PALAEONTOGRAPHICA

CONTRIBUTIONS

TO THE NATURAL HISTORY OF THE PAST

J. F. POMPECKJ

WITH THE COOPERATION OF F. BROILI, H. RAUFF AND G. STEINMANN as representatives of the german geological society SUPPLEMENT VII

> 1ST. PART VOLUME II

STUTTGART SCHWEIZERBART'S PUBLISHING HOUSE (ERWIN NÄGELE) G. M. B. H. 1929

SCIENTIFIC RESULTS OF THE TENDAGURU EXPEDITION 1909–1912

NEW RESULTS FOUNDED BY GEOLOGICAL-PALAEONTOLOGICAL INSTITUTE AND MUSEUM OF THE UNIVERSITY OF BERLIN

THROUGH W. JANENSCH IN BERLIN

STUTTGART SCHWEIZERBART'S PUBLISHING HOUSE (ERWIN NÄGELE) G. M. B. H. 1929

THE VERTEBRAL COLUMN OF THE GENUS DICRAEOSAURUS

BY

W. JANENSCH^{*}

WITH PL. I–VII, 79 TEXT-FIGURES AND 6 TABLES

^{*} Original citation: Janensch, W. 1929. Die Wirbelsäule der Gattung *Dicraeosaurus*. *Palaeontographica*, Supplement VIII, Part I, Vol. II: 37-133. Translated by Simone Klutzny, May 2002. Original author's footnotes are translated without notation. Translator and editor comments appear in footnotes as [Tr] or [Eds].

Contents.

	Page
Foreword	39
Outline of the material of Dicraeosaurus	41
General remarks on the external architecture of the presacral vertebrae and the	
nomenclature of the laminae system	43
Positive and negative sculptural elements	44
The direction of stress in the architecture of the laminae	44
Nomenclature of the vertebral laminae system	46
Dicraeosaurus hansemanni	50
Presacral vertebrae Skeleton m Second presacral vertebrae, axis Presacral vertebrae 3–24 Comments on individual presacral vertebrae Presacral vertebrae from locality dd Proatlas Atlas	50 50 51 69 72 72 73
Sacrum	74
Caudal vertebrae Skeleton m Caudal vertebrae from locality dd	78 78 84
Ribs of the presacral vertebrae Short ribs from cervical vertebrae 2–11 Long ribs of the last cervical vertebra and the 12 dorsal vertebra	87 87 90
Chevrons	95
Physiological and histological conclusions Flexibility of the vertebral column Significance of the architecture and position of the neurapophyses Significance of the laminar system of the diapophysis and the parapophysis	99 99 100 102

Connections of the laminae Interspinous lamina Supraspinous lamina Nuchal ligament Supraneural lamina Summary of the laminar support apparatus of the neck	103 103 104 105 106 106
Bifurcation of the neurapophyses of the presacral vertebrae	107
About the muscles of the spinal column	108
Dicraeosaurus sattleri	109
Presacral vertebrae Skeleton M Excavation site E Isolated dorsal vertebrae from other localities	109 109 114 118
Sacrum	118
Caudal vertebrae Skeleton M Caudal vertebral centra from locality O	121 121 123
Ribs	124
Chevrons	125
Caudal vertebrae from Dicraeosaurus of uncertain species affinities	126
Caudal vertebrae from excavation site GD	126
Caudal vertebrae from excavation site Ob	127
Caudal vertebra[e] La	127
Caudal vertebral column s	128
Isolated caudal vertebrae from different excavation sites	130
Characteristics of the vertebral column of the genus <i>Dicraeosaurus</i> and comparison of both species	131
Literature	133

Foreword.

The study presented here is concerned with the spinal column and its appendices from both species of the genus *Dicraeosaurus*, established in my preliminary report on the vertebrate fauna of the Tendaguru Beds (1914). The exceptionally good preservation, for sauropods, of one skeleton (m) of *Dicraeosaurus hansemanni* gave cause for, and also justifies, the morphological description of the particularly distinguished external architecture in thus far not executed comprehensiveness of detail. This thorough morphological description forms the basis for revealing and interpreting the significance of some characters of this architecture.

The organization of the description is the result of the composition of the material. The older species, *Dicraeosaurus hansemanni*, will be dealt with first, skeleton m of this species forming the main part; the description of its spinal column provides the backbone of the entire investigation. A second part contains the description of the vertebral column of *D. sattleri*, less completely preserved yet remarkable due to its higher specialization. The description of a larger collection of caudal vertebral series and also of isolated caudal vertebrae from different excavation sites is given separately, as the assignment of these specimens to a species is uncertain. The precise position of the locations at which the specimens have been found can be observed on the previously published survey map of the excavation sites (1925).

The difficult preparation of the material described here was executed with excellent results by Mr. Senior Preparator G. Borchert; the gentlemen Mr. Preparator J. Schober and to a lesser extent Mr. Senior Preparator E. Siegert also deserve merit.

The exquisite drawings of the skeletal elements are merited to Mr. Hugo Wolff from Berlin-Karlshorst.

The fact that this treatise could be richly outfitted with drawings worthy of the material must be gratefully accredited to the generous support presented by the Prussian Ministry for Science, Art, and National Education to the Geological–Paleontological Institute and Museum of the University of Berlin for the publication of the Tendaguru project.



Outline of the material of Dicraeosaurus.

Dicraeosaurus hansemanni JANENSCH.

Skeleton m.

The skeleton from the Middle Saurian Bed near Kindope, north of Tendaguru, lay with its right side downward in the sediment. It was found articulated from the 19th caudal vertebra to the 9th cervical vertebra inclusive¹. The proximal part of the neck from the 8th cervical vertebra up to the axis was bent ventrally and lay at right angle to the distal part of the neck. The left side of the vertebral column, from the 13th presacral vertebra to the sacrum and the first caudal vertebra inclusive, were damaged by abrasion. The left diapophyses of the vertebrae are more or less completely lost because of this damage. The left parapophyses of the posterior dorsal vertebrae and the left sides of the neurapophyses were removed. The left sides of the centra of the posterior dorsal vertebrae have also been more or less strongly abraded. The atlas and skull were not found at the excavation site, nor anywhere in the more distant surroundings. The vertebral column of the tail exhibits a concave bend, which can also be observed in the other dinosaurs from Tendaguru (compare HENNIG 1915). The ribs of the right side are in almost undisturbed articulation with the vertebrae, on the other hand the ribs of the left side are only incompletely preserved; they were not found in articulation with the vertebrae due to the loss of the tips of the left diapophyses, but were scattered over the nearer surroundings of the skeleton. The pelvic bones and femur of the right side lay in situ. The left femur was found a short distance dorsal to the sacrum. The left tibia, fibula, and astragalus lay still in articulation above the proximal part of the distal section of the neck that is connected to the body. Only the distal part of the left ischium was preserved, it was positioned slightly above the end of the tail. Three caudal vertebrae that match the skeleton in size were found at a farther distance from the skeleton in the weathered zone of the marls.

The process of its embedding can be deduced from the position in which the skeleton was found. The carcass of the sauropod had been transported by water until it came to rest at the excavation site. On its way it lost the skull, both anterior limbs including the sternal plates, the right lower leg, both feet, and the larger part of its tail. Prior to the final positioning and embedding of the body in the sandy marls, an additional movement resulted in the bending of the proximal part of the neck. Later on, abrasion cut off the prominent tips of the left diapophyses of the dorsal and sacral vertebrae including the ribs, the left half of the pelvis, and the left hind limb. These parts were transported into the neighboring area. Concerning the left hind limb: it might well be possible that it was not disconnected after the positioning, but, like the proximal part of the neck, fell into its two parts which were then separated from each other prior to the final positioning of the skeleton.

¹ A figure of skeleton m *in situ* was presented earlier [JANENSCH 1924, text-fig. 17 and pl. IV, Fig. 2]

The vertebral material investigated in this study includes: 24 presacral vertebrae, the sacrum consisting of five vertebrae grown together, 19 articulated and three isolated caudal vertebrae. Additionally, there is a number of more or less incomplete short cervical vertebrae, the right distalmost long cervical rib, 12 right and three left dorsal ribs, as well as 17 chevrons.

Vertebrae from excavation site dd.

The numerous vertebrae from *Dicraeosaurus hansemanni* from excavation site dd from the Middle Saurian Bed near Kindope, north of Tendaguru, belonged to two animals which must have been of exactly the same or at least of nearly the same size. At the moment, the presacral vertebrae are only partially prepared, 13 of the cervical vertebrae are completed, while almost all caudal vertebrae are still unprepared. The bones from excavation site dd are generally much less well-preserved than the bones of skeleton m, therefore no particularly interesting information can be expected from the preparation of these presacral and caudal vertebrae. For this reason, a thorough preparation of these vertebrae has been set aside in favor of more pressing preparatory work. Among several badly preserved sacra which are difficult to determine to species, two seem to belong to the two skeletons of *Dicraeosaurus hansemanni*. All of the caudal vertebrae that can be safely separated for the two individuals are prepared, because this material complements skeleton m in an important way. There are 63 caudal vertebrae present. The preparation of the atlas, proatlas, one cervical rib, and a smaller number of chevrons is also completed.

Dicraeosaurus sattleri JANENSCH.

Locality M.

In 1909, the first year of the excavation, excavation site m close to the south knoll of Tendaguru in the Upper Saurian Bed provided the remains of one animal, scattered over an area of approximately 20 m². The bones lay closely beneath the surface, but were also weathered out in parts, and in this case were more or less disintegrated. Only the 2nd and 3rd, and the 4th–7th caudal vertebrae lay in natural articulation. The parts of the skeleton present include two cervical vertebrae, two arches of the neurapophysis of one presacral vertebra, four caudal vertebrae, the sacrum, seven anterior and one mid-caudal vertebra, a number of incomplete ribs as well as parts of ribs, five chevrons, two ilia, of these the right one in connection with the sacrum, two pubes, one ischium, two femora, and further a large number of weathered and disintegrated parts of bones. Even on the vertebrae that were excavated and not weathered out, due to the shallow depth in which they were found, the finer elements of the external architecture were for the most part not at all or only incompletely preserved.

Locality E.

At site E in the Upper Saurian Bed near Tendaguru, ten more or less incomplete presacral vertebrae were found, one of these belonging to a not fully grown individual. One cervical rib was also excavated. Whether there are more parts of the skeleton that belong to the same animal from which the cervical ribs originate among the other bones found at this excavation site can only be determined after all the material has been prepared.

Locality o.

Excavation site o from the Upper Saurian Bed at Tendaguru is important because it provided, together with the centrum of a dorsal vertebra and one from a caudal vertebra, also the scapula, coracoid, humerus, and ulna from the forelimb girdle. From the pelvic girdle, the ischia, femur, tibia, fibula, and 5th metatarsal were found. Even though the preservation leaves a lot to be desired, important conclusions about measurements can be made from these finds. Nothing contradicts the assumption that all these parts belong to one individual only. The shape of the available vertebrae proves their certain assignment to the genus *Dicraeosaurus*; certain limb bones such as the femur and humerus indicate that the species must be *Dicraeosaurus sattleri*.

Locality Ob.

A dorsal vertebra from a *Dicraeosaurus* was found together with a larger number of caudal vertebrae at Obolello, southeast of Tendaguru. This single dorsal vertebra will be described in addition to the finds identified as *Dicraeosaurus sattleri*, even though their assignment to a species cannot be deduced with certainty from the characters of this part, neither from this vertebra nor from the caudal vertebrae that apparently go with it. What speaks indirectly in favor for the assignment to this species is the association with *Gigantosaurus robustus*, which is only found in the Upper Saurian Bed, the only deposit from which *Dicraeosaurus sattleri* is known.

Caudal vertebrae of *Dicraeosaurus* indeterminate to species.

Series from locality GD. Series from locality Od at Obolello, southwest of Tendaguru. Articulated series s. The caudal vertebrae from the LADEMANN Collection. Isolated caudal vertebrae from various localities.

General remarks on the external architecture of the presacral vertebrae and the nomenclature of the laminae system.

Of the many variables that determine the shape and structure of the vertebrae, apart from the inheritance of certain basics, are the stresses that are put upon each vertebra by gravity and the active work of muscles in their ligamentous connections. The problem of deducing the shape of the vertebrae of fossil reptiles such as dinosaurs, which are not represented now by related forms, according to the requirements that are put upon them, is made much more difficult by the fact that the results of anatomical and physiological investigation of the few thoroughly studied recent species can only be taken into account with uncertainty, because of their distant relationship and their morphological divergence. On the other hand, we do not lack data for the interpretation of the significance and purpose of certain morphological characters of the vertebral column of Sauropoda. These characters can be deduced from the very special peculiarities of this architecture, which is, as almost nowhere else in the vertebrate kingdom, an architecture perfected on its surface into the most elaborate detail.

Positive and negative sculptural elements.

The external architecture of the presacral and sacral vertebrae—to some extent also the caudal vertebrae of certain genera—shows elements of a positive and negative nature. Positive elements are the elevated points where the muscle ligaments, muscles, and tendons insert. Of these points, the insertion of muscle ligaments are even more distinguishable due to their rugose surface which shows especially clear protuberances and ridges, however, the insertion points of muscles and tendons are not as easily marked and defined. Positive elements are in particular the laminae on the neural arch and its appendages, also to an extent on the vertebral centra, that had to withstand the strains of pressure. These ridges, functioning as reinforcements, dominate the entire sculpture of the vertebrae to a very high degree.

These positive architectural elements are elevated even more strongly for the above-mentioned purpose by the tendency to reduce bone substance wherever it is not necessary, thereby building a kind of negative sculpture. The effect of this tendency to build negative sculptures can be divided into two modes. In one case the reduction of bone material is achieved by concave depressions and folds between the elevated elements, which determine the shape of these depressions. These depressions are deepened to an important extent which allows the ridges to protrude even more prominently. The second mode of bone material reduction occurs as grooves and holes on the surfaces. The shape and size of such reliefs is not determined by the demand to withstand stresses and strains and can therefore change considerably from one vertebrae to the next, and can even vary strongly between the left and the right side of the same vertebra. The determining factor was obviously the molding of the laminae system; the positioning of the muscles and their tendons seems to be more or less adjusted or submitted to this system. interpretation of these architectural factors is especially valid for the neural arch and its laminae, meaning these parts of the vertebrae that were foremost submitted to the tensile forces of the inserting muscles. tendons, and muscle ligaments. The vertebral centra, which had first and foremost to absorb direct compression, show mostly the negative sculptural elements. This occurred to a high degree in all the cervical and proximal caudal vertebrae. Considerable variation of these structural elements occurs in the posterior dorsal vertebrae in the various genera.

The direction of stress in the architecture of the laminae.

Concerning the dorsal vertebrae of *Diplodocus*, H. F. OSBORN (1899) remarked generally that the occurring laminae^{*} (which is probably the best German translation for OSBORN'S "lamina buttresses" or "laminae"), connect all the major points where tension and compression occurs.

The ridges are mainly built to counteract the strains of compression, and are constructed for this purpose according to the force and direction of this compression. These requirements of compression occur directly at points where two neighboring vertebrae touch and press against each other due to the influence of gravity or due to movements, namely at the end surfaces of the vertebral centra and at the zygapophyses.

To withstand the compression executed by the adjacent vertebrae these end surfaces of the centra have their abutment of course in the centrum itself. The pleurocentral pits show that the passages along which compression is transmitted circumvent the areas of these pits, the edges of

^{* &}quot;Leisten" = "laminae" [Tr]

which are often shaped as ridges. The zygapophyses that are exposed to compression from the presacral vertebrae withstand this compression by the presence of laminae that are positioned in a certain way. These laminae always lead to a point designed to withstand this compression due to its strong construction. For the prezygapophyses this point is the anterior end of the centrum, for the postzygapophyses these points are the neurapophyses and their forked branches, respectively. In certain genera, two dorsally diverging laminae can occur among the lower-positioned prezygapophyses of the cervical vertebrae, which indicate that compression was not transmitted in only one direction, but was absorbed and diffused in different directions.

The second, more common method of the laminae to counteract compression is that at the epiphyses of the vertebrae, distally occurring tensile forces produced by muscles and ligaments are absorbed in the laminae as in the vertical part of a T-beam, and diverted to points developed to act as a counter-force against these pressures. These points are namely the ends of the vertebral centra, which act as strong counter-forces by attaching to the next vertebrae.

The tensile forces that are transmitted medially through the interspinous ligament, and by inserting muscles more or less sagittally at the neurapophyses and at their branches respectively, are absorbed by paired laminae running along the anterior and posterior and leading to the pre- and postzygapophyseal laminae that both form a stable counter-force; the prezygapophyseal laminae by means of their laminar connection with the centrum and the postzygapophyseal laminae because of their position on top of the prezygapophyseal lamina of the following vertebrae. On both sides of the undivided neurapophyses runs a lamina that gets more prominent terminally (as for example in *Dicraeosaurus*) and that obviously functions to support the laterally much-broadened distal end of the neurapophyses. It can be assumed that tensile forces, caused by the supraspinal lamina to which these ridges had to withstand, begin at this enforcement.

The different points of the laminae, which strengthen the attachment points of the ribs as well as the diapophyses and the parapophyses, correspond to the variability in the shape and the joints of the ribs and to the direction of stress in the neck and body. The laminae run from these points to the ends of the centra. The direction of the laminae that run from the diapophyses towards the anterior and posterior of the centra in the long cervical vertebrae is naturally not the same as in the short dorsal vertebrae. They are positioned more horizontally in the former, almost at the same angle as the longitudinal axis. The same laminae run by nature ventrally in the anteroposterior direction in the short vertebra of the distal part of the trunk, with a high insertion point of the diapophyses. The anterior lamina is always more weakly developed and often completely missing. Other laminae run over the dorsal surface of the diapophysis and strengthen it and the neurapophysis against each other. The laminae running from the parapophysis towards the anterior and posterior of the centra are well developed: they enclose the ventral surfaces of the centra laterally. The lamina running anteroventrally is always present in the dorsal vertebrae, the lamina running posteroventrally is often absent but is developed in *Diplodocus*, for example. With the ascent and approximation of the parapophyses to the diapophyses and the fusion of both elements into one single process in the dorsal vertebrae, the reinforcement is also unified, as both structures together are only supported by one lamina that descends anteriorly from the parapophysis, and by another lamina that descends posteriorly from the diapophysis.

Nomenclature of the vertebral laminae system.

The complicated external architecture of the vertebrae of sauropods, especially of all their different laminae, makes the need for clear terms for this architectural elements necessary. The first comprehensive nomenclature was developed by H. F. OSBORN in his treatise on the distal part of the skeleton of *Diplodocus* (1899). Because only the distal part of the skeleton is described, the cervical vertebrae were not taken into consideration. HATCHER (1901) adopted OSBORN'S nomenclature in his work on Diplodocus. Later, LULL (1919) used also OSBORN'S terms in his work on Barosaurus, with just a few additions and changes. The first significant improvement of OSBORN'S first nomenclature was achieved in his joint publication with MOOK, the monograph on the genus Camarosaurus* (1921), in which the laminae were named in terms that describe their course much more clearly. A nomenclature of the laminae would then be the most comprehensive and easiest to use when the terms would allow immediate recognition of the position of each lamina. This would be achieved most clearly if the name included the two points that are connected by the lamina in question. But following through with this principle would mean completely rejecting the nomenclature introduced by American authors. This seems to me neither desirable nor necessary, because a number of these terms characterize the position of the laminae quite clearly, and these terms can be easily taken over into the German language, although slightly altered. In cases in which an American term seemed to me in need of improvement, I employed the principle of naming the lamina after the points at which they are aimed. Therefore, the terms "horizontal lamina" and "oblique lamina" seemed unfavorable to me. These terms give no clear idea of the course of these laminae. The term "horizontal lamina", when it is used for a lamina that connects the diapophysis with the zygapophysis, labels a lamina with horizontal course in dorsal vertebrae; yet the same lamina takes on a sloping position in the cervical vertebra. Therefore, LULL names the lamina between the diapophysis and zygapophysis "oblique lamina". However, the author uses the same term also for the lamina that runs on the lateral surface of the neural arch posteroventrally from the prezygapophysis toward the centrum, as well as for the laminae that frame the pleurocentral grooves. This usage demonstrates that terms that only describe the laminae as horizontal or oblique are better avoided. I replaced these terms—apart from the term for the last-mentioned lamina, which I do not name specifically—with terms that clearly explain the points at which the laminae in question are aimed. This was achieved by including the syllable "centro" when terms were introduced in which the aiming points were the parapophyses or centrum of the respective vertebrae. For this reason the term "infraprediapophysial lamina" used by LULL and OSBORN had to be eliminated, as this name is useful for the dorsal vertebrae but not for the elongated cervical vertebrae, in which the diapophyses are not at all as ventrally supported as the name indicates.

The included synopsis arranges the laminae in definite terms according to the two landmarks they connect and between which they act as a reinforcement, and at the same time this table contains a comparison of the American nomenclature.

Additional to the main laminae summarized in the table, accessory laminae of minor significance often occur. These accessory laminae may be positioned parallel to the main laminae and in this case serve obviously as reinforcement solely to this lamina; they, too, absorb compression and transmit it in the same direction as the main laminae to which they are related.

sic = *Camarasaurus* [Tr]

Cedi = centrodiapophyseal lamina Cedih = anterior centrodiapophyseal lamina Cediv = posterior centrodiapophyseal lamina Cepah = anterior centroparapophyseal lamina Hy = hyposphene Jfdi H = infradiapophyseal groove Jfhy = infrahypophyseal lamina Jfpo = infrapostzygapophyseal lamina Jfpol = lateral infrapostzygapophyseal lamina Jfpr = infraprezygapophyseal lamina Jfpr = lateral infraprezygapophyseal lamina Jtpr = intraprezygapophyseal lamina Lasp = lateral spinal lamina N = neurapophysis Padi = parapophysis Padi = paradiapophyseal lamina Pl = pleurocentral groove Po = postzygapophysis Podi = postzygodiapophyseal lamina Posp = postspinal lamina Pr = prezygapophysis Prdi = prezygodiapophyseal lamina Prsp = prespinal lamina Sudi = Spinodiapophyseal lamina Supo = Spinopostzygapophyseal lamina Supr = Spinoprezygapophyseal lamina

Laminae of the presacral vertebrae of sauropods.

Fig. 1. Middle cervical vertebra of Brachiosaurus brancai, lateral view.

Fig. 2. Posterior cervical vertebra of Dicraeosaurus hansemanni, anterior view.

Fig. 3. Posterior dorsal vertebra of *Dicraeosaurus hansemanni*, lateral view.

Fig. 4. Posterior dorsal vertebra of Dicraeosaurus hansemanni, posterior view.

Course of laminae		Osborn 1899	LULL 1919	Osborn-Mook 1921	JANENSCH 1929	
Running on neurapophysis	unpaired on anterior midline unpaired on posterior midline running laterally	prespinal lamina postspinal lamina diapophyseal lamina	prespinal lamina postspinal lamina	supradiapophyseal lamina	prespinal lamina postspinal lamina spinodiapophyseal lamina	
Extending from diapophysis Extending from parapophysis	connecting with neurapophysis connecting with prezygapophysis connecting with postzygapophysis connecting with parapophysis running ventrally toward centra if present twice: running toward anterior end of centrum running toward posterior end of centrum	diapophyseal lamina horizontal lamina horizontal lamina diapophyseal lamina diapophyseal lamina prezygapophyseal lamina prezygapophyseal lamina	posterior oblique lamina anterior diapophyseal lamina posterior diapophyseal lamina diapophyseal lamina horizontal lamina anterior diapophyseal lamina	supradiapophyseal lamina horizontal lamina horizontal lamina infrapredia-pophyseal lamina infradiapophyseal lamina infrapostdia-pophyseal lamina horizontal lamina infraprezyga- pophyseal lamina	supradiapophyseal lamina prezygodiapophseal lamina postzygodia-pophyseal lamina paradiapophyseal lamina centrodiapophyseal lamina same anterior prezygapara-pophyseal lamina anterior centropara- pophyseal lamina	
purupopnysis	running toward posterior end of centrum				posterior centropara- pophyseal lamina	
Extending from prezyga- pophysis	connecting with neurapophysis running ventrally toward centrum if present twice: medial lateral running anteromedially running laterally on neural arch from anteroventral toward centra	prezygapophyseal lamina prezygapophyseal lamina oblique lamina	prezygapophyseal lamina oblique lamina	spinoprezyga- pophyseal lamina infraprezyga- pophyseal lamina	spinoprezyga-pophyseal lamina infraprezyga-pophyseal lamina same medial same lateral intraprezyga-pophyseal lamina lateral infraprezyga- pophyseal lamina	

Course of laminae		Osborn 1899	LULL 1919	Osborn-Mook 1921	Janensch 1929
Extending from postzyga- pophysis to hyposphene	connecting with neurapophysis if present twice: medial lateral running ventrally toward centra running laterally on neural arch from anteroventral toward centra running anteromedially running ventrally from hyposphene	postzygapophy- seal lamina diapophyseal lamina postzyga- pophyseal lamina oblique lamina	postzygapophyseal lamina	suprahyposphenal lamina suprapostzyga- pophyseal lamina infrapostzyga- pophyseal lamina	suprahyposphenal lamina same medial same lateral paradiapophyseal lamina infrapostzyga- pophyseal lamina lateral infrapostzyga- pophyseal lamina intrapostzyga-pophyseal lamina centropostzyga- pophyseal lamina

The accessory laminae can also be arranged at a diverging angle to the main laminae, in this case they transmit the pressure that is transmitted towards the main lamina in a different direction.

HATCHER introduced the term "pleurocentral laminae" for the struts that often divide the pits in a more or less irregular manner. I have so far not found a reason to employ this term. I also avoided names for laminae that form the frame and reinforce the borders of the variable pits and fossae, as for example the infradiapophyseal fossa.

As has been explained above, a nomenclature was also created for the fossae and niches that owe their shape to negative architectural elements because they are formed by the reduction of bone substance, as opposed to the laminae that have to withstand positive strains. HATCHER (1901) distinguished between a number of fossae in his treatise on *Diplodocus* (1901); OSBORN and MOOK (1921) employed some of HATCHER'S terms. I limited myself to naming only fossae that are truly individual elements, and not for fossae that are merely concave niches between laminae. In the first category, for example, belong the pleurocentral pits in the vertebral centrum as well as the infradiapophyseal fossae. The only cavity that does not fall into this category and does deserve a name of its own seems to be the deep, unpaired, medially positioned niche between the spinopostzygapophyseal laminae of the cervical vertebrae of most genera, and so I suggest the name "supraspinous fossa".

Presacral Vertebrae.

Skeleton m.

The design and structure of the presacral vertebrae is best described in continuity with and with special emphasis on the constant and the iterative characters of the vertebrae. The axis will be described separately because of its distinctive shape.

There is no definite border between the vertebrae of the neck and those of the trunk. If one would be willing to define this border by the position of the parapophysis relative to the pleurocentral suture, the 13th vertebra would have to be included in the neck, because the parapophysis lies under that suture; the parapophysis, at least with the largest part of it, lies above this suture only in the 14th vertebra. Therefore, the neck-trunk border has to be postulated as posterior to the 13th vertebra. However, the deciding factor here must be the shape of the ribs. Within the series of ribs, there is a morphologically distinct break between the short rib of the 11th presacral vertebra and the long rib of the 12th vertebra. However, as will be demonstrated below, the rib of the 12th vertebra cannot be described as thoracic rib despite its elongation, because the distal end is pointed and was therefore certainly not connected with the sternum. It therefore has to be regarded as the last of the cervical ribs, because the next following rib widens distally and therefore counts as the first dorsal rib. Therefore, out of the 24 presacral vertebrae, 12 belong to the trunk and the same number belong to the neck.

Second presacral vertebra, axis.

Pl. I, Fig. 1 a-c.

The anterior end surface of the centrum shows a rounded, four-sided outline of ca. 7 cm height and 6.5 cm width. The surface is divided by a horizontal groove into a convex lower section and a ca. 3 cm high, slightly more elevated, equally convex part. The lower part represents the anterior surface of the intercentrum, its suture against the atlantal centrum being clearly recognizable as a wavy border on its ventral surface. Slightly below mid-height, the margin of the anterior surface projects strongly posteriorly in a short semicircle. Therefore it forms a frame in the center for the sunken, vaguely developed parapophyseal facet, while it protrudes anteriorly in the dorsolateral corner. The dens^{*}, which was broken off the centrum but was fixed again, has the general shape of a cone with a rounded tip into which the neural canal is cut showing a flat and concave basal surface, tilted slightly downwards anteriorly. The posterior surface of the dens is distinctly concave. The end surface of the posterior centrum is circular and deeply concave. The centrum shows laterally wide pleurocentral fossae that extend forward to the anterior surface so that only a thin wall of bone remains; the left pleurocentral fossa is far more concave then the right one, so that the separating transverse wall lies on the right side of the median plane. Ventrally, the pleurocentral fossae are bordered by a ridge running toward the parapophysis. This ridge is clearly expressed on the left side, but on the right side it is only vaguely visible in its middle. This sharpedged ridge forms a roof over a distinct pocket anterior to both ends. On the right side this pocket is completely missing anteriorly, and posteriorly it is only weakly outlined. The ventral side shows a flat, triangular

dens = odontoid [Tr]

plane behind the anterior end, which grades into a sharp-edged median ventral lamina, extending over the central third of the centrum.

The neural arch is very tall when compared with the centrum; it extends 21 cm above the 6.8 cm high anterior end of the centrum and consists mainly of an in anteriorly convex plane that ascends at an angle of ca. 55°. This plane shows the actual neurapophysis in its upper very strongly built part, is 7.5 cm wide, and the dorsal end is a generous 2 cm thick. Posteriorly, there is a postspinal lamina sculptured ventrally with tubercles that gain depth ventrally to about 3 cm height, separating two deep pockets here. A weaker prespinal lamina runs medially over the ventral two-thirds of the neural arch. The prezygapophysis lies close to the lateral wall of the neural canal with an elliptic, slightly convex facet, which is at an angle of ca. 60° , laterally tilted, ca. 2.5 cm long and 2 cm wide, and projects slightly along the anterior margin of the neural canal. The postzygapophyseal laminae are strongly built and project laterally and anteriorly distinctly in the posterior direction; their ascending posterior margins form a sharp spinopostzygapophyseal lamina, which turns into the margin of the neurapophysis. The horizontal facets are ca. 4.8 cm long and ca. 3.5 cm wide, posteriorly descending in the medial direction at an angle of ca. 20°. A rugosity runs parallel to it about 1 cm above the outer margin of the postzygapophyseal lamina. The postzygodiapophyseal lamina leads anteroventrally towards the diapophysis from the outer margin of the postzygapophyseal lamina, but is not fully symmetrical on both sides. This lamina, only well preserved on the right side, forms a thin convex sheet that is ca. 3.5 cm broad and projects freely at an oblique slant for about 3 cm in the posterior direction. The facet for the tuberculum is not recognizable with certainty. The anterior and posterior parts of the neural canal are simply roofed. Its diameter increases considerably anteriorly, being ca. 2.6 cm wide and ca. 3.6 cm high in the central and posterior parts.

3.-24. Presacral vertebrae.

Pl. I, Fig. 2a, b, c, c–23a, b, c.

Vertebral centra.

The increase in length of the cervical vertebrae is small compared to the dorsal vertebrae. The average lateral length of the centra, minus the anterior convexity, measures 16 cm in the middle of the trunk, compared to 23 cm in the 7th presacral vertebra as the largest lateral length in the cervical vertebrae, only 1.44 of the latter. Apart from the constant increase in size of the end surface and therefore the changing main dimensions, the shape and structure of the centra are relatively constant from the 3rd to the 9th presacral vertebrae. The condyle is very strongly built, and the volume of the centra is greatly reduced by the deeply indented fossae; the deeply concave end surfaces, especially of the last vertebra, show a bulge on the outside that corresponds to this hemispherical hollow.

The common formation of a plane on the ventral surface of the cervical vertebrae is not present, but rather the high and very thin ventral lamina runs along the midline. Between this ventral lamina and the centroparapophyseal laminae, running posteriorly from the steeply overhanging and equally very thin and posteriorly high parapophyses, lie correspondingly extensive cavities. With the shortening of the centra of the posterior cervical vertebrae, the length of the posterior centroparapophyseal laminae is simultaneously reduced, and amounts to only a couple of centimeters in the 11th presacral vertebra.

The central ventral lamina preserves its character as a long, thin, high ridge from the 2nd to the 9th presacral vertebrae. Then it becomes shorter in accordance with the shortening of the centra, and also becomes rapidly thicker from the 11th vertebrae onward. At the 13th vertebra it has become a rounded ridge, which is only weakly indicated in the following vertebra. The lamina gets stronger in its anterior part, where it has a coarse surface, a character that is not clearly expressed only in the anterior neck vertebrae. This coarse thickening might be interpreted as an indication for a hypapophysis. A ligament was probably attached to this hypapophysis, and the very thin and often sharpedged remaining part of the lamina can also have only served as an insertion point for a ligament, namely one of membranous nature. It was probably a ligament that supported the esophagus.

	Length	Length of	Width of	Height of	Width of	Height of	Height of	Distance	Length of
	of entire	centrum minus	anterior	anterior	posterior	posterior	entire	between ends	neural
No.	centrum	anterior	end of	end of	end of	end of	vertebra	of the	canal roof
		convexity (free	centrum	centrum	centrum	centrum		diapophyses	
		lateral length)							
2	17.3 cm	16 cm	7.1 cm	7.2 cm	7.1 cm	6.7 cm	27.3 cm	8.8 cm	
3	19.5	18.5	6.7	4.8	8.3	8.4	23.9	11.7	11.3 cm
4	24.3	21.5	7.9	6.2	10.0	9.6	41.1	13.1	11.4 (+)
5	25.5	22.5	8.9	8.3	11.7	11.5	43.0	14.2 (+)	13.2
6	28.5	23	11.1	10.8	11.8	12.0	43.6	15.5	14.5
7	28.3	23	11.2	10.7	13.0	12.4	42.1	16.9	14.2
8	28.5	23.5	12.2	11.3	14.7	13.4	42.9	18.8	12.1
9	27.4 (+)	22	13.8	11.1	17.0 ±	14.0	41.9	21.8 (+)	11.7
10	26.4	21	15.2(+)	13.2 (-)	17.0	14.0	47.3	?	10.4
11	21.9	15.5	15.5	11.1	15.7 (±)	13.4 (±)	51.3	28 ¹⁾	9.4
12	19.3	14	15.0	12.5	15.2	12.9	54.6	34.2	7.7
13	18.4	13	14.6	12.6	15.3	12.9	62.8	42 ¹⁾	6.8
14	17.4	14	14.2	12.4	14.2	13.3	69.5	40 ¹⁾	4.0
15	18.3	14	12.2	12.3	13.2	13.3	74.5	40 ¹⁾	3.5
16	18.2	15	12.8	12.9	12.5	12.5	74.6	44 ¹⁾	1.9
17	18.4	16	12.8	13.0	14.9 ±	14.9 ±	76.7	49 ¹⁾	1.6
18	18.4	16	13.5	13.4	14.3	14.3	78.8	47 ¹⁾	1.5
19	19.8	16	12.8	13.6	12.8 ±	12.8 ±	77.6	41 ¹⁾	1.1 (±)
20	18.6	16	10.7 +	13.2 (+)	13.5 (±)	13.5 (±)	79.2	38 ¹⁾	1.4 (±)
21	18.4	15.5	11.9 (+)	14.2	13.8 (±)	13.8 (+)	81.4	36 ¹⁾	?
22	17.3	14.5 (+)	12.1 (+)	16.1 ±	14.1 (+)	14.1 (+)	82.8	34 1)	0.9
23	18.4	14.5 (+?)	?	17.7 ±	15.6 (+)	15.6 (+)	84.4	35 ¹⁾	2.9
24	16.3	14 +	12.6 (+)	18.3 ±	17.8 ±	17.8 ±	86.2 (±)	35	4.7

Measurements of the presacral vertebrae of Dicraeosaurus hansemanni, skeleton m.

