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Pneumatic structures in the cervical vertebrae of the Late Jurassic Tendaguru sauropods *Brachiosaurus brancai* and *Dicraeosaurus*

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Key words: Sauropoda, *Brachiosaurus*, *Dicraeosaurus*, vertebral pneumaticity, cervical vertebrae, computed tomography

ABSTRACT

The presacral vertebrae of sauropod dinosaurs were surrounded and invaded by a complex system of pneumatic diverticula, which originated most probably from cervical air sacs connected with the respiratory apparatus. Cervical vertebrae of *Brachiosaurus brancai* and *Dicraeosaurus* sp., two sauropods from the Late Jurassic (?Oxfordian-Kimmerian-Tithonian) eastern African locality Tendaguru, were examined with computed tomography to visualize internal pneumatic structures. With this method, comparative reconstructions of pneumatic diverticula in the neck of these sauropods were done that help to understand the biomechanical role of vertebral pneumaticity in sauropods. Internal pneumatic structures in *Brachiosaurus brancai* are semicamellate with few large camerae in the vertebral centrum, surrounded by pneumatic camellae. *Dicraeosaurus* exhibits a procamerate pneumatization pattern with few deep fossae penetrating to a broad median strut in the vertebra, but no internal pneumaticity was found. The semicamellate pneumatization pattern of *Brachiosaurus brancai* corresponds with another Late Jurassic *Brachiosaurus* specimen, whereas in Cretaceous brachiosaurid taxa like *Sauroposeidon*, the complexity of internal pneumatization increases to form a fully camellate pneumatization pattern. In *Dicraeosaurus*, internal pneumatization has most likely secondarily been reduced.

Brachiosaurus and *Dicraeosaurus* possess a similar distribution of main external pneumatic diverticula, with *Brachiosaurus* having much more subdivided diverticula. Due to the weight reduction achieved by these pneumatic diverticula, the neck of *Brachiosaurus* was up to 25 per cent lighter than without pneumatic structures, whereas that of *Dicraeosaurus* was only 6 per cent lighter. Pneumatization of the cervical vertebrae therefore can play an important role in lightening some sauropods.

ZUSAMMENFASSUNG

Die Präsacralwirbel sauropoder Dinosaurier waren von einem komplexen System pneumatischer Diverticula umgeben und ausgehöhlt. Die pneumatischen Diverticula entstammten wahrscheinlich einem paarigen cervicalen Luftsack, der mit dem Atemapparat verbunden war. Zur Darstellung der internen pneumatischen Strukturen wurden Halswirbel von *Brachiosaurus brancai* und *Dicraeosaurus* sp. der spätjurassischen (?Oxfordium-Kimmeridgium-Tithonium) Fundstelle Tendaguru aus dem östlichen Afrika mit Computertomographie untersucht. Die daraus resultierenden vergleichenden Rekonstruktionen der pneumatischen Diverticula im Halsbereich dieser Sauropoden-Taxa dienen dazu, die biomechanische Bedeutung pneumatischer Strukturen in den Wirbeln von Sauropoden besser zu verstehen. Interne pneumatische Strukturen bei *Brachiosaurus brancai* sind semicamellat mit wenigen großen Camerae in den Wirbelkörpern, welche von Camellae umgeben sind. *Dicraeosaurus* zeigt hingegen ein procamerates Pneumatisierungsmuster ohne interne Pneumatisierung, bei dem wenige tiefe pneumatische Fossae bis zu einem breiten medianen Septum im Wirbel vordringen. Das semicamellate Pneumatisierungsmuster von *Brachiosaurus brancai* entspricht dem anderer spätjurassischer *Brachiosaurus*-Arten, während kretazische Brachiosauriden wie *Sauroposeidon* ein komplexeres, vollständig camellates Pneumatisierungsmuster besitzen. Bei *Dicraeosaurus* wurde die interne Pneumatisierung höchstwahrscheinlich sekundär reduziert.

Für *Brachiosaurus* und *Dicraeosaurus* kann eine ähnliche Verteilung der hauptsächlich externen pneumatischen Diverticula rekonstruiert werden, welche bei *Brachiosaurus* jedoch viel stärker unterteilt waren als bei *Dicraeosaurus*. Aufgrund der Gewichtsreduzierung durch die pneumatischen Diverticula war der Hals von *Brachiosaurus* wahrscheinlich bis zu 25 % leichter als ohne pneumatische Strukturen, derjenige von *Dicraeosaurus* hingegen nur ca. 6 % leichter. Die Pneumatisierung der Halswirbel kann demnach eine bedeutende Rolle für die Gewichtsreduzierung bei verschiedenen Sauropoden spielen.

1. Introduction

Sauropod dinosaurs are the largest land vertebrates that ever existed. One of the most remarkable features of these gigantic herbivores is the long neck, reaching more than 10 metres in sauropods such as *Brachiosaurus*. The presacral vertebrae of

most sauropods are hollowed out by a complex system of cavities, which in analogy to extant birds, is interpreted to be the osteological correlate to a system of pneumatic diverticula (Seeley 1870; Janensch 1947; Britt 1993; Wedel 2003a). In birds, pneumatic diverticula in the neck originate from cervical

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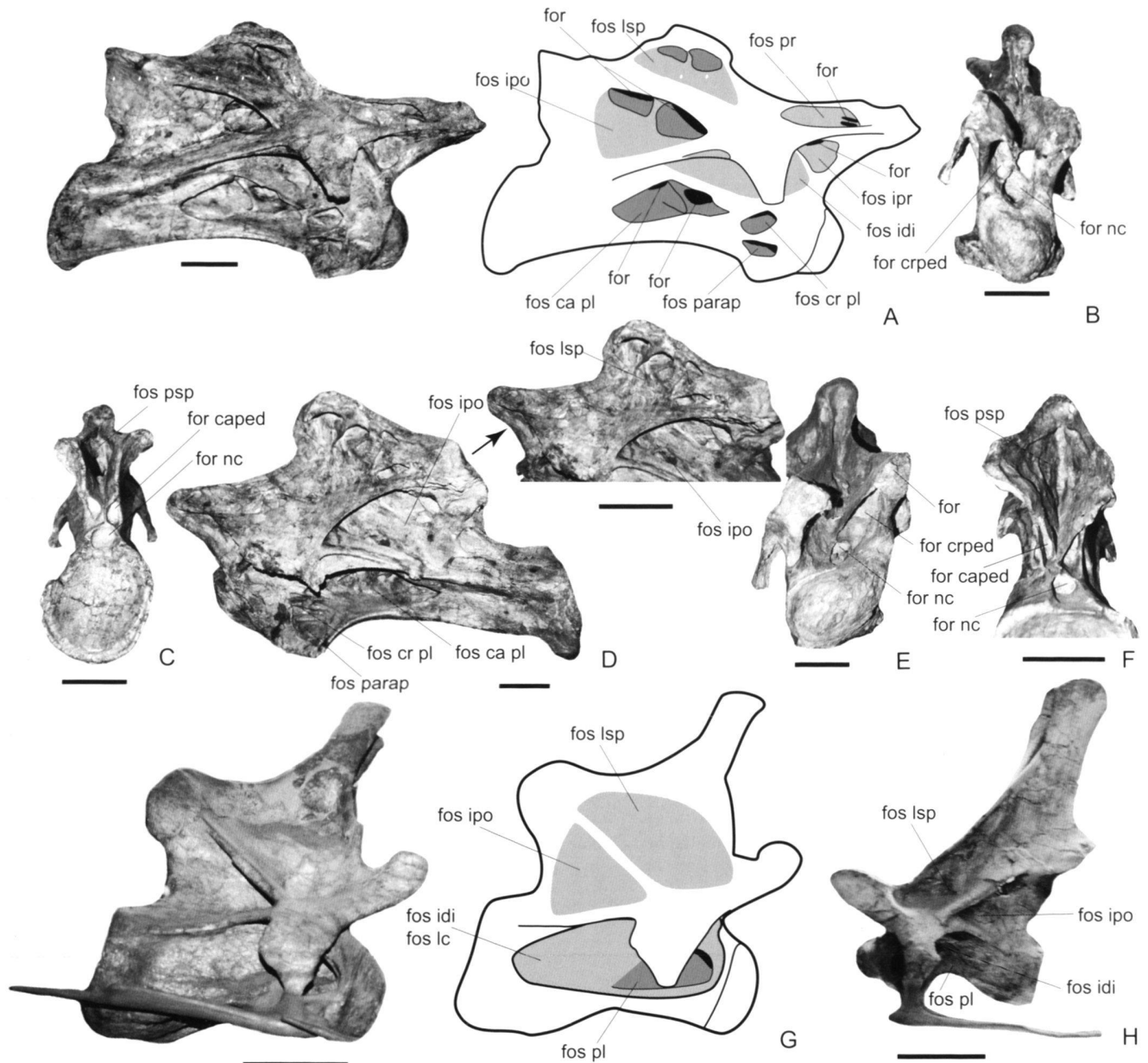


