

## IS THERE AN OPTION FOR A PNEUMATIC STABILIZATION OF SAUROPOD NECKS? – AN EXPERIMENTAL AND ANATOMICAL APPROACH

Daniela Schwarz-Wings and Eberhard Frey

### ABSTRACT

The reconstructed distribution of the major pneumatic diverticula systems in the sauropod neck might hint towards pneumatic stabilization or operation of the long neck, which was investigated considering anatomical and mechanical aspects of soft-tissue reconstructions in the neck of sauropods as well as experimental data. The mechanical role of pneumatic bodies in a generalized segmented beam of Styrodur™ blocks, which was stabilized by air-filled tube-like balloons, was tested with an experiment. A support effect was evident already with one ventral pneumatic system. Adding further pneumatic systems increased the load capacity of the beam. Furthermore, the presence or absence of proximal intersegmental blocks, pressure changes within the balloons, proximal fixation of the balloons or their fixation at each segment respectively, and the degree of segmentation of the pneumatic systems changed the efficiency of support.

In the necks of sauropods, pneumatic support would hinge on the specific reconstruction of the pneumatic diverticula, sufficiently high pressures and a possibility for regulating pressure of the pneumatic system. Only if pneumatic diverticula would extend beyond their bony boundaries at the vertebral surface, and if one or more pressure regulating mechanisms were present, would a support effect be an option. Because none of these factors can be reliably reconstructed on an osteological basis, the hypothesis of pneumatic neck support in sauropods remains hypothetical. However, the combination of pneumatic support with other bracing mechanisms in the sauropod neck results in a consistent constructional morphological model for a pneu aided neck support in sauropods.

Daniela Schwarz-Wings, Naturhistorisches Museum Basel, Augustinergasse 2, 4001 Basel Switzerland  
Current address: Museum für Naturkunde der Humboldt-Universität Berlin, Invalidenstraße 43, 10115 Berlin, Germany. [d.schwarz-wings@museum.hu-berlin.de](mailto:d.schwarz-wings@museum.hu-berlin.de)  
Eberhard "Dino" Frey, Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstr. 13, D-76133 Karlsruhe, Germany. [DinoFrey@aol.com](mailto:DinoFrey@aol.com)

**KEY WORDS:** sauropod; pneumaticity; air sacs; vertebra, cervical; neck support; Styrodur™ model

PE Article Number: 11.3.17A

Copyright: Palaeontological Association October 2008

Submission: 28 January 2008. Acceptance: 13 October 2008

Schwarz-Wings, Daniela, and Frey, Eberhard, 2008. Is There An Option for a Pneumatic Stabilization of Sauropod Necks? – An Experimental and Anatomical Approach. *Palaeontologia Electronica* Vol. 11, Issue 3; 17A: 26p; [http://palaeo-electronica.org/2008\\_3/155/index.html](http://palaeo-electronica.org/2008_3/155/index.html)

## INTRODUCTION

With an enormous weight and a length of nine or more meters, sauropod necks must have been equipped with efficient bracing structures to keep off ground and move. Dorsal ligaments (Tsuihiji 2004), strongly segmented axial muscles (Wedel and Sanders 2002; Schwarz et al. 2007) and overlapping cervical ribs (Martin et al. 1998) certainly were parts of the cervical bracing system in sauropods. Additionally, sauropod dinosaurs had a pneumatized axial skeleton, in which at least the presacral vertebrae were surrounded and/or invaded by pneumatic diverticula. The vertebral pneumatic diverticula in sauropods most likely derived from pulmonary air sacs in the thorax (Figure 1.1) and were connected to the respiratory apparatus (Wedel et al. 2000; Wedel 2003b, 2005), but not necessarily obligatory ventilated.

Several possible functions of vertebral pneumaticity in sauropods have been proposed, such as weight saving, increased strength of the vertebrae, increased buoyancy of the body, respiration or thermoregulation (Janensch 1947; Coombs 1975; Britt 1993; Wedel et al. 2000). It is evident, that the invasion of pneumatic diverticula into the vertebrae led to a lightening of the axial skeleton (Wedel 2005; Schwarz and Fritsch 2006), which was certainly a prerequisite for the evolution of long necks.