¹⁾ Distance between the ends of the preserved right and the symmetrically restored left diapophysis; deformation, which reduces the distance, has not been considered.

Explanation of the signs. (Also valid for following measurement-tables)

- + Amount too small due to incomplete preservation or deformation.
- (+) Amount only slightly too small due to incomplete preservation or deformation.
- Amount too large due to deformation.
- (-) Amount only slightly too large due to deformation.
- \pm Amount uncertain, too large or too small. Also estimated original amount.
- (±) Amount only slightly uncertain. Also estimated amount.

The pleurocentral fossae of the anterior cervical vertebrae have an extraordinarily wide circumference, and only the small lateral zone of the posterior end of the lateral surfaces remains; these fossae are in general relatively shallow, only in the anterior end above the parapophysis are they more deeply depressed in a pouch-like manner. With the shortening of the cervical vertebrae, these fossae get increasingly narrower in circumference in the more distal cervical vertebrae, so that the 12th vertebra shows only short, but deeply depressed fossae. From the

13th vertebra onward, the pleurocentral pits become shallower and lose their sharp ventral borders. With the rise of the parapophyses, the pits extend dorsally, but also lose their sharp dorsal borders in this process. From the 16th vertebra onward, they remain only wide, shallow depressions, which extend over half the height of the centrum and do therefore no longer deserve the name "pleurocentral pits".

The centra become more and more like the dorsal vertebrae from the 15th vertebra onward. This assimilation occurs due to the rise of the lateral pits and the simultaneous change in the shape of the vertebrae into equally centrally retracted cylinders, which are very simply shaped due to a uniform curvature of their flanks and ventral surface. The curvature of the anterior end surface, which is almost semispherical in the 13th vertebra, is rapidly reduced in the following vertebrae. It is flat from the 16th vertebra onward, from the 21st vertebra onward only a small dome is visible in the dorsal part of the anterior end surface; but it cannot be readily concluded how much this is an effect of deformation. In accordance with the reduction of the convex curvature in the anterior surface of the anterior dorsal vertebrae, the concavity of the posterior one is also reduced, yet it is still relatively well expressed until the 24th vertebra. The almost circular outline of the anterior surface in the dorsal vertebrae gets slightly higher than wide from the 17th vertebra onward. In the last dorsal vertebrae, the outline is irregularly narrowed as a result of lateral pressure.

Neural arch and neural canal.

Because the appendages of the neural arches and the laminae attached to these appendages are described separately, only the parts surrounding the neural canal upward to the line of the joint process and the neural canal itself are dealt with in this paragraph.

The main characteristics of the transformation of the neural canal and its progressive reshaping in the presacral vertebral column are as follows: in the anterior cervical vertebrae the neural canal consists of a long tube, the roof of which has a length of 11.5 cm in the 3rd vertebra, and a length of 13 cm in the 4th vertebra, amounts that are only a scant one-third shorter than the base of the canal. The length of the roof is absolutely and relatively at its largest in the 5th vertebrae at 16.5 cm. The length of the roof amounts to 14.5 cm in the 6th vertebra, but decreases to 7 cm in the 13th vertebra, lessens abruptly to 4 cm in the following vertebrae, then to 2 cm in the 16th vertebra, and amounts to only 1-2 cm in the following vertebra. However, in the last two presacral vertebrae the length of the neural canal roof increases again to 3 cm in the 23rd vertebra and to 4.5 cm in the 24th vertebra.

This list demonstrates that the roof of the spinal cord is very incomplete in the trunk; yet on a higher level the gaps in the neural canal roof are bridged by the zygapophyses, albeit incompletely.

It is characteristic that the neural canal roof decreases in length as soon as the parapophysis shifts to the level of the prezygapophysis (from the 16th vertebrae onward). The requirements to withstand the compressive stress transmitted via the capitulum toward the parapophyses needed a strong abutment in the preceding vertebrae.

The table on p. 52 contains the lengths of the neural canal roof in each vertebra. The lengths of the bases are not given because they differ only insignificantly from the free lateral lengths of the centra that are also listed in the table. The comparison of the free length of the neural canal roof with the free lateral length of the centra therefore also demonstrates the approximate ratio between the length of the roof and the base of the neural canal.

Between the 3rd and the 11th presacral vertebrae, the roof of the neural canal is a sharply edged, thin lamella at its exit, an impression that is due to the fact that above the neural canal, a pocket is inserted on its left and right side. This pocket is framed laterally by the centroprezygapophyseal lamina and dorsally by the intraprezygapophyseal lamina. The roof of the neural canal is relatively strong at the posterior exit of the 3rd vertebra with a thickness of about 11 mm; its upper margin, from which the intrazygapophyseal lamina extends, projects about 1 cm over its lower margin. In the 4th vertebra, a pocket is inserted above the neural canal, framed dorsally and ventrally by a thin lamina. The very thin ventral lamella, the edge of which when viewed posteriorly is positioned much more deeply and further back than the edge of the dorsal lamina, represents the actual roof of the neural arch. But this lamella leaves the posterior end of the neural canal uncovered, so that here the 1-2 cm more highly positioned. concave, thin dorsal lamina, which can also be understood as the medially joined intrazygapophyseal laminae, forms the dorsal cover. In the following vertebrae a change occurs only in so far as this pocket, positioned between these laminae and the roof of the canal, is divided by a strong medial wall into two deeply depressed holes of triangular outline. This wall is only weakly expressed in the 4th vertebra. Obviously, this medial wall serves as a strengthening of the medially inclined intrapostzygapophyseal lamina and for the absorption of the pressure transmitted from the postzygapophyseal lamina by this laminae. This formation continues, except that the projection over the roof of the neural arch by the edges of these laminae disappears completely at the 9th vertebra, and, in accordance with the shortening of the entire neural arch, all the edges achieve a wider distance from the posterior end of the centrum. The pockets in the anterior surface next to the entry of the neural canal disappear from the 11th vertebra onward, yet the pockets on the posterior surface are still strongly expressed; these pockets become shallow only from the 13th vertebra onward and disappear completely further on.

The entire nature of the transformation of the shape in the neural arch at the transition from the cervical to the dorsal vertebral column is based on the fact that the tube-like casing of the spinal cord changes into a structure that consists of two massive, high, strong, and longitudinally running lateral walls connected by a transverse wall, so that a distinct H-profile in achieved. This transformation is accomplished by the rise of the zygapophyseal lamina, which creates panels next to and mostly above the entry and exit of the neural canal, which together build a wall. The minimum thickness of this wall amounts to 4 cm in the 14th presacral vertebra, but decreases to 3 cm in the 15th. Yet this transverse wall is not totally massive; a pocket, the infradiapophyseal fossa, extends from the lateral surface so deeply into the wall ventrally to the diapophysis that only a thin bone layer remains. The strength of this wall can decrease to 5 mm; it will be dealt with separately below. The pockets achieve a wide circumference in the posterior dorsal vertebrae. As the lateral pocket rises from the 15th vertebra onward, a substantial cavity inserts increasingly deeply into the anterior surface of the transverse wall. From the 16th vertebra onward, an equally deep cavity presses into the posterior surface ventral to the zygapophyses, both depressions result in the already mentioned decrease in thickness of the transverse wall. The wall is reduced to 13 mm in the 16th vertebra, 10 mm in the 18th, and 5 mm in the 21st vertebra. The posterior cavity again decreases in depth in the more posterior dorsal vertebrae, and disappears completely in the last free vertebrae. The anterior edge of the lateral walls of the presacral vertebra, on which the parapophysis of the dorsal vertebrae rises, is bent outward and extremely strong up to the 16th vertebra. However, from the 17th vertebra onward, in which the parapophysis has almost reached the height of the prezygapophyseal lamina, the anterior rim is very thin and forms the anterior centroparapophyseal lamina up to the 21st vertebra. From this vertebra onward, it suddenly gets very thick again. The lower part of the posterior edge of the lateral

wall is very strongly built, and extends dorsally into a thin centropostzygapophyseal lamina.

For the determination of the shape of the cross-section of the neural canal, only those vertebrae were used that show no signs of the so often occurring lateral deformation of their walls. The anterior opening of the neural canal shows a dorsally slightly pointed cross-section in the vertebrae that show a decreasing size of the pockets above or lateral to it, such as from the 3rd to the 9th vertebra; in the 13th vertebra the cross-section is almost exactly circular, and in the next two following vertebrae it is slightly dorsoventrally elliptical. However, the posterior opening is immediately roundish from the proximal vertebrae onward, it is as slightly dorsoventrally elliptical as the anterior opening in the 14th and 15th vertebrae. In the anterior cervical vertebrae, the base of the neural canal is almost horizontal. In the following vertebrae, the base is indented by a shallow furrow, and in the posterior vertebrae an additional mold appears in longitudinal direction, with its deepest point anterior to the center. In the 16th vertebra the flatly rounded upper contour of the cross-section of the neural canal is still detectable. In the adjacent dorsal vertebrae the cross-section again becomes dorsally pointed, this is obviously due to the deformation of the overhanging bone wall into which it is cut, yet this pointed dorsal shape appears to have been present originally to a certain degree. In addition to the pointed dorsal end of the neural canal, the lateral walls of the neural arch converge ventrally in the anterior half of the presacral vertebral column, so that each vertebra has a narrower cross-section ventrally. The transverse wall into which the neural canal is carved is positioned at the posterior end in the posterior dorsal vertebrae, and the ventral narrowing of the cross-section is not present here.

The dorsal surface of the actual neural arch of the presacral vertebrae with their deeply bifurcated neurapophyses, i.e. the surface at the bottom between both these neurapophyseal branches, deserves special description. It would be incorrect to address such a surface in the 3rd vertebra, because the space between both neurapophyseal branches is very narrow and ends far above the dorsal surface of the prezygapophyses. However, from the bottom of the cleft a very thin-not completely preserved-median bony lamella stretches ventrally. Only the anterior part of the lamella was connected ventrally, as the preserved remains show, and the distal half of this bony lamella is freely suspended. The lamella shows a very irregularly rugose, plate-like thickening, pointing posteriorly, which might have borne an unpreserved lateral connection with the postzygapophyseal lamina, but which definitely served as the insertion point of a ligament (supraneural ligament). At the bottom of the 4th presacral vertebra lies a horizontal plane between the neurapophyseal branches that ascends laterally up their medial walls. This plane has a total length of ca. 8 cm, and the branches of the neurapophysis are at this point ca. 3 cm apart from each other. Positioned anterior to this horizontal surface is an irregularly shaped rugosity that projects anteriorly and bears the insertion point of the aforementioned ligament that runs toward the 3rd vertebra. On the ventral surface of this rugosity sits a thick, abruptly ending structure: the insertion of the nuchal ligament. In a position almost 2 cm below lies a flat, longitudinally concave, depressed lamella formed by the intrapostzygapophyseal lamina, which forms a dorsal covering for the neural canal. The position of the insertion points of the nuchal ligament, as well as the space between them [the branches of the neurapophysis], is more or less as in the 4th vertebra. Yet the anterior insertion of the ligament is always more weakly developed in the following vertebrae; in the intermediate cervical vertebrae, especially from the 7th to the 9th, the insertion point is shaped like a small groove, roofed by a slightly bulging edge. A corresponding, yet insignificant, rugosity can be traced posteriorly to the 16th vertebra. The posterior insertion point for the nuchal ligament gets increasingly more pronounced, and from the 6th vertebra onward this insertion point takes on the character of an irregular nut- or egg-shaped structure that projects freely posteriorly. On the posterodorsal surface of this structure are usually two irregular, coarse, short, deeply excavated grooves that provided the rough surface for the insertion of the nuchal ligament.

This projecting structure is most extensive in the 10th vertebra, where it is 38 mm long, 33 mm broad, and 22 mm thick. Along the adjacent vertebrae, this projection for the insertion of the nuchal ligament is quickly reduced in size. It is already rather insignificant in the 12th vertebra, almost not visible any longer in the following vertebra, and from the 14th vertebra onward the structure is absent. In its place now appears a hole, which seems to still be a bit rugose at the bottom. From the 17th vertebra onward, the postspinal lamina begins to ascend at this point.

The pleurocentral^{*} suture is in general not at all recognizable in the anterior half of the presacral vertebral column. It is uncertain whether a several centimeter long, slightly gaping cleft on the posterolateral end of the neural arch of the 5th vertebra in the posterior wall of the neural canal, slightly above the base, represents a section of the pleurocentral suture. The pleurocentral suture can only be determined with certainty for the first time on the external surface in the center of the 13th vertebra, as a ca. 5 cm long, slightly bulging line that describes a flat, dorsally open arch. Indications of this suture are also visible on both sides ventrally on the anterior lateral walls of the neural arch. This section of the 15th ca. 4 cm above the base of the neural canal and remains at this height to the last presacral vertebra. The pleurocentral suture is represented from the 16th vertebra onward as a coarsely serrated, bulging line that runs in its entirety relatively straight and almost horizontal or just slightly ascending posteriorly. In the 19th vertebra the sutures gape on both sides, and in the following three vertebrae even a disarticulation along both sutures has occurred.

$Neurapophysis^2$.

The overall impression of the presacral vertebral neurapophyses is determined by their considerable height in connection with a deep bifurcation, not only in the proximal trunk, but also in the neck. The vertebrae are divided from the 3rd to the 16th along their entire length, from the 17th to the 19th vertebra this bifurcation is shortened in three increments, and from the 20th vertebra onward the neurapophyses are in one piece; a very clear inclination is furthermore expressed in the neurapophyses of the cervical vertebrae. In the 3rd vertebra, the neurapophyses show a ca. 60° inclination of their terminal part against the axis of the neurapophyses lie nearly vertical, but already show a weak anterior inclination of the upper part of the anterior edge. In the following vertebrae up to the 9th, the neurapophyses show an increasing anterior inclination, so that an angle of 52° against the long axis of the neural canal is achieved.

In vertebrae positioned horizontally next to each other, the angle enclosed by the neurapophyses of the 3rd and the 9th vertebra amounts therefore to ca. $180^{\circ} - (61^{\circ} + 52)^{\circ}$, thus 67° . However, as demonstrated during the mounting of the skeleton, in life the neck must have described a flat, ventrally open arch in its anterior part, so this angle must have been smaller in reality. The

^{*} pleurocentral = neurocentral [Tr]

² The common expression "neural spine", which evokes the image of a strongly projecting, more or less stick- or wand-like process, is completely unsuitable when applied to structures that are shaped like a low ridge or a low roundish protrusion. Much more useful is therefore the term neurapophysis as used by some authors (V. HUENE, MÜLLER), which is not limited to a certain shape, but only addresses a structure that projects from the neural arch. Now, we find in sauropods a bifurcation of the neurapophysis, which can divide this structure into two fully separated parts, or, as in the transitional vertebrae that lead to the distal dorsal vertebrae, a neurapophysis of one piece only divided in its upper part, so that it appears bifurcated. MARSH termed the divided paired parts of the neurapophysis "metapophyses", OSBORN used this name too. Yet the use of this term can hardly be recommended, as in mammals a completely different process dorsal to the prezygapophysis bears the same name. I use the term "neurapophyseal branch" for the bifurcated parts of the neurapophyses in *Dicraeosaurus*.

apex of the arch has to be assumed at the 5th presacral vertebra, or even better between the 4th and 5th vertebrae.

Approaching the trunk, the neurapophyses become erect again, which results in a vertical position of the neurapophyses in the trunk at the 14th presacral vertebra; additionally a distinct posterior inclination occurs, but in the 21st and 22nd vertebrae the neurapophyses are again vertical. The two last free neurapophyses in front of the sacrum are again weakly bent anteriorly, behind the sacrum the neurapophyses again gain a strong posterior inclination in the proximal part of the tail.

The neurapophyseal branches of the 3rd presacral vertebra have a narrow, wand-like shape, in this vertebra they are in contrast to the completely independent ones in the following vertebrae, ventrally joined together for ca. 1/5 of their length. Their cross-sections are dorsally triangular, but distinctly U-shaped ventrally. With increasing length the neurapophyseal branches of the 4th vertebra exhibit the shape of two thin, broad, sharply edged, laterally completely flat, almost parallel wands that are on their inside immediately behind the lengthwise-reinforced anterior end, and which get only slightly broader ventrally.

The terminal flat parts are smaller in the next following vertebrae, but do transcend into a wide triangular thin plate, concave and depressed, that shows a deeply excavated cavity directly above the diapophysis; the inner lengthwise reinforcement separates slightly ventrally from the anterior edge. From the 9th vertebra onward, the free neurapophyseal branches become more wand-like with a more triangular cross-section and with still strong, but in the last cervical vertebrae only insignificantly broadened, ends. Their square ventral dimension is reduced, and simultaneously they separate increasingly until the 10th vertebra. When seen from the front, ventrally the branches resemble two wands that are slightly bend toward each other with their upper ends approaching each other, while in the following vertebrae they also approach each other ventrally. Viewed from the side, the neurapophyses of the 8th to 11th vertebrae describe a flat, posteriorly open curve. The lateral bend remains as long as the bifurcation of the neurapophyses is present; it is particularly clearly visible in the inner contour of the anterior parts. On the back of these triangular processes ventral to the terminal broadening of the plate, a longitudinal indentation becomes increasingly deep posteriorly, causing a weak, U-shaped profile that gets even weaker from the 12th vertebra onward. The cross-section of the central part of the neurapophyseal branches is squarer in the 13th vertebra, with a distinctly rounded anterolateral corner; the cross-section of the branches of the neurapophyses changes quickly further on. A lateral lamina appears in the 14th vertebra: the spinodiapophyseal lamina. This lamina gets more and more pronounced and has a particularly sharp, triangular cross-section in the 15th vertebra, and broadens the upper part of the crosssection increasingly laterally. The division of the neurapophyseal branches into two parts is incomplete in the 16th vertebra; here both branches are joined together about 15 cm above the medial edges of the prezygapophyses, with a complete height of 49 cm as measured from the prezygapophyses to the dorsal end of the neurapophyseal branches. The point of bifurcation on the next following vertebra lies 25 cm, and on the 18th vertebra it is 30 cm above the medial edges of the prezygapophyses. Simultaneously, the free branches broaden more and more laterally. The ventral part of the neurapophyseal branches of the 16th vertebra become U-shaped in cross-section above the bifurcation point at their medial surface; the U shows very dissimilar arms, the lateral one being much longer. On the right side this shape is more strongly developed than on the left in this and the following vertebra. However, in the 18th vertebra the short neurapophyseal branches show only a hint of this U-shaped cross-section and only in their most In general the neurapophyses show the same high undivided shape ventral part.

from the 19th vertebra to the sacrum, with a constant broadening of the lateral contour in the dorsal direction. Because of the strong development of the medial and lateral laminae, the cross-section achieves a distinct cross-shape (+). The width of the neurapophysis, the left edge of which is not preserved in the posterior dorsal vertebrae, is increasingly reduced from the 20th vertebra onward. Its width is estimated at 21 cm in the 20th vertebra, but is reduced to 16 cm from the 20th to the 24th vertebra. The extent of the medial plane is simultaneously reduced from 13 cm to 10.5 cm.

Laminar system of the neurapophysis. Among the neurapophyseal laminae one has to distinguish functionally the ones that serve as the insertion point for ligaments, such as the prespinal and postspinal laminae; these laminae are unpaired and positioned in the medial plane. Then there are those that serve as the insertion for the dorsal ligaments and are terminally reinforced. These laminae are paired, and they are positioned laterally on the neurapophyses and contribute to their lateral extent: the spinodiapophyseal laminae (OSBORN'S supradiapophyseal lamina). The third kind are the laminae that serve as reinforcements for the neurapophyses against strains coming from other structures, namely from the prezygapophyseal lamina, the postzygapophyseal lamina, and the diapophyses, and which are directed toward these points of strain.

The median prespinal lamina, which deserves an especially thorough description because it is important for its relationship with the nuchal ligament, does not appear in the deeply bifurcated neurapophyses of the cervical and anterior dorsal vertebrae. It is only in the 3rd vertebra, with ventrally joined neurapophyseal branches, that a delicate, somewhat nodularly reinforced lamina is visible on the ventral surface. In the 17th presacral vertebra, which has neurapophyseal branches that are bifurcated over 2/3 of their length, a thin, sharply edged median lamina appears for the first time ventral to the bifurcation point, which is only about 6 cm long. The length increases to 18 cm in the following vertebra. The prespinal lamina is laterally effectively "overgrown" by the supraprezygapophyseal lamina in the 19th presacral vertebra, where the bifurcation point is in the upper 1/3 of the neurapophyseal branches. The prespinal lamina, framed by both supraprezygapophyseal laminae, discloses its presence as the support of a median ligament by characteristically clear longitudinal creases. The dorsal end shows a steep, ca. 4.5 cm long anteroventral slant. This surface is irregularly wrinkled and continues ventrally as a short, pointed ledge, roughly sculptured on its ventral surface. The inclination continues less steeply between the neurapophyseal branches in the posterodorsal direction. The prespinal lamina is prominent in the subsequent, unbifurcated neurapophysis, but the remains of the spinoprezygapophyseal lamina extend just above mid-height, framing a longitudinally wrinkled groove like a dam. The dorsal part of the prespinal lamina is ca. 9 cm long, indistinct, and incompletely preserved. Two strikingly tiny laminae, much better preserved on the right side then on the left, run perpendicularly ventrally to the prespinal lamina toward its distal end. The well-preserved ventral part of the lamina, positioned ventral to these small laminae, has a length of ca. 8 cm; it is distinguished from the upper part by projecting slightly more anteriorly. The lower part longitudinally bulges anteriorly and has a similar corrugation and surface structure to the upper part. The prespinal lamina protrudes freely from the surface in the other posterior presacral vertebrae except along a short distance in the ventral section. The lamina is a strong vertical ridge that ends abruptly anteriorly and shows a longitudinal corrugation here again. The prespinal lamina is "cut off" in a tilted, slightly concave line in the 21st vertebra, a condition less clearly expressed in the next vertebra. The prespinal lamina is developed along the entire length in the 23rd and 24th vertebrae. The dorsal part of the prespinal lamina projects anteriorly in the 23rd vertebra, and moreover sticks out plug-like dorsally.

A postspinal lamina, as well as a prespinal lamina, is present, apart from the axis, for the first time in the 17th presacral vertebra. Here, it forms a ca. 9.5 cm long, sharply edged lamina, somewhat irregularly reinforced in its dorsal part, that reaches up to the bifurcation point. The prespinal lamina is ca. 20 cm long in the following vertebra, where it is stronger, increases dorsally in thickness, and shows a longitudinal corrugation along its edge. The prespinal lamina extends higher in the 19th vertebra due to the rise of the bifurcation point. It is irregularly framed by the spinopostzygapophyseal laminae along most of its extent. As а consequence of the shortening

of these laminae, the spinopostzygapophyseal lamina emerges freely as a strong, marginal, longitudinally corrugated lamina in the dorsal two-thirds of the neurapophysis in the 20th vertebra. The spinopostzygapophyseal lamina projects slightly less highly in the 22nd vertebra, again higher in the 23rd vertebra, and in the 24th has almost the same height as the free neurapophysis. The free edge of the spinopostzygapophyseal lamina runs straight in the posterior vertebrae. However, in the dorsal part of the 21st vertebra this lamina is cut off in a tilted, slightly concave line of ca. 11 cm above a projecting lug. A similar cut-out of a smaller dimension appears on the dorsal end of the previous vertebra.

The spinodiapophyseal laminae appear for the first time in the 14th vertebra, indicated as a blunt edge that runs almost straight on both sides on the upper two-thirds of the outer surface of the neurapophyses. Both edges run toward each other anteriorly. The spinodiapophyseal laminae get more pronounced in the following vertebrae and simultaneously get more and more concave in their middle, in accordance with the course of the anterior edge of the neurapophyseal branches. The spinodiapophyseal lamina protrudes as a sharp-edged blade in the dorsal part of the 17th vertebra, and causes a wider lateral extent of the neurapophyseal branches. The course described by the spinodiapophyseal lamina straightens in the 18th vertebra, in which the bifurcation point is in the center The course curves slightly inward in the 19th vertebra, as do the entire of the neurapophysis. neurapophyseal branches. The spinodiapophyseal laminae run in the following vertebra with an unbifurcated neurapophysis approximately to the middle of the lateral surface of the neurapophysis, where they impinge on the supradiapophyseal lamina. Only in the 24th vertebra does this connection with the supradiapophyseal lamina not occur, because the spinodiapophyseal lamina, bending ventrally, turns into the inner suprapostzygapophyseal lamina. With the spinodiapophyseal laminae, the neurapophyses reach their widest lateral extent, their thin and therefore often not preserved edge thickening only in the upper part. Their lateral extent increases continuously from ventral to dorsal and reaches its widest extent a short distance from the dorsal end. On the right side, which is the only preserved side from the 20th to the 22nd vertebrae, the width amounts to ca. 10 cm but decreases in the following two vertebrae to 9 cm and 8 cm. The width of the ventral end is reduced accordingly.

The end-surface ligament insertion points of the neurapophyses deserve special attention because of their significance for providing insertion surfaces for the terminal neurapophyseal ligaments. In the second presacral vertebra, this surface presents a diagonal, roughly sculptured surface that slopes laterally in accordance with the cross-section of the unpaired neurapophysis. Its posterior border is relatively straight, and the anterior border is arched. The posterior edge is cornered, and the anterior edge descends smoothly and convexly. On the other hand, the neurapophyseal branches of the four following vertebrae show narrow end surfaces. The linear extension of these end surfaces is axially positioned. The surfaces descend anteriorly and posteriorly, their medial edges are decidedly sharpedged, and their lateral edge is rounded. This dissimilar condition of both of the edges is still observable in the 9th vertebra. Both edges are almost equally rough in the 11th and 12th vertebrae. The end surfaces widen form the 13th vertebra onward in accordance with the increasing thickness of the neurapophyses. From the 14th vertebra onward, that is with the emergence of the spinodiapophyseal laminae, the end surfaces stretch obliquely downward on the lateral surfaces in the ventrolateral direction. Therefore they form a wide, slanting lateral surface on the ends of the neurapophyseal branches. These surfaces show a more rounded transverse profile in the more uniform neurapophyses of the posterior dorsal vertebrae. In these vertebrae a more or less distinct, shallow medial depression in the terminal profile is also evident. When seen in dorsal view, the end surfaces show a stretched oblong shape in the posterior dorsal vertebrae, from which center the end surfaces of the pre- and postspinal laminae extend as thin twigs. These laminae extend slightly laterally and then become narrowly pointed.

Diapophysis.

In the 3rd presacral vertebra, the diapophysis is a 3 cm wide lamella that points ventrally and extends into a rounded, anteroventrally pointing tip. This downward-pointing lamella quickly widens to 4 cm and 5.5 cm respectively in the following vertebrae, the extent of the widening diminishing from these vertebrae onward. The ventral edge of the lamella becomes a more horizontal, straight ventral edge; this character is retained up to the 8th vertebra; the ventral end of the diapophysis is not preserved in the 9th vertebra. The tubercular facet on the ventral edge of the lamella is only very indistinctly expressed in the 3rd and 4th vertebrae. From the 5th to the 9th vertebrae, the small tuberculum is firmly united with the diapophysis, but only at the anterior end of the ventral edge of the diapophysis, so that the distal end of the overhanging lamella forms a noticeable ledge. The diapophyses are incompletely preserved in the 10th vertebra. The 11th vertebra shows a modification in the character of the diapophysis: it is positioned higher, projects more strongly in both lateral and obliquely anterior directions, and it develops a triangular, laterally pointing end surface. The slightly pulled-out and also sharpest-angled corner of this triangular end surface is directed anterodorsally and bears a distinct tubercular facet that points ventrally. The diapophysis protrudes in the next vertebra, but much more distinctly so in the following ones, with a strong elongation in the diagonally anterolateral direction, changing shape during this process and developing into a long, narrow process. While this process shows an anterolaterally pointing component in the 11th vertebra, this component is rapidly reduced; it has completely disappeared in the 15th vertebra, the diapophyses are tilted more posteriorly from the 16th to the 19th vertebra and stand more vertically again from the 19th vertebra onward. The external shape of the diapophyses changes as well, in so far as it gets shorter from the 19th vertebra onward, and simultaneously widens strongly from the 18th to the 20th vertebra, narrowing again in the 23rd vertebra. The diapophysis of the 24th vertebra is again a very small process. The laterally pointing end surface of the diapophysis in the 11th vertebra already develops into a slightly domed, furrowed end surface in the next vertebra, whose contour changes in the further course of the vertebral column. The outline of this surface is triangular in the 13th vertebra, with the sharpest corner pointing ventrally; in the next vertebra this triangular outline becomes oval, in the 16th vertebra this outline changes to rhomboidal with its longest diagonal pointing anteroventrally, and in further progress longitudinal flutings are cut into the laterally pointing end surface of the diapophysis from anterior and ventral. The end surface in the 20th vertebra is simple and roundish, and becomes narrow in the 23rd vertebra. In the 13th vertebra a special facet for the tuberculum separates very vaguely from the end surface, but gets more distinct in the 22nd and 23rd vertebrae, in which it takes on the shape of a small concavity. Concerning the position of the diapophyses, it is necessary to clarify whether their steep position has not been exaggerated by the lateral position of the skeleton due to the overlying pressure. The diapophysis of the 17th vertebra obviously did not suffer any mentionable distortion, and it forms an angle of 40° with the horizontal axis. The posterior dorsal vertebrae, on the other hand, were affected by distortion as is indicated by numerous fractures and displacements, and were probably pushed into a too steep position.

Lamina e system of the diapophysis. One lamina each runs from the diapophysis toward the anterior end of the centrum, the prezygapophyseal lamina, and the postzygapophyseal lamina. These laminae are subject to considerable shape changes due to the change in position and form of the diapophysis within the presacral vertebral column. In the cervical region, the exceptionally strong laminae run toward the posterior end of the centrum and toward the postzygapophyses, the postzygodiapophyseal lamina and the posterior centrodiapophyseal lamina, forming a well rounded crest. They obviously act to reinforce the diapophysis against a pull in the posterior direction executed by the muscles attached to the diapophyses and cervical ribs.

The posterior c e n t r o d i a p o p h y s e al l a m i n a slants posteriorly and laterally, its rounded anterior edge descending slightly posteriorly up to the 10th cervical vertebra; from the 12th presacral vertebra onward, in which the diapophysis begins to ascend considerably, this lamina achieves an increasingly vertical position. It is positioned in an almost transverse plane in the 14th vertebra, slightly bent posterolaterally. This position remains almost unaltered to the 23rd presacral vertebra; only the edge of the centrodiapophyseal lamina is cut out of this transverse plane in a shallow arch to the 19th vertebra. This condition might continue in the next two vertebrae, but this cannot be determined with certainty because of deformation. In the 23rd and 22nd vertebrae, however, the edge of the lamina is not cut out in the described manner, but projects more strongly laterally; still, a complete clarification of this condition is also prevented by the deformation in this vertebra. In the 24th presacral vertebra, which has a strongly reduced diapophysis, this condition could not to be determined due to insufficient preservation. In the true dorsal vertebrae the anterior edge of the centrodiapophyseal laminae is relatively sharply extended, especially in their ventral part. A membranous ligament was supposedly attached here, but its course cannot be deduced from the morphology of the vertebrae.

Anterior centrodiapophyseal lamina. The anterior centrodiapophyseal lamina is generally more or less exactly positioned on an extension of the postzygodiapophyseal lamina, and stiffens the diapophysis against the anterior end of the centra during a muscular pull in the anterior direction. The lateral view of the centrodiapophyseal lamina in the cervical vertebra is obscured by the diapophysis, except for the very last ones. In the 3rd vertebra the lamina is insignificant, a low sharp crest; however, in the following vertebrae the anterior centrodiapophyseal lamina runs posterodorsally as a short, strong ridge with a thick, rounded edge. In the 12th presacral vertebra the lamina is positioned almost vertically and interrupts the line in which the postzygodiapophyseal lamina is pointing. The lamina in the same position is hardly present in the following vertebra any longer, and it is completely missing from the 14th vertebra onward. Because of the shortening of the vertebrae and the higher and more posterior position of the diapophysis, such a lamina is no longer necessary. As there are already laminae running closely and almost parallel to each other from the diapophysis toward the back of the centrum and from the parapophysis towards the front of the centrum, such a lamina becomes superfluous as its direction of reinforcement would almost collide with those of the others.

Prezygo di a pophyseal la mina. The ridge forming the anterior edge of the diapophysis and the ventrolateral edge of the prezygapophysis hangs relatively steeply ventrally as a sharp-edged lamella. It joins the infraprezygapophyseal lamina anteriorly, and together they support the anterior part of the prezygapophysis, but only up to the 8th vertebra; from the 9th vertebra onward, both structures only meet ventral to the facet. The edge becomes increasingly erect along the cervical vertebral column. The lamina naturally gets shorter with the ascent of the diapophysis, but at the same time also stronger. From the 11th to the 13th vertebra, in which the diapophyses and prezygapophyses are only a few centimeters apart, the connecting lamina is accordingly short but thickly rounded, and eventually trails horizontally. With the elongation and the erection of the diapophysis in the 14th and 15th vertebrae, the lamina gets longer, more sharply edged, and rises anterolaterally. The rise of the parapophysis results in the paradiapophyseal lamina forming the edge of the diapophysis at the expense of the prezygapophyseal lamina. The prezygapophyseal lamina runs only for a short distance in the 17th vertebra as a sharp ridge, and further on ascends as a rounded edge on the diapophysis; the lamina is absent from the 18th vertebra onward.

The postzygodiapophyseal lamina is not present in the 3rd cervical vertebra. This lamina is very strongly developed from the 4th presacral vertebra onward, with a thick, rounded edge. It rises posteriorly at an angle of ca. 45° , and slopes laterally in the ventral direction.