Fig. 1. External pneumatic structures in the cervical vertebrae of *Brachiosaurus brancai* and *Dicraeosaurus hansemani* from Tendaguru. 4th cervical of *Brachiosaurus brancai* A) Photograph (left) and schematic drawing with external pneumatic structures (right) in right lateral view, B) cranial view, C) caudal view. 7th cervical vertebra of *Brachiosaurus brancai* D) left lateral view with close-up to lateral surface of the neural arch showing the subdivided laterospinal fossa, E) cranial view, F) neural arch in caudal view showing the postspinal fossa. G) right lateral view of 8th cervical vertebra of *Dicraeosaurus hansemani* as displayed on the mounted skeleton in the HMN with photograph (left) and schematic drawing with pneumatic structures (right). H) 5th cervical vertebra of *Dicraeosaurus hansemani* in left lateral view. Abbreviations: for, foramen; for caped, caudal peduncular foramen; for crped, cranial peduncular foramen; for nc, neural foramen; fos cau pl, caudal pleurocoelous fossa; fos cr pl, cranial pleurocoelous fossa; fos idi, infradiapophyseal fossa; fos ipo, infrapostzygapophyseal fossa; fos ipr, infraprezygapophyseal fossa; fos lsp, laterospinal fossa; fos parap, parapophyseal fossa; fos psp, postspinal fossa. Scale bar: 10 cm.

air-sacs in the cranial thorax region and are part of the respiratory apparatus (Müller 1908; Duncker 1971). In sauropods, similar cervical air-sacs can be reconstructed, from which diverticula emerged to pneumatize the presacral vertebral col-

umn (Wedel 2003a). Several ideas and hypotheses about the functions of postcranial pneumaticity in sauropods, such as weight-saving or cooling device or as a part of the respiratory apparatus have been proposed (Janensch 1947; Britt 1993;

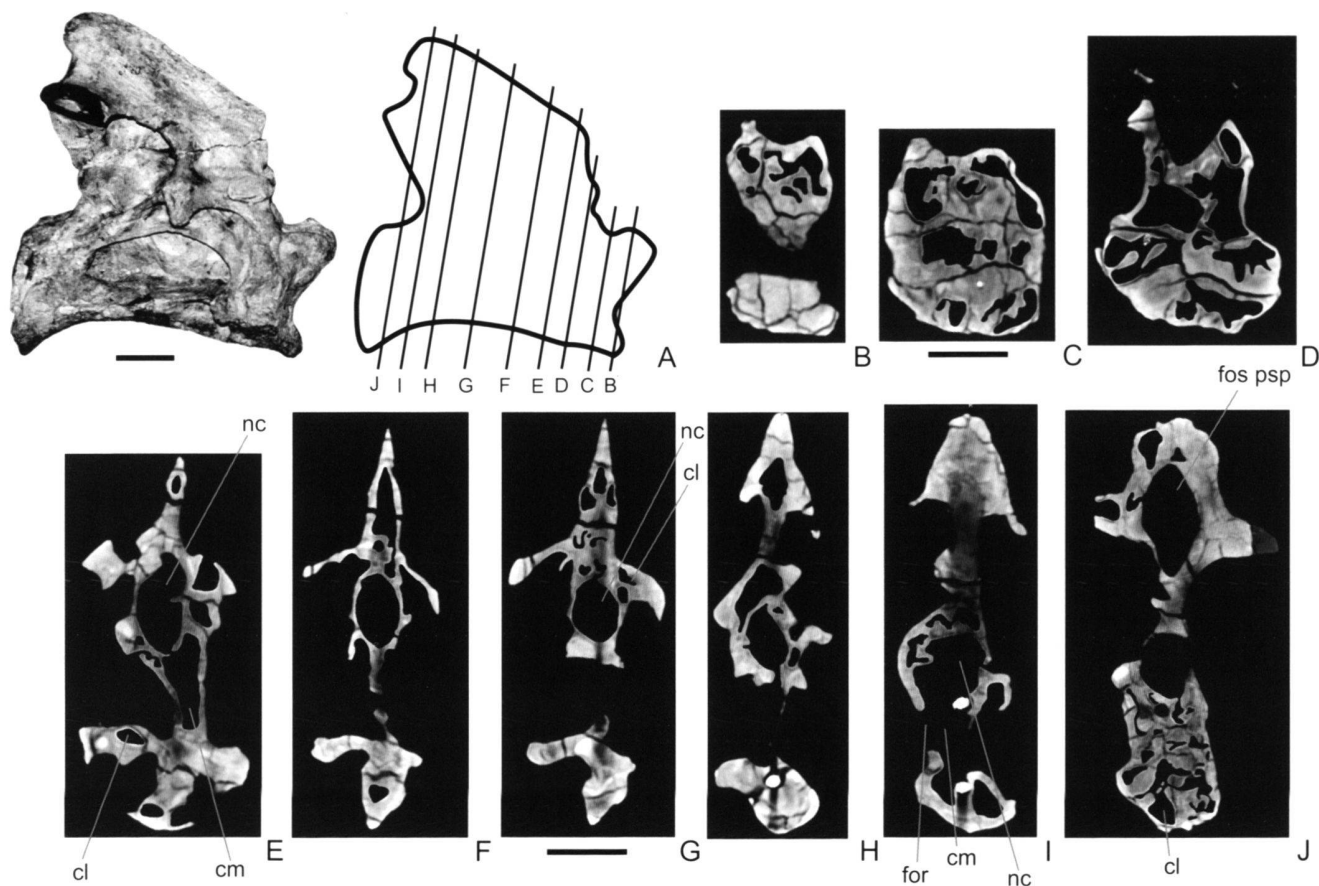


Fig. 2. Transverse sections through axis of *Brachiosaurus brancai* (HMN SI 70) with computed tomography. A) Photograph (left) and schematic drawing (right) of the vertebra in right lateral view with levels of transverse cross-sections as displayed in B–J. Abbreviations as in Fig. 1 and: cl, camella; cm, camera; nc, neural canal. Scale bar: 5 cm.

Perry & Reuter 1999; Wedel 2003a), but none of them dealt so far with the biomechanical role of pneumaticity in sauropods. Therefore, finding reasonable explanations for the presence and possible biological role of pneumatic diverticula in sauropods is still problematic and the main purpose of a SNF (Swiss National Foundation) project in the Natural History Museum of Basel (Switzerland). In this project, sauropod vertebrae were studied with computed tomography to make comparative reconstructions of the distribution of pneumatic diverticula in sauropods. With the help of these reconstructions it will be possible to devise models for the construction of the extremely long sauropod necks and to explain the presence of pneumaticity in the sauropod axial skeleton.

The internal pneumatic structures in the neck of sauropods have been studied and described extensively (Janensch 1947; Britt 1993; Wedel et al. 2000a, b; Wedel 2003a, b), especially since computed tomography made non-destructive investigations of the remains possible. On the basis of these investigations, the differences between the amount and distribution of pneumatic cavities in major sauropod taxa could be defined (Britt 1993; Wedel 2003a, b). In the present study, the distribu-

tion of internal and external pneumatic structures in the cervical vertebrae of *Brachiosaurus brancai* and *Dicraeosaurus* from the Late Jurassic (?Oxfordian–Kimmeridgian–Tithonian) Tendaguru beds of Tanzania (Aberhan et al. 2002) are described in detail, leading to a reconstruction of the distribution of pneumatic diverticula in the neck of these taxa. Pneumatic structures in both taxa were described for the first time by Janensch (1929a; 1947; 1950b), but exclusively in German and only on the basis of broken remains or thin sections through single vertebrae. Our goal herein is to use computed tomography to provide a new exhaustive description of these structures and make them available for a broader range of scientists.