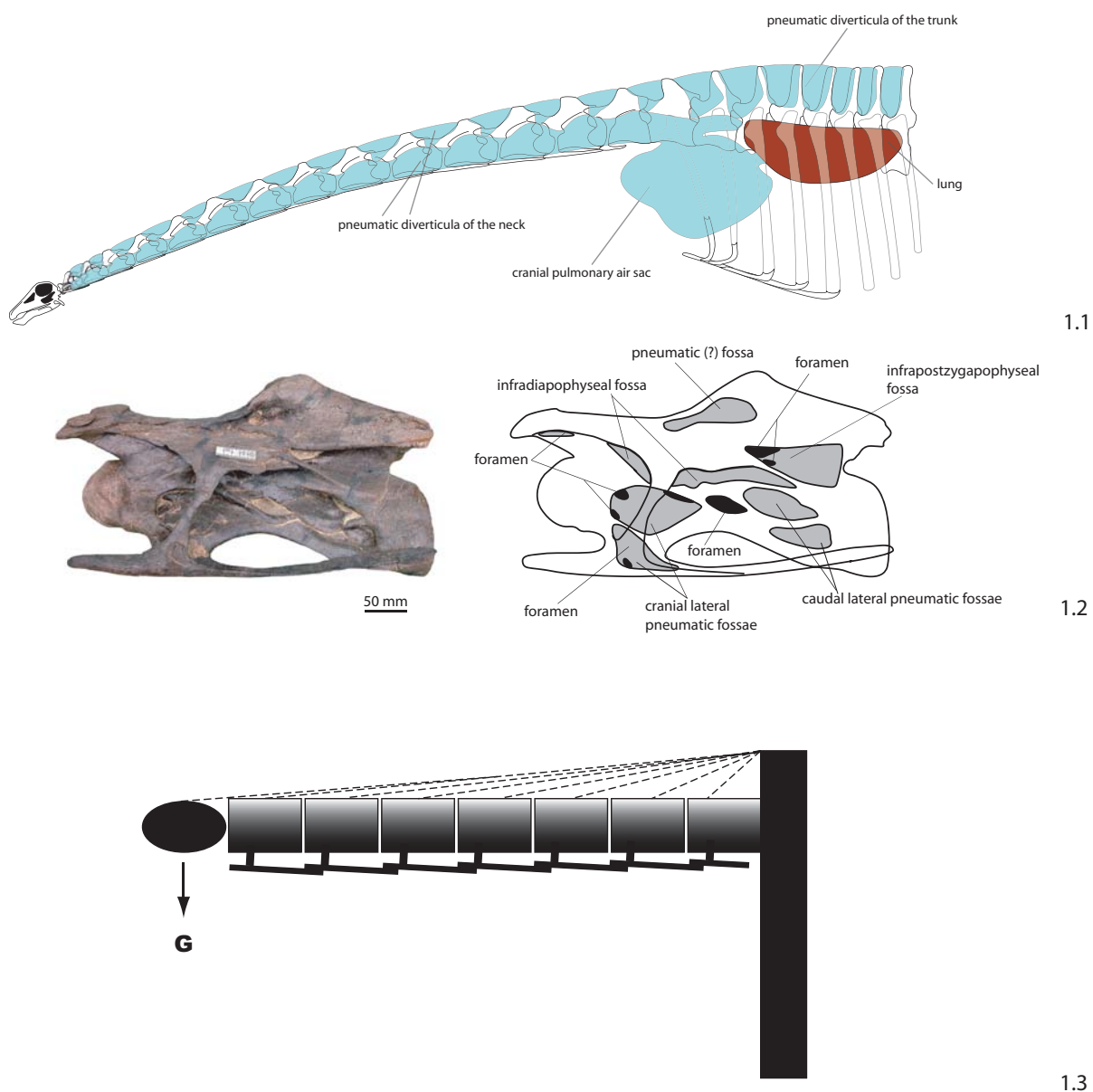
The shape of the cervical vertebrae of sauropods strongly suggests that a variety of pneumatic diverticula accumulated around them. In analogy with extant birds, Akersten and Trost (2000, 2001, 2004) assumed that these diverticula might have contributed to a stabilization of sauropod necks. According to this assumption, the system of pneumatic diverticula lying laterally to the vertebral centra provided passive support of the neck beam, making nuchal or other dorsal ligaments obsolete (Akersten and Trost 2000, 2001, 2004). However, strong dorsal ligament systems are well known in birds (Boas 1929; Tsuihiji 2004) and a dorsal ligament system able to brace the neck has also been reliably reconstructed for sauropods (Tsuihiji 2004; Schwarz et al. 2007). Furthermore, the analyses of Akersten and Trost (2000, 2001, 2004) only refer to ventral diverticula, neglecting the dorsal ones – but in birds, the dorsal diverticula in the neck can be nearly as large as the ventral ones, overgrowing the neural spines as big intermuscular diverticula (Müller 1908; O'Connor and Claessens 2005). The pressure regulation and possible ventilation of the cervical pneumatic systems of sauropods and birds have not been discussed in these papers.

