the 2nd to 17th. An isolated right branch can be associated with the haemapophysis of the 2nd vertebra. There does not appear to have been a haemapophysis of the first tail vertebra, to which the absence of any indication of an associated facet on the first centrum speaks in favour. According to OSBORN (1899) a haemapophysis I is also absent in *Diplodocus* while RIGGS (1903) holds the presence of one as possible for *Apatosaurus excelsus* and C. W. GILMORE (1936) indicates one for *Apatosaurus louisae*.

The particulars of the morphology and the modifications in the series may be seen in the figures. The branches of all haemapophyses are free proximally; are thus not connected by a bridge.

Haemapophyses of Find no. Eight haemapophyses of the anterior tail section are present in Find no, and one that had its position considerably farther back and was mounted on the 19th caudal vertebra of the skeleton. The eight anterior haemapophyses were mounted on the caudal vertebrae number 3 to 10 in the skeletal reconstruction. The haemapophyses of no conform substantially to those of Aa; they only differ slightly in that in no the distal shaft is noticeably longer in relation to the depth of the haemal canal. The length measurements are greater than in Aa, since Skeleton no must have been considerably larger.

The various genera of sauropods differ considerably in that the haemal canal of the haemapophysis was completely open in some, in others in contrast, the anterior haemapophyses, at least in a longer series, is closed dorsally by a bridge that connects the forks. Beside *Brachiosaurus*, the closest related genus *Camarasaurus* and *Haplocanthasaurus* [sic] belong to the first group; *Diplodocus*, *Apatosaurus*, *Dicraeosaurus* belong to the other group. It appears that the genera with relatively low neurapophyses of the caudal vertebrae exhibit haemapophyses that are open dorsally, while the genera with tall neurapophyses have haemapophyses that are closed dorsally. The development of the bridge between the branches likely does not signify more than the enlargement of the articular surface on the centra of the associated caudal vertebrae. A stiffer connection may have been established thereby, just as the taller neurapophyses might also have more strongly restricted the motion of the vertebrae against one another than the lower neurapophyses. It does not appear impossible that a similar kind of the haemapophyses also indicates points of affinity.

Haemapophyses (Find Aa), Views from the left side 1/4 nat. size  
Fig. 109–118. Haemapophyses 3–12.  
Fig. 119–122. Haemapophyses 14–17.

Haemapophyses (Find Aa), Views from the front. 1/4  
nat. size  
Fig. 123–132. Haemapophyses 3–12.  
Fig. 133–136. Haemapophyses 14–17.

## Summary of the results.

As a probable vertebral formula there resulted: 24 presacral vertebrae, 5 sacral vertebrae; at least 50 caudal vertebrae. Of the presacral vertebrae 13 belong to the neck, 11 to the trunk. The number of missing rod-shaped terminal vertebrae of the tail cannot be estimated. The cervical vertebrae are elongated to a great degree with the exception of the first and last. The free length (without condyle) of the centra in the 8th to 11th cervical vertebrae reaches almost three times that of the middle dorsal vertebrae.

The very strongly excavated centra of the presacral vertebrae from the axis onward possess a pronounced pneumatic character in their pleurocentral depressions that hollow them out up to the median septum, and in the large-celled structure of the condyles. The external architecture of the presacral vertebrae is specialized to a high degree by extensive refinement of the laminae, deeply invading niches between these, by development of external caverns and laminae of the second order. The neurapophyses are obviously entirely unbifurcated; in the neck they are low, knob-shaped; in the trunk and sacrum they are medium tall; tallest in the vertebrae prior to the middle of the trunk. The relatively long lateral processes in the sacrum are characteristic. The tail is relatively short, the middle vertebrae are not elongated, and the posterior vertebrae are rod-shaped and shortened. The construction of the caudal vertebrae is simple, primitive, without overlap of the presacral features, the pleurocoels and the lateral laminae on the lower neurapophyses. The centra are somewhat biconcave, almost without lateral ridges; the lateral processes are weakly developed, not distributed plate-like on the anterior vertebrae.

The cervical ribs are extraordinarily long; they reinforce the cervical vertebrae, particularly against lateral bending. The ribs of the axis exhibit a differentiation that might perhaps be interpreted as a secondary sexual difference. The head is somewhat cavernous in the second and third dorsal rib. Of the ribs of the trunk, the anteriormost ones exceed in strength to a high degree the very weak posterior ribs.

The articular connections between the 2nd and 3rd presacral vertebra permit extensive motion; only sagittal bending was possible in the majority of the remaining cervical vertebrae and the middle and posterior dorsal vertebrae as well as in the anteriormost caudal vertebrae.

The vertebral column of *Brachiosaurus brancai* conforms extensively with the American species *B. altithorax*. Of the forms with unbifurcated neurapophysis, the next closest is the dorsal vertebra of *Ornithopsis (Pelorosaurus) hulkei* SEELY [sic] from the English Wealden. In the genus *Camarasaurus*, shown to be related to *Brachiosaurus* by the construction of the skull, the mostly bifid presacral vertebrae are similar to the posterior dorsal vertebrae and the caudal vertebrae of *Brachiosaurus*.

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## Explanation of the plates.

### Plate I.

Presacral vertebrae of *Brachiosaurus brancai*. 1/10 nat. size

- Fig. 1. Axis (Find be 1).
- Fig. 2. 3rd cervical vertebra (Find be 2).
- Fig. 3. 4th cervical vertebra (Find be 3).
- Fig. 4. Axis (Find be 1), rear view.
- Fig. 5. 3rd cervical vertebra (Find be 2), front view.
- Fig. 6. 3rd cervical vertebra (Find be 2), rear view.
- Fig. 7. 4th cervical vertebra (Find be 3), rear view.
- Fig. 8. Middle cervical vertebra (Find Y 4).
- Fig. 9. Posterior dorsal vertebra (Find AR 1), front view.
- Fig. 10. The same dorsal vertebra. Right lateral view.
- Fig. 11. The same dorsal vertebra. Rear view.

### Plate II.

Caudal vertebrae of *Brachiosaurus brancai* (Find Aa), 1/10 nat. size

- Fig. 1a-18a. Front views of the 1st-18th caudal vertebra.
- Fig. 1b-18b. Right lateral views of the 1st-18th caudal vertebra.
- Fig. 1c-18c. Posterior views of the 1st-18th caudal vertebra.

### Plate III.

Caudal vertebrae of *Brachiosaurus brancai*. (Find D),  
close to 1/10 nat. size

- Fig. 1-23. 1st-23rd caudal vertebra. Lateral views.
- Fig. 24. Posterior caudal vertebra, separated from the 23rd caudal vertebra by a gap. Lateral view.
- Fig. 25-29. Posterior caudal vertebra, separated from Fig. 24 by a gap.
- Fig. 30-36. 1st, 2nd, 9th, 11th, 16th, 20th, 23rd caudal vertebra, anterior views.
- Fig. 37. The same caudal vertebra as Fig. 27, front view.
- Fig. 38-44. 1st, 3rd, 9th, 11th, 16th, 20th, 23rd caudal vertebra, rear views.
- Fig. 45. The same caudal vertebra as Fig. 27, rear view.

### Plate IV.

Caudal vertebral column of *Brachiosaurus brancai* (Find no).  
about 1/40 nat. size

### Plate V.

Rib cage of the skeletal reconstruction of *Brachiosaurus brancai* in the atrium of the Geol. Palaeontol. Institute and Museum (Museum für Naturkunde) in Berlin.  
About 1/20 nat. size