Brachiosaurus is one of the largest sauropods and phylogenetically represents a basal titanosauriform (Upchurch 1998; Wilson & Sereno 1998; Wilson 2002). It has been suggested that the eastern African *B. brancai* JANENSCH 1914 and the western North American *B. altithorax* RIGGS 1903 should be distinguished from each other on a subgeneric level (Paul 1988), but this suggestion has not been widely accepted (see e.g. Wilson & Sereno 1998; Upchurch et al. 2004). *B. brancai* pos-

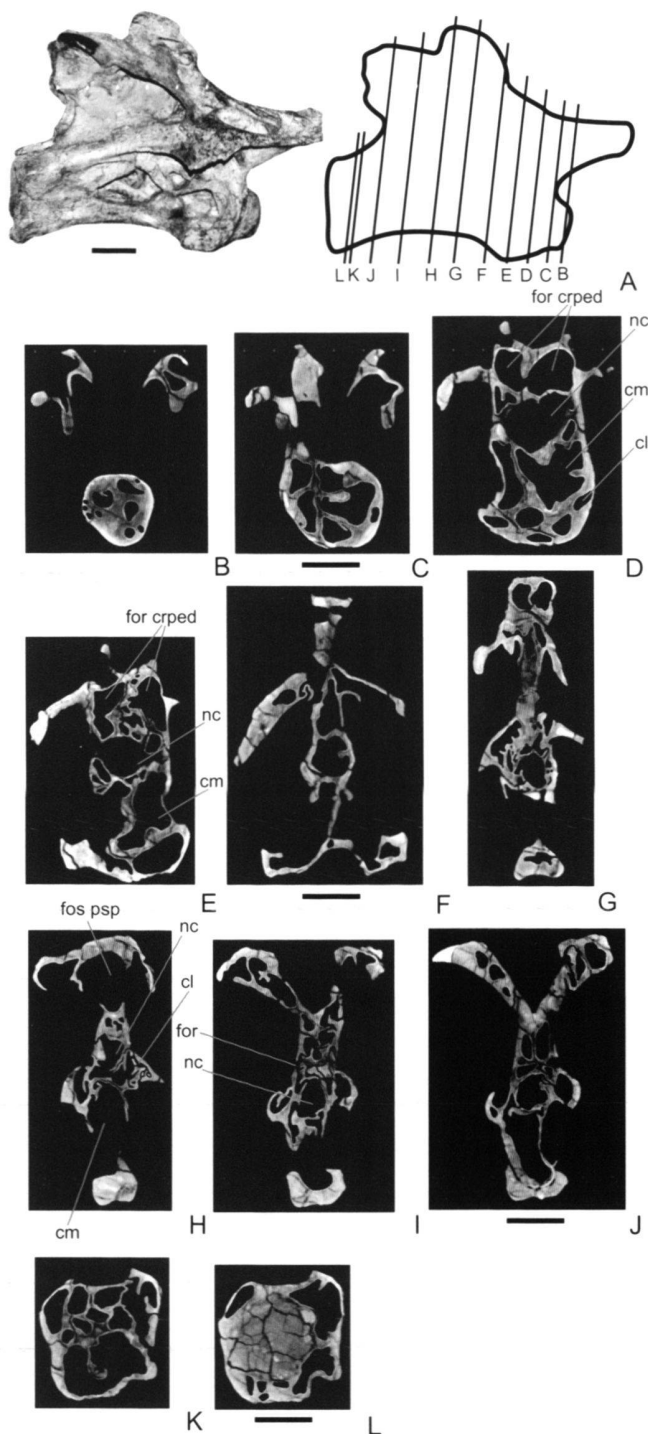


Fig. 3. Transverse sections through 3rd cervical of *Brachiosaurus brancai* (HMN SI 51) as obtained from computed tomography. A) Photograph (left) and schematic drawing (right) of the vertebra in right lateral view with indicated levels of transverse cross-sections as displayed in B–L. Abbreviations as in Figure 1 and 2. Scale bar: 5 cm.

sesses 13 cervical vertebrae, of which the medial and caudal cervicals have extremely elongated vertebral centra (Fig. 1A–F) (Janensch 1950b; Wedel et al. 2000a, b; Naish et al. 2004). The neural spines in the cranial cervicals are low and increase in height towards the cranial dorsal vertebrae, so that each neural spine is taller than the one in front of it. There is a transition point in neural spine height between the 6th and 7th cervical vertebra, with the 7th neural being remarkably higher than the 6th cervical neural spine (Wedel et al. 2000a; Wedel & Cifelli 2005). All neural spines of the cervicals are undivided. The cervical ribs exceed three cervical vertebrae in length (Janensch 1950b; Wedel et al. 2000a), becoming thin and rod-like in their caudal part. Apart from descriptions of internal pneumatic structures visible in broken vertebrae of *B. brancai* by Janensch (1947; 1950b), previous studies of internal pneumatic structures in brachiosaurids were restricted to a cervical vertebra of *Brachiosaurus* sp. (Wedel et al. 2000b) and cervical vertebrae of *Sauroposeidon* (Wedel et al. 2000a, b; Wedel 2003a), both from North America. A report of CT sections of cervical vertebrae of *B. brancai* therefore increases the knowledge about internal pneumatic structures in brachiosaurids and is the first description of CT sections of non-North American sauropod vertebrae.

Dicraeosaurus is one of the smallest sauropod taxa and exclusively reported from Tendaguru with the two species *D. hansemanni* and *D. sattleri* (Janensch 1914, 1929a, 1929b; Aberhan et al. 2002). The taxonomic assignment of *D. sattleri* is uncertain. It has been suggested that this species should be referred to the genus *Amargasaurus* (Salgado 1999), but this has not been adopted so far (see e.g. Wilson 2002; Upchurch et al. 2004). *Dicraeosaurus* possesses a short neck with 12 cervical vertebrae (Janensch 1929a; Salgado 1999). The cervical neural spines are tall and increase in size in the caudal direction (Fig. 1G, H). From the 3rd cervical vertebra onwards, all neural spines are deeply bifurcate. The cervical ribs are not completely preserved, but they are interpreted to be shorter than their respective vertebral centra and morphologically similar to those of *Diplodocus* (Janensch 1929a). The pneumatic structures found in the cervical vertebrae of *Dicraeosaurus* are simple and restricted to the external surface of the vertebrae (Janensch 1929a, 1947), and represent according to the scheme of Wedel et al. (2000b) the procamerate condition. In recent studies on the evolution of pneumaticity in sauropods (Wedel 2003a, b), *Dicraeosaurus* is completely left out. Though it could not be expected to reveal internal pneumatization in *Dicraeosaurus* cervicals, CT sections were helpful for getting an insight into the general distribution and development of pneumatic spaces in this taxon.

2. Material

The mounted skeletons of *Brachiosaurus brancai* (Janensch 1950a) and *Dicraeosaurus hansemanni* (Janensch 1929b) in the HMN (Museum für Naturkunde der Humboldt-Universität Berlin), as well as cervical vertebrae of the skeletons SI and

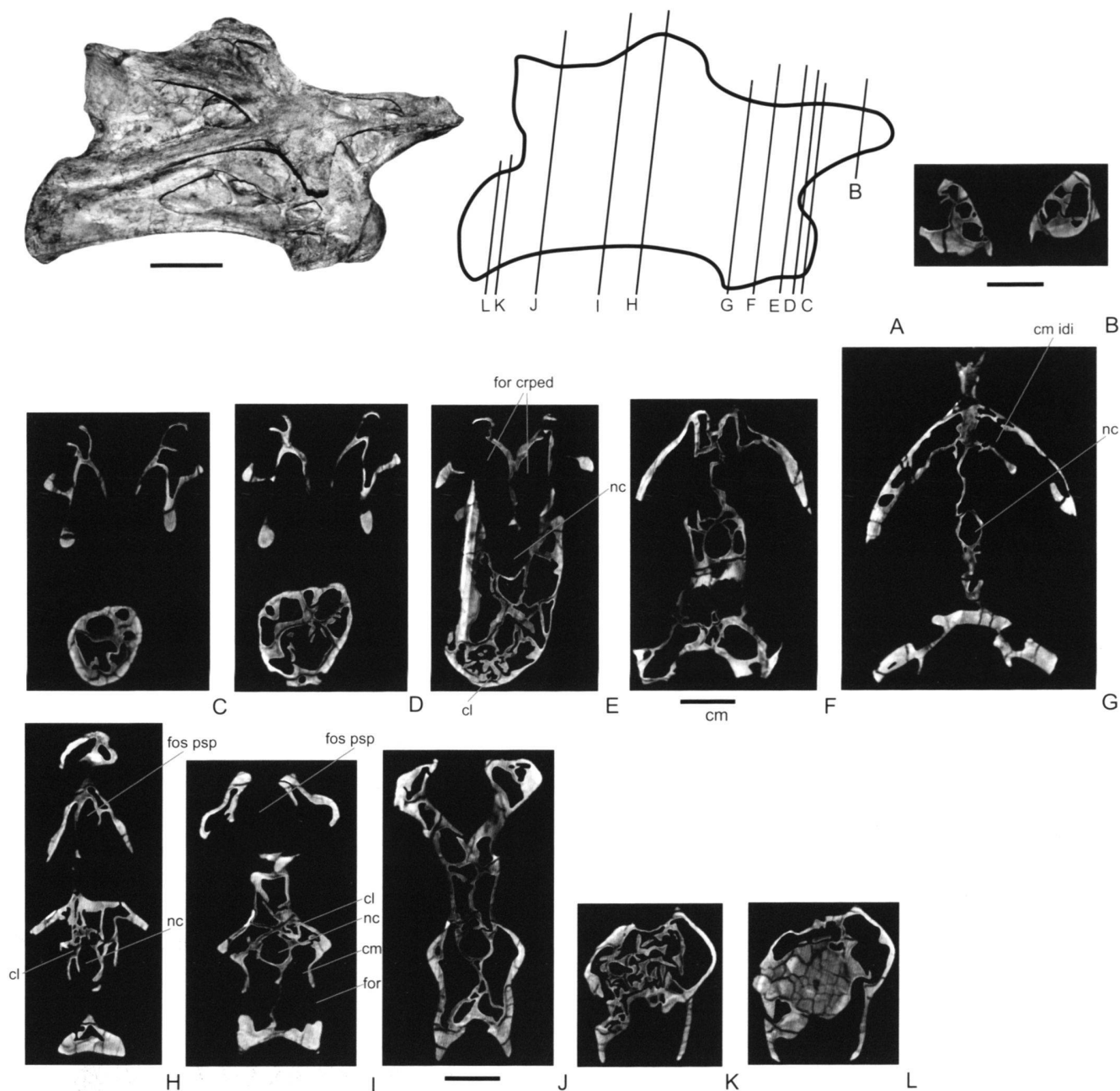


Fig. 4. Transverse sections through 4th cervical of *Brachiosaurus brancai* (HMN SI 71) with computed tomography. A) Photograph (left) and schematic drawing (right) with indicated levels of transverse cross-sections as displayed in B-L. Abbreviations as in Figs. 1 and 2 and: cm idi, camera within diapophysis. Scale bar: 10 cm.