The concept of pneumatic stabilization in the sauropod neck is intriguing, because it would yield a bracing mechanism in support of the tendino-muscular and bony bracing systems without adding weight and opening the option for the reduction of the dimensions of the non-pneumatic bracing systems. However, it remains speculative whether or not the cervical pneumatic systems were mechanically able to take load and if they could, which anatomical and mechanical configuration of pneumatic systems could have taken maximum load. Therefore, the hypothesis of pneumatic stabilization of sauropod necks was tested experimentally, taking into account the anatomy and topography of pneumatic diverticula reconstructed for sauropods (Wedel et al. 2000; Wedel and Cifelli 2005; Schwarz and Fritsch 2006; Schwarz et al. 2007). Hereby, we did not stress the exact morphology and mechanical properties of an anyway reconstructed sauropod neck construction, but tried to model the basic construction of a pneumatically stabilized segmental beam. This beam consisted of a chain of Styrodur™ blocks. A pneumatic system was modeled with tube-shaped party balloons, tied up with gauze tissue. The basal approach applies to the analogy of a tetrapod neck to a segmented cantilever (Kummer 1959; Alexander 1989; Martin et al. 1998; Hildebrand and Goslow 2001). The objective of the experiment was to investigate the mechanical possibility to stabilize a segmented beam with pneumatic bodies, as well as the effects of different arrangements, fixation and segmentation of pneumatic bodies. The results of the experiment were then applied to different sauropod neck constructions in the frame of the limits of soft-tissue reconstructions for sauropods and with the presumed respiratory apparatus.

## MATERIAL AND METHODS

### Material

Sauropod material was examined in the following collections: American Museum of Natural History (AMNH), New York, USA; Chengdu University of Technology (CDUT), Chengdu, China; Carnegie Museum of Natural History (CMNH), Pittsburgh, USA; Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing, China; Museo Argentino des Ciencias Naturales, Buenos Aires (MACN); Museum für Naturkunde, Berlin (MNB), Germany; Naturhistorisches Museum Basel (NMB), Basel, Switzerland; Saurier-Museum Aathal (SMA), Switzerland; Naturmuseum Senckenberg (NMS), Frankfurt, Germany; National



**Figure 1.** 1.1. Reconstructed distribution of pneumatic diverticula along the neck. Note that this reconstruction does not represent a model for respiratory mechanisms in sauropods: neither the direction of air flow, nor the connection of the cranial pulmonary air sac to the trachea or the presence of further pulmonary air sacs are known. 1.2. 8<sup>th</sup> cervical vertebra (SMA L25-3) of *Diplodocus* sp. with osteological correlates assigned to pneumaticity, left as photograph and right as schematic drawing. 1.3. Model of the tetrapod neck as a segmented cantilever fixed at the shoulder girdle. Loading by gravity  $G$  places the dorsal part of the cantilever under tension and the lower part under compression. The segmented cantilever needs to be braced to prevent its sagging, which can be achieved by dorsal tensile (tendons, muscles) and/or ventral compressive elements (cervical ribs).

Museum of Natural History, Smithsonian Institution (NMHNSI), Washington, USA; Yale Peabody Museum (YPM), New Haven, USA; Zigong Dinosaur Museum (ZDM), Zigong, China.

For comparative anatomy, the skeletons of *Rhea americana* (NMB 2670), *Struthio camelus* (NMB 8180), *Dromaeus novaehollandiae* (NMB 2978), *Casuarus casuarus* (NMB 1829), *Sarcoramphus gryphus* (NMB 3295) and *Cygnus cyg-*

*nus* (NMB 10588) were investigated. The necks of *Meleagris gallopavo*, *Columba livia* and *Ardea cinerea* were dissected. CT scans of a crane (*Grus grus*) and a white-tailed eagle (*Haliaeetus albicilla*), produced in the Clinic for Small Pets of the Free University of Berlin with a high-resolution Multislice-CT scanner (GE Healthcare Light Speed advantage QXi), were examined.