The angle increases from the 8th vertebra onward, however, the ridge decreases strongly in length with the continuous shortening of the vertebrae and the rise of the diapophyses. The lateral suspension of the ridges decreases and has disappeared in the 11th vertebra. Then an ascent of the ridge in the lateral direction occurs so that the ventral surface becomes visible when viewed laterally. With the increase in diapophyseal length the ridge becomes increasingly a sculptural element of the latter, which it lies now close to as a thin narrow lamella that only broadens slightly in a plane-like way toward the postzygapophysis in the ventral direction. This ventral plane extends slightly in the posterior dorsal vertebrae.

A paradiapophyseal lamina is indicated for the first time in the 15th presacral vertebra, in which it runs dorsally as a thin rib, less than halfway toward the diapophysis. In the 16th vertebra, in which the parapophysis rises almost to the height of the prezygapophyses, the paradiapophyseal lamina is to some extent more clearly visible as a thin, although incompletely preserved, crest. This crest runs dorsally along the diapophysis up to about one-third of its length and converges with the prezygodiapophyseal lamina, forming a ventrally overturned rim, so to speak. At the end of the paradiapophyseal lamina, both laminae separate again from the prezygodiapophyseal lamina in the ventral direction, enclosing an area shaped like a stretched triangle. The paradiapophyseal laminae then runs as an independent short, sharply ridged edge toward the ventral end of the diapophyseal facet. The ridge is almost identical in the 17th vertebra. In all the following vertebrae, the ridge is not ventrally overturned any longer, but runs anteriorly as a sharp edge. The stretched and elongated triangular area between the paradiapophyseal lamina and the prezygodiapophyseal lamina gets smaller in the posteriormost vertebrae. The paradiapophyseal lamina obviously served as an attachment area for the membranous ligamentum colli costae, which stretched between the parapophysis, diapophysis, capitulum, and tuberculum; its delicacy and sharp edge indicate that it was rather insignificant as a reinforcement.

The supradiapophyseal lamina, which runs from the diapophysis toward the neurapophysis, appears only in the dorsal vertebrae, next to each other in singular and plural. The supradiapophyseal lamina first appears in the 14th presacral vertebra, where it stretches from the dorsal surface of the diapophysis, slightly behind its midline as a moderately extended, vertical wall in the deep pocket between the diapophysis and neurapophysis, toward the neurapophysis. However, the supradiapophyseal lamina is very strongly developed in the 15th vertebra. It emerges from the neurapophyseal branch in such a way that the anterior rim of the diapophyseal lamina is overturned laterally for one-third of its length and merges with a lamina situated on the midline of the dorsal surface of the diapophysis. The rim of this lamina is particularly strong. The ventral turnover of the rim of the anterior end of the neurapophysis is insignificant in the next vertebra, but the diapophyseal section of the edge is higher and more significant. A second, very weak ridge runs parallel to the main ridge, and lies in the deep pocket posterior to the supradiapophyseal lamina, at least on the right side. The anterior ridge has become considerably weaker in the 17th vertebra and has almost completely retracted from the diapophysis. The second ridge, however, is gets stronger and reaches almost halfway up the midline of the diapophysis. On the left side, even a third dainty ridge is developed in the deep area, which aims toward the posterodorsal rim of the diapophysis. The second posterior ridge becomes the main ridge from the next vertebra onward, joining the supradiapophyseal lamina which descends from the neurapophysis in the three anterior vertebrae with undivided neurapophyses, the 20th-23rd; in the 23rd vertebra this connection is less clearly developed, and it is no longer present in the 24th vertebra. On the other hand, the anterior ridge remains present as a modest extension up to the last presacral vertebra, but is only indicated toward the end of the presacral vertebrae. Rudiments of the middle ridge are present up to the 19th vertebra and then again in the 22nd.

Parapophysis.

The parapophysis of the 3rd presacral vertebra is a button-like structure with a roundish outline of the pitted articular face for the capitulum, and has a diameter of 2.7 and 2.2 cm; it extends dorsally and ventrally over the cavities in the centrum. The articular face is oriented ventrolaterally; its ventral rim hardly extends ventrally over the ventral contour of the centrum. The parapophysis of the 4th vertebra is altogether similar to the previous, but it is slightly larger, 3.2 cm long and 2.6 cm broad; its pitted articular face is deeply concave. In the following vertebra the capitulum lies close to the parapophysis or is broken off together with it (5th vertebra). The articular face shows a rather long, stretched outline in the 7th vertebra, as well as in the following ones. The parapophysis in the 11th vertebra is positioned immediately behind the rim of the articular condyle of the centrum, slightly below half of its height, as a roundish, basin-shaped depression of ca. 3 cm diameter. The smooth surface of the concavity is remarkable. The parapophysis of the 12th vertebra is slightly larger (3.5 cm), flatter, not quite as evenly hollowed out, and positioned marginally higher, at about half the height of the condyle. The parapophysis gets larger, flat, and dorsoventrally stretched in the following vertebrae, and it is still relatively smooth in the 12th vertebra but then obtains a rugose surface on the facet. The parapophysis shifts strongly dorsally from vertebra to vertebra; it lies still ventral to the base of the neural canal in the 13th vertebra, it already lies with the larger part of it above the base of the neural canal in the 14th vertebra, in the 16th vertebra the upper rim of the parapophysis reaches up to the center of the prezygapophyseal facet, and from the 18th vertebra onward the dorsal rim of the parapophysis extends dorsally above the prezygapophysis. From the 22nd vertebra onward, the parapophyses are incomplete or not preserved at all. From the 14th to the 19th vertebra onward, the size and shape of the capitular facet remain almost unchanged, being about 6.5 cm long and 3.5 cm wide, the width narrowing in the succeeding vertebrae.

The ridge system of the parapophysis. Among the laminae that reinforce the parapophysis against the centrum, the anterior centroparapophyseal lamina is naturally undeveloped in the anterior presacral vertebrae, because the parapophysis is positioned immediately at the anterior end behind the rim of the condyle, and thus there is not enough space for the centroparapophyseal lamina. The centroparapophyseal lamina is strongly developed, extending ventrally from the end of the centrum, in the 15th and 16th presacral vertebrae, in which the parapophysis rises desultorily above the centrum. However, in the following vertebra the lamina is, as far as is actually preserved, developed as a very thin and laterally directed lamella. The considerable strength of the centroparapophyseal lamina in the 15th and 16th vertebrae shows remarkable strain, which is in striking contrast to the otherwise thin-walled character of the laminar system.

The posterior centroparapophyseal lamina runs from the parapophysis of the cervical vertebrae to the posterior end of their centra; in the 3rd presacral vertebra it forms a rather strong wall, raising dorsomedially and posteriorly, and running horizontally as a rounded crest further on along the centrum; in lateral view this results in a dorsally inturned contour. The posterior part of the lamina is developed as a thin, ventrally suspended wall in the following vertebrae. The edge becomes shorter in the posterior half of the neck, and it lies flatter from the 10th vertebra onward and disappears from the 13th vertebra onward.

Prezygapophysis.

The continuous development of the prezygapophyses of the presacral vertebrae shows altogether the following picture: in the 3rd vertebra it forms a strong, anteriorly jutting, relatively slim process that is mainly supported by the infraprezygapophyseal lamina, which leads to the anterior end of the centrum; the prezygapophyseal lamina, which leads to the diapophysis, branches off the lateral surface; the very delicate intraprezygapophyseal lamina inserts on the medial surface of the prezygapophysis and runs to the center of the roof of the neural canal. Between these three laminae lie excavated pockets that are ventrally open. The 4th lamina, the spinoprezygapophyseal lamina, forms a dorsally directed, increasingly sharper crest of the articular process. The prezygapophyses already shorten considerably, shift slightly more laterally, and move further away from each other from the 5th vertebra onward. At the transition into the trunk, they lose most of their character as independent, anteriorly jutting processes as they lean against the rising diapophysis; with this rearrangement the deeply excavated pockets almost completely disappear. The prezygapophyses move close together until they have an average inner distance of 2 cm in the anterior dorsal vertebrae, and take on the character of medially directed and also medially narrowing wedges from the 16th vertebra onward.

For the exact description of the prezygapophyseal facets, their shape and position and the disturbances of their shape, which are also present in the otherwise very favorable preserved spinal column of *D. hansemanni*, have to be taken carefully into consideration. Thus it can be observed that the rims of the facets have been pushed open in several cases. The borders of the facets in the direction toward the vertebrae are often not clearly visible and cannot be determined, and it is also obvious that the character of the curvature has been influenced by pressure in certain cases, and that namely the inclination of the facets has been altered to a considerable degree.

During measurement of the length and width of the facets, considerable differences were often found between the right and left sides that probably cannot be entirely attributed to subsequent deformation or to inaccurate measuring, but might partly be natural. Also, the measurements of the prezygapophyseal facets of one vertebra may not correspond to the postzygapophyses of the preceding vertebra.

The contour of the prezygapophyseal facets of the 3rd vertebra is elliptical, 4.5–5 cm long and 4 cm wide. The contour of the two following vertebrae is nearly circular (ca. 4.5 x 4.5 cm); but the facets are broader than long in the 6th and 7th vertebra $(3.5 \times 4-5 \text{ cm})$; however, their surfaces are slightly smaller than in the preceding vertebrae. The surfaces are again nearly circular from the 8th to the 12th vertebra, but increase in size (6.5 x 6.5 cm in the 12th vertebra). In the 13th vertebra the length increases to ca. 8 cm, still retaining the same width of 6.5 cm; in the 14th vertebra the length has increased to ca. 9 cm, yet the width has decreased to ca. 4.5 cm. The width decreases further; the measurements in the 16th vertebra are 3 x 9 cm, in the 18th vertebra $3.5 \times 8-8.5$ cm; the length also decreases further to 6.5-7 cm. The posterior rim, and therefore the width, is often not clearly recognizable in these vertebrae, but seems to be generally around 4 cm. The facets get broader again in the penultimate presacral vertebra; the contour acquires a special characteristic in the last presacral vertebra, as here the anterior rim is slightly bent inward, measuring ca. 4.5–6 cm. In the vertebrae in which a hyposphene^{*} articulates between the prezygapophyses, i.e. from the 15th vertebra onward, the facet extends ventrally over the straight, cut-off medial rim; this inner section of the facet, which achieves the greatest heights of ca. 3 cm in the 19th vertebra and 3.5 cm in the 24th vertebra, bends ventrolaterally; in the three last vertebrae it rises increasingly steeply, standing almost completely vertically in the last vertebra. The surfaces of the facets of the prezygapophyses, which are convex in the axis, are almost level in the 3rd to the 5th vertebrae; in the two following vertebrae they are concave to different degrees, obviously representing sections of pillar-like rotational bodies with an axially directed axis of rotation; in the 8th and 9th vertebra the facets are either level or insignificantly convex; in the 10th vertebra a concave facet

^{*} Janensch uses "zygosphene" here *et seq*. [Tr]

can be found on the right side and a convex one on the left; the curvature is precisely reversed in the next two following vertebrae: the only preserved right facet of the 13th vertebra is level, the facets are concave in the sense described above in the 14th and 15th vertebra, in all following vertebrae the surfaces are nearly level, and it is distinctly convex only in the last one. The prezygapophyseal facets all show a medial angle of incidence, except for the last vertebra. Considerable differences were discovered during measurement of the inclination on both sides, which, as far as they were not natural, might have been caused by pressure but might have also occurred to a certain degree due to a not exactly vertical orientation of the vertebrae during mounting on the plaster pedestals. The inclination of the prezygapophyseal facets were measured medially in the transverse plane. In facets with a curvature in the transverse plane, an average straight inclination was estimated and forms the basis for the measurement. It turned out that in the first cervical vertebrae the inclination increases from an angle ca. 28° to one of ca. 40°, slightly more in the 3rd, and still more in the 4th to the 7th vertebrae. Then a strong decrease to less then 20° in the 10th and 11th vertebrae takes place, and again an increase in the inclination angle to 40° and slightly more in the 15th and 16th vertebrae. Then again a decrease occurs: from the 19th vertebra onward the inclination angles are ca. 20° or a little above, in the 23rd vertebra a strong decrease to slightly above 10°, and in the 24th vertebra eventually a reversal is measured in the lateral direction to ca. 12°.

Prezygapophyseal laminar system. Spinoprezygapophyseal lamina. This lamina is developed as a weak lamella in the 3rd vertebra that does not extend beyond the bifurcation point of the neurapophysis; the exact position of its dorsal end cannot be determined due to incomplete preservation. In the 4th vertebra, the sharp ridge of the prezygapophysis turns into the anterior rims of the vertical neurapophyseal branches, of which the right one is very thin and the left is slightly stronger and The anterior part of the anterior rims therefore represent the not particularly set off curved. spinoprezygapophyseal laminae. The anterior rims of the spinoprezygapophyseal laminae become thicker in the following vertebrae with anteriorly inclined neurapophyseal branches, they are at their greatest extent on the strongly anteriorly inclined neurapophyseal branches of the 8th and 9th vertebrae. They are already much weaker in the less steeply positioned neurapophyseal branches of the 10th vertebra, at least the only preserved left one. The anterior parts of the anterior rims of the spinoprezygapophyseal laminae are bent laterally in the following vertebrae. In the 15th vertebra, in which the anterior rim of the neurapophyseal branches bends laterally towards the supradiapophyseal lamina, only very short, sharp laminae remain of the spinoprezygapophyseal laminae, and in the next vertebra even these are no longer noticeable but reappear again very weakly in the 17th vertebra. The same weak spinoprezygapophyseal laminae are present in the 18th vertebra, which has a half-divided neurapophysis. Here they lie close to the strongly developed laminae, which run ventrally in continuance of the anterior rims of the neurapophyseal branches. They still bend ventrolaterally toward the diapophyses, but due to their direction can best be described as the main spinoprezygapophyseal laminae. The main spinoprezygapophyseal laminae shift very close together in the following vertebrae. They are, by the way, very irregularly developed in the 19th vertebra. They enclose the rough, longitudinally furrowed edge of the prespinal lamina in the 19th and 20th vertebrae, between them over half the height of the neurapophyses, but both over differently long distances. In the following vertebrae the main spinoprezygapophyseal laminae run considerably lower along the neurapophyses.

In fr a prezygapophysis, forms a rather strong wall in the cervical vertebrae, the anterior rims of which rise anteriorly in the 3rd vertebra at a rather steep angle. The angle gets even steeper in the succeeding vertebrae and in the last cervical vertebrae faces increasingly laterally. The strength of the lamina increases along the anterior dorsal vertebrae. Then the parapophysis rises upward along the infraprezygapophyseal lamina from the 14th to the 16th vertebra; the part positioned ventral to the parapophysis becomes the centroparapophyseal lamina during this course. It will be dealt with in the chapter on the parapophysis. Intraprezygapophysis is mostly developed as a thin, sharp, distinctly projecting lamella. It projects far less from the 11th vertebra onward, in accordance with the posterior shift of the prezygapophyses. This lamina disappears simultaneously with the medial moving together of the prezygapophyseal laminae in the anterior dorsal vertebrae from the 16th vertebra onward.

Postzygapophysis and hyposphene.

In the presacral vertebrae with completely divided parts of the neurapophysis, The postzygapophysis forms a wedge-like, ventrally increasing thickening on their posteroventral end, which carries the ventrolaterally pointing facet.

In the anterior part of the neck, i.e. in the main part of the anticline of the cervical vertebrae, a rugosity is visible above the facet that might have served as a muscular attachment area. This rugosity is positioned above the lateral rim of the facet as a bulging inflation parallel to it in the third cervical vertebra, which by the way is also present in the axis. In the 4th vertebra this rugosity still lies on the lateral surface, but is shifted posteriorly and causes a projection above the posterior end of the facet. This projection appears more clearly in the following vertebrae with increased anterior inclination of the neurapophyseal ranches, because by an angular turnover of the contour, the rugosity remains limited to the point of this turnover. Only a small bulge is still present in the 8th vertebra. But further anteriorly on the 9th vertebra, approximately above the anterior end of the facet, a hint of this swelling is still present. The rugosity has disappeared further anteriorly.

With the increasing strength of the vertebral centra in the posterior half of the neck, the postzygapophyses move further apart from one other, only to shift closer together again with the increase in height and the rise of the parts of the neurapophysis at the transition into the trunk. The postzygapophyses are joined in the middle and form the zygosphene in the 15th presacral vertebra, which forms a medial, ventrally broadening, wedge. The postzygapophyseal facet extends to the lateral end of the zygosphene. Besides, the zygosphene is already indicated in the 14th vertebra, in the shape of an only partly preserved peg. The zygosphene gets increasingly stronger in the 16th and successive vertebrae, and has a ventral width of ca 4.5 cm in the 17th vertebra. The wedge shape is very slightly tilted, a character that is probably not, or not only, caused by deformation. The zygosphene gets narrower in the posterior dorsal vertebrae and shows a medial groove that is enclosed by sharp rims on the posterior surface. Additionally, the zygosphene gets dorsoventrally higher in the two last vertebrae, its lateral facets being almost parallel here. A medial crest is formed on the ventral surface of the zygosphene of the last three vertebrae, asymmetrically shifted to the right in the last one, which continues ventrally as a weakly projecting edge up to the level of the roof of the neural canal. In lateral view, the zygosphene projects posteriorly to a changing degree; for example, it is remarkable how much longer the ventral contour of the zygosphene is in the 20th vertebra compared to the 21st. This difference stems from the fact that the posterior rim of the lateral walls of the neural arch in the 20th vertebra extend dorsally a considerably greater distance from the posterior end of the centrum than in the 21st vertebra.

A triangular area is developed on the posterior surface of the postzygapophyses from the 16th vertebra onward, which is very narrow dorsally and shows wide angles laterally. This angle is blunt in the 16th vertebra and decreases to an R^* in the 18th vertebra, the enclosed field becoming simultaneously concave. This triangular field is not present in the 19th vertebra; a corresponding

^{*} This expression is unclear, but may refer to a "right angle" [Tr].

field is present again from the 20th to the 22nd vertebra, which is enclosed by two spinopostzygapophyseal laminae. Instead of the triangular field, the 23rd vertebra shows a deep groove between these two laminae, which disappears again in the last vertebra due to the regression of the medial spinopostzygapophyseal lamina. Therefore, there is not at all a continuous shape, but a continuous change in the form.

As was to be expected, the postzygapophyseal facets show in their entirety the same alteration of shape as the prezygapophyses, even though the measurements do not always correspond, as was mentioned before.

In the axis, the contour of the postzygapophyseal facets is a long ellipse (5 x 3.5 cm), and in the following vertebrae more roundish (4.5–5.5 x 4.5–5 cm). In the 5th and 6th vertebrae the facets are slightly shorter than wide (4 x 5 cm), they are missing in the 7th vertebra, in the 8th vertebra the facets measure ca. 5.5×4.5 cm, the facets increase in width in the 10th and are 5×6 cm, and in the 12th vertebra $5.5-6 \times 8-9$ cm. The length of the facets decreases in the dorsal vertebrae; the measurements in the 16th are $4 \times 8-8.5$ cm, in the 17th $3 \times 8.5-9$ cm. Toward the end the length increases again, however the width decreases; the facets measure 4.5×8.5 cm in the 20th, 4.5×7.5 cm in the 21st, and $6.5 \times 5.5-6$ cm in the 24th vertebra.

In the dorsal vertebra with a zygosphene, i.e. from the 15th presacral vertebra onward, the facets continue in a sharp bend along the lateral surface of the zygosphene. The facets of the zygosphene diverge ventrally in the anterior dorsal vertebrae, here they have a vertical extent of 3-3.5 cm. The facets are positioned more steeply in the posterior vertebrae, almost parallel in the two last ones, and the vertical extend also increases up to 4.5 cm in the 23rd vertebra, and up to 5–6 cm in the 24th vertebra.

The inclination of the postzygapophyseal facets is similar to that of the prezygapophyses, but is altered by deformation to an even higher degree. The inclination increases from slightly more then 20° in the axis to ca. 50° in the 6th vertebra. The inclination then decreases, as far as the measurements, unreliable in this region, allow judging. The inclination increases again to ca. 40° at the transition into the trunk. Decrease in inclination occurs again along the dorsal vertebrae, which leads to a reversal of the inclination in the last two vertebrae that—in accordance with the shape of the prezygapophyses—leads to an increase of the lateral inclination. The surfaces of the postzygapophyseal facets are generally almost level, only a divergence in some postzygapophyses appears, in which case the right and left facets of a vertebra may appear differently, as in the prezygapophyses. So only the right facet is convex in the 5th vertebra, the right one is concave in the 10th vertebra, the left side is convex in the 12th vertebra, whereas both sides are convex in the 13th and 16th.

Laminar system of the postzygapophysis including hyposphene. Spinopostzygapophyseal laminae. The spinopostzygapophyseal lamina runs posterodorsally from the postzygapophysis and is rather strongly developed in the 3rd presacral vertebra; in contrast it is thin and sharp-edged in the 4th vertebra and the following one, in which it runs anterodorsally and grades into the posterior rim of the flat dorsal part of the neurapophysis. With the occurrence of the posterior slant of the latter from the 8th vertebra onward, the lamina gets thicker again, being very strong in the anterior dorsal vertebrae up to and including the 19th, which has a high, dorsally positioned bifurcation point. From the 18th vertebra onward, an inner spinopostzygapophyseal lamina appears, in this vertebra only as a short blunt ridge running obliquely dorsolaterally from the medial junction of the postzygapophyses; its left side is strongly developed in the successive partly asymmetrical vertebrae, and further dorsally it encloses the longitudinally grooved rim of the postspinal lamina on both sides. The inner laminae dominate over the outer ones in the following vertebrae with an undivided neurapophysis, the outer laminae run close to the inner lateral surface of these vertebrae, in the form of short edges that converge strongly dorsally. The outer spinopostzygapophyseal lamina is insignificant in and 22^{nd} 21st vertebrae, the

while the inner one is strongly developed and reaches almost to the upper half of the free neural spine. The outer lamina is again more strongly developed in the 23rd vertebra, and it is positioned parallel to the inner spinopostzygapophyseal lamina, which is still considerably longer and stronger. The outer spinodiapophyseal lamina does not lie close to the inner spinodiapophyseal lamina, but lies much closer to the spinodiapophyseal lamina. In the 24th vertebra the inner lamina has almost disappeared, while the outer one is even more dominant and shifted slightly more laterally.

C entropostzygapophysis, forms a strong wall in the neck whose the posterior rim rises almost vertically. In the anterior cervical vertebrae, this wall also forms the lateral wall of the neural canal. The wall shifts laterally at the start of the posterior half of the neck and gets very strong from the 9th vertebra onward. The position changes, insofar as the right and the posterior laminae increasingly converge in posteriorly. In the 14th vertebra, but only on the right side, two parallel laminae are present close to each other, instead of just one.

From the 13th vertebra onward, the centropostzygapophyseal lamina shortens and the ventral end lies higher and achieves a more medially directed position; in the 13th vertebra the ventral end lies at the height of the roof of the neural canal, but considerably higher in the 14th vertebra. The centropostzygapophyseal lamina is the lamina only a very short and delicate lamella in the 15th vertebra, which runs laterally from the ventral end of the facet. In the following two vertebrae only short rudiments of the lamella can be found, and even these occur only on one side; the lamella becomes slightly longer again and achieves a more posteriorly directed position from the 18th vertebra onward. The thickness, but not the length, of the lamina increases further. The indistinct preservation of the centropostzygapophyseal lamina in the 24th vertebra does not allow a determination of its shape.

Intrapostzygapophysis. In the 3rd and 4th presacral vertebrae, the laminae drop steeply ventrally from left to right and join in a uniform curve into a single horizontal lamella which lies at a distance above the roof of the neural canal. The left and the right laminae join at an angle on the midline from the 5th vertebra onward, which was obviously pushed together by lateral pressure in the 5th vertebra but is also pointed in the succeeding vertebrae; the angle is wide in the 10th vertebra, as it might have been increased by vertical pressure, and the angle is pointed again in the following vertebrae. The lamina disappears from the 15th vertebra onward, which has joined postzygapophyses and a developed zygosphene.

In fr a h y p o s p h e n a l la m i n a. With the first occurrence of the hyposphene in the 15th presacral vertebra, the hyposphenal laminae appear as well; they are very asymmetrically developed in this vertebra. The right one is much more prominent, inserting on the center of the ventral surface of the zygosphene, whereas the left one inserts on the lateral surface; both diverge ventrally at an acute angle and are thickly rounded. This asymmetry is probably caused by the fact that the zygosphene is shifted to the right and is positioned obliquely. In the next vertebra, the laminae run from the lateral edges of the zygosphene and are much thinner, more highly developed, and very weakly ventrally diverging. The right one is still slightly longer than the left and reaches not quite halfway down to the base of the neural canal. With the upward shift of the zygosphene over the centrum, the laminae become accordingly longer and bend with their rim slightly medially as well; but this stops from the 22nd vertebra onward. The laminae get increasingly shorter in the 23rd vertebra, and they are almost insignificant in the 24th, at the same time being irregular and asymmetrical. This developed reduction is caused by the fact that the transverse wall suspended between the lateral walls of the neural arch has shifted fully to the posterior end and has become the support of the zygosphene.

Infradiapophyseal fossa. The infradiapophyseal fossa not only consists of a cavity enclosed by laminae, positioned ventral to the diapophysis and in front of the posterior centrodiapophyseal lamina, but also shows a particular depression. Thus the depression forms an independent element and deserves a separate account. It appears clearly developed for the first time in the 14th vertebra, in which it is represented on the right side by a roundish fenestra of almost 4 cm diameter. and on the left by a cavity which widens considerably behind an irregular square-shaped rim of 3 cm widest diameter. In the following vertebra, the cavity shows a rather wide circumference on the right side, with 5 cm widest diameter, but is very narrow on the left, measuring 1.4 cm in diameter; similar cavities lie on both sides of the 16th vertebra, vertically excavated at the bottom, which measure 4-4.5 cm; these cavities are somewhat larger still in the 17th vertebra, but with a flatter ventral excavation. A new character appears from the 17th vertebra onward on the left side, from the 19th vertebra onward on the right. With the continuous increase of the vertical diameter to 8 cm in the 22nd vertebra, the ventral part of the posterior enclosure takes on the character of a lamina, which encloses the cavity like part of a frame, with its free anteriorly pointing rim rising steeply posterodorsally and abutting closely to the anterior rim of the laterally projecting posterior centrodiapophyseal lamina, almost an extension of the latter and only slightly shifted posteriorly.

The narrowest and highest development of this posterior frame-like lamina is found in the 21st vertebra, and it gets broader and lower in the following vertebrae. From the 22nd vertebra onward, an additional, but slightly less strongly developed anterior frame-like lamina appears, which extends anterodorsally and rises as an anterior, frame-like lamina, forming a ventral angle of 90° with the just-described posterior frame-like lamina. Both laminae are somewhat less clearly developed in the 24th vertebra. Concerning the significance of the posterior frame-like lamina, it is unmistakable that it counteracted the pressure that was transmitted from the postzygapophyses via the infrapostzygapophyseal lamina onto the posterior frame-like lamina, which is actually always very broadly rounded rather than typically lamina-shaped, shows stress from pressure that affected the prezygapophyses from front to back.

Comments on individual presacral vertebrae.

To avoid possible mistakes when making use of the images, I now wish to add the following comments on the individual presacral vertebrae, by which those shape changes resulting from mechanical pressure will be elucidated in particular. Additionally, individual characteristics of the vertebrae that could not be considered in the general descriptions of the various shape elements will be dealt with.

2nd presacral vertebra (axis). On the anterior surface, in front of the left postzygapophysis, a small part is pressed outward. The roof of the neural canal is dislocated by some millimeters due in the middle of its posterior end to a break. Small fractures and deformations appear immediately ventral to the postzygapophysis, namely on the left side. The left parapophysis is slightly pushed laterally and is incomplete distally.

In front of the right postzygapophyses lies a large, ventrally facing opening, which is small on the left side; thus on the anterior end of the prezygapophysis a genuine fenestra seems to have been present, which has subsequently been enlarged by additional bone loss.

3 rd presacral vertebra. Ventral to the right postzygapophysis, the roof of the neural canal is thrust medially about 1 cm due to lateral pressure, which results in a somewhat reduced width. The left prezygapophyseal facet is pressed into a steeper position than the right one.
The right diapophysis was apparently pushed slightly medially.

Substantial fenestrae occur in front of the prezygapophyses, and in the medial wall between them, which probably are not solely due to loss of substance, but might originally have been smaller natural fenestrations. A smaller individual pocket lies ventral to the anterior end of the posterior centrodiapophyseal lamina.

4th presacral vertebra. Only the postzygapophyses are slightly pushed medially. In front of the right postzygapophysis lies a large, broken-through hole in front, which is small in front of the left one; a section of undamaged rim seems to be present anteroventrally in the right ones, so that a natural fenestra of smaller circumference can be assumed. The right prezygapophyseal facet is positioned more steeply than the left. The dorsal rim of the condyle appears eroded. Ventral to the anterior rim of the centrodiapophyseal lamina lies a special pocket, which is much larger on the left side than on the right; it merges with the pleurocentral groove in the following vertebrae. The rim of the left supraprezygapophyseal lamina is asymmetrically much stronger the right one.

5th presacral vertebra. A medially directed deformation appears ventral to the postzygapophyses and seems to have affected these also to a certain degree. The right diapophysis, including the cervical rib, was slightly pushed medially. The lateral rims of the prezygapophyses were pushed upward. The dorsal rim of the condyle appears eroded, so that a transverse depression is developed. The right postzygapophysis is distinctly convex, but the left one is flat.

6th presacral vertebra. The upper half of the neurapophyses are slightly bent to the right, and the left one is medially deformed at half its height. Parts of the rim of the right diapophysis were pushed slightly medially. The right prezygapophysis shows an unnaturally strong concave facet, although deformation caused by pressure is hardly noticeable otherwise.

The curvature of the condyle is very irregular, its center is depressed, the top is vaulted and projects anteriorly, and the bottom shows flat depressions on the right and left sides.

7 th presacral vertebra. The dorsal part of the left neurapophysis, the postzygapophyses, and the distal section of the diapophyses were not preserved and have been restored. The entire neural arch is slightly obliquely pushed to the left. The distal diapophyses are partly incomplete and have been restored. The condyle shows a groove centrally and on the left lateral surface.

8th presacral vertebra. The left neurapophysis is twisted along the longitudinal axis; the anterior side medially, the posterior side laterally. The condyle is dorsally vaulted and projects anteriorly, and its center is irregularly rugose and depressed.

9th presacral vertebra. The left neurapophysis was found detached and without direct connection to the vertebra, but could be reattached with a perfect fit. The neural canal is slightly crushed posteriorly. The articular cavity of the centrum is restored on the right rim, and it is also slightly depressed on the left dorsal surface.

The condyle shows a depression on the left side.

10th presacral vertebra. The right neurapophysis was detached and has been reattached without a proper fitting surface. The left diapophysis is completely restored, the right one distally so. The centrum and the neural arch, especially on the left side, show fractures and displacements, but the entire shape seems not to have been significantly disturbed. The walls surrounding the neural are not preserved on the left side.

11th presacral vertebra. The neurapophysis is missing on the right side, and the diapophysis including the postzygapophyseal lamina, the roof of the pleurocentral groove, and the supraprezygapophyseal lamina are missing on the left side. The entire neural arch is shifted to the left, especially anteriorly, and the central section is broken into pieces, as is the right side. The articular cavity shows cracks and displacements. The left postzygapophyseal facet has been forced

into too concave a shape by a fracture. The position of the preserved left neurapophysis might be considerably disturbed.

12th presacral vertebra. The neurapophysis is slightly bent to the left.

13th presacral vertebra. The left diapophysis and prezygapophysis are not preserved. On the left side, a depression lies next to the center of the condyle, which might have been weathered out. The left neurapophysis has been affected by an oblique transverse fracture and has also been affected by slight compression.

14th presacral vertebra. The distal part of the left diapophysis is not preserved. A ca. 2.5 cm wide furrow, which deepens medially, lies on the anterior surface ca. 10 cm below the upper end of both neurapophyseal branches. It is not impossible that a transversely lying bone has been pressed into this area. This fact is supported by the fractures and small dispositions that are present on the left neurapophyseal branch. The right diapophysis has been pressed into a probably too steep position.

Asymmetry: On the left side there is one centropostdiapophyseal lamina, but on the right side there are two.

15th presacral vertebra. The largest part of the diapophysis is not preserved. The prezygapophyseal facets are disturbed by gaping cracks. The right diapophysis has been pushed into a too steep position.

Asymmetry: The right centropostdiapophyseal lamina is much stronger than the left one. The right infradiapophyseal fossa is much larger than the left one.

16th presacral vertebra. The lateral parts of the left neurapophyseal branch, the left diapophysis, and the medial end of the prezygapophysis are not preserved.

The left diapophysis has been pushed somewhat posteriorly.

17th presacral vertebra. The larger part of the left diapophysis, the left parapophysis, and the lateral end of the left neurapophyseal branch are missing.

Only the ventral section of the anterior centroparapophyseal laminae is preserved. The ventral section of the neural arch is slightly dislocated to the left toward the centrum. This causes a slightly tilted profile of the neural canal. The left diapophysis is pushed medially into a steeper position.

Asymmetry: The right neurapophyseal branch carries medially a much more strongly developed lamina than the left one, in connection with a bend in the dorsal part of the side of the postspinal lamina.

18th presacral vertebra. The left posterior rim of the centrum, the distal half of the left diapophysis with the entire paradiapophyseal lamina, the medial, and on the right side also the dorsal sections of the centroparapophyseal laminae are missing. The hyposphene is incomplete at a gaping transverse fracture (later filled with plaster) ventral to the postzygapophyses. The postzygapophyses themselves and the neurapophysis are pushed apart for ca. 1.5 cm and displaced ca. 1 cm to the left. At a horizontal fracture approximately at the height of the postzygapophysis facet, the right diapophysis is displaced obliquely ventrally and medially for about 1.5 cm, and therefore shortened for this amount of length. The preserved proximal section of the left diapophysis is slightly medially pushed upward. The right postzygapophyseal facet is slightly compressed and shortened at the fractures.

19th presacral vertebra. The left side of the centrum is somewhat abraded. The left diapophysis including the left parapophysis, the lateral section of the postzygapophysis, the right paradiapophyseal lamina, and the centroparapophyseal lamina are largely missing. The left neurapophyseal branch is incompletely preserved.

Asymmetry: Spinoprezygapophyseal laminae and medial postzygapophyseal laminae.

20th presacral vertebra. The left side, the right, and the ventral rim of the centrum, as well as the left lateral surface of the ventral part of the neural arch positioned dorsal to it, are abraded. The left diapophysis, together with parapophysis and the lateral section of the left prezygapophysis, the complete left centroparapophyseal lamina, and the largest part of the

right lamina, are missing. Also missing are the left lateral spinodiapophyseal lamina and a large portion of the right, and the left posterior rim of the neural arch ventral to the infrahyposphenal lamina. The right diapophysis is medially compressed, and this deformation obviously caused too steep a position.

21st presacral vertebra. The left surface of the centrum is abraded. The left wall of the neural canal, the left diapophysis together with the parapophysis and the centrodiapophyseal lamina, the left spinodiapophyseal lamina, and a section of the rim of the right spinodiapophyseal lamina are missing. The proximal section of the right diapophysis is compressed dorsomedially and is obviously pressed upward.