SII of *B. brancai* (Janensch 1914, 1929a, 1950b) and isolated cervical vertebrae of *Dicraeosaurus* sp. (Janensch 1929a, 1929c) were examined personally.

For the CT study, only the cranialmost cervicals of the individual SI of *Brachiosaurus brancai* could be transported:

- HMN SI 71 (Fig. 2) is the complete and well preserved axis. The CT scan revealed a pair of metal bars within the vertebral centrum, presumably added during the original preparation.

The left postzygapophysis of the specimen is modelled with plaster.

- HMN SI 51 (Fig. 3) is the 3rd cervical vertebra, which is slightly lateromedially distorted with the right diapophysis and postzygapophysis modelled in plaster.
- HMN SI 70 (Fig. 4) is the nearly complete and only weakly lateromedially distorted 4th cervical vertebra with parts of its right pre- and postzygapophysis broken away.

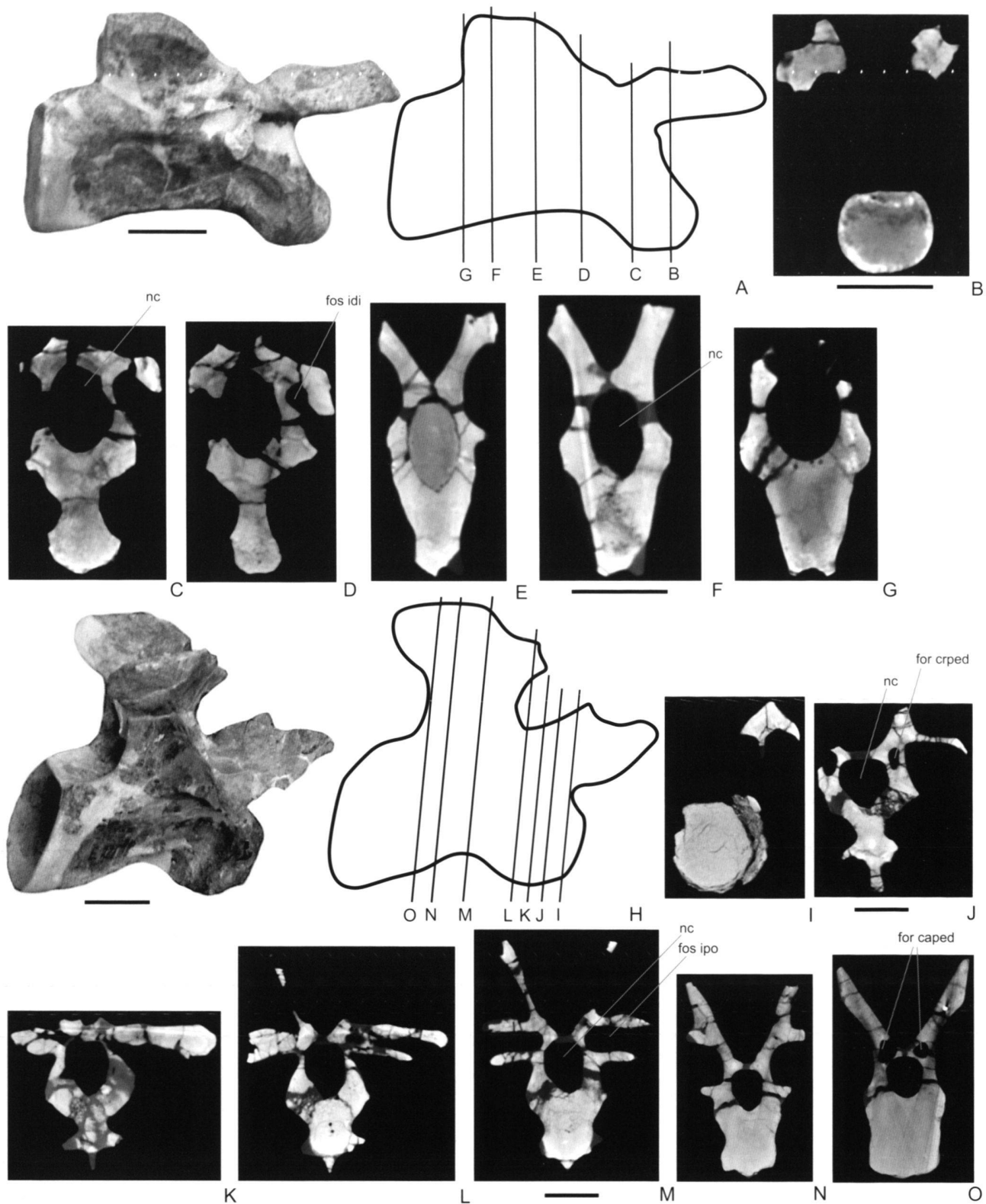


Fig. 5. Transverse sections through cervical vertebrae of *Dicraeosaurus* sp. with computed tomography. A) Photograph (left) and schematic drawing (right) of 4th cervical (HMN E14) with indicated levels of transverse cross-sections as displayed in B-G. H) Photograph (left) and schematic drawing (right) of 12th cervical (HMN E27) with indicated levels of transverse cross-sections as displayed in I-O. Abbreviations as in Figs. 1 and 2. Scale bar: 5 cm.

As the cervicals of *Dicraeosaurus hansemanni* are on the skeletal mount, and those of *Dicraeosaurus sattleri* are strongly modelled and covered with plaster and resin materials, only some isolated smaller cervical vertebrae of *Dicraeosaurus* sp. from the locality “E” of the Tendaguru deposit were available for CT scans. Those isolated cervicals were described by Janensch (1929a; 1929c) as *Dicraeosaurus sattleri*, but currently labelled only as “*Dicraeosaurus* sp.”. As no diagnostic features are visible, a specific assignment is impossible.

- The cervical vertebra E14 (Fig. 5A–G) represents a 4th cervical of *Dicraeosaurus* sp. Its postzygapophyses are broken away and parts of the neural arch are modelled with plaster.
- E27 (Fig. 5H–O) represents a 12th cervical vertebra of *Dicraeosaurus* sp. The left neural spine is broken away. The vertebral centrum and neural arch are badly fractured and have been repaired and modelled with plaster.

3. Method

The computed tomography was performed in the Clinic for Small Animals, Free University of Berlin, using a high-resolution Multislice-CT scanner (GE Healthcare Light Speed advantage QXi). A spiral scan with a 0.6 mm interval was made, leading to DICOM stacks between 326 and 927 images, according to the size of the objects. The settings were 140 kV and 220 mA. Data were reconstructed in bone algorithm with a GE Advantage Workstation 4.2 and Volume Viewer Plus, using the software Voxtool 5.4.46.

Due to the distortion and preservation of the remains, the total area of pneumatic spaces could not be isolated with a software program. On the basis of the CT scans, the reduction of bone material by pneumatic structures was calculated manually as follows. From each vertebra, several transverse cross-sections were chosen and with the software ImageJ 1.30v surrounded by an “ideal vertebra” outline. The total amount of pixel covered by pneumatic structures was subtracted from the total amount of pixel of the “ideal vertebra” outline. Transformed into percentages, these values give a rough estimate of how much of the bone material has been replaced by pneumatic structures. A similar method has been employed by Wedel (2004b; 2005), who defined the Air Space Proportion (ASP) as a value for the estimated proportional amount of air in a pneumatized bone.

As the only extant vertebrates possessing postcranial pneumaticity, birds were taken as models for the reconstruction of postcranial pneumaticity in sauropods (Britt 1993; Wedel et al. 2000a, b; Wedel 2003a, b). The reconstruction and description of pneumatic diverticula for *Brachiosaurus brancai* and *Dicraeosaurus* sp. are based on comparisons with extant birds in this work, i.e. with the dissections of necks of *Meleagris gallopavo*, *Columba livia*, *Struthio camelus* and *Ardea cinerea*.

The terminology applied here is based on Wilson (1999) for sauropod vertebral laminae and Britt (1993), Wedel (2000b), and O'Connor (2003; 2004) for vertebral pneumaticity with external and internal pneumatic structures (see also Fig. 1).