### **Reconstruction of Pneumatic Soft-Tissue in the Sauropod Neck**

Topographical similarities between soft-tissue attachment sites of related extant and extinct vertebrates can be used for reconstructing such soft-tissues in extinct taxa, following the method of Extant-Phylogenetic-Bracketing (EPB) (Bryant and Russell 1992; Witmer 1995, 1997; Carrano and Hutchinson 2002). In the case of sauropods, extant Crocodylia and Aves provide the anatomical framework for these soft-tissue reconstructions (Gauthier et al. 1988; Witmer 1997; Benton 2004). The presence of osteological correlates for vertebral pneumaticity exclusively in extant avians permits the reconstruction of these soft structures only by one-way phylogenetic comparison, corresponding to a Level II inference (Witmer 1995, 1997).

Criteria for recognizing osteological correlates of pneumatic structures in sauropod vertebrae (Figure 1.2) are based on comparison with extant avians and follow the works of Britt (1993), O'Connor (2004, 2006), Wedel (Wedel et al. 2000; Wedel 2005) and Witmer (1990, 1997). Because of these avian-based comparisons, standard nomenclature of pneumatic structures for birds was used (Müller 1908; Duncker 1971; O'Connor 2006), supplemented by topographical descriptors for additional pneumatic structures. For the intraosseous pneumatic structures of the vertebrae, established terms for sauropods (Britt 1993; Wedel et al. 2000; Wedel 2003a, 2005) were used. The terminology of the external laminae in sauropod vertebrae follows that of Wilson (1999).

### **Objective of the Experiment**

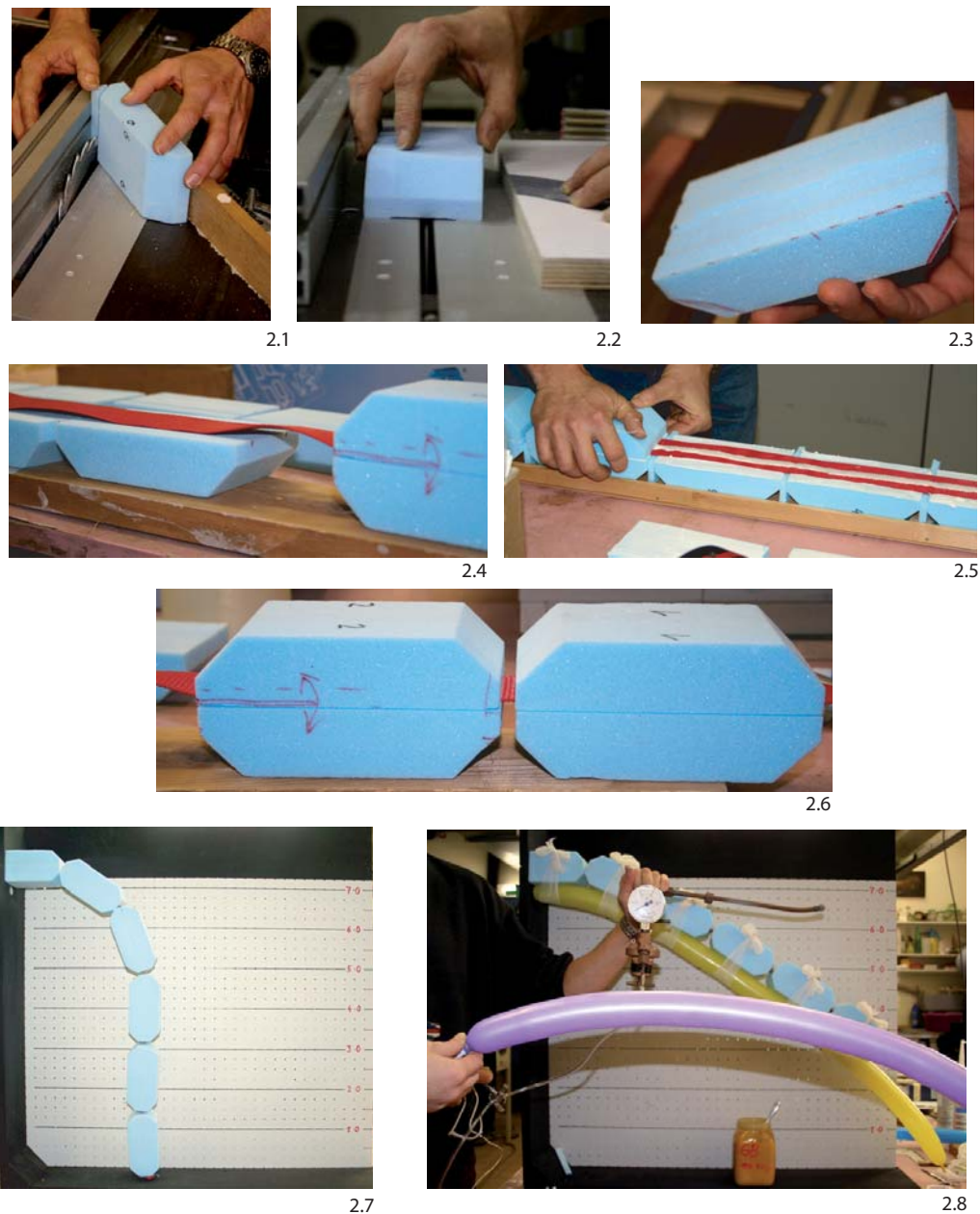
The objective of the experiment was to test the effect of pneumatic support on a chain-beam with different arrangements of pneumatic bodies as a model for the tetrapod neck (see below). Specifically, we wanted to find out whether or not simple pneumatic tubing would be able to hold the chain beam in a near horizontal position and how different arrangements and numbers of pneumatic tubings would influence the stability of the chain beam