22nd presacral vertebra. The left side of the centrum and the lateral surface of the left wall of the neural canal are abraded. Lacking the left diapophysis together with the left parapophysis, a large part of the surface of the right diapophysis posterior to the parapophysis, the posteriorly jutting part of the hyposphene, the larger part of the left spinodiapophyseal lamina, and parts of the right spinodiapophyseal lamina. The right diapophysis is pressed dorsomedially and has been shortened.

23rd presacral vertebra. The left side of centrum and the lateral surface of the left wall of the neural canal are severely abraded. The left diapophysis together with the parapophysis and centroparapophyseal lamina, part of the anterior surface of the right diapophysis together with the right parapophysis, and large parts of the rims of the spinodiapophyseal laminae are missing. The diameter of the neural canal is diminished due to lateral pressure. The right diapophysis has been shortened by compression.

24th presacral vertebra. The left side of the centrum is abraded. The left diapophysis together with the left parapophysis and extensive parts of the rims of the spinodiapophyseal laminae are missing. The right diapophysis is strongly compressed proximally and therefore perhaps positioned in a somewhat incorrect orientation.

Presacral vertebrae from locality dd.

The presacral vertebrae from dd merit only a few comments. A comparison between the same vertebrae of both animals from this excavation site and of skeleton m shows individual differences of not too much relevance. The design of the pleurocentral grooves on the axis does not correspond in detail, and the diapophyses show somewhat different widths and orientations. The anterior cervical vertebrae from dd show slightly more extensive zygapophyseal facets than the vertebrae from the skeleton, moreover the facets on the 5th cervical vertebrae from dd are much shorter than on the same vertebra of m.

It must also be noted that the intrapostzygapophyseal laminae meet medially horizontally in this 5th vertebra from dd, so that it must be assumed that the acute angle at which the intrapostzygapophyseal laminae meet medially in the corresponding vertebra of m is the result of lateral pressure.

"Proatlas".

Fig. 5a, b.

Two scale-like structures, dd 514 and dd 513, can with the greatest probability be interpreted as the so-called left and right proatlantes. Both specimens, which differ from each other in minor details, possess a thick anterior end with an elliptical to egg-shaped, slightly depressed posterior surface, ca. 4 cm long and 2.5 cm wide. A dorsally pointing, flat, longitudinally curved scale grows out of the anterior end; it quickly thins and evenly narrows, its anterior and lateral rims simultaneously form a blunt angle, and both specimens extend posteriorly into an unpreserved, but obviously pointed end. The anteromedial corner is coarse and rugose in both proatlas specimens, but in different ways. The total original length must have been approximately 7.5 cm. According to their size, both proatlas specimens fit much better on the skulls of *Dicraeosaurus hansemanni* than on the much smaller ones of *Barosaurus* from dd. With the depressed anterior surface, the right proatlas fits with its depressed anterior surface on a dorsolateral curvature of the foramen magnum of skull dd 307, and also fits so perfectly onto the dorsal surface of the atlantal neural arch of dd 511, so that an assignment of both elements to one another, and therefore to the same species of sauropod, must be strongly assumed. The proatlas of *Brachiosaurus* differs by the lack of such a strongly developed and sharply circumscribed anterior attachment area.

Left proatlas (dd 514) of *Dicraeosaurus hansemanni*. Fig. 5a dorsal view Fig. 5b anterior view. 1/2 original size.

Atlas.

Fig. 6a-c, 7a, b.

The altogether rather heavily built intercentrum (dd 511) shows the anterior, deeply depressed cavity for the occipital condyle ventrolaterally circumscribed by a vault, which is sharply edged and slightly protruding ventrally. Accordingly, the rather flat ventral surface, slightly depressed medially and toward its posterior end, shows an anteriorly protruding rim. A medially rounded, very deeply depressed longitudinal groove lies dorsally; transverse to this groove, the profile is strongly rounded so that this dorsal part resembles the cross-section of a thick, narrow ring in dorsal view. The low posterior surface is bordered dorsally by an edge, which runs in a dorsally open

Fig. 6a. Intercentrum (dd 511) in anterior	Fig. 7a. Right neural arch (dd 512) in lateral					
view.	view.					
Fig. 6b. The same, posterior view.	Fig. 7b. The same, anterior view.					
Fig. 6c. The same, ventral view.	1/4 nat. size.					

curve; it is relative deeply depressed on both sides next to the center. The nearly square lateral surfaces stand very steeply, almost vertically from the ventral surface. The obliquely dorsolaterally positioned sutural areas for the neural arches have an egg-shaped contour ca. 3.5 cm long and 2.5 cm wide. Possible rib facets are not recognizable. In size the intercentrum definitely fits both skulls of

Largest length (ventral)	4.8 cm	
Largest width (dorsal)		7.8 cm
Width (ventral)	6.2 cm	

Dicraeosaurus hansemanni from the same excavation site dd and can unobjectionably be assigned to this species. A significantly smaller intercentrum from the same excavation site, which according to its size fits one of the smaller skulls, probably belonging to Barosaurus africanus, differs namely by a flatter dorsal depression and a projection on both sides of the ventrolateral corner of the posterior surface. These characters that are also present in the intercentrum of Diplodocus. are two

closely related to *Barosaurus*, which is also evident from HOLLAND'S drawings (1905 Fig. 11–13). The much larger intercentrum of *Brachiosaurus*, which was found with the skull at excavation site t, is much lower and has a flat posterior surface.

The right n e u r a 1 a r c h dd 512 (Fig. 7a, b) has a ventral sutural surface, which according to its shape and size fits positively on one of the intercentra, and probably belongs to this intercentrum, or perhaps to one from the other skeleton of *Dicraeosaurus hansemanni* from dd. Directly above the mentioned sutural surface lies a slightly narrower, broad, crescent-shaped surface that is divided by a vault into an anterior flatly depressed facet for the occipital condyle and a larger, posterior one for the odontoid process. Both surfaces border the ventrally broadening, ventral section of the neural arch ventromedially. The dorsal section is very incompletely preserved and allows only to observe that it continued anteriorly as a short arched structure, and posterodorsally as a flatter arch. The dorsal section of the neural arch bears a deeply incised furrow medially, shaped like half of a tube, that forms the lateral wall of the neural arch.

Sacrum.

Skeleton m.

Pl. III.

Preservation.

Because of the lateral burial posture, the sacrum suffered some, although inconsiderable, compression in the direction perpendicular to the medial plane, as can be observed on the right lateral processes [diapophyses + sacral ribs]. These are completely missing on the left side, except on the 4th sacral vertebra, in which the dorsal part of the lateral process is preserved. The five neurapophyses are all preserved. The 2nd to 4th sacral centra were disarticulated and were found embedded in isolation, but could be refitted. As mounted, the distance between the dorsal arches of the 4th and 5th vertebrae, and therefore also between their neurapophyses, is obviously wider than it would have been in the undisturbed condition.

Centra.

The middle sections of the centra are moderately constricted ventral to the articulation of the sacral ribs, both medially and dorsally. The lateral constriction is most pronounced in the 4th vertebra, but even here a very sharp ventral keel does not occur, and the ventral surface is still rounded. The lateral surfaces of the centra show no indications of pleurocentral fossae. The surfaces and contours of the end facets of the first sacral vertebra, those of the three following vertebra, and the anterior facet of the 5th vertebra are incompletely preserved. Therefore the articulating end surfaces do not fit perfectly together. The posterior end surface of the 5th sacral vertebra is well preserved, almost circular, and has a width of 20 cm and a height of ca. 19.5 cm. The dorsal half of the end surface is rather strongly inclined anteriorly toward the ventral half, and is in addition slightly concave. The ventral half is nearly level, with only a weak depression slightly ventral to the center of the entire end surface. The margin of the end surface is formed by an up to 2 cm wide, slightly elevated, ring-shaped zone with fine concentric fluting, demarcated from the center by a shallow, weakly developed furrow. The upper half of the outer rim protrudes

sharply due to a surrounding narrow outer furrow. As mounted, the length of the entire row of five centra measures 73 cm from the center of the anterior end surface of the first vertebra to the posterior one of the last; the lengths of the individual vertebrae, measured ventrally from anterior to posterior, are 16 cm, 12 cm, 13 cm, 14 cm, and 17 cm.

Neurapophyses.

Of the neurapophyses, those of the 2nd to the 4th vertebrae are fused without trace of a suture with the medial prespinal and postspinal laminae along their entire lengths, whereas the 1st and 5th are free along their entire lengths. The neurapophysis of the 1st vertebra is almost perfectly vertically positioned and only very weakly inclined anteriorly. The median wall, formed by the prespinal and postspinal lamina, shows a minimum width of ca. 8 cm at one-third of its height; it broadens dorsally to ca. 11 cm. The median wall in the three middle sacral vertebrae, formed by the fusion of these same laminae, has a minimum width of about 17.5 cm at one-third of its height, and its height is 28.5 cm. The anterior contour of the prespinal lamina of the 2nd sacral vertebra is slightly bent inward in its ventral third, and it is slightly bent forward dorsally. The posterior contour of the postspinal lamina of the 4th sacral vertebra is bent moderately strongly inward in its ventral third, and dorsally it is nearly straight. The median wall in the 5th (caudosacral) sacral vertebra has an almost consistent width of 8–9 cm; the anterior and posterior rims run parallel to one another, are anteriorly inclined for about one-quarter of their height, and then bend in a narrow arch posteriorly in such a way that the dorsal section runs straight with an inclination of ca. 60° to the axis of the neural canal. As far as they are unfused, the rims of the prespinal and postspinal laminae show the characteristic longitudinally fluted, coarse-grained rugosity. The spinopostzygapophyseal laminae appear on the ventral third of the sides of the free prespinal laminae of the 1st (dorsosacral) and 2nd sacral vertebra, whereas they are not developed on the 5th vertebra. The spinopostzygapophyseal laminae are barely indicated on the 1st sacral vertebra, but on the 4th and 5th they project so strongly that they enclose a deep slit between them. The development of the spinopre- and spinopostzygapophyseal laminae is obviously connected with the physical demands to which they were exposed. The above-mentioned laminae had to counteract the anterior tension on the first two vertebrae by stiffening. These laminae are missing on the neurapophysis of the 5th sacral vertebra, which was exposed to tensions coming from the rear. These tensile forces on the neurapophyses must have been very strong in the 4th and 5th sacral vertebrae, as indicated by the posterior inclination of both neurapophyses. Both neurapophyses therefore possess very strong spinopostzygapophyseal laminae. The spinodiapophyseal laminae are not positioned continuously perpendicular to the wall that is formed by the pre- and postspinal laminae, but rather are slightly bent anteriorly in the anterior four neurapophyses; on the other hand, in the 5th sacral vertebra they are directed slightly more posteriorly. In dorsal view, in accordance with the position of the neurapophyses of the first sacral vertebra, a very insignificant anterior inclination appears on the dorsal half of the rim. A very weak inclination occurs on the second sacral vertebra, an increasingly stronger one on the 3rd and 4th, and a really strong posterior inclination on the 5th. The spinodiapophyseal lamina of the 3rd vertebra is particularly thin, and ventrally it strongly approaches the next one, which is characterized by particularly strong development. The neurapophyses show almost the same shape in anterior or posterior view, a broadening in the dorsal direction, just as in the posterior dorsal vertebrae. The dorsal width of the neurapophyses increases posteriorly; it is 18.5 cm on the 3rd sacral vertebra and 20.5 cm on the 4th. The dorsal rims get broader by vaulting and descend in a lateral curve. The spinodiapophyseal laminae are weakly developed and thin on the 1st, 2nd, 3rd, and 5th sacral vertebrae; they can be traced dorsally on the 2nd and 3rd for over half the height of the neurapophysis, but are fused with the

spinopostzygapophyseal lamina in their dorsal part. Whereas the spinodiapophyseal lamina is positioned anterior to the lateral spinal lamina in the anterior sacral vertebrae, in the 5th vertebra it is positioned posterior to this lamina, obviously because of the obliquely posteriorly inclined position of the diapophysis.

Lateral processes.

The lateral processes, a term I use in the sense of VON WIEDERSHEIM for the processes inserting on the lateral ilium, are very differently shaped in the individual vertebrae. Two sections are easily distinguished: a dorsal one that represents the diapophysis, and a ventral one that corresponds to the rib and therefore forms the actual sacral rib. The diapophyseal section of the lateral processes of the 2nd and 3rd vertebrae—the one from the 1st is missing, as already mentioned —still shows the bauplan of the diapophyses of the posterior dorsal vertebrae, whereas the diapophyseal sections of the 4th and 5th vertebrae are already modeled according to the type of the caudal vertebrae. However, the actual sacral vertebrae are ventrally fused with each other. In the three middle vertebrae these ventral parts are represented by massive processes, which extend dorsolaterally from the centra. At first they become thinner, but then thicken again so that they abut each other along rather extensive sutural surfaces. Their lateral ends form a uniform, bumpily sculptured attachment area for the ilium, which is ca. 13 cm wide and 41 cm long, and which extends in a weak curve at an inclination of $40^{\circ}-50^{\circ}$ to the frontal plane. The diapophysis is not preserved on the 1st lateral process, but it could have been only a relatively weak process because the broken surface at the insertion point of the process, immediately behind the prezygapophysis, measures only 5 cm in length. Only the lateral section of the sacral rib is preserved. It is represented by a strongly anterodorsally projecting, chevron-like, folded open, thin bar, 34 cm long but obviously slightly shortened by compression, which gets thicker ventrally where it abuts the ventrally thickened part of the 2nd sacral rib along a suture; here it bears the ca. 4 cm broad, dorsally pointed, ca. 10 cm long attachment area for the ilium, which runs dorsally perpendicular to the attachment area for the central vertebrae. The missing parts, which connect the sacral ribs with the vertebra, were restored ventrally as a thick rod, which bears a thin transverse wall dorsally. The diapophysis, on the other hand, was not restored. The diapophysis of the 2nd lateral process is a process with a T-shaped, anterolaterally positioned cross-section that extends ventrally ca. 60° against the body axis. Here the thin, vertical ventral wall shifts anteriorly along the diapophysis, so that the cross-section forms a right angle close to the end. The free end is thickened and shows a triangular contour. The minimum width of the process, ca. 5.5 cm, is in the middle and increases to 7.5 cm at the end; its free length is 21 cm, but has probably been shortened by compression by a few centimeters. A thinly walled, slightly curved bar with a low. Tshaped cross-section with expanded ends can be identified with certainty as the ascending lateral process of the parapophyseal section of the 2nd presacral rib, and was mounted as such even though it did not fit onto the broken surface of the 2nd presacral rib. The diapophysis and sacral rib are medially fused into a 43 cm high bony wall, which shows a rising, vaulted, elevated suture that occurs dorsally slightly above mid-height. The completely preserved 3rd lateral process has, like the 2nd, a diapophysis with a Tshaped cross-section; the strong transverse beam reaches a width of 11 cm laterally, is positioned exactly transversely, and extends 27 cm laterally as measured from the middle of the corresponding neurapophysis, but here also shortening has taken place due to compression. The vertical wall is positioned relatively exactly parallel to the midline ventral to the cross-beam, extends for only ca. 7 cm beyond the anterior end of the latter, and is very thin dorsally but gets stronger toward the slightly laterally rising suture alongside the much more substantial wall of the sacral rib. From the wall of the sacral rib. there extends laterally а

flat, 8.5 cm broad ventrally, dorsally strongly reduced process, which ascends vertically and lies with its dorsal end close to the end of the diapophysis, but is not fused with the latter. At its lateral rim lies a very pronounced incision dorsal to the lower part, which supports the ilium. The rising tubercular process lies with its upper half close to the ilium. Between this rising process, the horizontal beam of the diapophysis, and the vertical-medial wall formed by both structures, lies a 13 cm long, about ca 6 cm wide dorsally, ventrally narrowing opening. In contrast to the preceding one, the 4th lateral process is formed from the diapophysis and the sacral rib as a uniform, slightly posteriorly inclined wall. On the lateral rim, at about the mid-height of the process, lies a very significant thickening that bears a 10 cm high, 7.5 cm wide upper attachment area for the ilium; the lateral rim retreats slightly from here, has a thickness of only about 2 to 3.5 cm, and shows a bumpy dorsal surface; the wall is thin and sharply edged ventral to this thickening. The dorsal horizontal rim of the wall is smoothly rounded and increases its outward thickness from 2.5 to 3.5 cm. The suture between both elements rises laterally and emerges 7 cm on the outer rim below the dorsal rim. An opening is not present. In the incompletely preserved left 4th lateral process, a separation has even taken place along this suture. Like the 4th lateral process, the 5th is developed as a uniform wall. A medial section is missing over the entire height of the vertebra and was restored. The diapophyseal section has a very thin wall, and its dorsal rim is also much thinner than on the 4th lateral process. The connection with the ventral part, representing the sacral rib, is not preserved but was restored. The latter is developed as a plate, strongly concave toward the front and thickened ventrally, the anterior end of which lies close to the lower process of the 4th vertebra, supporting the ilium. Ventrolaterally it bears an obliquely posterodorsally rising, ca. 20 cm long and 8 cm wide, centrally constricted, ca. 5 cm wide attachment area for the ilium, which considerably elongates the ventrally connected attachment area of the anterior sacral vertebrae.

Zygapophyses.

The prezygapophyses of the 2nd sacral vertebra extend about 20 cm above the base of the neural canal. The walls carrying the neural canal are relatively strong, 2 cm thick dorsally and sharp-edged anteriorly, rounded on the outside, medially flat and slightly depressed in places; their inner distance is ca. 5.5 cm. The facets, with imperfectly preserved outlines, droop slightly laterally, and they are longer than in the preceding vertebrae, ca. 8 cm long and 6 cm wide; their medial rims approach each other to a distance of 2 cm. The mediovertical part of the facet is medially protruding, as is clearly visible on the right side; it is ca. 4.5 cm high.

As in the preceding dorsal vertebrae, a bony wall descends between the walls bearing the prezygapophyses, and the anterior surface is concave and positioned 8–9 cm from the anterior rims of the prezygapophyseal walls; its ventral rim, which is not completely preserved, leaves an opening for the spinal cord about 8 cm high.

The postzygapophyses of the 5th sacral vertebra are represented by two weak, posteriorly inclined, laterally protruding projections that are separated by a depression. They bear slightly vaulted facets extending obliquely anterodorsally, the inner rims of which merge dorsally into the spinopostzygapophyseal laminae.

Neural canal.

Concerning the shape of the neural canals of the sacral vertebrae, the question arises as to how far the canals differ from those in the following free dorsal and caudal vertebrae. In the 1st

sacral vertebra (dorsosacral vertebra), the neural canal and its surroundings present in general the same picture as the preceding last dorsal vertebra. The opening for the spinal cord in the descending transverse wall is not higher than in the latter. Also, regarding the shape of the neural canal, the 5th sacral vertebra (caudosacral vertebra) shows absolutely the same picture as the 1st free caudal vertebra; the neural canal also has about the same height of 5 cm as in the first free caudal vertebra. An assessment of the neural canal in the three middle vertebrae, i.e. in the actual sacral vertebrae, is made difficult by the fact that their centra have been dislocated, and on their dorsal sides the basal surfaces of the neural canal are not preserved. The original base of the canal naturally could not be reconstructed with certainty while reassembling the sacral vertebrae. The lateral walls of the neural arches, extending from the centra to the zygapophyses and to the bases of the diapophyses in the anterior four sacral vertebrae, are fused dorsally over a length of 10 cm; there remain small openings ventrally which served as exits for the nerve branches of the sacral plexus. The corresponding opening between the both posteriormost sacral vertebrae was obviously considerably shorter than the one between the two preceding vertebrae; but this is not clearly visible. The hollow space that lies between the lateral walls of the neural arch in the 1st sacral vertebra has almost the same shape as in the last dorsal vertebrae, i.e. the neural canal is bordered dorsally by the ventral surface of the thick descending bone wall only in the posterior section, whereas the anterior part is not closed dorsally but merges with the hollow space enclosed by the laterally rising walls of the neural arch carrying the prezygapophyses. In the three middle sacral vertebrae, the parts corresponding to the lateral walls are laterally strongly and roundly inflated, and thus form bulbous, widely extended caverns, while each of these vertebra is closed posteriorly by the deeply lowered bone wall. Aside from the lateral expansion of the caverns, there is apparently no vertical expansion present to any mentionable degree.

Caudal vertebrae.

Skeleton m.

Pl. IV.

Preservation.

The caudal vertebra did not suffer much deformation. The neurapophysis is completely missing in the 19th vertebra. In the first two caudal vertebrae the left spinodiapophyseal lamina is for the most part not preserved. The missing parts of the prezygapophyses in several vertebra and the suprapostzygapophyseal laminae in the most anterior vertebrae had to be restored. The lateral process of the 1st vertebra was lost on both sides, the right one in the 2nd and 4th vertebrae.

Centrum.

The thick, disc-shaped centra in the first caudal vertebrae become slowly more elongated, so that in the 13th vertebra their length equals their height. The anterior caudal vertebrae are concavo-convex. The convexity of the posterior end surface is most pronounced in the 2nd caudal vertebra and decreases from this vertebra much faster than the concavity of the anterior end surfaces. The anterior end surface in the 7th vertebra is still strongly concave, but the posterior one is almost flat but slightly irregularly developed, inasmuch as the upper half bulges slightly anteriorly and the lower half is slightly depressed. In the following vertebrae a posterior concavity slowly develops and is clearly marked in the 15th vertebra. The anterior concavity has actually disappeared in the same vertebra, but reappears again to a very small degree in the following vertebra. In the isolated caudal vertebrae (m94–m96), which probably belong to the same animal and may be regarded as the 22nd, 23rd, and 25th caudal vertebrae, both end surfaces are moderately concave, the posterior one slightly more.

The lateral surfaces of the caudal vertebrae are strongly constricted. A median area, which is separated by rounded edges, shallowly concave, and depressed transversely and longitudinally, appears ventrally and is increasingly better developed from the 6th vertebra onward. In the same vertebra a lateral, ventrally pointing keel emerges more clearly, which is more pronounced from the 9th vertebra onward because a horizontally positioned rounded ridge appears on the flanks at mid-height, paralleling the neural canal. In the latter vertebra, the ridge is only developed on the posterior half; in the following vertebra it runs along the entire flank, but is positioned slightly more deeply. It descends more and more in the following vertebrae, so that it lies only slightly above the ventral surface in the 15th vertebra, and grades into the rounded edges that connect the chevron attachment facets of one side with the other. The cross-section of the vertebrae with deeply positioned edges results in a rather square shape. From the 15th vertebra onward, a second, more highly positioned edge appears, which lies first slightly above, but from the 18th vertebra onward lies exactly at the mid-height of the centrum. From the 17th vertebra onward this edge is again strongly developed, and especially characterizes these caudal vertebrae.

	No. in	Dorsal	Ventral	Height of	Height of	Width of	Width of	Complete
Catalog	vertebral	length of	length of	anterior	posterior	anterior	posterior	height of
no.	column	centrum	centrum	end of	end of	end of	end of	vertebra
				centrum	centrum	centrum	centrum	
m 24	1	13.4 cm	13.0 cm	20.1 cm	20.8 cm	20.0 cm	19.0 cm	81.0 cm
m 23	2	11.5	10.2	20.1	18.8	20.6	18.6 (+)	73.6
m 22	3	13.3	11.7	19.3	17.9	20.2	18.2	66.8
m 21	4	12.6	11.6	18.1	17.0	18.8	17.8	62.0
m 20	5	12.4	12.5	17.4	16.2	18.2	17.1	?
m 19	6	13.1	11.3	16.4	15.5	17.4	16.7	51.3
m 18	7	12.3	12.1	15.4	15.3	17.1	16.4	47.5
m 17	8	12.4	11.6	14.8	15.0	16.3	16.1	42.9
m 16	9	12.4	11.7	14.2	14.1	15.8	15.5	39.5
m 15	10	11.7	11.8	13.6	13.9	15.9	15.5	37.7
m 14	11	11.9	12.2	13.3	13.6	14.6	14.1	34.9
m 13	12	11.9	12.2	13.2	13.6	14.3	13.1	34.2
m 12	13	12.5	12.9	13.0	13.6	13.8	13.2	33.0
m 11	14	13.0	13.2	12.8	13.4	13.6	13.1	31.2
m 10	15	12.9	13.3	12.3	12.3	13.6	12.4	29.2
m 9	16	13.3	13.4	11.9	12.6	12.7	12.7	28.2
m 8	17	14.0	13.9	12.0	12.7	13.0	12.9	26.5
m 7	18	14.7	14.8	12.1	12.3	13.2	13.0	27.7
m 6	19	15.2	15.1	12.4	12.2 (+)	13.1	12.5 (+)	?
m 95	22 (?)	16.7	16.4	10.1 (+)	9.8 (+)	12.1	?	?
m 94	23 (?)	?	15.4	?	9.5 (+)	12.0 (+)	10.5 (+)	?
m 96	25 (?)	?	15.5	9.0 (+)	?	?	?	?

Measurements of the caudal vertebrae of Dicraeosaurus hansemanni, skeleton m.

The terminal surfaces of the centra are positioned perpendicular to the axis of the neural canal only in the 17th and 18 vertebrae, whereas in the preceding vertebrae the anterior end surface encloses an acute angle with the axis. A rod was inserted through the neural cord, resting

on the rims of the end surfaces, and the angle enclosed by the rod and the anterior surfaces in lateral view was measured. The results are the following:

1st vertebra	79°	10th vertebra	85°
3rd "	77°	13th "	86°
6th "	77°	16th "	86°
8th "	81°	17th–19th "	90°

The pleurocentral grooves are completely missing on all caudal vertebrae. The chevron attachment facets are already developed ventrally toward the posterior end surface of the centrum from the 1st vertebra onward. They are triangular in shape and set onto the posterior surface of the ventral edges. They are from the 4th onward they are slightly depressed and consistently connected by a rugose lamina, less clearly so in the first three vertebrae. The transverse distance between the facets is in accordance with the not very large ventral keel on the centra, and their centra are separated from one another for ca. 7 cm on the 4th vertebra, and for ca. 5.5 cm from the 7th onward to the 19th. Below the anterior end surface of the centrum the chevron attachment facets appear as beveled surfaces of the rounded ventral edges on the 3rd vertebra. They become more distinct posteriorly and are connected by rugose bumpy projection from the 13th vertebra onwards.

Neural arch.

The neural arch forms a very strong lateral wall for the neural canal. It shows a transverse plane on the posterior surface of the anterior vertebrae, which grades into the transverse processes. This transverse plane disappears gradually with the decrease in size of the transverse processes from almost the 9th caudal vertebra onward, so that simple, transversely positioned walls are developed, which get increasingly thinner.

Neural canal.

Regarding the shape of the neural canal, it is evident that a median depression was present in the center of the basal surface in almost all vertebrae, and furthermore that projections, shaped as short, low ridges and only slightly above mid-height on both sides emerge out of the lateral walls in about the middle between both ends of the canal. The lumen of the neural canal, which expands toward both ends, does not change with respect to its minimum width in the preserved row of vertebrae, being 2.8–2.9 cm. In the first two vertebrae the measurements are a few millimeters less, but this could be due to deformation. In contrast, the height of the neural canal differs consistently. In the first vertebra, the anterior and posterior heights measure almost 5 cm—a figure that might be slightly influenced by pressure—3.8 cm anteriorly and 3.2 cm posteriorly in the third vertebra, and 2.6 cm and 2.6 cm in the 17th. Thus, there is the usual noticeable decrease in height of the neural canal, but a small increase occurs again in the posterior vertebrae.

Neurapophysis.

In the anterior caudal vertebrae the neurapophyses show on the whole still the same character as in the posterior dorsal vertebrae. They are still high and possess strongly projecting post-, pre-, and spinodiapophyseal laminae. At first the height decreases quickly along the vertebral series, then more slowly; in the 1st caudal vertebra it rises 59 cm above the base of the posterior exit of the neural canal, 46 cm in the 4th, 29 cm in the 8th, 19 cm in the 12th, and 14.5 cm in the 18th. The neurapophyses show remarkable differences regarding their position and curvature. In the 1st vertebra the neurapophysis is anteriorly inclined in its ventral third with respect to the axis of the neural canal. It is curved posteriorly dorsal to this inclination, but again shows some indication of an anterior inclination in the dorsalmost part. The point at which the neurapophysis curves posteriorly shifts ventrally in the following vertebrae. The curvature gets weaker from the 3rd vertebra onward and is hardly visible in the 5th vertebra; thus the neurapophysis rises straight posterodorsally. On the other hand, the anterior curvature of the dorsalmost section of the neurapophysis becomes more and more pronounced. It is most prominently developed from the 7th to 10th vertebrae, but then gets weaker again to the 14th vertebra. In the two following vertebrae an anterior curvature appears again that results in a slightly concave anterior rim of the entire neurapophysis, but the curvature is insignificant again in the 17th vertebra.

The prespinal lamina strongly exceeds the postspinal lamina in extent in the first anterior vertebrae, being about twice as wide in the 1st vertebra; this dominance is reduced toward the 6th vertebra, in which the prespinal and the postspinal laminae show equal dimensions. The rim of the prespinal lamina on the 1st vertebra is more then 0.5 cm thick in its middle section, but gets thinner ventrally and dorsally. This ventrally directed decrease in thickness continues along the column, but the dorsal decrease is not present from the 3rd vertebra onward. The postspinal lamina shows almost the same thickness as the prespinal lamina in the anterior vertebrae. There is no decrease in thickness at all in the dorsal direction, but very much so ventrally in the anterior caudal vertebrae. Here the lamina disappears dorsal to the postzygapophyses, between the projections of the spinodiapophyseal laminae that enclose the postzygapophyses. With the reduction of the spinodiapophyseal laminae anterior to the 6th vertebra, the pre- and postspinal laminae alone basically form the uniform, flat spine of the neurapophysis, effectively losing their character as independent laminae completely. The width of the neurapophysis in the median plane, measured perpendicular to its longitudinal axis, is on average ca. 9 cm in the 1st vertebra, 8–8.5 cm in the following vertebrae, ca. 7.5 cm in the 5th, ca. 7 cm in the 8th, and about 6 cm from the 10th onward. The spinodiapophyseal lamina projects far laterally in the anterior caudal vertebrae, and gets lower and thickly rounded ventrally and turns over at its ventralmost point from a laterally pointing position to an anteriorly pointing position by merging with the prezygapophyses, thereby from this point taking on the character of the supraprezygapophyseal lamina. The extent of the spinodiapophyseal lamina decreases quickly from the 2nd vertebra onward. So the width of the neurapophysis in the lateral direction decreases from 19 cm in the 1st vertebra, to 14 cm in the 2nd, to 12.5 cm in the 4th, and to ca. 8 cm in the 6th; moreover the lamina becomes more and more indistinct ventrally by getting shallower. Its ventral part cannot be recognized at all, or if so then only as a flat swelling, from the 8th vertebra onward. The dorsal part of the lamina persists as a rough, elevated, ventrally blurred zone alongside the middle of the lateral surfaces of the neurapophyses, which consistently decrease in length. However, it is still visible as an insignificant rugosity below the dorsal rim of the neurapophysis on the 17th vertebra.

The anterior and posterior rims of the neurapophysis, that is the pre- and postspinal laminae, are always rough and longitudinally fluted. These rugose zones widen dorsally from the 7th vertebra onward. The anterior rugose zone is enclosed laterally by thin, rounded, smooth, small laminae that end somewhat below the upper rim from the 7th vertebra onward. The rugose zones indicate a strong ligamentous connection (interspinous ligament) between the neurapophyses of neighboring vertebrae; it must have been particularly strong toward the top of the neurapophysis. A part of the ligament is preserved as an irregular ossification on the 8th vertebra.

In dorsal view the distal end surfaces of the neurapophysis describe an anteriorly convex curve in the first caudal vertebra, descending laterally along a curved course, and also shows a rounded profile transverse to the lateral curvature. Their curved course becomes flatter with the decreasing width of the end surfaces in succeeding vertebrae; the end surface is only as wide as long in the 8th vertebra, it is longer than wide from the 11th vertebra onward, and the end surface has a width of only 3.5 cm and a length of 17.5 cm in the 17th vertebra. The end surfaces show a very irregular surface from about the 7th vertebra onward. The anterior and posterior rims of the end surfaces are elevated: two prongs on the anterior rim protrude only on a few middle and posterior vertebrae in this series, the posterior rim, however, protrudes in all vertebrae with the exception of the first and last. The dorsal rims of the right and left spinodiapophyseal laminae are connected by a rounded transverse ridge. This ridge is median to a more or less saddle-like depression; a mostly well-marked depression lies anterior and posterior to this transverse ridge on the median line. The dorsal end of the neurapophysis shows a highly characteristic profile in lateral view: anteriorly and posteriorly rising projections are separated from a central convexity by depressions. The development of the end surfaces of the neurapophyses allows concluding that a thick layer of nonfossilized tissue, a ligament (supraspinous ligament) or ligament and cartilage, respectively, were present.

Prezygapophyses.

In the 1st caudal vertebra the prezygapophyses are hook-shaped, slightly anteriorly rising processes, which are very slightly vaulted on their lateral surface. The facets are very peculiar in shape as they consist of two areas, a dorsal one that inclines steeply medially, and another, separated from the first by an edge, that inclines steeply laterally and at the same time is slightly longitudinally concave. A prezygodiapophyseal lamina, which extends from the transverse process, is so short that it hardly reaches the prezygapophysis. The prezygapophyses of the 2nd vertebra are, as far as they are preserved, of the same type. The lateral surfaces of the prezygapophyses in the succeeding vertebrae show strong longitudinal vaulting, which continues to said lamina; but the vault is already indistinct in the 5th vertebra and disappears completely from here on. The prezygapophyses of the following vertebrae are processes with a strongly vaulted outer surface. They decrease in length slightly but remain essentially similar. The rounded, in some places rough, edge changes somewhat ventrolaterally on the 15th and successive vertebrae. The facets on the 3rd vertebra are not distinctly preserved. The following vertebrae no longer show the division into two areas as on the 1st vertebra, but form simple, steep, medially inclined surfaces. The medial inclination is 70° up to the 6th vertebra, decreases to 50° , but increases again in the last vertebra. As far as can be determined, the contours of the facets are more or less regular ellipses. The long axis of the facets is steep and obliquely anteroventrally directed from the 4th vertebra onward, but is less inclined and more anteroventrally directed in the posterior vertebrae in combination with the narrow The planes of the facets are mostly relatively level; but there are also contour of the facets. prezygapophyses with slightly concave facets and occasionally some with convex facets. It is very likely that some parts of the non-level facets become concave and convex by deformation; how much this might be the case for all of them escapes our judgment.

Postzygapophyses.