4. Description of pneumatic structures

4.1. Pneumaticity in the neck of *Brachiosaurus brancai*

First detailed descriptions of the internal pneumatic structures of the cervical vertebrae of *Brachiosaurus brancai* were made on the basis of broken remains and cross-sections of the vertebrae by Janensch (1947; 1950b), who was one of the first scientists to describe and interpret vertebral pneumaticity in sauropods in detail.

The computed tomographies allow a description of the connection between external and internal pneumatic structures. The cervical vertebrae of *Brachiosaurus brancai* display a complex pattern of external pneumatic fossae and foramina (Janensch 1950b). The subdivision of pneumatic fossae and the number of pneumatic foramina increases caudally. Intraosseous pneumatic structures in the cervical vertebrae of *B. brancai* are semicamellate (*sensu* Wedel et al. 2000b). In the CT study, the axis (HMN SI70) (Fig. 2) and the third cervical vertebra (Fig. 3) (HMN SI51) show fewer and larger, more rounded camellae than the fourth cervical (HMN SI71) (Fig. 4). Except the unpneumatized odontoid process, the axis (HMN SI70) is pneumatized (Fig. 2B).

Vertebral centrum

In lateral view, the cranial third of the vertebral centrum is adjacent to the vertebral condyle slightly depressed and possesses an irregular rugose surface with at least three distinct, longitudinally oval pneumatic fossae (Figs. 1A, D; 2–4). The ventral-most of the cranial pleurocoelous fossae is bounded by sharp bone margins and bears a pneumatic foramen, by which the parapophysis is hollowed out from dorsolaterally. The large, nearly circular interparapophyseal camella extends far medially and leaves a broad median bone strut with a few small camellae.

The pneumatic fossae positioned dorsally and cranially to the parapophysis each bear a pneumatic foramen, which opens into the vertebral condyle into lateral camellae. Within the vertebral condyle, the lateral camellae branch out into several smaller, rounded camellae surrounding a large median camella (Figs. 3C; 4C, D). The vertebral condyle is pneumatized, and the complexity of the camellae within the vertebral centrum increases medially to the cranial pleurocoelous pneumatic fossa. The camellae open into a left and a right high-oval camera level with the cranial margin of the diapophysis. The paired camerae enclose a thin median bone strut (Figs. 2E; 3E; 4F) and extend dorsally as far as to the lateral margins of the neural canal and caudally open into the caudal pleurocoelous fossa.

In lateral view, the longitudinally oval caudal pleurocoelous fossa is positioned caudally to the diapophysis and in the medial third of the vertebral centrum length and bounded by sharp bone margins. From the caudal pleurocoelous fossa, at least three longitudinally oval to circular pneumatic foramina penetrate into the neural arch and lead into camellae laterally to the neural canal. Caudomedially, pneumatic foramina

connect the caudal pleurocoelous fossae with paired internal camerae (Figs. 2G, I, J; 3G, I, J; 4G–J). The median bone strut left between these camerae is broader than in the medial part of the vertebral centrum and pneumatized itself by camellae. In the caudalmost part of the vertebral centrum, the size of the internal camerae decreases strongly and the medial part of the vertebral centrum is filled by a meshwork of small pneumatic camellae (Figs. 3K; 4L). Immediately cranially to the opening of the vertebral cotyla there remain only one dorsal, one ventral and a left and right lateral camera, which diminish parallel to the opening of the caudal vertebral cotyle.

Neural arch

The base of the prezygapophysis is deeply excavated at its lateral face by a longitudinally oval, internally rugose supraprezygapophyseal pneumatic fossa (Fig. 1A). Within this supraprezygapophyseal fossa, two pneumatic foramina lead cranially into the prezygapophysis to run into two main camellae. These main camellae branch out cranio-laterally into smaller camellae, so that the prezygapophysis is very strongly hollowed out and only thin lamellae of bone walls remain (Figs. 3B; 4B, C).

An infraprezygapophyseal fossa is positioned ventrally to the prezygodiapophyseal lamina and caudally blends into the infradiapophyseal pneumatic fossa at the lateral surface of the vertebral centrum ventrally to the diapophysis. The infradiapophyseal fossa cuts dorsally to the neural canal deeply into the neural arch, forming a left and right infradiapophyseal camera (Fig. 4F). In the cranial half of the diapophysis the left and right infradiapophyseal camerae enclose a high-oval medial camella (Fig. 3F). A thin median bone strut can be observed in the caudal half of the diapophysis (Fig. 4H).

In its cranial two thirds the diapophysis is internally completely hollowed out, with the resulting intradiapophyseal camera extending far medially into the neural arch and ventrally separated by a thin bone wall from the ventrally adjacent infradiapophyseal camera (Figs. 3F; 4H). The ventral wall of the diapophysis is perforated by a large medial foramen. The lateral third of the diapophysis is massive and houses a small, circular camella. Between the axis and the 6th cervical vertebra, the caudal third of the diapophysis is massive bone and bears some small camellae. From the 7th cervical vertebra onwards, the caudal margin of the diapophysis is medially indented.

The postzygodiapophyseal lamina roofs a large infrapostzygapophyseal fossa (Fig. 1A, D), which very strongly undermines the postzygodiapophyseal lamina dorsally. The resulting infrapostzygapophyseal camera leaves only a thin median bone strut of the neural arch and blends cranially into the intradiapophyseal camera. Dorsally, the infrapostzygapophyseal camera branches out in some smaller camellae. In the axis (HMN SI70), the postzygapophysis is not pneumatized (Fig. 2J), but in the 3rd (HMN SI51) and 4th (HMN SI71) cervicals, a canal leads caudally from the infrapostzygapophyseal

camera into the postzygapophysis to form rounded camellae positioned dorsoventrally to each other (Figs. 3I, J; 4J, K). In these two vertebrae, the postzygapophysis therefore is strongly hollowed out with only thin bone walls left.

In lateral view, the lateral face of the neural arch is slightly depressed to form a strongly rugose laterospinal fossa (Fig. 1D). The laterospinal fossa is divided into several smaller pneumatic fossae, separated from each other by bony laminae (Janensch 1950b). Cranioventrally, the laterospinal fossa bears a pneumatic foramen that leads into a small camella within the neural arch. Caudally, the laterospinal fossa blends into at least two longitudinally oval pneumatic fossae, which are positioned ventrally adjacent to the broadened, rugose dorsal margin of the neural spine. These two pneumatic fossae deeply medially excavate the neural spine (Figs. 3F; 4H, I).

In caudal view, the single neural spine is undermined by a median postspinal fossa (Figs. 1C and F; Janensch 1950b). As it is visible in the CT sections (Figs. 2J; 3H–J; 4J, K), little pneumatic foramina penetrate the lateral walls of the postspinal fossa and lead into the postzygapophyses and the neural spine.

Neural canal

The neural canal is bounded by a paper-thin bone wall and surrounded ventrally by and laterally and dorsally by small camellae (Figs. 2–4). Caudally to the diapophysis region, foramina connect the neural canal with the dorsally adjacent camellae, and with the ventral camera (e.g. Figs. 2G, H; 3G–J; 4H–K).

The cranial face of the cervicals exposes paired, rounded triangular cranial peduncular foramina laterodorsally to the neural canal (Fig. 1B, E). The foramina are twice as high as the opening of the neural canal and dorsally excavate the base of the prezygapophysis. The cranial peduncular foramina open into a paired cranial peduncular canal, which caudally unites with the infradiapophyseal camera (Figs. 3D, E; 4E, F). Similarly, the caudal face of the vertebrae bears paired caudal peduncular foramina with a rounded triangular outline and half as wide as the neural canal (Fig. 1C, F). The caudal peduncular foramina open into the paired caudal peduncular canal, which end in a system of small camellae (Fig. 3I, J) or cranially blends into the infrapostzygapophyseal camera (Fig. 4J, K). Within the neural arch, the cranial and the caudal peduncular canal lie dorsally to the neural canal and contact the small dorsal and lateral camellae around the latter. The axis only possesses a depression laterodorsally to the cranial vertebral foramen, but no cranial and caudal peduncular foramina or canals.