against application of load at its free end. The experiment was designed to answer the following questions: 1) Is it mechanically possible to stabilize a chain beam with pneumatic bodies? 2) How do arrangement and fixation of the pneumatic bodies influence the load capacities of the chain beam? 3) How does the system react to symmetrical and asymmetrical changes of the pneumatic pressure? 4) Is it possible to move the chain beam with pressure changes?

### **Theoretical Background for Building the Model**

From a mechanical viewpoint, the tetrapod neck is comparable to a segmented cantilever fixed at one end (Koch 1917; Gray 1944; Slijper 1946; Kummer 1959; Alexander 1989; Frey and Martin 1997; Martin et al. 1998; Hildebrand and Goslow 2001; Salisbury and Frey 2001). The cervical vertebrae form the segments of the cantilever, and the vertebral column of the trunk and the shoulder girdle form its fixation. The cantilever is loaded by gravity, which places its dorsal part under tension, whereas the ventral part is compressed (Figure 1.3). Each segment is free to move against its neighbors on an intersegmental articulation. The tensile and compressive stresses are accommodated by tensile dorsal and/or compressive ventral bracing elements.

Typical bracing structures in the tetrapod neck are the zygapophyseal articulations and their articular ligaments and dorsal ligaments. Additional bracing is brought about by the hydraulic effects of the cervical muscle mass. The zygapophyseal articulations are positioned dorsally to the intervertebral articulations and limit the mobility of the vertebral segments against each other by ligament and bone lock (Stevens and Parrish 1999; Stevens 2002; Stevens and Parrish 2005). Dorsal ligaments (Figure 1.3) extend along the neck of tetrapods either as a single, continuous supraspinal ligament (e.g., in extant crocodylians: Wettstein 1937; Frey 1988a), or as a multisegmental fan-shaped nuchal ligament originating from the trunk region (e.g., in extant mammals and birds; Boas 1929; Slijper 1946) and forming tensile structures (Bennett and Alexander 1987; Alexander 2002). In some tetrapods, such as extant crocodylians (Frey 1988b; Salisbury and Frey 2001) and sauropods, overlapping cervical ribs positioned ventrally to the vertebrae (Figure 1.3) form additional compressible bracing structures connected to each others by intercostal ligaments (Frey 1988a, 1988b; Frey and Martin 1997; Martin et al. 1998).



**Figure 2.** Experimental setup: building the chain beam of 6 segments. For further explanations, see text in “Material and Methods.”

### Experimental Setup

First, Styrodur™ blocks were cut into shape with the blade saw so that the mobility of the chain beam in one plane was guaranteed (Figure 2.1-2.3). The blocks were cut horizontally in two halves, which were glued to a 30 mm wide polyester belt with heavy-duty universal resin dispersion glue (“Pattex Montage Kraft-Kleber Original”) (Figure 2.4-2.6). The most proximally situated segment was cut vertically and formed the fixation base of

the chain beam. The finished chain consisted of six segments and was 650 mm long with a total weight of 200 g.

The chain beam was fixed on a vertical plywood pivot board 700 mm above the stand board, on which the vertical pivot board was mounted (Figure 2.7). The polyester belt was inserted into a horizontal slit cut into the pivot board and fixed with screw clamps in a way that the base segment was absolutely immobile. Pivot and stand board were

linked to each other by a scale panel with a 100 mm grid, in order to record the load effects during the experiment.