The postzygapophyses of the anterior caudal vertebrae are shaped thusly: the facets are cut into the lateral surface of the extensive spinopostzygapophyseal laminae, which extend ventrally immediately next to both sides of the postspinal laminae. Along their course, the laminae become stronger and eventually merge with each other above the neural canal. The facets are steeply positioned and curved inward in a way that makes them almost look like cross-sections of horizontally positioned cylinders. The contour of the facets is not clearly recognizable in the anterior caudal vertebrae, seeming to be more or less high elliptical to high oval. The postzygapophyses of the 1st caudal vertebra are rather peculiarly shaped, as these facets, as well as those of the prezygapophyses of the 2nd caudal vertebra, show an additional ventral ventrolaterally inclining area, supported laterally by ventrally diverging processes. Between the strongly projecting spinopostzygapophyseal laminae of the anterior caudal vertebrae lies a deeply incised narrow cavity, which is created by the retreat of the rugose rim of the postspinal lamina. The spinopostzygapophyseal laminae decrease in length posteriorly along the vertebral series. They eventually lose the character of laminae and take on the shape of strong, laterally projecting structures which bear facets with slightly protruding rims. The steep inclination of the facets decreases in the anterior vertebrae; it is ca. 45° - 50° from the 7th vertebra onward, but increases again slightly in the posterior vertebrae. The slit-like depression on the posterior surface of the neurapophysis decreases in length along the vertebral series and is eventually limited to the area between the facets.

Lateral processes.

The lateral processes of the anterior caudal vertebrae are far upward reaching, transversely positioned bony walls. It has to be assumed, by analogy with the caudosacral vertebrae, that they consist not only of a part that is homologous to a rib, but additionally include a part that corresponds to a diapophysis. In particular, in the 3rd caudal vertebra traces of a suture between rib and diapophysis still appear to be recognizable, as shown in more detail below. I will use the neutral term "lateral process" for the entire structure. The preserved remains of the left lateral process of the 1st caudal vertebra allow recognizing only that a very thin bony wall rises dorsally to the proximal part of a strong, ventral, weakly laterally ascending rim. The lateral process of the 2nd vertebra forms an extension, an almost exactly transversely positioned wall. The very thick, longer ventral rim and the much thinner dorsal rim of this wall run almost parallel to one another and rise laterally at an angle of ca. 20°. The lateral rim runs vertically in its dorsal part, and ventrally it juts far laterally. The lateral rim of the lateral process is ca. 21 cm high, and the distance between its ventral end and the lateral rim of the anterior end surface of the centrum is ca. 14 cm. The posterior rim of the lateral process is rather flat, very slightly convex, and weakly corrugated in such a way that its mediolateral part is slightly depressed. A large depression is located on the anterior surface, resulting in a thinning of the wall, which in turn causes the partial loss of bony material. The lateral surface of the rim of the lateral process is dorsally narrow, up to 5 cm wide ventrally, and directed posterolaterally. The lateral processes of the two successive caudal vertebrae change insofar as the extent of their surface and the depression in the anterior surface, and therefore the thinning of the lateral process, decrease considerably. This is not at all the case in the 5th vertebra, in which the lateral process is particularly plump with an ca. 11.5 cm high lateral rim. The distance between the ventral and anterior rims of the centrum is ca. 7 cm, and its distal thickness measures ca. 5 cm. The transverse extent of the surface decreases rapidly further on, the thickness of the process in the 6th vertebra rising to a preliminary 7 cm, but then decreasing strongly in the following

vertebrae. The ventral part of the lateral process of the 9th vertebra forms a low vault, the main direction of which is posteroventral, as it is in the two succeeding vertebrae. The dorsal part of the lateral process has become very flat. Its dorsal end is still recognizable by a rugosity that can be traced over some additional vertebrae. A ca. 5 cm long and ca. 3 cm wide rugose protuberance is all that remains of main part of the lateral process in the 12th vertebra. This protuberance narrows in the posterior vertebrae to a rough edge that runs along a flat, dorsally concave curve.

Caudal vertebrae from locality dd.

Among the caudal vertebrae of the two specimens of *Dicraeosaurus hansemanni* from excavation site dd, the anterior caudals of each individual are easily distinguished by the different shapes of their neurapophyses. The neurapophyses of the caudal vertebrae of one specimen, dd A, are similar to those found on skeleton m. These neurapophyses—at least those in the tail section behind the very high, anteriormost vertebrae-have a moderately rising anterior rim. The anterior rims of the neurapophyses rise much more steeply in the other animal, dd B (Fig. 8). The anterior contour of the neurapophyses shows the same steep slope in those caudal vertebrae in which the centra are elongated and the neurapophyses lower. The caudal vertebral series of dd B end with a vertebra that might be identified as the 20th caudal by comparison with the caudal vertebral column of skeleton m. The vertebrae of the succeeding section all belong to dd A according to the similar shape of their neurapophyses. It is therefore more likely that the vertebrae at hand from the most posterior tail section, in which the continuously decreasing neural arches are not, or are incompletely, preserved, belong to dd A rather than to dd B. The 64 prepared caudal vertebrae from dd were found isolated, and when reassembled resulted in incomplete vertebral series separated by a number of gaps. It is therefore enough that these vertebrae are described inasmuch as they complement the caudal vertebral column of skeleton m. The individual vertebrae will be referred to by the position they occupy in the restored and mounted tail of skeleton m.

Fig. 8. Anterior caudal vertebra of *Dicraeosaurus hansemanni*, dd 11. 1/8 natural size

The posteriormost and only incompletely preserved vertebrae of skeleton m, which were inserted into the tail of skeleton m as the 22nd, 23rd, and 25th caudal vertebrae, show in contrast to the last one, number 19 in the m series, a decrease in centrum diameter combined with an initial slight increase in length; the neurapophyses are not present in these vertebrae. Two vertebrae from dd A, dd 80, and dd 114, which might belong in the section between the 22nd and 25th vertebrae, show an increasingly reduced height of the neurapophysis. The neurapophyses in these vertebrae get slimmer, and the anterior and posterior contours become less inclined.

In the following vertebrae a slow but permanent decrease in the absolute length of the centrum occurs, along with a relatively stronger decrease in centrum diameter, and a neurapophysis that gets continuously slimmer. The completely preserved vertebra dd 111, the 27th in the skeleton (Fig. 9a, b), has a dorsal length of 15.1 cm along the centrum, and the anterior end surface is 9.1 cm high and 9.4 cm wide. The neurapophysis, which might be slightly compressed, forms a low,

longitudinally stretched plate. This plate has a long, dorsally longitudinally depressed end surface that forms a low curve, as well as a pointed posterior end. Compared with those of the previous vertebrae, the prezygapophyses have a more wand-like shape.

Vertebra dd 79, the 30th in the skeleton, measures 13.7 cm in dorsal length, 7.3 (+) cm in anterior height, and 7.6 (+) cm in anterior width. It therefore has a slimmer overall shape, and

Middle caudal vertebra (dd 111) of *Dicraeosaurus hansemanni*. Fig. 9a lateral view Fig. 9b posterior view. 1/4 natural size.

moreover the neurapophysis is not plate-like but more rod-like, showing a mostly rounded, triangular cross-section, obviously slightly compressed by pressure.

Five smaller vertebrae, which could well form a continuous series and thus were mounted in skeleton m as the 33rd to 37th vertebrae, are very much of the same type. The third (dd 97) of

Middle caudal vertebrae of Dicraeosaurus hansemanni

Fig. 10 a. dd 97 in lateral view.	Fig. 11 a. dd 133 in la
Fig. 10 b. The same, anterior view.	Fig. 11 b. The same, a
Fig. 10 c. The same, posterior view	1/4 natural

1 a. dd 133 in lateral view 1 b. The same, anterior view 1/4 natural size Fig. 12 a. dd 14 in lateral view. Fig. 12 b. The same, anterior view.

Fig. 12 c. The same, posterior view.

these vertebrae is depicted in Fig. 10a, b. The fifth, which is very similar to the previous one (dd 133), is depicted in Fig. 11a, b. The measurements of the two vertebrae shown above are: dorsal length of the centra 13.0 cm and 12.1 cm, height of the anterior ends 6.4 cm and 5.6 (+) cm, and widths of the anterior ends 6.5 cm and 5.6 (+) cm. All these caudal vertebrae still show a rounded

longitudinal edge at the mid-height of the centrum. The end surfaces are almost circular and strongly biconcave. Short edges emerge from the anterior surface at the base of the chevrons. The neurapophyses show a low, triangular cross-section in their proximal part, the only part that is preserved. The postzygapophyseal facets are not clearly delineated, but might have become blurred by the mode of preservation.

The next smaller vertebra, dd 14 (Fig. 12a–c), is separated from the previous one by four restored vertebrae in the skeleton. It differs from the previous vertebra by its centrum being more strongly constricted in the middle and by the fact that the longitudinal edge is no longer recognizable. Furthermore, the base length of the almost entirely missing neural arch is shortened to ca. 4.3 cm, more strongly so posteriorly than anteriorly. The measurements of the vertebra are: dorsal centrum length 10.6 cm, height and width of the obviously somewhat inflated anterior rim 5.0 (+?) cm each, and height and width of the obviously somewhat inflated anterior rim 5.0 (+?) cm each, and height and width of the weaker posterior rim 4.3 cm and 4.0 (+) cm. A 9.5 cm long vertebra, dd 77, follows in size but it is so distorted that it is suitable neither for description nor reconstruction of the tail of the skeleton. The following vertebra, dd 83 (Fig. 13a–c), shows a more strongly constricted centrum compared to dd 14, and therefore a more highly arched ventral profile. It shows a similar inflection of the anterior rim as well as a further decrease in the basal length of the anterior end to 3.8 cm and 4.1 (\pm) cm, and the height and width of the posterior end to 3.2 cm and 3.6 cm. Three restored vertebrae were inserted in the skeleton between dd 14 and dd 83, so that the previous vertebra is assigned to position 46.

Posterior caudal vertebrae of Dicraeosaurus

hansemanni. Fig. 13 a. dd 83 lateral view. Fig. 13 b. The same, anterior view. Fig. 13 c. The same, posterior view. Fig. 14 a. dd 88, lateral view. Fig. 14 b. The same, anterior view. Fig. 14 b. The same, anterior view. Fig. 15 a. dd 120, lateral view. Fig. 15 b. The same, anterior view. Fig. 15 c. The same, posterior view. Fig. 16 a. dd 398, lateral view. Fig. 16 b. The same, anterior view. Fig. 16 c. The same, posterior view. Fig. 16 c. The same, posterior view. 1/4 natural size

An assembled line of six vertebrae (dd 88, 492, 120, 114, 84, 398) that is separated from the previous vertebrae by two restored ones, shows, apart from the one that has been inserted as the 2nd and is very distorted, no decrease in length, only a decrease in thickness. The centra take on the shape of straight, rounded sticks with inflated ends. The concavity of the rather irregularly shaped end surfaces of these vertebral centra is strongly diminished or too obscure, especially in the last vertebrae. Vertebra dd 88 has a posteriorly rising neural arch of 2.5 cm basal length. At the end fracture that lies ca. 1 cm in front of the posterior end of the centrum, its incompletely preserved neurapophysis has a low and ventrally concave cross-section 1.7 cm wide and 0.8 cm high. The roof of the neural canal is deeply incised in the median plane posteriorly from the prezygapophysis. The neural canal is thus opened dorsally almost to the posterior end of the base. The basal length of the neural arch measures ca. 2.2 cm in vertebra dd 120 (Fig. 15a-c). The median incision in the roof of the neural canal reaches even beyond the posterior end of the base of the neural arch. The lengths of the centra of vertebrae dd 88, 120, 114, and 84 are 7.7 7.7 7.7 and 7.3 cm. cm. cm. cm.

The width and height of the anterior ends of the centra measure 3.6 cm and 3.2 cm; 3.0 cm and 3.3 cm; 3.0 cm and 2.8 cm; 2.6 cm and 2.5 cm. The incompletely preserved and presumably somewhat shortened vertebra dd 398 (Fig. 16a–c) shows an incompletely preserved neural arch with a basal length of 1.7 cm and a preserved length 6.8 cm. The preserved proximal part of the neurapophysis roofs the neural canal with an acutely angled transverse profile which is high elliptical in cross-section. However, the roof of the neural canal is not incised medially as in dd 88 and dd 120. Like the 54th vertebra, dd 398 is separated from the next preserved one by four intervening vertebrae in the skeleton.

Posteriormost caudal vertebrae of							
Dicraeosaurus hansemanni.							
Fig. 17. dd 86	Fig. 19. dd 85						
Fig. 18. dd 118	Fig. 20. dd 90						
1/4 natural size							

All the other preserved vertebrae are decidedly stick-like. A narrow, short break surface shows the position of the lost, but surely only insignificantly developed neural arches in the two largest stick-like vertebrae, dd 74 and dd 86 (Fig. 17). They measure only 7.2 cm and 7.3 cm in length; the slightly irregularly circular to short transversely elliptical end surfaces are 2.4–2.6 cm wide and 2.3–2.4 cm high. The anterior end surfaces are slightly convex with a shallow central depression, and the posterior ones are strongly convex. The thickness of the central cylindrical part of the centra, which show a flattened ventral surface enclosed between two edges, is 1.1-1.2 cm. Two other weaker stick-like vertebrae, dd 118 (Fig. 18) and dd 87, still measure 6.6-6.8 cm in length, but the diameters of their end surfaces measure only 1.5-2.0 cm, and those of their middle sections 0.8-1.0 cm. The position of the neural arch is indicated only by a weak protuberance. These two stick-like vertebrae occupy positions 64 and 65 in the skeleton, separated from the previous ones by three intervening vertebrae. Posteriorly they are separated from vertebra dd 85 (Fig. 19) by two intervening vertebrae. Vertebra dd 85 measures 6.0 cm; the diameters of its end surfaces are 1.6–1.7 cm, and those of its middle section are 0.8–0.9 cm strong. It is followed, again separated by three intervening vertebrae, by two vertebrae, dd 93 and 90 (Fig. 20), which are 5.0 cm and 4.6 cm long. The diameters of their end surfaces are 1.2-1.4 cm, but combine with undiminished thickness of the center. Eventually, after two more intervening vertebrae, a thin vertebra (dd 95) follows that is 4.9 cm long. It concludes as the 76th vertebra the tail of the skeleton.

Ribs.

Ribs of the presacral vertebrae.

For the description of the presacral vertebrae, it seems practical to describe the short ribs of the 2nd to 11th cervical vertebrae, and the long ribs of the 12th cervical and the dorsal vertebrae, which are similar in type as a unit, in two separate sections.

Short ribs of the 2nd to 11th cervical vertebrae.

Skeleton m.

Preservation: During excavation it was not possible to completely recover all the cervical ribs. A number of them are completely or almost completely missing. The thin ends are lost to a more or less great extent in all those present.

Description: Right and left proximal sections, which were found isolated, can only be interpreted as ribs of the second vertebra. The sections have two very thin, flat, longitudinally depressed laminae on the medial side. These laminae widen at the proximal end and carry the capitulum ventromedially in the shape of a flat-elliptical vaulted protuberance; the capitulum measures ca. 2.75 cm long and 1.75 cm wide on both ribs. The dorsal corner of the proximal end opposite the capitulum is only slightly thicker. The left rib is somewhat stronger than the right one, in particular the width of the proximal end is considerably larger, at 4.7 cm compared to 3.8 (\pm) in the right. The minimum width of the left rib, which is 10 cm long as preserved, measures 2.5 cm right behind in the middle of the fragment, and the width slightly increases distally. The width of the right rib, preserved for a length of 6.5 cm, measures 2.2 cm. Despite their different measurements these two sections must be parts of the opposing ribs from the 2nd vertebra, as can be shown by comparison with the corresponding ribs in *Brachiosaurus*. It is therefore incorrect to assign the smaller rib to the unpreserved atlas, because the atlas from site dd (see page 73) that is attributed to *Dicraeosaurus hansemanni* shows no indication of a parapophyseal facet, as is also the case in *Brachiosaurus*. By analogy with the eight following vertebrae, it must be assumed that the rib was pointed distally.

Ribs from the axis of *Dicraeosaurus* hansemanni. Skeleton m. Fig. a. Right rib, lateral view. Fig. b. The same, medial view. Fig. a. Left rib, lateral view. Fig. b. The same, medial view. 1/5 natural size.

The ribs of the 3 r d and 4 th vertebrae were, like those of the second, not fused with the vertebrae and were not excavated in articulation with them. Two ca. 5 cm long fragments, which show an irregular, acutely angled transverse profile at their thick end, obviously represent rib sections from one of these two vertebrae.

The ribs of the 5 th vertebra were fused to it. In the better preserved right rib, the suture between the capitulum and parapophysis has a length of ca. 4 cm and a considerable width of about 3 cm. The rising tuberculum is a thin bar narrowing down to 1.6 cm, which is fused with the diapophysis along a 2.3 cm long suture. It is reinforced by a well-developed medial lamina. The lateral extent of the costal head, despite having been reduced by pressure, was definitely relatively small. A very short prong juts anteriorly. The strangely acutely angled transverse profile between both costal heads flattens rapidly in the posterior direction. About 4.5 cm from the anterior rim of the tuberculum, the rib is already transformed into a simple rod that first narrows down to a width of ca. 1.8 cm, but widens again to 2.2 cm at the distal break. The plane of the rib shaft, which is first positioned sagittally, then turns its ventral surface rather strongly laterally.

In the 6th vertebra, only the end of the tuberculum of the left cervical rib is present, which is tightly fused to the vertebra along a 2.9 cm long and 1.7 cm wide suture. On the right side, the preserved half of the articular surface of the parapophysis lies free, and therefore the rib was not fused to the parapophysis.

The right capitulum in the 7th vertebra articulates with the parapophysis along a ca. 5 cm long and 3 cm wide suture; however, as there is a gaping cleft between them, they were at best incompletely fused. An isolated left capitulum most probably also derives from this vertebra.

The right rib of the 8 th vertebra (Fig. 21) is almost completely preserved, and the entire proximal part is hardly deformed. The flat capitulum, which is 5.8 cm along the suture, descends laterally to a moderate degree. A thick, rounded lamina leads from the thick left anterior end of the capitulum to the strongly developed, but incompletely preserved anterior tip. A second, similarly built lamina runs toward the rising capitulum, which presents a thin, flat, minimally 2.5 cm wide bar. The lateral extent of the rib is 4.6 cm, and the lateral height along the tuberculum is 6.7 cm. Posteriorly the rib quickly acquires the character of a thin, flat bar which narrows at first down to 2.8 cm and then widens continuously to 3.4 cm at 18 cm from the anterior end of the capitulum. Here there is a sudden narrowing to an awl-like end part, which is not completely present and measures only ca. 0.5 cm at the break. This narrowing occurs only in the dorsal section; the ventral rim continues undisturbed. Ventrolaterally, the free part of the rib turns caudally at the vertebra, but is it impossible to decide how much of this is caused by deformation. The entire preserved length of the rib is ca. 25 cm, and hardly more than a few centimeters should be missing.

Cervical ribs of Dicraeosaurus hansemanni. Skeleton m.

Fig. 21. Right rib of the 10th vertebra, lateral view.

Fig. 22 a. Left rib of the 10th vertebra.

Fig. 22 b. The same, anterior view.

Fig. 23. Right rib of the 11th cervical vertebra.

1/5 natural size.

The right rib of the 9th vertebra was obviously still partially fused with the vertebra, and the left one was found detached. Compared to the previous rib, the change in shape is that its lateral extent is slightly greater, the tubercular part slightly wider, and the distal part narrows earlier and less abruptly.

The ribs of the 10th vertebra, of which the right one is preserved only as a fragment and the left (Fig. 22a, b) lacks the tuberculum and the capitulum, still match the previous ones. However, they show a larger lateral extent of 7.5 cm measured from the capitular facet.

The character of the ribs changes completely with the ribs of the 11th vertebra, which are preserved from both sides. The distance between the ends of capitulum and tuberculum is larger, in accord with the shift of the diapophyseal facet to a more dorsolateral position. In anterior view, both appear hardly inclined toward each other any more. This shift causes the entire anterior part of the rib to achieve the character of a flat structure. Instead of the anteriorly jutting prong, there is now a crest with low, curved contour. A very delicate bony lamella stretches between the tuberculum and capitulum, which both terminate in rounded or slightly elliptical facets. Both facets are preserved on the left rib, the outer distance between both being 13.7 cm. Strikingly, there is a flat, lamella-like protuberance behind the tuberculum, which is thin in the right rib but more strongly developed in the left. This lamella gets lower and continues as a thin ridge on the distal part of the rib, of which only a short section is preserved. The distal part of the rib shows a more or less triangular cross-section, but its original length cannot be judged.

5th cervical rib from excavation site dd.

The left cervical rib dd 40 obviously corresponds almost perfectly to the right rib of the 5th cervical vertebra of skeleton m. The anterior tip is slightly more extended. The width of the nearly completely preserved tuberculum, as well as the incomplete free ends of the rib, is the same as in the right one. As this cervical rib is almost undeformed, in contrast to those of the skeleton, it was possible to determine the external angle between both rami; the angle measures almost exactly 90°.

Long ribs of the last cervical vertebra and the 12 dorsal vertebrae.

Skeleton m.

Material.

The 13 long ribs, which were found in situ on the right side of the 12th to the 24th presacral vertebrae, that is the last cervical and the 12 dorsal vertebrae, are completely preserved, apart from

Fig. 24. 12th cervical rib. Fig. 25–29. 1st–5th dorsal ribs of *Dicraeosaurus hansemanni*. Skeleton m. 1/10 natural size.

minor damages. The last cervical rib of the left side is only represented by a short fragment (capitulum), but the 1st and 3rd dorsal ribs are nearly complete. The 2nd, 4th, and 6th ribs are for the most part preserved, and the 9th is half preserved.

General description.

The bauplan of the long, continuously two-headed ribs is such that the more or less flat rib shaft, with its generally laterally facing plane, grades into the tuberculum. A proximally expanding ridge emerges from the inner surface of the rib shaft at different distances from the distal end, and this ridge merges with the ventral rim of the capitulum. Between the posterior rim of the outer surface and this ridge lies a longitudinal, medially directed depression which is short and flat in the 1st cervical and 1st dorsal ribs. The depression gets deeper and longer in the two following ribs until it covers about one-third of the entire length of the 3rd dorsal rib. This depression shortens considerably in the next ribs and gets very shallow in the two last ones. The cross-section of the shaft of the last cervical rib is rounded triangular and square. The rib shaft is flattened in the

Fig. 30–36. 6th to 12th dorsal ribs of Dicraeosaurus hansemanni. Skeleton m. 1/10 natural size.

proximal distal section of the 1st dorsal rib, and rounded triangular in the middle section. It is only in the 10th rib that the shaft has a continuously flattened cross-section. The rib shaft takes on a roundish cross-section distally only from the 10th rib onward, whereas in the proximal section the plane of the depression is almost perpendicular to the plane in which lie the bifurcated parts. This transverse positioning is even more distinct in the 11th rib. The rib shaft is straight in the last cervical rib, and only the distal end curves away from the capitulum in a short arch. The entire length of the shaft of the 1st dorsal rib is slightly curved in a direction opposite to the capitulum. The shafts of the 2nd and 3rd ribs are almost straight when viewed perpendicular to the plane of the side of the capitulum, strongly so in the five following ribs. This curvature is again much reduced in the 10th and 11th ribs, and the short last rib is almost straight. The curvature of the rib that lies more or less in a transverse plane of the body is always under great threat of distortion by pressure in the rock. However, such deformation is small in the ribs of skeleton m, and most specimens are not afflicted at all. The transverse curvature, which is weak in the first cervical and two first dorsal ribs, is only clearly developed in the distal quarter of the 3rd and 4th ribs.

The original curvature in the middle section might have been obliterated by deformation in these ribs. All the following ribs show a rather strong, uniform transverse curvature of the rib shaft. The maximum width of the shaft, i.e. on its outer surfaces and on the continuation into the capitulum, still lies within the widening caused by the separation of the tuberculum in its proximal section, up until the 3rd dorsal rib. The greatest width lies in the second quarter of the 4th rib, and in the middle sections of the five succeeding long and especially flat ribs. The greatest width has shifted close to the proximal end in the next two short ribs, in which the plane of flattening is transversely positioned. The last very short rib has a nearly uniform shaft width.

The tuberculum is always the shorter and stronger of the two proximal bifurcated parts, and the capitulum is always the weaker and longer. In the last cervical and 1st dorsal ribs, the tuberculum runs almost as a continuation of the longitudinal axis of the rib shaft. It curves out of the plane of the proximal part, weakly in the 4th rib, more strongly in the 5th. In combination with this bend there is an anterior inclination of the tuberculum out of the transversal plane of the bend of the rib shaft, up until the 7th rib. The angle enclosed by the hypothesized longitudinal axes running through the centers of the tuberculum and capitulum is ca. 80° in the last cervical rib. It stays at nearly 85° from the 1st through 8th dorsal ribs. Then the angle increases to more than 95° in the 9th rib, and to ca. 110° in the 10th and 11th ribs. The angle formed by the ventral contour of the capitulum with the longitudinal axis of the rib shaft is just about 90° in the 2nd rib. The angle is wider in the previous as well as the succeeding ribs, i.e. almost ca. 125° in the 6th and 7th dorsal ribs. The angle measures just about 90° in the 10th and 11th vertebrae. The delicate proximal rim between the tuberculum and capitulum shows a deeply rounded, incised contour in the last cervical rib. The cut-out is very flat in the dorsal ribs, and it is almost lost in the posterior ones, in which the contour is nearly straight. The last rib, the 12th, has a special shape because of its position relative to the pelvis.

Details of the individual ribs.

Last cervical rib, right side. The posterior rim of the outer surface of the rib shaft shows a swelling about 11 cm from the tubercular facet that is in the ca. 1.5 cm wide and ca. 5 cm long center. This swelling could have been the attachment point for a muscle or tendon, but with its even shape it does not look like a abnormal pathological growth. The rib shaft shows a triangular cross-section in the middle section, a more roundish one ventral to this, then a triangular one again over a short distance. A piece that can only have been short is missing at the distal end of the shaft, which is strongly bent toward the side of the tuberculum. As the rib end obviously terminated in a point rather than being flat, an original connection with the sternum cannot be assumed; the rib must therefore still be considered a cervical rib, even though it has the character of a dorsal rib due to the long rib shaft. The 12th vertebra belonging to this rib must therefore be referred to the cervical vertebrae. The capitular facet is 2.8 cm wide by 3.8 cm long. The tubercular facet is 2.4 cm wide and 4.6 cm long.

Last cervical rib. Only the capitulum is present.

1 st dorsal rib, right side. The head of the capitulum is missing and has been restored. The distal end, which is not completely preserved, gets wider and distinctly double-edged. An original connection with the sternum was obviously present. The rib is therefore the first right dorsal rib.

2 n d dorsal rib, right side. The posterior rim of the outer surface of the rib shaft is developed as a sharp, projecting edge. At 43 cm from the end of the tuberculum, it decreases so much that the width of the rib shaft becomes considerably reduced. The completely preserved distal end increases in width from 37 mm to 59 mm and gets simultaneously flatter distally.

2 n d d o r s a l r i b, left side. The completely preserved rib is essentially similar to the left one, but lacks the aforementioned sudden narrowing of the rib shaft.

3 r d d o r s a l r i b, right side. Apparently only a small part of the distal end is missing. An increase in width is not present, but only because the rims of the shaft are not preserved.

3 r d d o r s a l r i b, left side. The missing central third has been restored. The widening of the distal end is distinct, but not completely preserved.

4th dorsal rib, right side. The distal end is missing.

4 th dorsal rib, left side. The tuberculum is missing. The rib is otherwise completely preserved, but is slightly compressed at ca. 1/4 of its length from the proximal end. The distalmost end is well preserved. It simultaneously gets flatter and wider, from 43 mm to 64 mm, which is caused only by the protruding contour on the side of the capitulum. The end surface is transversely cut off and rugose.

5th dorsal rib, right side. The rib shaft bends distinctly forward toward the side of the capitulum at ca. 80 cm from the end of the tuberculum. The completely preserved distalmost end is flattened over the last 10 cm and has a relatively uniform width of 54 mm, swelling to 26 mm in thickness at the end.

5th dorsal rib, left side. The tuberculum and a ca. 15 cm long section of the proximal part of the rib shaft are missing. The rib shaft is deformed distal to the missing section. The completely preserved distal end is ca. 5 cm wide.

6th dorsal rib, right side. The rib shaft is almost straight at 70 cm from the end of the tuberculum, and then describes a smooth curve to the incompletely preserved distal end. The width decreases continuously toward the end, where it measures 40 mm, the reduction therefore being considerably stronger than on the previous rib.

7 th dorsal rib, right side. The last 20 cm of the distal rib shaft decrease in width suddenly and distinctly to 34 mm. The terminal part is missing.

7th dorsal rib, left side. The rib is slightly deformed. The distal third of the rib shaft is missing.

8th dorsal rib, right side. The sudden narrowing of the distal end occurs as it did in the previous rib. A pathological growth is visible on the posteromedially facing surface of the rib shaft ca. 32–40 cm from the tubercular end. The growth juts out on both sides about 1 cm over the rib shaft.

9 th r i b, right side. The sudden narrowing of the distal part of the rib shaft is more uniform than in the two previous ribs. A similarly strong bony growth is in the same position as on the 9th rib at ca. 32-42 cm from the tubercular end. The distalmost part of the rib shaft is missing.

9th rib, left side. The tuberculum and most of the of the distal half of the rib shaft are missing.

11th rib, right side. This rib is distinguished from all previous ones by the fact that the rib shaft has a strongly compressed cross-section in the area from which the capitulum emerges, as well as distal to this area. The maximum diameter of the cross-section in this area is 4.8 cm, with a transverse diameter of 2.5 mm. When viewed from dorsally onto the extended surface of the proximal part of the rib, one looks at the narrower side of the rib shaft. The capitulum is apparently slightly bent out of its original orientation by pressure. Distal to its mid-length the rib shaft has a cylindrical shape with a hint of four indicated longitudinal edges. The largest and smallest diameters of the rib shaft measure 3.1 cm and 2.9 cm at 50 cm from the tubercular end. It seems that only a very small piece of the distally flattening and, towards the end, distinctly anteriorly bent distal end of the rib shaft is missing.

11th rib, right side. The extended surface between both bifurcated articular processes is much reduced compared to the previous rib. It extends only to a point ca. 13 cm from the tubercular end. A concavity on the posterior side is hardly visible any longer. The rib shaft is comparatively even more laterally compressed, emerging abruptly out of the anterior surface of the proximal widening. The height of the cross-section is 4.6 cm by a 1.7 cm wide at 14 cm from the tubercular end. The height decreases continuously and rather evenly in the distal direction. The compressed shape is retained to the end to a certain degree. where it is 2.0 by 2.1 cm cm.

In the middle section of the rib shaft, a rounded longitudinal edge appears on the tubercular side over a short distance.

12th rib, right side. This rib has a very peculiar shape, probably due to its position in the region of the ilium. The capitulum is not preserved. The width of the tuberculum has been insignificantly reduced to 2.5 cm by the crumbling away of material. The proximal widening is even on both sides. The short rib shaft is proximally compressed and in the same area irregularly rectangular. The plane of the extended surface is flatly inclined to the proximal widening. The ventral edge that extends from the capitulum continues onto the shaft and forms the ventral inner edge of the entire anteriorly directed width of the rib shaft. An edge extending from the tuberculum forms the opposite edge on the rib shaft. This edge is somewhat elevated over several centimeters at 10 cm from the tubercular end, and extends the width of the rib shaft in this area to 3.8 cm at a thickness of 2.0 cm. The rib shaft flattens to 1.6 cm in the middle section; it now measures 24 mm, but must have been larger originally.

Chevrons^{*}.

Chevrons of skeleton m.

(Figs. 37–57.)

Material: 17 chevrons are present. Only some of these were found in articulation with the ventral sides of the vertebral centra, but were detached from the centra and more or less far dislocated. A referral to a certain vertebra on the basis of the position in which they were found was only possible for some of the chevrons, and even for these not with absolute certainty. There are no indication that one or more are missing within the row of chevrons or anteriorly to it. The chevrons could be easily ordered in a row according to their change in size and shape, which also reflects essentially the position in which they were found, as far as this position allows such a conclusion. As the centrum of the 1st caudal vertebra is already outfitted with facets for the chevron, it seems likely that the 17 chevrons present belong to the 1st through 17th caudal vertebrae.

Preservation: The chevrons are mostly complete or nearly complete preserved. The distal end is lost in the 2nd one. The larger part of the left part of the proximal bifurcation is missing in the 5th chevron. The 9th, 12th, and 13th chevrons are missing the proximal section of the right part of the bifurcation, the left in the 16th is missing, and in the 17th the right and the left parts entirely. The 13th chevron has lost a longer distal part, and the 15th and 16th chevrons the distalmost tips.

Description: The general shape of the chevrons is as commonly found in sauropods. In the anterior chevrons, the parts of the proximal bifurcation are connected by a proximal bridge, which is best developed with ca. 2 cm thickness in the first chevron, and averages only about half as thick in the five following ones. In dorsal view the bridge shows a deep central notch anteriorly, which is only weakly developed on the posterior side. The bridge is interrupted in the middle in all other vertebrae. The cross-section of the space enclosed between the bifurcated parts of the chevron tapers ventrally to an acute point, and is ventrally rounded only in the first chevron. The vertical diameter of this space measures 6-7 cm in the chevrons with a complete bridge, increases slightly in the succeeding ones, and decreases again to 6-7 cm from the 12th chevron. The width of this space enclosed in the anterior chevrons

^{*} Here and elsewhere, substituted for original "haemapophyses" [Eds].

by the proximally connected bifurcated part is approximately 3.5 cm. The width of the enclosed space might have been changed by pressure in those chevrons with free bifurcated parts. It is hard to decide whether the width decreases posteriorly. The proximal facets for the vertebral centra are positioned oblique to the longitudinal axis of the bone. Usually there is an especially marked attachment at the posterior rim of the anterior one and another for attachment of the anterior rim to the posterior one, indicated by different inclinations. The parts of the bifurcation are always thin and flat, with more or less sharp rims. The posterior chevrons from the 12th onward show a

Fig. 37–53. Chevrons of the 1st through 17th caudal vertebrae of *Dicraeosaurus hansemanni*. Skeleton m. 1/6 natural size.

transverse elevation on their lateral surface at a distance of 3.5–4 cm from and parallel to the proximal edge. The width of the rami—in lateral view—in the two first chevrons is smaller than in the following ones. It decreases in the posterior half of the preserved series, but changes erratically from one vertebra to the next, and can even be rather different on the right and left sides of the same vertebra.

The principal changes in shape of the chevrons mainly concern the form and length of the parts that are positioned distal to the bifurcation point. In the anterior section of the tail, this part has the form of a rod, which is completely straight in the first chevron. It is

only this chevron that shows an increase in width, to a small degree anteriorly but to a much larger degree posteriorly, which results in an obliquely arrow-like shape with long anterior and short posterior edges of the tip. In the second chevron the rod-like distal part is also still straight, but longer and stronger. From the 3rd chevron, the longest one, onward, we find a distinct,

Chevrons of Dicraeosaurus hansemanni. Skeleton m, posterior view.

Fig. 54. Chevron of the 1st caudal vertebra.