Cervical ribs

No cervical ribs could be examined with computed tomography, so that only their external pneumatic structures can be described. The remains of the cervical ribs (isolated remains HMN S36 and remains from the individuals SI and SII) possess a through-shaped depressed internal surface. A rounded crest

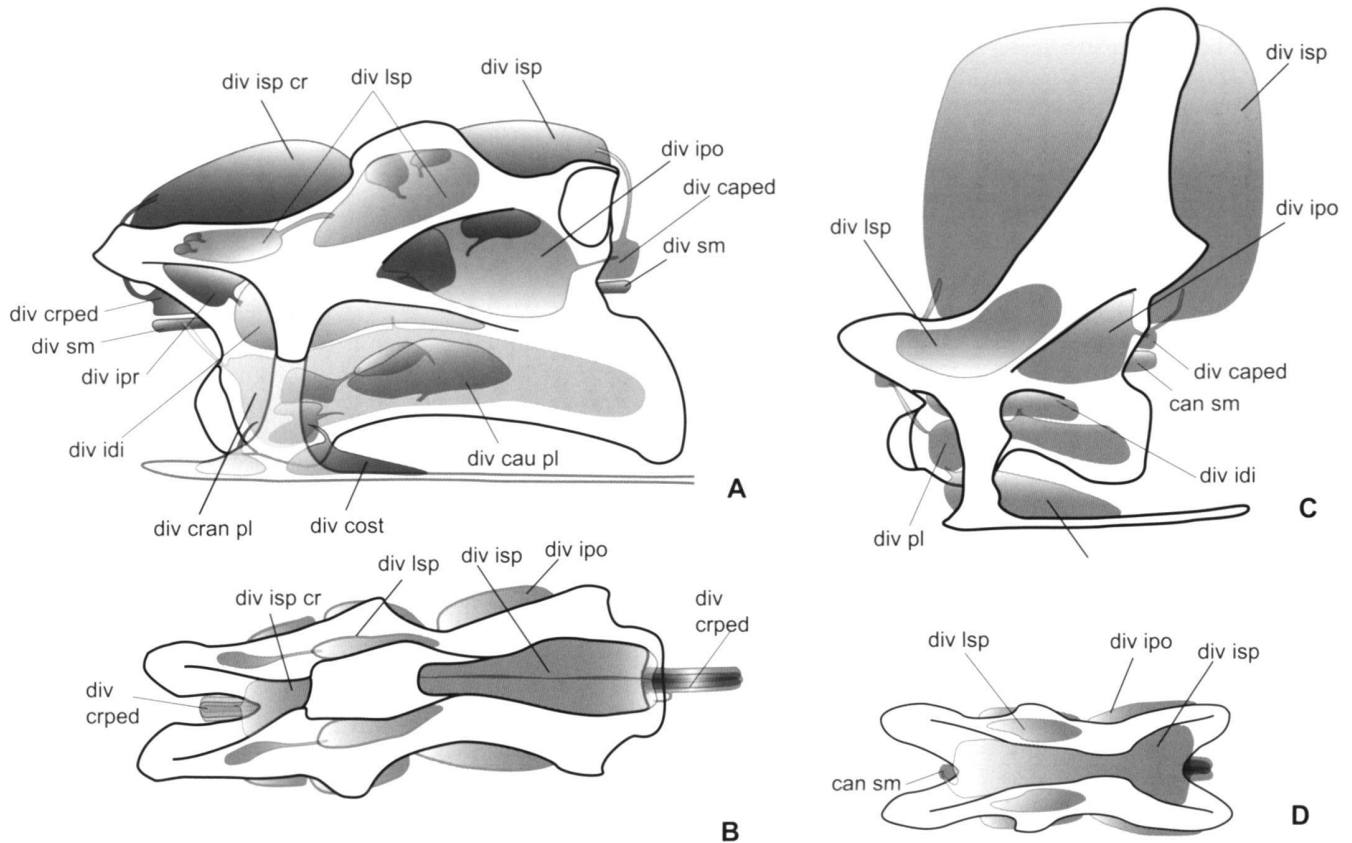


Fig. 6. Reconstruction of pneumatic diverticula in the cervical vertebrae of *Brachiosaurus brancai* and *Dicraeosaurus*. Cervical vertebra of *Brachiosaurus brancai* A) in left lateral view, B) in dorsal view. Cervical vertebra of *Dicraeosaurus* C) in left lateral view and D) in dorsal view. Figures are not to scale. Abbreviations: div caped, caudal peduncular diverticulum (paired); div cau pl, caudal pleurocoelous diverticulum; div cran pl, cranial pleurocoelous diverticulum; div crped, cranial peduncular diverticulum; div idi, infradiapophyseal diverticulum; div ipo, infrapostzygapophyseal diverticulum; div ipr, infrapraezygapophyseal diverticulum; div isp, (caudal) interspinal diverticulum; div isp cr, cranial interspinal diverticulum; div lsp, laterospinal diverticulum; div sm, supramedullary diverticulum.

at the internal surface of the rib connects the capitulum with the tuberculum (Janensch 1950b). Caudally to the capitulum-tubercular crest, a pneumatic foramen penetrates from the internal rib surface cranially into the rib body and the internal rib surface can be subdivided by further rounded crests.

Reduction of bone material at the cervical vertebrae

The external cortical bone of the cervical vertebrae has mostly a thickness of 6 mm, but regionally (i.e. in the medial region of the vertebral centra) it reaches only 3 mm in thickness. The thickness of the septa separating pneumatic cavities from each other varied between 1 mm and 6 mm, with most septa having a thickness of 1–2 mm. In the axis, approximately 50 % of the bone material is replaced by pneumatic structures. The transverse cross-section of the neural canal is ca. 8 % of the total transverse cross-sectional area at the axis. In the third cervical vertebra, approximately 47 % of the bone material has been resolved by pneumatic diverticula. The neural canal comprises 6 % of the total transverse cross-sectional area of the verte-

bra. The 4th cervical has approximately 60 % of the bone mass replaced by pneumatic structures, and the neural canal is approximately 4 % of the total transverse cross-sectional area of the vertebra.

Reconstruction of pneumatic diverticula in the neck

The pneumatic fossae and camerae of *Brachiosaurus brancai* correspond most probably to pneumatic diverticula (Wedel et al. 2000b; Wedel 2003a). The strongly divided and complex pneumatic fossae in the cervical vertebrae indicate a strong subdivision or branching out of these main diverticula, which increased caudally within the neck.

The consistent appearance of pneumatic foramina and fossa on the lateral faces of the cervical vertebral centra, the parapophyses and the medial face of the cervical ribs of *Brachiosaurus brancai* indicates the presence of a unit of pneumatic diverticula that formed similar to extant birds paired canales intertransversarii, running along the vertebral centra of the neck vertebrae through the foramina intertransversaria

(Müller 1908; Wedel 2003a; O'Connor 2004). These canals intertransversarii formed the connection from the cervical air sacs to the neck vertebrae, supplying the latter with air. The cervical vertebrae of *Brachiosaurus brancai* can be reconstructed as having possessed a costal diverticulum (Fig. 6A). The costal diverticulum extended for approximately one third of the length of the costal body, according to the pneumatic structures found at the cervical ribs at least between parapophysis and costal tuberculum. At the lateral surface of the vertebral centrum, there was probably one large pleurocoelous diverticulum, which divided cranially into some smaller cranial pleurocoelous diverticula and caudally into a larger caudal pleurocoelous diverticulum (Fig. 6A). The cranial pleurocoelous diverticula invaded the vertebral condyle and the cranial part of the vertebral centrum. The foramen intertransversarius was most probably filled by the cranial part of the pleurocoelous diverticulum, the infradiapophyseal diverticulum and the laterocostal diverticulum.

The infraprezygapophyseal diverticulum was separated from the infradiapophyseal diverticulum by a thin lamina (Figs. 1A; 6A). There was one infradiapophyseal diverticulum (Fig. 6A), which invaded the vertebral centrum and the neural arch and cranially continued beneath the prezygodiapophyseal lamina. A large infrapostzygapophyseal diverticulum can be reconstructed, which exclusively pneumatized the neural arch (Fig. 6A). The pneumatic canals connecting the neural canal with surrounding cavities, and the connection between the neural canal and the intracorporal camerae indicate the presence of supramedullary pneumatic diverticula.

The lateral face of the neural arch of *Brachiosaurus brancai* bore most probably a laterospinal diverticulum. The strongly pneumatized prezygapophysis resulted either from a cranial extension of the laterospinal diverticulum, or from a dorsal extension of the cranial peduncular pneumatic canal (Fig. 6A, B). It is indicated by the pneumatic foramina connecting the neural arch and the postzygapophyses with the interspinous cavity, that the caudal interspinous cavity housed an interspinous pneumatic diverticulum (Fig. 6A, B). The interspinous diverticulum most probably was divided into two lateral parts enclosing a medial interspinous elastic ligament as in extant birds (Boas 1929) and reconstructed for other sauropods (Wedel et al. 2000b; Tsuihiji 2004). It is possible that cranially to the neural spines a cranial interspinous diverticulum was present, which originated from an ascending branch of the supramedullary diverticulum (Fig. 6A, B).

4.2. Pneumaticity in the neck of *Dicraeosaurus*

The external pneumatic structures in the cervical vertebrae of *Dicraeosaurus* are generally simple fossae with few subdivisions. Rarely, small pneumatic foramina occur. Pneumatic structures of *Dicraeosaurus* have been described by Janensch (1929a), but because they form the basis for reconstructing pneumatic diverticula in the neck of *Dicraeosaurus*, we regard it necessary to give a detailed account on their distribution on

the basis of the complete cervical vertebral column of *Dicraeosaurus hansemanni*.

In *Dicraeosaurus hansemanni*, the lateral surface of the vertebral corpus bears a large pleurocoelous fossa that is divided into a craniodorsal and a caudoventral half (Fig. 1G, H). The surface of the pleurocoelous fossae is slightly rugose, showing the typical "woven" texture that can occur at the contact between bone surface and pneumatic epithelium (Britt 1993; Wedel et al. 2000b). From the cranial pleurocoelous fossa, a foramen ventrally perforates the surface of the parapophysis. Cranially, the cranial pleurocoelous fossa tapers to a "bottleneck" leading into the vertebral condyle. From the 5th cervical onwards, a longitudinally oval foramen lies dorsally within the cranial pleurocoelous fossa. In the axis, an infradiapophyseal fossa extends from the cranial pleurocoelous fossa in dorsal direction, whereas in the caudalwards following cervicals, the infradiapophyseal fossa is caudoventrally to the diapophysis. The infraprezygapophyseal fossa is united with the infradiapophyseal fossa. An infrapostzygapophyseal fossa is present and dorsally bounded by the postzygodiapophyseal lamina (Fig. 1G, H).

The lateral surface of the neural arch of the cervical vertebrae of *Dicraeosaurus hansemanni* bears a rugose laterospinal fossa (Fig. 1G, H). In the axis and the 3rd cervical, a foramen connects the laterospinal fossa with the postspinal fossa, which might be a preparation artefact. With the exception of the axis, the neural spines of the cervical vertebrae of *Dicraeosaurus hansemanni* are bifurcate. In the axis and the 3rd cervical, a caudal postspinal fossa is developed, divided by a median crest into two lateral halves. Between the 3rd and 7th cervical vertebra, a fossa lies cranially to the neural spine at the dorsal surface of the neural arch.

Description of the CT sections

The 4th cervical vertebra of *Dicraeosaurus* sp. (HMN E14) (Fig. 5A) shows less invasive external pneumatic structures than that of *Dicraeosaurus hansemanni*, but is also one third smaller than the latter. The cranial vertebral condyle is not pneumatic. The pleurocoelous fossa in the cranial half of the vertebral corpus extends medially into the vertebral corpus, leaving a median bone strut of one third of the total width of the vertebral centrum (Fig. 5C, D). The ventral third of the median bone strut consists of unpneumatic spongiosa having presumably contained erythropoietic bone marrow. Similar unpneumatic spongy bone is found in the caudal half of the vertebral centrum (Fig. 5D). The infradiapophyseal fossa undermines the diapophysis and lateral fourth of the neural arch (Fig. 5C, E). The infrapostzygapophyseal fossa is a shallow concave depression, which ends far laterally from the neural canal (Fig. 5E, F). The bifurcate neural spine branches are massive bone.

The 12th cervical vertebra (HMN E27) (Fig. 5H) is identical in size and in the amount and distribution of external pneumatic structures to the 12th cervical of *Dicraeosaurus hanse-*

manni (Janensch 1929a). At the cranial third of the vertebral centrum, the cranial pleurocoelous fossa is divided by a crest into a ventral and a dorsal half (Fig. 5J, K). Therefore, in the CT section, the bone is reduced to a cross-shaped structure. Ventrally to the diapophysis, the vertebral centrum gets more massive than in the cranial part of the vertebra and bears a short lateral crest (Fig. 5L). The infradiapophyseal fossa is shallow and cuts ventrally to the diapophysis slightly into the neural arch (Fig. 5J, K). The caudal margin of the diapophysis is drawn out into a ventral and a dorsal sheet, with the ventral sheet extending caudally as the caudal centrodiaophyseal lamina, whereas the dorsal sheet becomes the postzygodiaophyseal lamina (Fig. 5L, M). The infrapostzygapophyseal fossa is very shallow. Janensch (1929a) describes the walls of the neural canal of the cervicals of *Dicraeosaurus* as very thin and with lateral excavations in the medial part of the neural canal. In contrast, in both vertebrae studied with CT, the wall of the neural canal appears massive (Fig. 5). Whereas the neural canal of HMN E14 exposes no lateral excavation, such an excavation can be seen in the neural canal of HMN E27 (Fig. 5K). In the caudal fourth of the neural canal, a paired caudal peduncular fossa is positioned dorsally to the neural canal (Fig. 5O). Laterally, the neural spine bears a shallow laterospinal fossa that has no connection to the internal structures of the vertebra.

Reduction of bone material at the cervical vertebrae

Whereas the bone of the cervical vertebrae is mostly massive, it can reach regionally (i.e. at the diapophyses and the metapophyses of the neural spine) only 3 to 10 mm in thickness. The maximum constriction of the vertebral centrum by the laterocorporal pneumatic fossae leaves a median bone strut of 10 mm thick. In the 4th (HMN E14) and the 12th (HMN E27) cervical of *Dicraeosaurus* sp., approximately 18 % of the bone material is replaced by pneumatic structures. The transverse cross-section of the neural canal reaches 20 % of the total transverse cross-section of the vertebra in the 4th cervical and 12 % in the 12th cervical.

Reconstruction of pneumatic diverticula in the cervical vertebral column

The rugose or “woven” resorption texture visible in the pneumatic fossae of *Dicraeosaurus* indicates that they housed pneumatic diverticula (Wedel et al. 2000b). In contrast to sauropods with camerate, polycamerate or camellate internal vertebral morphology (Wedel et al. 2000b; Wedel 2005) the pneumatic diverticula of *Dicraeosaurus* were simple and did not branch out further.

The cervical vertebrae of *Dicraeosaurus* bore a pleurocoelous diverticulum at least in the cranial half of the vertebral centrum (Fig. 6C). As in *Brachiosaurus brancai*, the consistent appearance of pneumatic fossae on the lateral faces of the cervical vertebral centra indicates the presence of paired canales intertransversarii, running as in extant birds along the verte-

bral centra of the neck vertebrae through the foramina intertransversaria. The infradiapophyseal diverticulum and the infrapostzygapophyseal diverticulum were the most invasive pneumatic diverticula at the cervical vertebrae, hollowing out the diapophysis and parts of the neural arch from laterally (Fig. 6C). At the lateral surface of the neural arch, a laterospinal diverticulum was present (Fig. 6C, D).

In the cervical vertebrae of *Dicraeosaurus*, the neural canal is not connected to other pneumatic structures, providing no osteological evidence for the presence of supramedullary diverticula (although this might also be a problem of preservation and the small sample size). The paired caudal peduncular fossae dorsally adjacent to the neural canal indicate that pneumatic diverticula might have been present within the neural canal. This is also supported by the large size of the neural canal in relation to the vertebral size in *Dicraeosaurus* (see above, Fig. 5). Furthermore, in extant birds with pneumatized cervical vertebrae, the supramedullary canal is formed by a dorsally ascending branch of the pleurocoelous diverticulum (Müller 1908; Duncker 1971; Wedel 2003a). Thus, the development of supramedullary diverticula depends on the presence of laterocorporal pneumatic diverticula. Since *Dicraeosaurus* possessed pleurocoelous diverticula, a large neural canal, and caudal peduncular fossae in the cervical vertebrae, the taxon most probably possessed also supramedullary diverticula.

In extant birds, a branch of the supramedullary diverticulum ascends dorsally between the intervertebral foramina to produce interspinous dorsal diverticula (Müller 1908; Wedel 2003a), which can form large protrusions dorsal to the vertebrae (O'Connor 2003). If *Dicraeosaurus* possessed supramedullary diverticula (see above), it would be also likely that the postspinal cavity of the axis and 3rd cervical, and the space between the bifurcate neural spine branches in the caudally following cervicals was filled by pneumatic diverticula (Fig. 6C, D), similar to *Diplodocus* (D. Schwarz, pers. obs.) and *Brachiosaurus brancai* (see above).

The presence of a costal diverticulum is not reconstructable from bone morphology, since the parapophyses are not pneumatized. The preserved cervical ribs in *Dicraeosaurus* are fragmentary and covered with plaster, so that they are useless for reconstructing vertebral pneumaticity. It can be assumed that the area of the foramen intertransversarium was at least filled by the laterocorporal and infradiapophyseal diverticula.

5. Discussion

5.1. Pattern of pneumatic structures and biomechanical implications.

The general distribution and amount of reconstructed pneumatic diverticula in the necks of *Brachiosaurus brancai* and *Dicraeosaurus* corresponds to those reconstructed for the neck of *Sauroposeidon* (Wedel et al. 2000b) and *Diplodocus* (D. Schwarz, pers. obs.). It corresponds also to the array of external pneumatic fossae generally found in sauropods, as de-

scribed by Britt (1993), Wedel et al. (2000a) and Wedel (2003a, b), indicating a common pattern of pneumatic structures in sauropod cervical vertebrae. For *Brachiosaurus* it is probable that the postspinal cavity housed a (eventually paired) pneumatic diverticulum, and was not completely filled by the interspinal elastic ligament. In *Dicraeosaurus*, the gap between bifurcate neural spines housed probably large interspinal diverticula, as has been reconstructed for the bifurcate cervical neural spines of *Diplodocus* (D. Schwarz, pers. obs.). These interspinal diverticula most probably shared the cleft between the neural spine branches with an interspinal elastic ligament, for which there is osteological evidence (Janensch 1929a; Tsuihiji 2004). In contrast, there is no osteological evidence for the presence of a dorsal cervical muscle invading the gap between the neural spine branches in *Dicraeosaurus*, which would not allow the construction of interspinal diverticula and increase the weight of the neck considerably.