Fig. 55. Chevron of the 6th caudal vertebra.

Fig. 56. Chevron of the 10th caudal vertebra.

Fig. 57. Chevron of the 14th caudal vertebra.

1/6 natural size.

although slight, anterior bending-through of the rod. The length is still the same in the 4th chevron, but along with the strength decreases from here continuously. From the 11th chevron onward the distal wand begins to buckle increasingly sharply posteriorly ventral to the bifurcation point, by simultaneous getting shorter and sharper distally. The angle of the anterior contour encloses ca. 130° in the last chevron, while the rami have again increased in width.

Measurements.									
	1	2	3	4	5	6	7	8	
Total length	23.3	25.9 +	31.9	31.2	30.0	28.3	26.2 (+)	26.0 (+)	
Width at proximal end	8.2	8.7	9.5	9.9	?	8.1 (+)	8.2	7.8	
	9	10	11	12	13	14	15	16	17
Total length Width at proximal end	24.9 (+) ?	22.9 (+) 6.9	20.0 (+) 7.2 (+)	19.3 (+) ?	? ?	17.0 ?	16.4 + ?	14.2 + ?	? ?

Chevrons from locality dd.

Several anterior chevrons are present from excavation site dd, two of which belong to *Dicraeosaurus hansemanni*. Furthermore, there is a strongly mutilated chevron from the region between the 15th and the 19th vertebrae that belongs to this species. Also present are three additional chevrons, of which one (dd 495) belongs to a vertebra which must have been positioned not far behind the last vertebra of this series in m, the 19th, while the others must have belonged to more distant following vertebrae. The referral to *Dicraeosaurus hansemanni* follows readily from the strong similarity with the last, the 17th chevron of skeleton m. The two posterior chevrons (dd 515 and dd 516) can also be referred to this species, as their shape connects them with the chevron. These chevrons cannot belong

to the genus *Barosaurus*, whose chevrons from the same excavation site are marked by their *Diplodocus*like shape and are definitely different. They also cannot belong to *Brachiosaurus*. The chevron in this genus do not show sharp edges along the much thicker rami of the bifurcation. This is a distinct trait, which is only present in chevrons from excavation site no, although it can only be shown from the anterior half of the tail of the specimen, but which most likely continues into the posterior half of the tail.

Chevron dd 495.

[Figs. 58 a, b.] The ends of the rami of the bifurcation as well as the distal ends are missing. The rami, of which the left is more strongly developed than the right, are sharp-edged posteriorly and show a transverse ridge on their lateral surface. The distal part of the chevron is so strongly bent that the ventral contour forms an angle of more than 90° with the anterior edge of the rami. A short median opening is positioned in the distal part, which exits asymmetrically on the left side of the very sharp ventral edge. A break surface indicates that the distal part must also have had an anterior projection. The only ascertainable measurement is the width of the left ramus, which is 3.1 cm at the bifurcation point. This chevron might have been positioned in the region of the 20th caudal vertebra.

Chevrons of *Dicraeosaurus hansemanni*. Fig. 58 a. dd 495 lateral view. Fig. 58 b. The same, dorsal view. Fig. 59 a. dd 515, lateral view. Fig. 59 b. The same, dorsal view. Fig. 60 a. dd 516, lateral view. Fig. 60 b. The same, dorsal view. 1/6 natural size

Posterior chevrons of dd 515 and 516.

The proximal rami of chevron dd 515 [fig. 59 a, b] form very thin, high, rectangular plates. These plates are about 7 cm high and show a width of about 5 cm in the proximal section, but widen distally and end in pointed tips anteriorly and posteriorly. The rami are fused in the area of these tips, while between them lies a median, 6.5 cm long, slit-like gap. The anterior surface of the chevron is marked by a more steeply inclined contour of the rami. The incompletely preserved posterior tip was obviously longer than the anterior one. The preserved distal length measures 12 cm.

The other chevron, dd 516 [Fig. 60a, b], is very similar to the already described one. Its height is slightly shorter, not quite 6 cm, and the anterior distal tip is longer and thinner. Posteriorly, only the bases of the tips are preserved, which are not yet joined at the end of the break. It is impossible to decide whether the ends were fused at all; in any case, this chevron had a longer medial slit than the other one, and was positioned more posteriorly in the tail.

It is easy to imagine that the type of chevrons dd 515 and 516 is derived from that of chevron dd 595 by a widening of the rami, a longer projection and sharpening of the anterior and posterior distal ends, and elongation of the median gap. Thus, it is certainly possible to refer this type to *Dicraeosaurus hansemanni* as well. It should be derived from the region between the 25th and 35th caudal vertebrae.

Physiological and histological conclusions.

Flexibility of the vertebral column.

The possibilities for flexion are determined by the mode in which the joints between two adjoining vertebrae are constructed, i.e. the connection between centra and zygapophyses. If the end surfaces of two centra were the exact halves of two spheres, they would allow flexion in every direction including rotation around the longitudinal axis. The glenoid cavities of the presacral vertebral centra represent more or less a hemisphere, that is if one ignores the mechanically induced subsequent deformation. Whether this was also the case in the posterior dorsal vertebrae cannot be decided, because of the incomplete preservation on the left side and also because some deformation has occurred. The hollow shape of the posterior dorsal vertebrae does not exactly reflect a hemisphere, but seems to be irregularly shaped. The articular head fits increasingly inaccurately into the cavity of its predecessor from the 9th cervical vertebrae forward. The articular head is cut off in the middle cervical vertebrae, and therefore a direct connection with the concave surface is not possible; it could have only been achieved if the deficient bone substance were somehow replaced, probably by cartilage. It is striking how much smaller the articular head in the anterior cervical vertebrae is compared to the corresponding cavity. Naturally a thicker layer of cartilage has to be assumed on the articular head of these vertebrae.

The incongruence between the articular head and the articular cavity does not necessarily indicate restriction of flexibility in any direction. Constraint on possible movements was caused by the connections of the zygapophyses. We can infer diverse conditions in different regions of the column from the orientations of the facets. From the 2nd presacral vertebra onward, torsion was impossible due to the interlocking of the zygapophyses. Flexion in the median plane was probably possible throughout the entire presacral vertebral series. During flexion, all the zygapophyseal facets, whether positioned steeply or flat, as well as the facets of the hyposphene moved in circles with the individual points of their articular surfaces, the centers of which lie on an axis of rotation that is perpendicular to the median plane and goes through the center of the hollow sphere of the posterior joint in the anterior presacral vertebrae with well-developed articular condyles. Indeed, the zygapophyses and hyposphene allow bending in the median plane within the presacral vertebrae, as shown by visual examination and moving the vertebrae against one another. This assessment is not even influenced by the distortions and deformations on the joint surfaces.

Secondly, it also has to be investigated whether and how far lateral flexion of the presacral column was possible in addition to flexion in the median plane. Lateral flexion requires gliding the zygapophyseal facets on planes of rotation around an axis of rotation, which has to pass dorsoventrally through the centers of the articular cavities of the vertebrae with well-developed articular condyles. The circles described on these planes of rotation are much narrower than those of the plane of rotation for median flexion, as their diameter is only as wide as the distance between symmetrically positioned points of the right and the left zygapophyseal facets of a vertebra. The mode of rotation should reveal itself much more strongly on the facet surface. Lateral flexion in the anterior cervical vertebrae—without the atlas—was nearly impossible because their steeply inclined zygapophyseal facets, more or less level and positioned close to one another, fall too far out

of the only very narrow circles that are permitted by the plane of rotation. The conditions are more favorable for lateral flexion in the posterior cervical vertebrae, in which the zygapophyses are further from each other and their facets are positioned more horizontally. Flexion in both directions simultaneously, lateral and median, would be theoretically possible in two ways: in the first scenario, the facets would slide on each other, but not onto their entire surface because they are incongruent; for example, in the most extreme cases both facets are convex or one is convex and the other level. Preservation does not allow assessing such a possibility. The other theoretical condition is that the facets are sections of spherical planes, the centers of which fall together with the centers of rotation of the condyles. Such a condition does not really apply for the facets of the posterior cervical vertebrae, but a certain approximation of this scenario is given by the fact that these facets are positioned much more horizontally. The circles on which the points of the facets glide get considerably larger due to the increasing distance between the facets in this region. This also increases the possible range of simultaneous lateral and median flexion. It can be assumed with certainty that a not insignificant lateral movement was possible in this region, which might have been caused by the slight incongruence of the facets gliding on one another, or was even enhanced by it. Such an incongruence is provable nowhere with certainty, because the facet surfaces have often been changed by deformation, especially in cases with more strongly developed vaulting.

The effect the hyposphene^{*} articulation has on the possibilities for flexion is obvious, and has already been explained in detail by OSBORN and MOOK (1921 page 302): it makes lateral flexion impossible and additionally prevents elevation of the postzygapophysis of one vertebra over the prezygapophysis of its successor. The latter is only relevant for vertebrae in which the hyposphene broadens wedge-like ventrally, and not for vertebrae in which the hyposphene presents nearly parallel plates, as in the two last dorsal vertebrae. The presence of the hyposphene results in a lack of lateral flexibility for the entire dorsal vertebral series from the 15th presacral vertebra onward.

Flexion in the median plane is not permitted by the shape of the zygapophyseal facets in the entire preserved series of caudal vertebrae, and it is out the question that such movement was performed in life. Lateral flexion is impossible in the anterior caudal vertebrae, in which the prezygapophyses have steeply inclined facets that project far anteriorly. With the shortening of the prezygapophyses and the flattening of the incident angle of their facets, i.e. from about the 8th vertebra onward, a slight degree of lateral flexion from vertebra to vertebra should have been possible. The range of lateral flexion of the entire tail was probably considerable because the weak individual swing of each vertebra added up.

Significance of the architecture and position of the neurapophyses.

The indubitable fact that the laminae served to reinforce and counteract distal tensile stress allows specifying the direction from which such tension originated. The strength of the laminae allows assessing the force of this tension. It is therefore possible to infer the direction of the predominant tensile forces from the variable strength of the lamina jutting out in several directions on the neurapophyses and the neurapophyseal rami. This results in the important observation that the inclination of these laminae is always directed toward the point from which the tension originated.

^{*} Here and elsewhere, substituted for original "zygosphene" [Eds]

The anticlinally arranged neurapophyses in the anterior section of the neck indicate that posteriorly directed tensile forces acted on the vertebrae anterior to the apex of the anticline, which is located between the 4th and 5th vertebra. The profile of the neurapophyses of the 2nd and 3rd vertebrae corresponds to these forces; it is M-shaped in the unpaired axial neurapophysis, but the profile is deeply U-shaped in the lower half of the neurapophyseal branches of the 3rd vertebra. The U-shaped profile is only weakly indicated in the 4th vertebra, and it is no longer present in the 5th. The increasingly strong anterior inclination of the neurapophyses in the anterior cervical vertebrae argues for strong tensile stress in the cranial direction. In connection with this tensile strain is the robust development of the supraprezygapophyseal laminae which form the anterior rim of the neurapophyseal branches and stiffen them against tension in the anterior direction. The supraprezygapophyseal laminae gain maximum strength exactly in those vertebrae with the furthest anterior inclination of the neurapophysis, namely in the 8th and 9th vertebrae. The neurapophyseal branches of the following vertebrae straighten up again and show a longitudinal depression on their posterior surface, again resulting in an U-shaped profile, to counteract the tension in the posterior direction. At the same point, the strength of the supraprezygapophyseal laminae diminishes, which leads to the conclusion that the tensile stress that came from the anterior direction has considerably decreased. It is very important to note the increasing development of anteriorly facing surfaces in the dorsal half of the very strong neurapophyseal branches of the 15th through 19th vertebrae, which is created by the lateral longitudinal edges of the neurapophyses, which were subsequently transformed into the spinodiapophyseal laminae. This additional surface can only be interpreted as a muscular attachment area. Thus it has to be assumed that the attachment areas of the respective muscles expanded laterally from vertebra to vertebra. This might have coincided with an increase in the circumference of the muscles. In the uniform neurapophyses of the posterior presacral vertebrae, from the 20th vertebra onward, thin lamellar spinodiapophyseal laminae give the impression that they served not so much as attachment areas for strong muscles, but had more the function of supporting the terminal expansion of the spine which served as an attachment area for the dorsal ligament. The anteriormost dorsal vertebrae up to the 17th show, by very robustly developed suprapostzygapophyseal laminae in accordance with the general posterior inclination of the neurapophyseal branches, that strong tensile forces acted upon them here posteriorly. The suprapostzygapophyseal laminae are almost completely missing, which indicates that anterior tensile stress was not much in evidence. However, they are slightly more strongly developed in the 19th presacral vertebra, in which the anterior section of the neurapophysis is curved anteriorly, indicating severe stress in the anterior direction. The posterior direction of this stress is clearly indicated in the still more or less visible supraprezygapophyseal laminae of the succeeding vertebrae with straight, vertical neurapophyses. The supraprezygapophyseal laminae get weaker in succeeding vertebrae and are stronger only in the 23rd and 24th vertebrae, in accordance with an anterior inclination of the neurapophyses. The very strong development of the suprapostzygapophyseal laminae along the entire spinal column, which occurs in the posterior vertebrae even in pairs, shows that there was a strong tensile force acting toward the sacrum, which required a strong reinforcement of the ventral part of the neurapophyses and neurapophyseal branches in the direction of the zygapophyseal joints. A remarkable character of the neurapophyseal branches of the 12th through 14th vertebrae must be mentioned: the laterally overturned anterior rim in the ventral part of the neurapophyseal branches is directed laterally toward the prezygapophyses, which in these vertebrae are shifted far laterally and act here as reinforcement against lateral stress. On the other hand, this rim runs toward the diapophysis in the 15th through 17th vertebrae, and is particular strongly developed in the 15th.

The robust development of the suprapostzygapophyseal laminae in the anterior caudal vertebrae indicates that these had to withstand particularly strong tensile forces in the posterior direction. These forces acted especially upon the ventral part of the neurapophyses, which is indicated by the overturning of the neurapophyses of the first vertebra. Throughout the entire series

of preserved vertebrae a tensile force was obviously acting in the anterior direction at the dorsal end of the neurapophyses, as is made plausible by the anterior inclination of their dorsalmost section. The anterior stress at the dorsal end of the neurapophyses was probably caused by tension in the strong dorsal ligamentous connections between the vertebrae. This tension might have been caused by the fact that the caudal vertebrae were pulled down posteroventrally by their weight. The posterior sagging of the vertebrae caused a stretch in the connecting ligaments, in their insertion points and with that stress. The ligamentous connection between the neurapophyses was obviously very strong. The dorsally widening rugose areas on the anterior and posterior surfaces of the neurapophyses indicate the presence of a very strong interspinous ligament. By their very irregular relief, which they all possess with the exception of the anteriormost vertebrae, the end surfaces of the neurapophyses indicate that they carried a thick layer of non-fossilized tissue, which, apart from a terminal cartilaginous layer, might have been a strongly developed supraspinous ligament.

Significance of the laminar system of the diapophysis and the parapophysis.

The stress that is visible in the laminar systems of both the diapophyses and parapophyses will be treated in connection, because a very important stress, namely that caused by the rib articulation, concerns both systems. In the anterior cervical vertebrae, the diapophysis is reinforced by the posterior centrodiapophyseal lamina, and the parapophysis by the posterior centroparapophyseal lamina, against a muscle pull at the cervical ribs that is directed caudally and causes a lateral or ventral flexion. The postzygodiapophyseal lamina counteracts a muscle pull that inserts at the diapophysis, is posterodorsally directed, and causes dorsal flexion. The postzygapophyseal lamina is particularly strongly developed in the 4th through 6th vertebrae which are positioned in the anticlinal part of the neck. This strong development seems to be somehow connected with the mechanics of the anticline. The striking fact that the postzygapophyseal lamina is not present in the 3rd vertebra shows that the diapophysis in this vertebra was not subjected to this kind of stress. In this vertebra it is the already-mentioned neurapophyseal branches that are adapted against dorsal tension, which is directed posteriorly by their posteriorly concave U-shaped profile. All the mentioned laminae act essentially in the same way in the posterior cervical vertebrae as in the anterior ones. It seems that the increasingly horizontal position of the postzygapophyseal laminae resulted in a more optimal reinforcement against lateral flexion of the neck. The postzygapophyseal laminae achieved a greater significance only in the posterior part of the neck, as can been concluded from the zygapophyseal facets.

The stresses on the diapophysis and parapophysis of course change significantly with the development of the cervical ribs into movable thoracic ribs. The stresses on the diapophysis a parapophysis are thus more varied in the trunk than in the neck. In the anterior part of the trunk, the shoulder girdle carries the rib cage, and the ribs carry the vertebral column. It is obvious that in the laterally far projecting, bifurcated proximal section of the anterior dorsal ribs the very strongly developed capitulum supports the respective vertebra to a large part. At first the capitulum articulates directly with the centrum up to the 14th presacral vertebra; in the next two following vertebrae, in which it rises dorsally onto the neural arch, the parapophysis is so strongly festooned that the significant stress on this rib connection is obvious. The load on the rib heads by the vertebral column

causes compression between these and their joints on the anterior dorsal vertebrae, which results in a particularly strong reinforcement of the diapophysis against the neurapophyseal branches by transversely directed laminae. The postzygapophyseal lamina alone has a transversely directed position in the 12th vertebra. In the 13th vertebra, in which the performance of the postzygapophyseal lamina is enhanced by a connection with the supradiapophyseal lamina, it is positioned in the same way. The transverse reinforcement of the two following vertebrae is enhanced in a remarkable manner: the anterior rims of the neurapophyseal branches are bent laterally and fuse with the strong supradiapophyseal lamina in these two vertebrae. The supradiapophyseal lamina weakens considerably in the following vertebrae, and with it the transverse reinforcement. The stresses on the diapophysis and the parapophysis can by no means have been limited only to medially directed compressive stresses. During walking compression must have been lifted (or at least very much reduced) on the side in the phase in which one anterior limb was elevated from the ground. A tensile stress from the suspended and downward-pulling weight of the ribs and the connected soft-tissue parts was now acting on the diapophysis. This tensile stress was absorbed by the more or less horizontally positioned centrodiapophyseal laminae in the dorsal vertebrae. The distribution of stress between the ribs and vertebrae must have been in the posterior section of the trunk. because the posterior pelvic girdle carries the vertebral column by a stiff connection combined with the elimination of movable ribs. Thus, the vertebrae anterior to the sacrum are not carried by ribs, and therefore are not subject to compressive forces from them. However, this could have been the case to a certain degree when the animal lay on its stomach. To counteract the compressive forces that might have occurred in this case, the weak supradiapophyseal laminae must have been sufficient. Otherwise, tensile stress must have been predominant on the diapophyses, which had to be absorbed by the thoroughly welldeveloped centrodiapophyseal laminae. I do not attempt to interpret the fact that these were particularly large and at the same time thinly developed in the last free dorsal vertebrae.

Ligamentous connections.

Pl. IV.

Interspinous ligament.

The median spinal laminae are especially robustly developed at the dorsal end of the neurapophyses in the last two dorsal vertebrae, in particular in the dorsal section, and even project slightly anteriorly. Similarly, the median spinal laminae are very strong in the first caudal vertebrae, especially at their dorsal ends. It is concluded that the interspinous ligament was particularly strong between the vertebrae next to the pelvis, connecting them particularly strongly and counteracting the median flexion of the vertebral column. It is especially the anterior projection of the prespinal laminae, which naturally occurred at the spatial expense of the ligament, that indicates the limited range of possible medial flexion. In the preceding dorsal vertebrae with undivided neurapophyses, however, the medial spinal laminae are weakly developed at the dorsal end and project less far anteriorly than those in more posterior positions. The connection was therefore slightly loosened here, favoring the possibility of median flexion.

the increasingly low position of bifurcation point in the neurapophyses, the interspinous ligament shortens rapidly in the cranial direction within the following series of vertebrae with such bifurcated neurapophyses; thus, the possibility for flexion in the median plane quickly increases. The ligament is not present anterior to the 16th presacral vertebra. Whereas the interspinous ligament fills the entire height of the space between the neurapophyses in the last dorsal vertebrae, it can only have been a couple of centimeters high between the 16th and 17th presacral vertebrae. It was probably also weak, because the prespinal lamina is very thin in the 17th vertebra, as well as in the 18th. The interspinous ligament was not developed anterior to the 16th vertebra. An interspinous ligament must only be hypothesized again between the 2nd and 3rd vertebrae. Between the ventral, reinforced end of the prespinal lamina of the 3rd vertebra and the rugose rim of the ventral part of the postspinal lamina of the axis, must have been spanned a lamellar ligament, which can be termed the interspinous ligament.

Supraspinous ligament.

In the section of the dorsal vertebrae with unbifurcated neurapophyses as well as in the sacrum, the nature of their end surfaces argues for the presence of a well-developed supraspinous ligament. These end surfaces are widened and additionally project anteriorly and posteriorly over the spinodiapophyseal lamina. The development of the end surfaces can only be interpreted such that ligamentous tissue extended from one rim of the terminally widened end of one vertebra to the next, as, for example, in crocodiles, in which ligaments stretch between opposite dorsal ends of the neurapophyses. The median depression, which is especially distinct on the dorsal surface of the ends of the neurapophysis of the anteriormost non-bifurcated vertebra, the 20th, seems to indicate a median reinforcement of the ligament, which continued anteriorly as the nuchal ligament, to be dealt with later. Apparently there was an additional connection to the median slope of the end surfaces of the neurapophyseal branches of the previous bifurcated vertebra, up to about 1/3 of its height, as indicated by the shape of the end surface in these areas. As the ends of the neurapophyses of the anterior caudal vertebrae are very similar to those of the sacral and posterior dorsal vertebrae, a corresponding ligamentous connection has to be assumed here as well. The median depression is present here as well, but only from the 2nd caudal vertebra onward. It becomes incorporated into the complex undulating and elongated end surfaces in the succeeding caudal vertebrae with a reduction of the spinodiapophyseal lamina. The structure of the end surfaces of the neurapophyses of these and of the middle caudal vertebrae indicates a very strong supraspinous ligament. the narrowness of which must also have allowed lateral flexion. In contrast, the width of the supraspinous ligament connection must have impeded or even prevented such movement in the posterior dorsal and anteriormost caudal vertebrae, in accordance with the function of the zygapophyseal joints. Conditions in crocodiles suggest that tendons and muscle fibers of the m. longissimus dorsi, i.e. the dorsal tail musculature, extended posteriorly from the lateral, ventrally running parts of the terminal expansion of the neurapophyses in the posterior dorsal, sacral, and anterior caudal vertebrae.

The structure of the dorsal end of the neurapophyseal branches in the anterior dorsal vertebrae with deep bifurcations, and in the cervical vertebrae, indicates a cartilaginous or ligamentous cap, but not paired, continuous ligaments, although insignificant connections might have been present. The hypothesis that muscles or their tendons, respectively, inserted at the rim of this cap seems plausible indeed, as there is hardly another imaginable reason for the high development of the neurapophyses.

Nuchal ligament.

The striking anterior projections at the base between the neurapophyseal branches that occur in most of the cervical vertebrae indicate a ligamentous connection, which must have run as a ligamentous string from the anterior dorsal vertebrae to the anterior cervical vertebrae, and therefore has to be named the ligamentum nuchae. The caudal insertion point of this nuchal ligament has to be assumed at the dorsal end of the prespinal lamina of the anteriormost vertebra with an unbifurcated neurapophysis, which would be the 20th. Even though only the ventral part of this area in the 20th vertebra is well preserved, it is possible to recognize that the prespinal lamina projects anteriorly and presents a particular fluting that is directed obliquely anteroventrally. Additionally, small laminae that are positioned transverse to the lamina indicate particular forms of stress. These small laminae are only visible on the better-preserved right side. The base between the neurapophyseal branches in the preceding vertebrae with 1/3 bifurcation shows a ventral inclination that continues even more steeply on the dorsally thickened end of the prespinal lamina. This oblique inclination was probably connected with the fact that the anteroventrally directed nuchal ligament was still attached here and might have been reinforced by the shape of this area. The dorsal vertebrae that follow anteriorly and show an increasingly deep bifurcation of the neurapophysis show no attachment area at the base of the bifurcation, but are completely smooth. Indications of ligaments that branch off dorsally are found in the cranial direction from the 12th presacral vertebra, the last of the cervical vertebrae. These ligament branches are only weak in this vertebra, however in the anterior vertebrae including the 5th, they are represented by very strong and strikingly nutshaped ligamentous attachments at the base between the neurapophyses. The observation that these projections for ligament attachments show notches on their dorsal and posterior surfaces indicates that the ligament section that attached here branched off posterodorsally. Therefore it can be assumed that the nuchal ligament inserting on the 20th and 19th presacral vertebrae ran freely anteriorly between the neurapophyseal branches and received additional smaller ligaments from the 12th presacral vertebra cranially. The incompletely preserved attachment area in the 4th presacral vertebra has not so much the shape of a distinct projection, but more of a posteriorly directed step in the roof of the neural canal. The anterior attachment of the now probably much weaker nuchal ligament must be assumed at this point. It is plausible that the nuchal ligament ended here, because the strong ventral bend of the anticline of the anterior cervical vertebral column begins here. Accordingly, the nuchal ligament descends from the level of the top of the high neurapophysis of the 20th vertebra to the level of the roof of the neural canal of the 4th vertebra, where the anterior insertion point is located. At this level, a ligamentous connection between the anterior end of the 4th vertebra and the 3rd vertebra was present, which cannot be called interspinous ligament any longer because of its low position, and it will be described below as the supraneural ligament.

The obvious question arises as to whether there was also a ligamentous connection between the axis and the skull. Such a connection is not indicated by the distinct development of an attachment area in the skulls in question. The end of the supraoccipital is very robustly developed in skull dd 3307, but an attachment area is not really developed toward the dorsal end of the neurapophysis of the axis. The rugose end surface of the neurapophysis extends so insignificantly onto the anterior surface of the axis that it does not seem plausible that a strong ligament was present here in the direction of the skull. Maybe there will be time to consider this question in more detail in the description of the skull material.
The ligamentum nuchae in mammals, especially in ungulates, differs from the ligament described here insofar as it runs dorsally at a distance from the neurapophyses of the spinal process of the cervical vertebrae, is connected with the ends of the neurapophyses by means of smaller individual ligaments, and inserts on the occipital region. Even though there are differences, these are not so severe as to make the term nuchal ligament for this ligament in *Dicraeosaurus* unjustified.

OSBORN and MOOK (1921 p. 302) assume, as did RIGGS, that the spinal notches (riding places) provided space for movement of the strong median dorsal musculature. They assume the median and dorsal surfaces of the branches of the spinal processes to be smooth, in contrast to the dorsal ends at which muscle fibers could have been attached. It seems more plausible to me that a ligament ran between the neurapophyseal branches, as described above. The striking, nut-shaped, strongly furrowed protrusions that show a rather unusual shape for a muscle attachment area argues against the view of the American authors, and in particular such an unpaired, median dorsal muscle can hardly be derived from other known muscles.

Supraneural ligament.

The number of ligamentous connections that can be recognized from their attachment areas is not exhausted with the three described ones. From the 16th vertebra onward, i.e. the vertebra at which the interspinous ligament ends, indications of another ligamentous connection can be found. At the wall that rises from the anterior exit of the neural canal steeply up to the base of the split between the neurapophyseal branches, and which decreases stepwise in height cranially in the following vertebrae, appears a rugose, median protrusion that is positioned within a roundish depression in the 13th and 12th vertebrae and gets much flatter further on. A ligament certainly originated at this area, which could have only run to the previous vertebra, respectively. The depression that lies behind a step at the base of the split between the neurapophyseal branches in the 15th and 14th vertebrae can be assumed to be the insertion point for this ligament, which by its position can be regarded as a ventrally displaced replacement of the interspinous ligament. The depression described above is shallow with an low inner protrusion in the 13th vertebra, but in the 12th and 11th is behind the posterior surface of the projections for the incoming branches of the nuchal ligament, which is no longer clearly developed. This ligament, if present at all, cannot have had any appreciable strength anterior to the 11th vertebra. Such a ligamentous connection must be assumed with certainty only between the 4th and 3rd vertebrae, as there is a strongly developed anterior prong at the 4th vertebra in opposition to a rather striking, vertically positioned, strongly bumpy plate that is positioned ventral to the posterior end of the slit between the neurapophyses in the 3rd vertebra. Considering their position close above the neural canal, these ligaments can legitimately termed supraneural ligaments.

Concluding remarks on the cervical ligamentous support apparatus.

The most remarkable conclusion resulting from the above descriptions of the ligamentous connections of the presacral spinal column of *Dicraeosaurus hansemanni*, which like all such histological reconstructions in fossil vertebrates necessarily includes some hypothetical and uncertain aspects, is the most likely presence of a ligamentum nuchae. Starting at the mid-dorsal

vertebrae, the 20th and 19th presacral vertebrae, and up to the 4th vertebra, this nuchal ligament must have stretched freely between the neurapophyseal branches of the preceding vertebrae, and supported the neck in conjunction with ligamentous branches emerging from the 12th through 5th vertebrae. The strikingly high, anticlinally arranged neurapophyses of the anterior cervical region show that a separate, more or less independent apparatus for support and movement existed in the first cervical vertebrae and the head. The nuchal ligament ended exactly at the apex of the dome of the anticlinal region. Possibly the entire support apparatus of the neck was hypertrophied, and the neurapophyses of the cervical vertebrae had such considerable height because the neck, rather short for a sauropod, was carried almost horizontally, and thus gravity fully affected it along its entire length.

The attempt at a reconstruction of the main ligamentous connections in the presacral column of *Dicraeosaurus hansemanni* is shown in Pl. IV, which illustrates a median section through the vertebral column and the inserting ligaments.

Bifurcation of the neurapophyses of the presacral vertebrae.

When trying to find a reason for the bifurcation of the neurapophyses, the particularly remarkable fact comes to my attention that, due to the bifurcation, the lateral rims of the neurapophyses are positioned more laterally in the anterior dorsal and posterior cervical sections, and that these rims are strengthened in comparison with the unbifurcated neurapophyses of the posterior dorsal vertebrae. This argues for the development of stronger and more laterally positioned muscle attachment areas. We are probably not mistaken in supposing that this improves the efficiency of lateral flexion of the neck. The fact that the divergence of the lateral rims did not result in a wide uniform neurapophysis, but is connected with the formation of a median split between two independent branches, must be attributed to the general principle of saving bone material whenever it is not mechanically necessary. The bifurcation must have also been causally connected with the ligamentous connections between the vertebrae. Moreover, the extremely deep position of the bifurcation points in the neurapophyses of *Dicraeosaurus* allowed very deep attachment points for the supraneural ligament, and thus more favorable conditions for the flexibility of the neck. This view is based on the following reasoning: with the attachment of a continuous ligament at the ends of unbifurcated neurapophyses, the ligamentous section between the neurapophyses becomes more stretched the higher the neurapophyses are during ventral flexion of the spinal column, i.e. more resistance against flexion is offered by the ligament. In other words, flexion is less hindered by the ligament the more deeply it is positioned. Moreover, the connection of the nuchal ligament with the cervical vertebrae via additional ligaments, which are attached deeply between the neurapophyseal branches, must have led to a different, more oblique position of these ligaments as their attachment areas were pushed further away from each other during ventral flexion, and so the nuchal ligament was not significantly stretched. The construction of the ligamentous support apparatus of Dicraeosaurus therefore created the possibility of strong ventral flexion, without causing, and being hindered by, considerable stress from stretching. The shortening of the interspinous ligaments, which goes hand-in-hand with the degree of bifurcation, must have increased the capacity for neck flexion.

Remarks on the musculature of the spinal column.

To draw conclusions on the development and course of the axial musculature on the basis of morphological characters of the vertebrae should only be attempted with the greatest caution. In general it can be said that considerable lateral flexion of the spinal column in the trunk and anterior part of the tail was prevented by the mode of joint articulation, and that this restriction should also have been expressed in the axial musculature. The axial musculature must have displayed considerable differences with that of recent crocodiles, lepidosaurs, and *Hatteria*, in which lateral flexion is of great importance. The fact that the very thin and high spinodiapophyseal laminae of the neurapophyses of the posterior dorsal vertebrae have no lateral surfaces for muscle attachment worth mentioning—in contrast to the development of the anterior dorsal vertebrae—and the fact that in the caudal vertebrae, apart from the most anterior ones, these lateral surfaces are strongly reduced, allows concluding that the development of the dorsal musculature was particular and probably weaker in a way.

I will attempt to determine the traces of certain muscles in two cases. The striking muscle attachment dorsal to the postzygapophyses in the cervical vertebrae, which increases in size from the 3rd onward and then decreases again to the 9th cervical vertebra and therefore is particularly strongly developed in the region of the anticline, can be related to the particular development of a muscle. As the development of the neck in sauropods resembles the one in birds more with respect to function, and the development of the muscle system can be expected to be more analogous to birds than to reptiles, the condition in birds will be used for comparison. From the descriptions of E. SELENKA (1891 GADOW-SELENKA) it can be learned that in Anser the musculus spinalis complex originates by tendons at the anterior rims of the spinal processes of the 2nd through 6th dorsal vertebrae, and at the lateral surface of the dorsal edge of the spinal process of the first dorsal and last cervical vertebrae, and that it inserts with two lobes on the posterodorsal surface of the postzygapophyses of the 16th through 10th cervical vertebrae. Muscles with a similar course might have run dorsally from the muscle attachments to the postzygapophyseal laminae of the cervical vertebrae of *Dicraeosaurus* to highly positioned origins on the neurapophyses of succeeding vertebrae. Such a muscle complex can only have served for dorsal flexion, specifically extension from a ventrally flexed position, and thus for raising the neck. It should be mentioned that this kind of muscle attachment, i.e. dorsal to the postzygapophyses of the cervical vertebrae, also occurs in other sauropods, for example in Brachiosaurus or Barosaurus.

Moreover, it can be assumed that the musculus longus colli anticus, a ventral flexor of the neck, inserted at the posteriorly pointed, and in *Dicraeosaurus* rather short, ends of the cervical ribs (GADOW-SELENKA 1891, p. 118).

Dicraeosaurus sattleri.

Presacral vertebrae.

Skeleton M.

Cervical vertebrae.

Sixth (?) cervical vertebra M 63. Fig. 61 a, b.

Preservation: The lateral laminae and the rim of the posterior articular condyle are missing on the centrum. Also missing are the parapophyses and diapophyses, the right prezygapophysis, the ends of the neurapophyseal branches, and most of the laminae of the neural arch or their rims.

Description: The largely preserved, strongly anteriorly jutting condyle had a somewhat transversely elliptical outline, ca. 8 cm wide and almost 6 cm in height. The height and width of the anterior end were slightly larger, the latter about 9 cm. The flanks of the centrum are almost completely occupied by very extensive pleurocentral pits, which reduce the median wall to 1.5 cm in thickness. The rather roundish diameter of the neural canal measures about 3-3.5 cm. Ventrally, in the most anterior section, the remains of a thin median lamina are found.