The reconstructed arrangement of pneumatic diverticula around the cervical vertebrae varies between *Brachiosaurus* and *Dicraeosaurus*: *Brachiosaurus* possessed most probably only isolate interspinal diverticula, whereas in *Dicraeosaurus*, pneumatic diverticula inside the gap of the bifurcate neural spines contacted each other, forming possibly a hose-like unit. Both in *Brachiosaurus* and *Dicraeosaurus*, large diverticula extended along the lateral face of the vertebral centra, forming a paired canalis intertransversarius. This suggests that at least parts of the cervical pneumatic system in sauropods could have contributed to neck bracing as passive support device (Akersten & Trost 2004).

The reconstructed amount of bone replaced by pneumatic diverticula in *Brachiosaurus* reaches up to 60%, so that the pneumatized neck vertebrae were two thirds lighter than they would have been without pneumatization. This value is similar to the mean ASP of sauropods in general, and the mean ASP given for *Brachiosaurus* (Wedel 2004, 2005). The value is also similar the amount of pneumatic camellae reported for the lithostrotian sauropod *Alamosaurus* (Woodward 2005). If it is assumed that the muscle mass of the neck comprises two thirds and the unpneumatized cervical vertebrae comprise one third of the total weight of the neck, pneumaticity would lighten the neck by approximately 25%. Considering the overall large size of *Brachiosaurus*, such a weight reduction of the neck is considerable, giving one possible explanation for the extensive pneumatization of the cervical vertebrae.

Pneumatic diverticula were present in *Dicraeosaurus*, but did not invade the vertebrae extensively. The amount of bone replaced by pneumatic diverticula reached not more than 20% in *Dicraeosaurus*, which is less than the smallest known ASP for sauropods (Wedel 2004, 2005). The neck of *Dicraeosaurus* was lightened only for 6% by its pneumatic structures, assuming the ratio of muscle and bone describe above. Therefore, the presumed effect of pneumaticity for lightening the neck in *Dicraeosaurus* is less important than in *Brachiosaurus*, and the reduced internal pneumaticity seems correlated with overall smaller body size and a shorter neck.

The multiple connections (canals, foramina) between the neural canal and the surrounding pneumatic structures of the cervical vertebrae found in camerate (e.g. *Diplodocus*), semicamellate (e.g. *Brachiosaurus*) and camellate (*Euhelopus*) sauropods (Britt 1993; Schwarz et al. 2004), show an interdependency between the supramedullary diverticula and internal pneumatization of the neural arch. Furthermore, no internal pneumatization of the neural arch has been found without the involvement of the neural canal. It is probable that internal pneumatization of the neural arch is triggered by a supramedullary diverticulum, the latter being a major factor for pneumatizing the neural arch. Therefore, a supramedullary diverticulum might be necessary for internal neural arch pneumatization, but might also persist without further internal pneumatization, as in *Dicraeosaurus*.

5.2. Pneumatic structures of *Brachiosaurus brancai* compared to other brachiosaurid sauropods

An isolated cervical vertebra of *Brachiosaurus* sp. (BYU 12866) has been figured and described by Wedel et al. (2000a, b) as possessing a semicamellate internal pneumatic structure, which is essentially identical to the cervicals of *Brachiosaurus brancai*. Thus, the CT scans of cervicals of *Brachiosaurus brancai* underline that pneumatic structures in the genus *Brachiosaurus* are identical, as it was postulated by Wedel et al. (2000b). Unfortunately, the type specimen of the genus and species *Brachiosaurus altithorax* (Riggs 1903, 1904) possesses no cervical vertebrae and therefore cannot be used for a comparison here. A cervical vertebra of the brachiosaurid "*Brachiosaurus*" *atalaiensis* (Lapparent & Zbyszewski 1957) shows no laterocorporal fossa, however, this material is very fragmentary and therefore not included here.

Sauroposeidon, as a different brachiosaurid genus, exposes some differences in pneumatic structures to *Brachiosaurus brancai*. An autapomorphy of *Sauroposeidon* is the extension of the laterocorporal fossae for nearly the whole lateral surface of the vertebral centrum (Wedel et al. 2000a, b), whereas in *Brachiosaurus brancai* the laterocorporal fossa covers only the cranial two thirds of the vertebral centrum. A recently described midcervical vertebra of an indetermined brachiosaurid from the Early Cretaceous of southern England (Naish et al. 2004) shows an intermediate pattern of pneumatic structures between that of *Sauroposeidon* and *Brachiosaurus*. Whereas *Sauroposeidon* has a camellate internal vertebral morphology with a meshwork of regularly spaced camellae, *Brachiosaurus brancai* exhibits besides camellae also some large camerae.

The comparison between these different brachiosaurids supports the hypothesis of a continuous development from camerate to camellate internal vertebral morphologies (Wedel 2003a; Wedel & Cifelli 2005: Figure 13) at least in the Brachiosauridae. Wedel et al. (2000b) assumed that the considerable elongation of the vertebral centra in brachiosaurids must be strongly correlated with the evolution of camellate internal vertebral structures. If the internal vertebral morphology of

brachiosaurids is discussed within a phylogenetic framework (see e.g. Wilson 2002; Wedel 2003a), the semicamellate condition of *Brachiosaurus* would have been derived from a camerate condition like in *Camarasaurus* (Wedel et al. 2000b; Wedel 2003a). Within brachiosaurids, through a time span from the Late Jurassic (Kimmeridgian-Tithonian, *Brachiosaurus brancai*) to the late Early Cretaceous (Barremian-Albian; indetermined southern England brachiosaurid, *Sauroposeidon*) a development from a semicamellate towards a completely camellate internal pneumatization pattern is therefore most probable.

5.3. Evolution of pneumatic structures in the Dicraeosauridae.

The pneumatic structures in the cervicals of *Dicraeosaurus* are similar to those of *Amargasaurus* (Salgado & Bonaparte 1991) the only differences being deeper fossae and more pneumatic foraminae in the latter taxon. The Dicraeosauridae form the sister-group to the Diplodocidae (Upchurch 1998; Wilson & Sereno 1998; Wilson 2002; Harris & Dodson 2004). The pneumatic structures in the cervicals of the Dicraeosauridae represent a procamerate pneumatization type, which differs strongly from the polycamerate condition of the cervicals of the Diplodocidae (Wedel 2003a). Unfortunately, few is known about a possible existence of internal pneumatic structures in the cervical vertebrae of rebbachisaurid sauropods (Calvo & Salgado 1995; Bonaparte 1999; Salgado et al. 2004), which are the sister-group to the Flagellicaudata (Harris & Dodson 2004; Upchurch et al. 2004). Judging from the external pneumatic features at the cervical and dorsal vertebrae (Calvo & Salgado 1995; Bonaparte 1999; Salgado et al. 2004), cervicals of rebbachisaurids could also possess a procamerate pneumatization pattern similar to *Amargasaurus*. If this would be the case, then pneumatic structures in the neck of dicraeosaurids could be interpreted parsimoniously to be primary and similar to those of procamerate eu- and neosauropods. However, the vertebrae of the rebbachisaurid *Nigersaurus* are described and illustrated as highly pneumatic (Sereno 2005), which points toward a secondary reduction of intraosseous pneumaticity in dicraeosaurids.

If the procamerate pneumatization pattern in dicraeosaurids would be secondary, it would have resulted from heterochrony. Histological studies (Sander 1999, 2000) show that *Dicraeosaurus* grew similar to other sauropods fast and continuously, but reached sexual maturity with 80 % of its maximum size at a relatively larger size than for instance sauropods like *Brachiosaurus* (sexual maturity reached with 40 % of maximum size). Together with their comparatively minor overall size, this could indicate an earlier stop of growth in the Dicraeosauridae. Truncated growth could explain the reduced pneumatization of the postcranial skeleton, which was arrested after external pneumatization, as is indicated by the simplicity of the external pneumatic structures in *Dicraeosaurus*. Thus, if the procamerate condition in the Dicraeosauridae had been secondary, it would have developed from an ancestor with in-

ternal pneumatization, their procamerate pneumatization pattern being therefore a reversal. The presence of extant birds without vertebral pneumaticity (Duncker 1971; Wedel 2003a, b) underlines, that a reduction of pneumatic structures is an evolutionary possibility. The procamerate pneumatization pattern in dicraeosaurids is correlated with a relatively short neck of not more than 12 cervical vertebrae and an overall small body size (Janensch 1929a; Salgado & Bonaparte 1991; Upchurch et al. 2004), indicating a unique and derived type of construction.

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