Fig. 61 a. Sixth (?) cervical vertebra of *Dicraeosaurus sattleri*. M63. Lateral view.
Fig. 61 b. The same, posterior view. a, Attachment knob of the nuchal ligament. 1/8 natural size.

As in *Dicraeosaurus hansemanni*, the neural arch is deeply incised to the roof of the neural canal. The roof is ca. 1.2 cm posteromedially, slightly less than 1 cm anteriorly, strong, and forms a rather wide, uniformly depressed groove. In its center, there is a ca. 3.4 cm long, anteriorly gradually flattening, posteriorly strongly bumpy protuberance, the insertion for the ligamentum nuchae. The prezygapophysis is a slim, steeply rising process, ventral to which lies a deeply inserted recess enclosed by the wall of the neural canal and the infraprezygapophyseal lamina. The prezygapophyseal facet is narrowly ovate and concave toward the steeply posteroventrally directed longitudinal axis. It inclines medially at an angle of 60° on average. The incompletely preserved neurapophyseal branches are narrow, thin, sharp-edged, and distinctly anteriorly inclined rods, the original height of which was obviously considerable. The incompletely preserved ventral continuation was very thin and lamellar down to the level of the neural canal. Dorsal to the unpreserved diapophysis, the lamella is deeply depressed toward the midline. The postzygapophyses grow with a horizontal dorsal edge as about 7 cm high, thin, platelike projections out of the bases of the neurapophyseal branches. The weakly convex, high, elliptical facets are steeply set in the postzygapophyses; the well-preserved right one has a length of 5 cm and a width of 3.2 cm. In lateral view the longitudinal axis rises very steeply anteriorly. The posterior contour rises steeply a further 3 cm above the dorsal rim of the facet and then turns with a rounded, slightly thickened

corner into the horizontal dorsal rim. Of the laminae of the neural arch, the steeply ventrally running prezygapophyseal lamina was rather strongly developed, judging by the preserved sections. Posterior to it, a recess deeply penetrates in the anteromedial direction. A comparison with the cervical vertebrae of *Dicraeosaurus hansemanni* suggested that vertebra M 63 is the 6th cervical vertebra according to the shape of the prezygapophyses and the inclination of the neurapophyses.

Eighth (?) cervical vertebra M 64 Fig. 62, a, b.

Preservation: The condyle and the rims of the posterior articular head of the centrum are incompletely preserved. The entire anterior part of the neural arch, the prezygapophysis, and the neurapophyseal branches are missing.

Description: The centrum is slim. The pleurocentral grooves are only weakly depressed on both sides, so that a relatively thick median wall persists. A central keel extends not exactly on the median plane, of which 3/4 of the posterior length are preserved. In addition a lateral ridge or edge (posterior centroparapophyseal lamina) was developed on both sides of the ventral surface. The preserved maximum length of the centrum is ca. 25.5 cm, and it was originally probably not more than 1– 2 cm longer. The overall dorsal length along the side measures almost exactly 22 cm. The median height of the posterior end of the centrum was ca. 8.5 cm, and its width cannot be determined but appears to have been slightly greater. The neural canal has a high, elliptical diameter. Its roof is ca. 1.5 cm strong posteriorly and forms a uniform, wide, longitudinal groove dorsally. The well-preserved right postzygapophysis is a dorsomedially slightly vaulted projection, which ends posteriorly in a curved, sharp rim. The rather flat facet inclines toward the midline at an angle of about 15°. It has a width of a good 5 cm, and its posterior end is indistinct. Anterior to the postzygapophysis, a very robust postzygodiapophyseal lamina extends anteroventrally, and a posteriorly, laterally, and dorsally positioned, moderately strong and low rim leads to the neurapophyseal branch. Comparison with the spinal column of D. hansemanni indicates that M 64 represents the 8th cervical vertebra.

Dorsal vertebrae.

Pl. V.

Only four dorsal vertebrae with neural arches and neurapophyses, three centra with insignificant remains of neural arches, three isolated neurapophyses, and two isolated neurapophyseal branches are present. The sequence of the four more complete vertebrae clearly results from the design of the neurapophyses, which shows a difference in the depth of the bifurcation in three vertebrae, whereas the fourth vertebra is not bifurcated.

Centra.

Preservation: The posterior rim of each centrum shows missing parts to various extents, and the rim of the anterior end is also incomplete in most cases. Several centra are laterally

compressed. The effects of this compression are also noticeable at the anterior ends of the centra in the form of cracks and displacement.

Description: The overall shape is very simple: constricted in the middle, with a ventrally rounded diameter and without any edges or pleurocentral grooves. The posterior end is always distinctly concave, the anterior end irregularly level and slightly convexly vaulted in its dorsal part. The contours of the end surfaces of vertebra M 9 are almost exactly circular; the anterior one has a estimated original diameter of 10–10.5 cm, the posterior one of 12 cm. The posterior end surface of M 10 is about 13 cm high and 12 cm wide. The posterior height measures ca. 16 cm in M 19, and the width is ca. 15 cm. The minimum thickness of the center of the centrum increases from 7 cm in M 9 to 8 cm in M 10, ca. 8.5 cm in M 45, and at least 10 cm in M 19. The dorsal lengths of these centra are consistently between 14–15 cm.

To determine the original sequence of the vertebrae, in addition to using the increase in the measurements of the end surfaces, the fact that a low depression is present in the most posterior vertebrae over half the height of their flanks was found useful. As these depressions are slightly more strongly expressed in M 37 than in M 19, I consider M 37 to belong to a more posterior position. The sequence resulting for the vertebrae is therefore M 9, M 11, M 10, M 45, M 12, M 19, and M 37.

Catalogue No.	Presumed position in vertebral column	Total length	Length of centrum minus anterior convexity (free	Width of anterior end of centrum	Height of anterior end of centrum	Width of posterior end of centrum	Height of posterior end of centrum	Entire height of vertebra	Distance between ends of diapophyses
			lateral surfaces)						
M 63		cm	cm	cm	cm	cm	cm	cm	cm
	6	$23.8 \pm$	20.6	90 ±?	7.2	—			—
M 64	8	25.1 (+)	21.8 ±		—	$10.2 \pm$	8.9		
M 9	17	15.2	—		—	—		$84.4 \pm$	$2x25.5 \pm$
M 17	18	14.8	—		—	—		84.5 +	$2x27.5 \pm$
M 10	19	15.9	13.8		12.6	11.7	12.9	89	
M 45	anterior	16.5 (+)	—		—	11.4 (+)	14.1 ±		
M 12	} dorsal		$18.8 \pm$			—		91.6 ±	$2x22 \pm$
M 19	y uortabraa	14.7	12.4	11.9 +	14.2	? 14.9	15.6		_
M 37	venteblae	14.2	12.3		—	—		—	—

Measurements of the presacral vertebrae of Dicraeosaurus sattleri, skeleton M.

Neural canal.

A transversely oriented bony wall descends ventrally between the longitudinally oriented bone walls forming the ventral portion of the neural arch; its lumen is 5.5–6 cm in height and ca. 3.5 cm in width. The descending wall is very thin in those vertebrae in which it is preserved. It roofs the neural canal in the median plane over a length of ca. 1.5 cm in M 9, over ca. 0.5 cm in M 11, and over ca. 1 cm in M 10.

Neural arch.

In the neural arch of the four more completely preserved vertebrae, and with their missing parts restored, the more delicate parts and the rims of the laminae are largely lost. The left diapophysis is missing in all four vertebrae, as is the right parapophysis and the left postzygapophysis in M 9, both postzygapophyses in M 11, the right diapophysis and the left parapophysis in M 10, and both parapophyses in M 12.

The entire neural arch is characterized by extraordinarily thin walls of the laminar system, very deeply recessed niches and fossae, and the extreme height of the neurapophyses.

Neurapophyses.

Of the two individual neurapophyseal branches, the distally complete left one has a length of 34.5 cm, and the right one, missing an end section estimated to be 7–8 cm long, has a length of 40 cm. Despite minor discrepancies, both could very well belong to the same vertebra. The overall shape is rod-like, the cross-section mostly irregularly four-sided. The narrow edges that enclose the median surface become indistinct distally, more proximally in the left branch than in the right one. An increase in width occurs proximally in the longer right branch, but only gradually, by a sharpening of the anterior edge and, to a greater degree, the posterior edge. The overall rounded, small distal terminal face is expanded ventrally more laterally than medially. The branches are strongly curved, which results in the distal ends facing slightly posteriorly. The proximal end of the right branch is only 5.3 cm wide and is thus still hardly expanded here, and therefore must have been very high.

Vertebra M 9 has two very high and slim neurapophyseal branches, whose free length was ca. 54 cm, and their point of bifurcation was positioned about 19 cm above the dorsal rim of the posterior end of the centrum. The neurapophyseal branches rise vertically, but in their dorsal half curve distinctly posteriorly. They also show a very slight lateral curvature in anterior view. The fact that the left neurapophyseal branch is more posteriorly curved than the right is probably due to deformation. The prespinal lamina is completely missing, but an incompletely preserved postspinal lamina is about 3 cm long. A weakly, longitudinally anteriorly vaulted spinodiapophyseal lamina is strongly developed in the dorsal half of the neurapophyseal branches; on the left side it reaches somewhat below the mid-height of the neurapophyseal branch, but can be traced much further down on the right side. The suprapostzygapophyseal lamina is well demarcated on the ventral half of the neurapophyseal branches, and faces obliquely posterolaterally here. On the left branch it can be traced as a posteromedial edge to the dorsal end of the ramus, but the right one is not as high. The suprapostzygapophyseal lamina emerges out of a flat area on the medial surface of each neurapophyseal branch. A special lamina arises out of the ventral third of this medial surface that leads to the dorsal end of the postspinal lamina. The anterior rim of the neurapophyseal branches is ventrally relatively sharp, but gets more and more broadly rounded dorsally. The distal end has a slight knob-like thickening, is slightly vaulted terminally, and shows an anterolaterally facing, facet-like slant that tapers ventrally.

The neurapophyseal branches of vertebra M 11 are quite similar to those of vertebra M 9, only shorter, with a free length of ca. 48 cm, and the bifurcation point is positioned higher, about 27 cm dorsal to the posterior end of the centrum. Accordingly, the unpreserved postspinal lamina must have been longer. Also, a short but irregularly running prespinal lamina is present. The dorsal ends of the branches are slightly carved anteriorly.

The neurapophyseal branches of vertebra M 10 lead up to the bifurcation point 52 cm above the dorsal edge of the posterior end of the centrum, and a depth only 24 cm beneath the undivided neurapophyses. The two branches are flat and wide, the wide surfaces being transversely positioned. The surfaces thin medially to an edge, which ends dorsally only below the distal end and is replaced by a ventrally pointed triangular area. The lateral margins of the triangle are formed by the well-developed, thin spinodiapophyseal laminae. Both neurapophyseal branches of vertebra M 10 are not completely identical, because on the left and slightly higher one the point of maximum thickness lies close to the medial margin, whereas on the right it lies more toward the middle. The neurapophyseal branches diverge ventral to their distal ends, which are in contact along a relatively well-expressed curvature. The prespinal lamina, which obviously also includes the supraprezygapophyseal laminae ventrally, is very robust.

It decreases in height dorsally, and the anterior margin terminates here on the floor of the crevasse between the branches, during the course of which the lamina thickens.

The entirely unbifurcated neurapophysis of vertebra M 12 shows the same distinctly cross-shaped cross-section as the posterior dorsal vertebra of *Dicraeosaurus hansemanni*. The well-preserved prespinal lamina is very thin and high, and the incomplete postspinal lamina was obviously similarly shaped. The neurapophysis is inclined anteriorly in the ventral half, but rather vertically above.

Of the three isolated neurapophyses, the least well-preserved one, of which only the dorsal 2/3 are present, is characterized by a weak, anteriorly concave curvature. It is probably derived from a vertebrae positioned anterior to M 12, and might belong to centrum M 45. Of the two other neurapophyses that are present with a complete length and also have the right postzygapophysis still attached, the better-preserved one shows a similar curvature to that of vertebra M 12. The poorly preserved neurapophysis probably ended up with too straight a shape when it was restored from numerous, partly ill-fitting pieces.

Prezygapophyses.

The prezygapophyses in M 9 project as more or less wedge-shaped, medially narrowing structures. They leave a medial gap ca. 2 cm wide and 2.5 cm deep for the zygosphene of the previous vertebra. The facets are only 2 cm wide, 9.5 cm long on the right side, and 10 cm long on the left. The lateral parts of the facets face posteriorly and slope medially at an angle of ca. 30°. The wedge shape of the prezygapophysis is less distinct in vertebrae M 11, M 10, and M 12, and they are generally thicker; as far as preserved, their facets are directed straight laterally. The width of the facets is slightly larger in M 10 and M 12; the angle of incidence is almost the same in M 11, but it cannot be determined in the two other vertebrae because of deformation. The gap for the zygosphene is slightly wider in these three vertebrae, and its depth is variable. It is remarkable that the facets of M 9 and M 11 are very slightly concave, which seems not to be the case for the incomplete facets of M 10 and M 12.

Postzygapophyses.

The postzygapophyses that are present in the four more complete vertebrae and the two isolated neurapophyses are quite similar to each other. They present medially fused, posteriorly sharpened wedges from which the suprapostzygapophyseal lamina emerges laterally. The postzygapophyseal facets which are attached to the unbifurcated neurapophyses show a weak concavity, whereas they are slightly convex on the bifurcated vertebra M 9. The zygosphene of vertebra M 9 has facets that converge dorsally at an angle of ca. 60°, whereas they enclose an angle of only 22° in M 12.

Diapophyses.

The only more or less well-preserved right diapophysis of vertebra M 11 is a flat, triangular, laterally acute wing that rises laterally at an angle of ca. 20°. It terminates laterally in an approximately triangular, rounded knob, under which lies the actual tubercular facet, which has the shape of a longish bulge. The centrodiapophyseal lamina is high and strongly developed, forming the largest part of the vertical posterior wall of the diapophysis, which only verv short to а

postzygapophyseal lamina is attached. The postzygapophyseal lamina was obviously much more strongly developed on the diapophysis of M 9. On this postzygapophyseal lamina a quite high, very thin supradiapophyseal lamina is additionally present. Two supradiapophyseal laminae are present on the left in vertebra M 10, and on both sides in vertebra M 12. In vertebra M 12, the preserved right postzygodiapophyseal lamina is extremely strong.

Parapophyses.

The left parapophysis of M 9 is an anteriorly vaulted plate running laterally and slightly ventrally from the prezygapophysis. The parapophysis carries a rugose, narrowly oval facet 6.5 cm long and 3 cm wide at ca. 5 cm from the prezygapophysis, which faces laterally and slightly anteriorly and whose vertical axis is very steeply positioned. The facets are positioned slightly higher in M 11, and still higher in M 10, just above the prezygapophysis.

Infradiapophyseal fossa.

The infradiapophyseal fossa is always very extended, occupying almost the entire available space anterior to the centrodiapophyseal lamina; in several cases its anterior margin is developed as a particularly peripheral lamina.

Positions of the individual dorsal vertebrae.

Combined with the observations on the centra and neurapophyses of these dorsal vertebrae, a comparison with the spinal column of *Dicraeosaurus hansemanni* provide clues for a more exact determination of their position. Accordingly, vertebra M 10 with only partial bifurcation of the neurapophysis can therefore be regarded with all certainty as the 19th presacral vertebra. A vertebra corresponding to the 18th of *Dicraeosaurus hansemanni* is not present. Vertebra M 11 might be the 17th vertebra and M 9 the preceding one, the 16th. Vertebra M 12, with unbifurcated neurapophysis as previously shown, should be inserted in the sequence M 45, M 19, and M 37 in an unknown position behind M 45. The three individual unbifurcated neurapophyses belong in the posterior five positions in the vertebral column. But the precise sequence of these specimens cannot be determined because of the narrow shape of the transverse processes. The vertebra to which to the two single, probably matching neurapophyseal branches belong must have been separated from dorsal vertebra M 9 by at least one vertebra.

Excavation site E.

Among the cervical vertebrae present, the incompletely preserved centrum E 4, with a total length of 15 cm and exposed neurocentral sutures, is derived from the posterior section of the neck. It must belong to a considerably smaller animal than the other cervical vertebrae, which can be matched so well by their size that there is no reason to assume that they did not all belong to the same animal. Of these specimens, E 16 is represented only by a centrum, but E 13–15 and E 27 possess tightly fused, more or less completely preserved neural arches. Only the isolated neurapophysis is preserved of the axis, and the neurapophyseal branches are missing in all other cervical vertebrae, along with the parapophyses and the most part of the lateral laminae. The diapophysis is only preserved on the right side of E 27, the prezygapophyses in E 14, 15, and 17, and the postzygapophyses in E 27, E 36, E 37, and E 4 are on the centra of dorsal vertebrae with free neurocentral sutures, from which the neural arches have separated.

Cervical vertebrae.

Pl. 63–67.

Centra: The order of the 6 cervical vertebrae derives, without doubt, from their changing measurements, from the posteriorly increasing diameter of the condyle and the posterior articular cavity, and in conjunction with the at first increasing, but in the most posterior cervical vertebrae again decreasing length of the centra. The sequence is E 13-E 17, E 27. As the table of measurements shows, the length of the vertebrae increases very much from E 13 to E 14, only slightly from E 14 to E 15, remains almost the same as in E 15 in the three following vertebrae, and has decreased again in the last one, E 27. The condyle is attached to the centrum with a strong ventral inclination that is the largest in the anteriormost vertebra. When well preserved, as in E 14 and E 15, the centrum shows a somewhat cone-shaped tapering. It also shows a depression in the condyle, which lies above the apex of the vault in E 14 but only slightly ventral to it in E 15. The basal, collar-like rim that surrounds the condyle is preserved in E 15. The posterior cavity in the

Cervical vertebrae of *Dicraeosaurus sattleri*. Fig. 63. Third cervical vertebra E 13. Fig. 64. Fourth cervical vertebra E 14. Fig. 65. Mid-cervical vertebra E 15. Fig. 66. Mid-cervical vertebra E 16. Fig. 67a. Twelfth cervical vertebra E 27 in lateral view. Fig. 67b. The same, posterior view. a = Knob for origin of the nuchal ligament. 1/8 natural size.

centrum is deeply depressed and irregularly shaped because a short, transversely positioned groove is developed at its deepest point. The pleurocentral grooves, which significantly reduce the actual mass of the centra, are deeply recessed posterior to the condyle, but are transformed into much lower depressions posteriorly that are not very distinctly delineated ventrally and posteriorly. In the anterior cervical vertebrae, the posterior half of the centrum has a narrow and rounded cross-section, which continuously widens along the vertebral series due to the dorsally diverging flanks, and which by E 27 is highly trapezoidal due to large, deeply depressed cavities. A median keel is always present on the ventral surface of the centra which extends over the anterior half or slightly further. The lateral margins of the ventral surfaces form mostly incompletely preserved edges, the posterior centroparapophyseal laminae. Between these laminae, and also between them and the median laminae in the anterior part of the centrum, the surface is more or less deeply depressed to form a longitudinal furrow. The lateral laminae are positioned slightly higher in the last vertebra, E 27.

The n e u r a 1 a r c h e s show the deep median incision reaching down to the roof of the neural canal that characterizes the genus. In E 14, a knob for the attachment of the nuchal ligament is preserved. It shows a posteriorly directed, rugose, 1.4 cm rising wall and descends anteriorly as an uneven surface that is extended into a median keel. The posterior surface of the knob sits roughly in the middle of the roof of the neural canal. A step that rose behind the middle of the thin roof of the neural canal, and which must have been higher than 1.2 cm, is visible in the first vertebra, E 13. As far as is discernible, the median rising walls of the postzygapophyses did not meet ventrally at an acute angle, but enclosed a rounded groove between them.

The prezygapophyses in E 14 and E 15 are represented by anteriorly rising, far projecting ledges—which taper off broadly posteriorly and form a surface lateral to the supraprezygapophyseal lamina that is concavely depressed in E 19, but more level and horizontal in E 15. Ventrolateral to this surface runs an almost sagittally positioned wall that is only about 1.5 cm high, the sharp ventral margin of which forms the actual prezygapophyseal lamina. The facets, which have a rounded outline and a diameter of just 3 cm in E 15, incline steeply medially. The prezygapophyses are shorter and already positioned more steeply in E 17. The strong anterior rim of the neurapophyseal branches rise vertically about 2 cm posterior to the posterior margin of their facet.

The postzygapophyseal laminae, which are only present in E 27 and even here with their margins incompletely preserved, are rather strong plates, projecting posteriorly with a roundish contour beyond the line of the vertically rising infrapostzygapophyseal laminae. As can be seen in the right postzygapophysis, their very weak convex facets have a dorsoventral extent of ca. 5.5 cm, a transverse extent of 4.5 cm, and incline ventrally at about 50°.

Of the diapophyses in E 13–15 and E 17 only the remains of their laminae that cross each other are preserved. In E 13 it is clearly visible that a postzygapophyseal lamina was not present. Therefore, by analogy with *D. hansemanni*, this vertebra must be regarded as the 3rd presacral vertebra, an opinion that agrees with the proportions relative to the other cervical vertebrae. The laminar system that supports and forms the right diapophysis is well preserved in E 17, but the distal descending end that bears the facet is completely missing. The prezygapophyseal lamina and the posterior centrodiapophyseal lamina lie almost in one plane and form a uniform, anteriorly rising at an angle of ca. 35°, level lamina, in which only the outer rim of the first mentioned lamina curves slightly laterally. Perpendicular to this lamina, which is steeply posterodorsally positioned, stands the strongly developed postzygapophyseal lamina. The short but still much stronger anterior centrodiapophyseal lamina runs almost exactly on its extension.

The position of the diapophysis, the inclinations of the laminae, and the shortness of the centrum of E 17 are in agreement with the 12th presacral and last cervical vertebra of *D. hansemanni*, and I assign the vertebra to the same position. The four remaining cervical vertebrae can be placed between the 3rd and 12th presacral vertebrae. Judging by the condition in *D. hansemanni*, vertebra E 14, which is much shorter than the mid-cervical vertebrae, must be the 4th. According to the form and circumference of the end surfaces, the distance between E 17 and E 27 is apparently so great that at least two missing vertebrae must be assumed in-between them. Vertebrae E 15, 16, and 17 therefore must be placed in the section between the 5th and 9th presacral vertebrae.

Axial neurapophysis.

A 17 cm long rod of bone, incomplete at its margins, forming a wand of triangular cross-section, is regarded as the axial neurapophysis, as shown by comparison with *Dicraeosaurus hansemanni*. The anteromedian edge shows an acute angle ventrally, but is flattened out dorsally. The original width cannot have exceeded 4.5 cm at 6 cm below the bumpy dorsal terminal face, which is only preserved to a small extent. The posterior surface is almost level dorsally. More ventrally, a longitudinal depression is added that is enclosed laterally by the converging insertions of the suprapostzygapophyseal laminae. In the ventralmost, ca. 2 cm long section, a particularly well-developed depression is found on both sides that encloses a median crest, i.e. a short postspinal lamina extending dorsally along a very low curve over half the length of the bone.

Dorsal vertebrae.

Dorsal vertebrae E 36 and E 37 are almost undeformed, and they are evenly constricted in their central section. In the thicker one, E 37, which must have been placed behind E 36, a flat, wide depression is visible dorsolaterally. The nearly level anterior faces show centrally positioned, rounded depressions. Depression of irregular shape and greater depth are found in the center of the strongly concave posterior faces. Although these two centra may originate from the middle of the trunk, the obliquely sheared centrum E 4 with an irregular, very insignificant concave anterior face and a deeper dorsolateral depression is probably the last dorsal vertebra.

Catalogue	Position	Entire length of centrum at mid-	Free dorsal lateral length of centrum	Height of anterior end	Height of posterior end	Width of anterior end	Width of posterior end
no.		half incl. condyle	without condyle	of centrum at median level	of centrum at median level	of centrum	of centrum
E 13	3	14.0 ±	13.0	5.0		4.9 +	_
E 14	4	$18.3 \pm$	16.6	5.0	_	5.2 +	
E 15		20.6 (±)	17.8	6.6 (+)	7.2 (±)	6.3 +	9.2 (+)
E 16	5–9	21.1(+)	18.3 (+)	5.9+	7.3 +	-	7.8 +
E 17		$21.6(\pm)$	19.3	7.2	8.4 (±)	7.4 +	9.2 (±)
E 27	12	18.0 +	15.8	9.1 +	$10.3(\pm)$		$11.2 \pm$
E 36		13.6	_	10.2	10.3(+)	10.3 (±)	11.4
E 37		13.4 (+)	—	11.6	_ ()	11.2(+)	
E 4	24 (?)	14.0	—	$13.8 \pm$		15.9 ±	

Measurements of the presacral vertebrae of *Dicraeosaurus sattleri* from excavation site E.

Affiliation of cervical and dorsal vertebrae.

The assignment of the cervical vertebrae from E to *Dicraeosaurus sattleri* is confirmed by the slim design of the centrum. The dorsal vertebrae also perfectly match the dorsals of skeleton M.

The question now arises as to whether these cervical and dorsal vertebrae belong to one individual. The cervical vertebrae from M surpass the cervicals from E in length by ca. 1/10. Such a size difference is not obvious in the dorsal vertebrae from both sites. However, when taking the deformation of the vertebrae from M into account, and comparing them with the undeformed centrum M, a size difference also results for the dorsal vertebrae. In addition, the exposed neurocentral sutures in the vertebrae from E demonstrate that these vertebrae originate from a younger animal. The affiliation of the cervical and dorsal vertebrae from E is considered as most likely.

Isolated dorsal vertebrae from other localities.

Dorsal vertebrae from excavation site O.

The centrum O 12, the margins of which are all eroded, is slightly compressed, which probably reduced is ventral length slightly but not its dorsal length, which must have been more then 12 cm. The anterior face is nearly level, and slightly vaulted anteriorly in the center of the dorsal part; the original height was somewhat over 10 cm, and the width measures hardly less. The posterior face is decidedly concave. The strongly constricted center part of the centrum has a simple, roundish diameter of 7.3 cm minimum thickness. The flanks show a weak, wide depression dorsally that extends onto the preserved left lateral wall of the neural canal, which rises dorsally and still exhibits remains of the suture. The relatively considerable thickness of the center part indicates that the centrum belongs to a vertebrae from the posterior half of the trunk.

The affiliation of this centrum to a dorsal vertebra that is derived from a not fully grown animal of *Dicraeosaurus sattleri* can be inferred, not from its shape, but from the associated limb bones.

Dorsal vertebral centrum from excavation site Ob.

The poorly preserved centrum of dorsal vertebra Ob 25, which has a crushed upper section and is altogether slightly obliquely deformed, shows a dorsal length of about 14 cm, and the average height of the deeply concave anterior end surface measures ca. 12 cm. The poor preservation does not allow determining its position within the column with certainty. The assignment of this dorsal vertebral centrum to *Dicraeosaurus sattleri* is not evident from the morphology. It was mentioned under this species because excavation site Ob probably lies in the Upper Saurian Bed.

Sacrum.

Skeleton M.

Pl. VI.

Considering of the complexity of the sacrum, the deformation is not significant. The neurapophyses almost completely lack the spinodiapophyseal laminae, while only small pieces of the spinal laminae are lost. The transverse processes, however, are only very incompletely preserved.

Centra.

The sacrum contains the normal number of five centra, which are tightly fused. The centra form a rod that curves ventrally. Whether this curvature was caused by deformation and compression that occurred in several places, or was at least enhanced by them, cannot be determined with certainty, but an originally present flexure certainly could have been intensified by such forces. The anterior face of the 1st sacral vertebra, which is compressed to a slightly oblique contour, was obviously once approximately circular. The diameter was about 17 cm and the ventral two-thirds of the surfaces were slightly concave. The posterior face of the 5th sacral vertebra is ca. 17.5 cm wide and 15.5 cm high, i.e. slightly transversely elliptical, but this shape might also have been affected by pressure. The posterior face is angled such that its surfaces faces posterodorsally. The dorsal margin extends significantly above the base of the neural canal. The fused areas, particularly visible in the terminal vertebrae of the sacrum, show a partially undistorted transverse width of about 13 cm between the first two and last two sacral surfaces in the 1st and last vertebra are broadly rounded, however they are narrowly compressed in the central vertebrae. There is no trace of pleurocentral grooves. The length of the series of five fused sacral vertebrae measures 67.2 cm ventrally.

Neural arches.

The anterior end of the first neural arch is similar to that in the posterior dorsal vertebrae, but its prezygapophyses barely project anteriorly. The five fused neural arches show fenestrae laterally between the individual vertebrae arising from the base of the neural canals, the fragile rims of which are mostly not preserved. The fenestra between the first two vertebrae is about 7.5 cm high and 3.5 cm wide, and narrows dorsally. The 2nd fenestra is enlarged because of loss of the peripheral areas, and therefore its size cannot be assessed. The 3rd fenestra is 11 cm high on the right side, and the last one is 7 cm in height and probably had a high, elliptical outline. The ventral part of the neural arch of the 1st sacral vertebra is similar to those in the posterior dorsal vertebrae, with a ca. 6 cm high gap cut out for the spinal cord in a ca. 4 cm thick transverse wall .

The lumen of the neural canal in the second sacral vertebra is slightly taller, ca. 8 cm, but shows only a dorsal length of 2 cm. The rim of the neural canal is not preserved in the 3rd vertebra, but was obviously sharply edged laterally and dorsally. These sharp edges are the result of a strong thinning and reduction of the transverse wall, and this is related to a vesicular inflation of the dorsal parts of the intervertebral cavities between the 2nd and 3rd, and the 3rd and 4th sacral vertebrae. In the first of these two inflations, the height of 16 cm hardly represents an increase compared to the distance between the base of the neural canal and the level of the prezygapophysis in the 1st sacral vertebra. But such an increase in height seems to have taken place in the succeeding intervertebral cavity, with an estimated height of 18 cm. Particularly striking is the lateral expansion, estimated at about 12 cm in both vertebrae. According to the preserved part of the wall, the two intervertebral cavities between the 2nd and 4th sacral vertebrae must have had a dorsally rounded, vesicle-like shape, and were characterized by a strongly expanded volume compared with the intervertebral cavities of the posterior dorsal vertebrae. On the posterior surface of the 4th sacral, the neural canal shows the usual form of a laterally compressed tube of 6 cm length and 7.5 cm height. It is similarly shaped in the 5th sacral vertebra, the dorsosacral, in which the posterior exit is 6 cm high.

Neurapophyses.

The neurapophyses of the three central sacral vertebrae are fused along their entire length. They form a very thin median bony wall that rises for about 64 cm above the level of the zygapophysis, and has a minimal ventral length of 19.5 cm and a dorsal length of ca. 35 cm, including the restored anterior prespinal lamina. The preserved ventral margin of the prespinal lamina of the 2nd sacral vertebra curves anteriorly, whereas the margin of the postspinal lamina of the 4th vertebra rises almost vertically. Only short ventral sections of the spinodiapophyseal laminae are preserved. The suprapostzygapophyseal laminae of the 4th sacral vertebra are clearly, yet delicately, developed. The neurapophysis attached to the 1st sacral vertebra was found isolated, but the contour fits so perfectly onto the anterior contour of the 2nd neurapophysis that there can hardly be any doubt that it belongs to it. This neurapophysis is shaped exactly like the neurapophyses of the dorsal vertebrae, but is characterized by the inclination of the ventral part extending over 2/3 of its length and only rising straight in the dorsal 1/3. The neurapophysis of the 5th sacral vertebra is characterized by a strong posterior curvature, which appears at mid-height. This neurapophysis rises for about 60 cm above the incompletely preserved postzygapophyses. At the base of the prespinal lamina, the individual supraprezygapophyseal laminae are still independent. The 3rd sacral vertebra has a total height of 97 cm including the neurapophysis, the 5th a total height of 80.5 cm.

Lateral processes.

A ca. 4.5 cm high and 2.5 cm thick bar must be regarded as the isolated diapophyseal part of the first lateral process. It has a rounded lateral face, and its cross-section is shaped like an inverted V medially, toward the fractured end. The 3rd diapophysis has an irregular U-shaped profile. The dorsally thin, horizontal beam is for the most part ca. 7 cm wide, reaching a maximum height of 2.5 cm and projecting transversely out of the median plane for ca. 31.5 cm. The diapophysis of the 4th sacral vertebra is by contrast a distally narrow, 2-3 cm thick rod with a rounded dorsal surface, which thins medially to form the well-developed supradiapophyseal lamina that in turn grades dorsally into the spinodiapophyseal lamina. On the anterior surface, the dorsal margin protrudes on its posterior surface, and the insertion of a lamina is visible ventrally. The more complete left diapophyses is directed rather strongly horizontally and posteriorly, and projects for ca. 33 cm out of the median plane. The lateral processes are naturally the robust ventral parts that insert on the centra, the best preserved parts of it. This capitular, bulky part with an irregular square cross-section is positioned posterior to the dorsal half of the anterior rim in the 1st vertebra. It sends out a dorsally and laterally rising plate, only preserved anteriorly in its ventral part, which also extends obliquely dorsolaterally and thereby makes contact with the capitular section of the 2nd lateral process. This 2nd lateral process is slightly more deeply positioned and has a more triangular cross-section ventrally. The corresponding parts in the 3rd and 4th vertebrae are similarly designed, but these show a ventral, posterolaterally running crest. These three capitular sections increase greatly in strength laterally and fuse here to form the strong, rod-like, structure that curves strongly toward the central sacral vertebrae, which carries the ilium on a ventrolaterally facing surface. Only the incomplete peripheral areas are preserved of the thin, extensive bone lamellae that rise dorsally from the capitular parts. The lateral process of the 5th sacral vertebra, of which the diapophyseal part is missing on both sides, is represented by a very strong bony plate. Only the ventral part is preserved, which is inclined anterolaterally. Its capitular part is very moderately developed.

It is closely attached to almost the entire lateral height of the centrum. The capitular part of the 5th sacral vertebra sends a strong process to the lateral part of the 4th lateral process. This projection rises steeply posteriorly, and toward the end the rim extends into a roundish surface of ca. 8 cm diameter, which takes part in forming the attachment site for the ilium.

Caudal vertebrae.

Skeleton M.

Pl. VII.

Seven posterior and one mid-caudal vertebrae are present from skeleton M.

Anterior caudal vertebrae.

The centra are completely preserved, except peripheral parts in the 2nd, 4th, and 6th vertebrae, which are lost. The entire length of the neurapophysis is preserved in the 6 anterior caudal vertebrae; a short, distal section is missing only in the 5th. A ventral section of the neurapophysis of the 7th vertebra is missing and was restored with plaster. The thin parts of the medial and lateral laminae of the neurapophyses are often not preserved. The prezygapophyses are only preserved in the 3rd and 4th caudal vertebrae on both sides; they are partially preserved on the right side of the 1st one. In the 1st and 7th vertebrae, the postzygapophyses are missing on both sides, and in the 5th caudal vertebra only on the right side. The lateral processes on the right of the first two caudal vertebrae are lost completely and are only incompletely preserved on the left side, as on both sides of the 3rd vertebra and the right side of the 5th. The left side of the 5th and 7th vertebral centra are deformed by compression to a small degree. The deformations on the neural arches are insignificant.

Sequences.

The sequence of the caudal vertebrae is clearly recognizable by their dimensions and shapes. Vertebrae 4–7 were found in situ. Moreover, the 3rd vertebra lay behind the 2nd in natural sequence. It follows clearly from the stepwise decrease in height of the neurapophyses, and the increase in lateral expansion of the lateral processes, that no vertebra is missing, either between the 1st and 2nd, or between the 3rd and 4th. The fact that the 1st vertebra is indeed the one following the sacrum results from the length of the neurapophysis.

Centra.

The heights of the centra exceed their widths. These proportions change along the sequence, as the width decreases much less than the height. The anterior and posterior faces have an almost circular outline, and the anterior ones are consistently strongly concave with a peculiar small, more or less central depression. The anterior margin of the centrum of the 1st vertebra projects anteriorly. Moreover, the posterior end surface is planoconvex on the centrum of the 1st vertebra with a hint of a cone-shaped tip. The convexity decreases in the next following vertebra and has almost completely disappeared from the 3rd vertebra onward. Hence, these vertebra must be termed planoconcave. The centra of all vertebrae are strongly constricted laterally. A ventral, rounded keel is visible on the 1st vertebra. The succeeding vertebrae

show a more or less clearly delineated, median, narrow longitudinal surface and a median longitudinal depression from the 4th vertebra onward, which is deeper and more like a furrow in the last vertebrae. Chevron attachment facets are present on the posterior margin of the centrum from the 1st vertebra onward. No longitudinal ridges or edges are present on the centra of these vertebrae, nor is there any trace of pleurocentral grooves.

Catalog no.	No. in vertebral column	Length of centrum, dorsal	Length of centrum, ventral	Height of anterior end of centrum	Height of ventral end of centrum	Width of anterior end of centrum	Width of posterior end of centrum	Entire height of vertebra	Largest width dorsal to lateral processes
M 18 M 35 M 36 M 13 M 14 M 15 M 16	1 2 3 4 5 6 7	13.6 cm 11.4 10.9 10.8 11.1 10.6 11.2	? ? 10.1 cm 9.9 8.7 9.4 10.6	$15.2 \text{ cm} \\ 15.6 \pm \\ 13.4 \\ 12.1 \\ 10.4 + \\ 11.5 + \\ 11.3 \\ 1.5 + \\ 11.3 \\ 1.5 + \\ 1.5 + \\ 1.3 \\ 1.5 + \\ 1$	14.6 cm 13.9 12.6 11.1 11.1 11.2 10.5	17.7 cm 16.6 (?+) 16.7 16.2 14.4 + 14.5 12.1 +	15.5 cm 15.2 14.4 14.3 13.4 (+) 14.0 13.3	82 cm 78 72 66 ? 54 ?	35 cm 31 (+) 26 + 24 20
M 17	?	13.4	13.4	9.4	9.4	10.3	9.7	?	

Measurements of the caudal vertebrae of Dicraeosaurus sattleri, skeleton M.

Neural canal.

In the 2nd vertebra, the anterior opening of the neural canal is highly elliptical, being ca. 4.9 cm high and 3.7 cm wide. The anterior and posterior openings in the following vertebrae are almost circular, with a diameter that decreases to ca. 3.2 cm in the 7th vertebra. A flat, longitudinal depression is always present in the mid-section of the floor of the neural canal.

Neurapophysis.

The neurapophysis of the 1st caudal vertebra shows the same extraordinary height as the neurapophyses of the sacral vertebrae, and the height of the neurapophysis decreases quickly, being reduced by about one-third of its free height in the 6th caudal vertebra. Measured from the base of the posterior end of the neural canal, the height is ca. 66 cm in the 1st caudal vertebra, and ca. 40 cm in the 6th. In all vertebrae the neurapophyses are strongly inclined, although in the anterior vertebrae they rise vertically from the centrum, curving gently posterodorsally. By the 6th vertebra, the neurapophysis angles straight posterodorsally. The prespinal laminae are much more defined than the postspinal laminae, but this difference diminishes in the posterior vertebrae. The spinodiapophyseal laminae are greatly widened dorsally in the anterior vertebrae, and their lateral margin is positioned posteriorly so that both neurapophyseal laminae describe a posteriorly concave curve in cross-section. The width decreases permanently and was obviously insignificant in the 7th vertebra.

Prezygapophyses.

The only well-preserved prezygapophyses of the 3rd and 4th vertebrae are directed slightly anterodorsally and show facets that steeply incline toward the midline. The character of these facets is not identical, as the facet on the right side of the 3rd vertebra is slightly concave, whereas the right one in the 4th vertebra is distinctly convex.

Postzygapophyses.

The postzygapophyses insert laterally underneath the strongly thickened suprapostzygapophyseal laminae, and are ventrally fused along the midline above the neural canal. Their facets incline medially at an acute angle of ca. 65° in the 2nd and 3rd vertebrae, but are positioned less steeply in the succeeding vertebrae.

Lateral processes.

In the 7 anterior caudal vertebrae the lateral processes (caudal ribs) are represented by transversely positioned walls that are obliquely attached to the vertebrae and show a more or less rectangular shape. Their ventral and dorsal margins rise dorsally, while their lateral margins are steeply dorsomedially positioned. The lateral extent decreases faster than the height along the sequence of 7 vertebrae. The slightly medially curved ventral rim is particularly strong in the anterior vertebrae. The lateral and dorsal margins, which are only preserved from the 4th vertebra onward, are reinforced, forming a lamina that is positioned transverse to the square dimension. The central parts of the lateral processes are strongly thinned in the 3rd and 4th vertebrae due to concave depressions, much more so on the right side than on the left. The posterior end is almost level in all vertebrae along the sequence, and the lateral processes are increasingly transformed into thick, plump, descending, ventrally strengthened bulges.

Mid-caudal vertebra M 17.

The neurapophysis, the ends of the postzygapophyses, and the right prezygapophysis are missing in M 17. The distinctly biconcave centrum is almost as high anteriorly and posteriorly as it is wide. It shows a hexagonal cross-section that results from a distinct ventral surface and a longitudinal ridge that runs slightly above the midline of the flanks. The mid-section of the centrum is moderately constricted. The left prezygapophysis narrows anteriorly, and the outer surface is longitudinally vaulted and bears a longish, level facet that inclines medially at an angle of ca. 45°. Nothing substantial can be said about the neurapophysis because of incomplete preservation.

> Fig. 68 a. Mid-caudal vertebra of *Dicraeosaurus* sattleri M, lateral view.
> Fig. 68 b. The same, anterior view. 1/8 natural size.

Caudal vertebrae from locality O.

Centrum O 17, which shows severely eroded margins, has very distinct lateral ridges and a widened, flat ventral surface that is clearly marked by edges. Both end surfaces are concave. The ventral length of O 17 is ca. 10.5 cm. The width of the posterior end surface measures 8 cm, and the original height can be estimated as about the same. The vertebra must have been positioned within the transition into the more elongated vertebrae of the mid-section of the tail.

Ribs.

Skeleton M.

Material and preservation: The skeleton includes a larger number of incomplete dorsal ribs and parts of dorsal ribs, which were found incompletely embedded in the matrix, or were restored from weathered-out surface fragments. The positions in the ribcage of the 10 specimens, in which the proximal bifurcation is more or less completely preserved, can be estimated in parts when compared with the completely preserved right rib series of *Dicraeosaurus hansemanni*. The approximate positions of the distal sections of the ribs could also be determined.

Ribs of Dicraeosaurus sattleri. Skeleton M.

Fig. 69. 12th cervical rib M 27. Fig. 70. Mid-dorsal rib M 25. Fig. 71. Mid-dorsal rib M 38. Fig. 72. 11th dorsal rib M 23. 1/10 original size.

Description: The design of the ribs is in general comparatively light and slim. A left dorsal rib, M 27 (Fig. 69), is identified with certainty. The expanded proximal part is evenly depressed posteriorly, and the sharp outer rim gets stronger only shortly behind the longitudinal, 2.2 cm wide tubercular facet. The incomplete capitulum is much stronger, being positioned at an angle of 125° to the main axis. An extremely thin lamina spans between both processes in a gentle curve. As in the rib of the 12th presacral vertebra of *Dicraeosaurus hansemanni*, the lateral margin shows a narrow, facet-like blunt area in the region where the proximal rib shaft widens. The curved ridge that borders the lateral surface in the area of the proximal expansion is very well defined; at its distal end a striking furrow extends over a certain distance close to the medial margin. The shaft is very slim, narrows gradually distally, and at the fracture that lies 36.5 cm from the proximal end shows an oval, laterally acute cross-section of 2.3 cm length and 1.7 cm width. By analogy with *D. hansemanni*, this rib must be regarded as the 12th, and thus the last cervical rib.

Nothing is preserved of the first dorsal ribs. The poorly preserved proximal rib section M 31, and the 70 cm long distal section M 24, probably originate from the area between the 3rd and 5th dorsal ribs. M 31 shows a minimal width of 4.5 cm and achieves a width of 6 cm more distally; M 24 is 7 cm wide and narrows toward the distal fracture to hardly 1 cm. A proximal half, M 39, might originate from the 5th or 6th dorsal rib. The strong capitular process shows a pathological thickening at the insertion with cross-section the shaft. The of the shaft below the is just

triangular bifurcation, with an only 3.8 cm wide base and a broadly rounded posterior prong. Distally the cross-section gets flatter and wider very quickly.

Fragments that must have belonged to more posterior ribs show a much weaker tuberculum. The capitulum of the right proximal rib half M 25 (Fig. 70) extends very steeply from the longitudinal axis, at a maximum angle of 135°. The shaft widens from the 3.8 cm narrow neck of the rib to only 5.2 cm; this fragment may represent the 6th, 7th, or 8th rib. The right rib M 38 (Fig. 71), 77 cm of which are preserved, is similarly shaped and shows a minimal width of 3.8 cm in the neck section, and a maximum width of 5.8 cm distally.

The distal ends of the ribs from the posterior part of the trunk must have been plate-like and very thin, as shown by a 5-mm-thick fragment. The posteriormost ribs possessed an even slimmer shaft that had the tendency to gain a high cross-section immediately below the proximal expansion. This is demonstrated by the short right proximal fragment M 65, which probably originated from the 10th dorsal rib. Here the shaft shows a blunt longitudinal edge on the anterior surface, and a much more distinct keel on the posterior surface.

In this specimen too, a pathological inflation of the capitulum is present. The high cross-section is even more distinct in the almost entirely (64.5 cm disregarding the curvature) preserved rib M 23 (Fig. 72), which represents the 11th dorsal rib, as comparison with the ribs of *Dicraeosaurus hansemanni* shows. The relatively short and strong capitulum, to which the thin and gently curved intermediate lamina is attached, is crushed towards the shaft. The shaft has a cross-section of 3.3 cm in height and 2.0 cm in width just below the bifurcation. The height of the cross-section first decreases slightly and maintains this height for a longer distance, followed by an increase in height due to sharpening of the anterior edge. The distal end flattens toward the fracture to a thickness of 0.5 cm with a width of 2.1 cm. In anterior view the rib shows strong curvature of the distal half. Another proximal rib fragment, M 21, obviously belongs to the left 11th dorsal rib, despite its slightly higher cross-section.

A comparison of the ribs of *Dicraeosaurus sattleri* with those of *D. hansemanni* shows that the former, even though of similar design in general, have a considerably slimmer and lighter build, as demonstrated e.g. by the 12th rib. In particular, they possess much thinner and weaker terminal sections.

Fig. 73 a. Chevron of *Dicraeosaurus sattleri*. Skeleton M, lateral view. Fig. 73. b The same, posterior view. 1/6 original size.

Chevrons.

Skeleton M.

Out of the 5 available chevrons, two are preserved for almost their entire length but possess only the right proximal ramus, while both rami are missing in the other three. When arranged according to the decreasing strength at the bifurcation point, an evenly increasing curvature is visible. The most anterior chevron is straight and distally strongly flattened. In comparison with the chevrons of *D. hansemanni*, the specimen may represent the 2nd chevron because it is too long and narrow to be the 1st. The next chevron is gently curved and the distal part is thicker. Apart from a variable curvature, the three other chevrons show a proximal flattening of the shaft which expands proximally from specimen to specimen. chevron 73 a, b)

has a length of 24.5 cm, to which only a very small missing end section should be added; the depth of bifurcation is 5 cm. The strangely laterally compressed left ramus widens mediolaterally to form the facet, which is 4.4 cm long and 3.3 cm wide, but does not touch the facet of the right side medially. A shallow depression, starting at the point of bifurcation, can be traced distally on the anterior margin to beyond mid-length. The distalmost end tapers somewhat and the anterior margin becomes thicker. Compared with the chevrons of *D. hansemanni*, these are of lighter and slimmer build and also more strongly curved.

Caudal vertebrae from *Dicraeosaurus* of uncertain species affinities.

Caudal vertebrae from excavation site GD.

The vertebral series from the Upper Saurian Bed of Tendaguru includes 17 entirely undeformed, and for the most part complete, centra of anterior and mid-caudal vertebrae. Parts of the neural arches are preserved in four vertebrae. The dorsal length ranges from 11.0 cm for an anterior and 12.6 cm for a mid-caudal centrum. The median height of the posterior end surfaces

Anterior caudal vertebrae of Dicraeosaurus sp.

Fig. 74a. GD 12, lateral view. Fig. 74b. The same, ventral view. Fig. 75a. GD 7, lateral view. Fig. 75b. The same, ventral view. Fig. 76a. GD 8, lateral view. Fig. 76b. The same, ventral view. Fig. 77a. GD 14, lateral view. Fig. 77 b. The same, ventral view.

1/8 nat. size.

ranges from 12.4 cm in an anterior and 8.8 cm in a posterior caudal centrum. The anteriormost centra show smooth, ventrally converging flanks and a median ventral furrow between the strongly defined projections, which carry the chevron attachment facet. The next following vertebrae show a squarer cross-section, as in vertebra GD 12 (Fig. 74). The central mid-caudal vertebrae show distinct lateral edges and a ventral flattening. The three centra GD 7, GD 8, and GD 14 (Fig. 77) show the increasingly narrow and flattened ventral surface when arranged in series from anterior to posterior. The basal part of neural arch preserved vertebra The vertebra the in GD 1. is

has a median height of 12 cm at the posterior end of the centrum. The lateral process attached to the neural arch is ca. 7 cm high. The lateral process is positioned so high that only a small fraction of its height reaches down below the posterior upper rim of the centrum. This vertebra was probably the 7th caudal, or one close to the 7th. The high position of the lateral processes argues for an assignment to *Dicraeosaurus sattleri*.

Catalogue no.	Dorsal length of centrum	Ventral length of centrum	Median height of anterior end of centrum	Median height of posterior end of centrum	Width of anterior end of centrum	Width of posterior end of centrum
G D 12	11.0	10.7	10.8	11.2	13.0 (+)	12.1 (+)
G D 7	11.9	11.9	10.4	10.3	11.6 (+)	11.0
G D 8	12.0	12.0	10.1 (+)	10.5	11.4	10.8
G D 14	12.4	12.2	9.5 (+)	9.0	10.2 (+)	10.1

Measurements of the illustrated caudal vertebrae of site G D.

Caudal vertebrae from excavation site Ob.

16 poorly preserved caudal vertebrae are available from the Upper Saurian Bed at Obolello, southwest of Tendaguru, which come from the anterior section and the anterior part of the mid-section of the tail. The centra from the mid-section of the tail show distinct lateral edges, and a ventral flattening when sufficiently preserved. Due to insufficient preservation there is not enough evidence for identification of the species.

Caudal vertebrae La.

The small collection of the deceased Captain LADEMANN from the Tendaguru region, which has been commendably donated to the Geological-Paleontological Institute and Museum of the University of Berlin by his sister Miss BIANKA LADEMANN, includes a number of caudal vertebrae of *Dicraeosaurus*, among others. Details of their stratigraphic position are unknown. These are vertebrae belonging to two animals of different sizes, which must originate from the same locality, as evidenced by their strikingly similar light coloration.

A complete anterior vertebra with a length of ca. 12 cm and an anterior height of more than 14 cm belongs to the larger of the two animals, in addition to fractions of four slightly smaller anterior vertebrae and a fairly complete mid-caudal vertebra with a distinct lateral edge, being ca. 12 cm long and a generous 10 cm high.

A sequence of 16 caudal vertebrae belonging to the smaller of the two animals includes vertebrae from the posterior part of the anterior section of the tail, which still show a square cross-section but already have visible lateral edges. Also belonging to this series is a larger number of mid-caudal vertebrae with well-developed lateral edges and flat ventral surfaces, as well as one complete and two half-complete centra from the anterior part of the posterior section of the tail. Their lengths vary between 9 and 10 cm. The height decreases from about 9 cm in the most anterior to 6–8 cm in the mid-caudal, and to 4–5 cm in the posterior caudal vertebrae.

Caudal vertebral column s.

Fig. 78.

Discovery site: Kijenjere, north of Tendaguru.

Horizon: Intermediate layers between the Middle and the Upper Saurian Beds, questionable whether above or below the *Trigonia smeei* horizon.

Material: Out of the available 23 vertebrae (s1, s2, s2a, s3 to s 22, counted from posterior to anterior), s5 to s19 obviously represent a series continuous with the three most anterior vertebrae in the series (s20 to s22), which for the most part were recovered in articulation. The immediate connection to s19, and whether they form a continuous sequence, cannot be determined with certainty but seems most likely. Obviously a gap of at least two vertebrae exists between s19 and s18. A gap of probably three missing vertebrae is likely between s5 and s4. For the five posteriormost vertebrae, s1 to s4, no direct succession can be established between any specimens.

Preservation: The centra of vertebrae s22 to s4 are completely or almost completely preserved, s3 is moderately well preserved, and s2 and s1 are strongly weathered. Centrum s2 is only

Fig. 78. Caudal vertebral series s of Dicraeosaurus sp. 1/8 nat. size.

half-preserved. Only half of the centrum of s2a is preserved. In the centrum of s22 the dorsal end of the neurapophysis is missing, in s21 the entire neural arch. Only the neurapophyses and zygapophyses of s20 to s5 are more or less completely preserved, and in s20 the zygapophyses are missing. In s19 half of the neurapophysis is missing, in s15 the neurapophysis to a large degree.

Description: The anterior faces of the 11 anteriormost centra are weakly concave, as far as they are freed of matrix. The posterior faces of the three anteriormost centra are concave as well, but they level out and stay flat to at least the 11th vertebra. The surface is still almost level in the 14th centrum, but shows a deep transverse incision in the center. The abutting, strongly concave anterior face of the 15th vertebra shows a corresponding notch. The posterior face of the 18th vertebra is deeply concave, as it is in the next smaller vertebra s4, from which it is separated by a gap. The anterior face of s4 shows a cone-shaped, blunt projection dorsal to a short, low depression. The incompletely preserved faces of the four smallest vertebrae show a roughly pitted surface. The very strong inclination of the neurapophyses relative to the neural arch in the anterior vertebrae of the series is noteworthy. The preserved stump of the neurapophysis in the anteriormost vertebra shows that here also the neurapophysis rose only to a small degree. The completely preserved neurapophysis of s20 forms a rather narrow, distally ca. 5 cm wide and 1.5 cm thick rod of bone, of which the anterior margin forms an angle of only 22° with the longitudinal axis. It is possible that this angle has been reduced by dorsolateral compression. The dorsal face shows a weak, S-shaped lateral profile with an average inclination

of ca. 25° to the longitudinal axis. The anterior and dorsal edges meet at a blunt angle. The neurapophysis thickens ventrally and carries the ventrolaterally facing facet of the postzygapophysis on both sides, although only on the right side is it distinctly preserved. In vertebra s18 the anterior edge extends in a flat curve onto the only very weakly curved dorsal margin, which ends in a posterior prong. The neurapophyses become narrower, and the anterior rims sharper, in the succeeding vertebrae. In the last vertebrae of the continuous sequence the neurapophyses take on the shape of thin, straight, obliquely posteriorly rising spikes, which no longer show postzygapophyseal facets. The prezygapophyses in the anterior vertebrae are rather wide processes with a medial inclination of the facets of ca. 70°. Beginning with the 6th vertebra of the series onward, the prezygapophyses get thinner and more pointed very soon. They rise slightly in the posterior vertebrae and also get shorter.

In order to determine the position of the vertebral series s within the entire caudal vertebral column, the skeleton of Dicraeosaurus hansemanni from the Middle Saurian Bed will be used. The proportional measurements of both series are obviously not fully in accordance. Individual s was considerably smaller than individual m. By using the ratio of dorsal length to anterior height of the centrum as the basis of comparison, and the degree of narrowness of the ventral surface, the best agreement is reached when vertebra s22 is equaled with m7, i.e. the 18th from skeleton m. Comparing the ratio of dorsal length to minimum thickness indicates that s22 is comparable to a much more anterior vertebra from m. However, s22 is shaped very differently from more anteriorly placed vertebrae, and it seems that the first calculation is more correct. Applying this procedure, vertebra s5 can be regarded as the 37th caudal vertebra, not counting the caudosacral vertebra as a caudal. A gap of about three vertebrae obviously exists between s5 and s4. Another gap of approximately three vertebrae has to be assumed due to the difference in size between s4 and s3, and a gap of the same size must have opened between s4 and s3 because of the difference in length. The most posterior vertebrae are too incompletely preserved to allow an assessment about their position in the series with an reasonable accuracy. It can only be stated that vertebra s2 was followed by a not inconsiderable number of caudal vertebrae, judged by the still strongly developed base of the neurapophysis of this vertebra.

When compared with those from the skeleton m of *Dicraeosaurus hansemanni*, the caudal vertebrae of individual s are slightly differently shaped. Only in the anteriormost 5 vertebrae are the lateral edges more or less well developed. Accordingly the ventral lateral edges are less distinct; they disappear relatively quickly in the vertebral series in the caudal direction, while they are still present in vertebrae of the same position of *D. hansemanni* from trench dd. The degree of elongation of the posterior caudal vertebrae is higher in *D. hansemanni* than in s, and also in a vertebra from trench XIV (Fig. 79) from the Upper Saurian Zone.

The spinal process of the anteriormost vertebra from s seems to be lower and less inclined than on the corresponding vertebra of m, as far as can be judged by the preserved parts. The lower-positioned spinal process in the posteriormost vertebrae correspond very well with this vertebra of *D. hansemanni* from excavation site dd.

The reduced elongation in the posterior caudal vertebrae could perhaps be a juvenile character. The absence of lateral and ventral edges in the mid-caudal vertebrae of s is a remarkable discrepancy with all others, which altogether originate from the mid-caudal vertebrae of 13 animals, among them also vertebrae from not fully grown individuals. However, I do not wish to segregate vertebral columns from the genus *Dicraeosaurus*. Whether it should be referred to *D. hansemanni* or to *D. sattleri* cannot be decided with the material at hand. As long as only *D. sattleri* is recorded

from the Upper Saurian Zone, the column is best included in this species. There seems to be not enough justification to establish a new third species on tail s.

Catalogue no.	Dorsal length of centrum	Ventral length of centrum	Median height of anterior end of centrum	Median height of posterior of the centrum	Width of anterior end of centrum	Width of posterior end of centrum
$\begin{array}{c} S \ 22 \\ S \ 21 \\ S \ 20 \\ S \ 19 \\ S \ 18 \\ S \ 17 \\ S \ 16 \\ S \ 15 \\ S \ 14 \\ S \ 15 \\ S \ 14 \\ S \ 13 \\ S \ 12 \\ S \ 11 \\ S \ 10 \\ S \ 9 \\ S \ 8 \\ S \ 7 \\ S \ 6 \\ S \ 5 \\ S \ 4 \\ S \ 3 \\ S \ 2a \\ S \ 2 \\ S \ 1 \end{array}$	11.2 cm 12.1 11.2 12.1 11.9 12.5 12.0 11.2 11.5 10.6 9.9 9.5 8.8 8.9 7.7 7.4 7.2 6.5 6.0 (+?) 6.0 (+?)	10.9 cm 11.2 11.1 11.7 12.1 (±?) 12.3 12.3 11.8 11.3 11.4 10.2 10.3 10.0 9.6 8.7 8.9 7.6 7.1 7.6 6.8	9.6 cm 8.6 9.1 8.9 8.1 7.2 (+) 7.3 6.8 6.6 6.3 6.1 5.6 5.4 5.0 4.6 4.3 4.4 3.4 2.8 2.7	9.2 cm 8.4 8.9 (+) 8.5 7.7 (+) 7.2 6.8 (+) 6.4 (+) 6.2 6.3 5.3 5.3 5.3 5.0 4.5 4.1 4.0 3.9 3.2 2.9	11.0 cm 10.3 9.9 + 10.1 9.2 9.4 9.0 (+) 8.9 8.1 7.8 (±?) 7.1 6.8 6.1 5.4 5.1 (+) 4.7 4.4 4.6 (-) 3.2	10.8 cm 9.9 10.4 10.0 8.9 (+) 9.0 8.8 8.4 7.5 7.1 6.0 5.4 5.1 4.7 4.2 4.1 (+) 4.0 3.0 (+) 2.6 +

Measurements of the caudal vertebrae of Dicraeosaurus sp. caudal vertebral column s.

Isolated caudal vertebrae from different localities.

There are a few isolated centra available, among them a poorly preserved one from the Middle Saurian Bed from the anterior half of the mid-caudal region of a subadult individual. Several other centra from the same section of the tail have been found at different sites in the Upper Saurian Bed, among them some in which the ventral edges are only very indistinctly indicated.

- Fig. 79 a Posterior caudal vertebra of *Dicraeosaurus* sp., lateral view. Fig. 79 b. The same, anterior view.
- Fig. 79 c. The same, posterior view.

1/8 natural size.

A posterior caudal vertebra with an incomplete neural arch from excavation site XIV in the Upper Saurian Bed, (Fig. 79) has a very elongated shape, evenly curved flanks, and a dorsal centrum length of 11.7 cm. Its anterior end surface is 5.7 cm high and very deeply excavated. The posterior end surface is almost level, hexagonal, 4.8 cm high, and 5.5 cm wide. The base of the neural arch is ca. 5.6 cm long and positioned far anteriorly. The entire shape is very similar to the caudal vertebrae of *Dicraeosaurus hansemanni* from excavation site dd, and much more elongated than the corresponding vertebrae of individuals s and La.

Characteristics of the vertebral column of the genus *Dicraeosaurus* and a comparison of both species.

The essential characteristics of the vertebral column of the genus *Dicraeosaurus* resulting from the foregoing description are as follows: 24 presacral vertebrae, of which 12 must be regarded as cervical vertebrae. Sacrum consists of five fused vertebrae. Cervical vertebrae comparatively moderately elongate. Anterior caudal vertebrae concavo-convex, mid-caudal vertebrae biconcave, posteriormost stick-like vertebrae biconvex. Mid-caudal vertebrae with lateral edge at half the lateral height, well demarcated and level ventral surface, and hexagonal cross-section in the central part. Dorsal vertebrae without pleurocentral grooves, except the most anterior ones. Structure of the centra fine-celled and spongiose. Neural arch and its processes lightly built, with a strongly developed laminar system and deeply excavated pockets. Neurapophyses in neck, trunk, sacrum, and the anteriormost part of the trunk very high, they are deeply bifurcated from the 3rd presacral vertebra onward; unbifurcated from the 20th onward. Very distinct anticline of the neurapophysis in the neck. Strong insertion areas for a ligament (L. nuchae) present on the roof of the neural canal between neurapophyseal branches of the cervical vertebrae. Diapophyses in the anterior part of the trunk not particularly robust. Proximal bifurcation of cervical ribs narrow.

The overview of the individual characters of the vertebral column of *Dicraeosaurus* shows a remarkable combination of highly specialized and primitive characters. Primitive characters are the shortness of the cervical vertebrae, the lack of pleurocentral grooves in the posterior part of the trunk, and the fine-celled structure of the presacral vertebrae. Specialized characters are the deep bifurcations of the neurapophyses, their extreme length, and their anticline in the anterior part of the neck. This combination of different, and also differently weighted, features sets the character of *Dicraeosaurus* in comparison with other genera. A close relationship with any other genus among sauropods is not evident from the architecture and structure of the vertebral column. The most striking character, the bifurcation of the neurapophyses, has, as discussed elsewhere (JANENSCH 1929), probably developed more than once within Sauropoda and should therefore be used only very cautiously to elucidate phylogenetic connections. Within Sauropoda, a group so diverse regarding the architecture of the vertebral column, *Dicraeosaurus* represents a special branch whose relation to other branches of this suborder cannot be determined with reasonable certainty by characters of the vertebral column, at least not with our current knowledge.

The comparison of the presacral vertebrae of *Dicraeosaurus sattleri* from the Upper Saurian Bed with those of *D. hansemanni* from the Middle Saurian Bed should not be diverted by details of the external architecture, especially since there is not enough material to gain a sufficient idea of the range of individual variations. The impression that immediately suggests itself is the difference in general character. In *D. sattleri*, the neural architecture of the vertebrae is more delicate, and in particular the neurapophyses are proportionally much higher, with the same kind of bifurcation. Also, when compared with the length of the centra, the diapophyses show a smaller degree of elongation in *D. sattleri*.

An overview of the entire caudal vertebral material of the genus *Dicraeosaurus* shows that the anterior caudal vertebrae of *D. hansemanni* and *D. sattleri* are easily distinguished by

the height of their neurapophyses. However, because the mid- and posterior caudal vertebrae have mostly no or only incomplete neural arches preserved-apart from the three individuals of the first species (skeleton m and two vertebral columns from trench dd) and the vertebrae of series s and Ob-a fundamentally distinctive character cannot be found. For this reason, mid- and posterior caudal vertebrae could not be used to answer the question of whether each of the two species of Dicraeosaurus is indeed restricted to only one horizon. When comparing all material of the mid-central and posterior caudal vertebrae, the centra differ so that within the series of vertebrae, the ventral narrowing, and in connection with this the rounded ventral edges that enclose the ventral area and always disappear in the posteriormost section of the tail, get indistinct in different parts of the tail; they disappear rather early in the small vertebrae of series s. Furthermore, the degree of elongation of the centra of this series is less in the posteriormost vertebrae than in the larger one of the three skeletons of Dicraeosaurus hansemanni or in the individual vertebrae from trench XIV from the Upper Saurian Zone. Such differences appear to me not sufficient enough to segregate specimens from the same horizon at the species or even genus level. I think it is more plausible to reckon such variability as within a single species of Sauropoda. I wish to point out that an examination of the caudal vertebral series of Camarasaurus supremus COPE, as arranged by OSBORN and MOOK, also shows considerable differences within the middle and posterior caudal vertebrae. How much dissimilarity can occur within the same species, with respect to the inclination and width of the spinal process of the mid-caudal vertebrae, is shown by the two individuals of D. hansemanni from excavation site dd, which are almost identical in size and certainly belong to the same species.

Literature.

GADOW, H. an 1891	d E. SELENKA. Vögel. I. Anatomischer Teil. Dr. H. G. Bronns Klassen und Ordnungen des Tierreiches.
Hatcher, J. B 1901	<i>Diplodocus</i> MARSH, its osteology, taxonomy, and probable habits, with a restoration of the skeleton. Mem. Carn. Mus. I. Pp. 1–63. Text-fig. 1–24. Pl. 1–13.
Hennig, E. 1915	Über dorsale Wirbelsäulenkrümmung fossiler Vertebraten. Centralbl. f. Min. usw. 1915. Pp. 575–577.
Holland, W. 1906	J. The osteology of <i>Diplodocus</i> MARSH. Mem. Carn. Mus. II. Pp. 225–264. Text-fig. 1–30. Pl. 23–29.
JANENSCH, W.	
1914	Bericht über den Verlauf der Expedition. Arch. f. Biontol. III. Pp. 15–58. Text-fig. 1–17. Pl. 1–6.
1914a	Übersicht über die Wirbeltierfauna der Tendaguruschichten, nebst einer kurzen Charakterisierung der neu aufgestellten Arten von Sauropoden.
1925	Die Grabungsstellen der Tendaguru-Gegend.
1929	Palaeontogr. Suppl. VII. Part I. Vol. I. Pp. XVII–XIX. Material und Formengehalt der Sauropoden in der Ausbeute der Tendaguru-Expedition. Palaeontogr. Suppl. VII. Part I. Vol. II.
LILL R S	
1919	The sauropod dinosaur <i>Barosaurus</i> MARSH. Redescription of the type specimen in the Peabody Museum, Yale University.
	Mem. Conn. Acad. Arts and Scie. 6. Pp. 1-42. Text-fig. 1-14. Pl. 1-7.
OSBORN, H. F.	
1899	A skeleton of <i>Diplodocus</i> . Mem. Am. Mus. Nat. Hist. I. Pp. 191–214. Text-fig. 1–14. Pl. 24–27.
Osborn, H. F. 1921	and Ch. C. MOOK. Camarasaurus, Amphicoelias and other sauropods of Cope. Mem. Am. Mus. Nat. Hist. N. Ser. III. Pp. 249–387. Text-fig. 1–127. Pl. 60–85.

Pl. I.

Presacral vertebrae of Dicraeosaurus hansemanni.

- 1a–23a. 2nd–24th presacral vertebrae, lateral view.
- 1b–23b. The same, anterior view.
- 1c–23c. The same, posterior view.

Pl. II.

Sacrum of Dicraeosaurus hansemanni.

- 1. Lateral view. a-18a. 1-18 sacral vertebrae, lateral view.
- 2. Anterior view. b-18b. The same.
- 3. Posterior view. c-18c. The same.

Pl. III.

Caudal vertebrae of Dicraeosaurus hansemanni.

- 1a–18a. 1st–18th caudal vertebrae, lateral view.
- 1b–18b. The same, anterior view.
- 1c–18c. The same, posterior view.

Pl. IV.

Reconstruction of the ligamentous apparatus of the presacral vertebrae of *Dicraeosaurus hansemanni*, represented in median section.

ssp. L. = supraspinous ligament.

isp. L. = interspinous ligament.

L. nu. = ligamentum nuchae, NACKENBAND.

sn. L. = supraneural ligament.

1/10 nat. size.

Pl. V.

Dorsal vertebrae of Dicraeosaurus sattleri.

1a-c. Anterior dorsal vertebra M 9.

2a-c. Anterior (17th?) dorsal vertebra M 11.

3a-c. Middle (19th) dorsal vertebra M 10.

4a-c. Posterior dorsal vertebra M 12.

1a–4a. Lateral view.

1b–4b. Anterior view.

1c-4c. Posterior view.

_

Pl. VI.

Sacrum of Dicraeosaurus sattleri.

1. Lateral view.

2. Anterior view.

3. Posterior view.

Pl. VII.

Caudal vertebrae of Dicraeosaurus sattleri.

- 1a–7a. 1st–7th caudal vertebrae, lateral view.
- 1b–7b. The same, anterior view.
- 1c–7c. The same, posterior view.