Tube-shaped party balloons were tied along the chain beam with gauze bandages according to the reconstructed positions of pneumatic diverticula in sauropod necks. The dorsal balloons were fixed proximally on the shelf by a clothespin. These balloons had a length of about 1.5 m and a diameter of about 50 mm when fully inflated (Figure 2.8). The muzzle of the balloons was connected to a T-switch, which was connected to a compressor and a WIKA manometer (gauge from 0.0-2.5 bar at a scale of 1/10 bar). In one experiment, the balloons were fixed to the segments with double-sided tape, in another experiment they were segmented by twisting parts of the balloons into pneumatic segments. Sometimes intersegmental wedges of Styrodur™ were needed for additional stabilization, especially at its base. At the distalmost segment, a cup was fixed and filled with iron powder to quantify the loads. In order to quantify the sagging effect, the quantity of iron powder was kept constant. For the quantification of the bracing effect, the cup was slowly filled with iron powder until sagging reached a defined level.

#### **Implementation of the Cantilever Model and Material Choices**

For the experiment we did not attempt to simulate any material properties of any organic tissue. Instead we tried to approximate the configuration of a generalized pneumatized chain beam system and its principal functionality as a model for the function of a pneumatized sauropod neck. In the cervical column of a tetrapod, the vertebrae can be regarded as a chain of stable inflexible elements, able to take compression loads and guaranteeing the constancy of length. In the experiment, Styrodur™ blocks formed these incompressible structures.

The complex synovial intervertebral ball and socket articulation of sauropods (Schwarz et al. 2007) would allow movement of the vertebral segments against each other in all directions. However, bending of the vertebrae against each other is limited or nearly blocked in the case of torque movements by the zygapophyseal articulations (see above) (Stevens and Parrish 1999; Stevens 2002; Stevens and Parrish 2005). This kind of movement limitation was simulated with the horizontally orientated polyester belt, which allowed the bending of the segments in the vertical plane until the contact of the Styrodur™ block. Horizontal

(lateral) movement and especially torque was limited. An investigation of lateral movements under pneumatic bracing was possible by arranging the chain beam with the polyester belt standing vertically. The most important mechanical property of the chain beam in any arrangement was the strongly limited torque, a feature essential for the position control of sauropod necks.

To monitor the support effect of pneumatic tubings alone, all other bracing elements were first omitted from the model. From its fixing point, the experimental chain beam with the polyester belt oriented horizontally would sag completely under its own weight into Styrodur body lock at its base. Later, additional Styrodur™ wedges were placed ventrally between the basal, representing additional ventral compressive bracing elements. The experiment was designed to (1) prove that a chain beam can be braced pneumatically, (2) quantify the effect of different arrangements and pressures of the pneumatic systems around the chain beam and (3) test the option of a pneumatically triggered movement of a chain beam. The results of the experiment are discussed in the frame of an optional utilization of extensive pneumatic systems as found among sauropods in the context of bracing and mobility.

Because the simulation of biomaterials is methodologically problematic if not impossible, the choice of the materials for the experiments was restricted to the material properties of the system in general. Bone is a biological composite material with a high compressive and poor tensile strength, therefore being mainly resistant against compression (Koch 1917; Currey 1987, 1999). For producing the simplified vertebral segments in the model, extruded high-resistance polystyrene foam Styrodur™ was chosen. Similar to bone, Styrodur™ has a higher compressive than tensile strength and is resistant against compression. Additionally, the material was cheap and easy to shape.

Pneumatic diverticula are air-filled pockets lined by pneumatic epithelium, thus they represent air-filled membrane constructions. The reconstruction of the pneumatic system of sauropods by comparison with extant birds implicates similarities in the properties of the pneumatic diverticula in both groups. In birds, the wall of the diverticula is formed by a smooth,  **cuboidal to columnar**  pneumatic epithelium (Duncker 1971; Maina 2005; O'Connor 2006). The pneumatic epithelium is covered by a thin layer of nearly avascular connective tissue, consisting of a loose network of elastic and collagenous fibers and a few blood vessels

(Duncker 1971; Carlson and Beggs 1973; Maina 2005). In the air sacs of the body cavity, the external wall of the pneumatic epithelium in many birds touches the peritoneal epithelium, which is a layer of mesothelial cells (Duncker 1971; Carlson and Beggs 1973; Fletcher 1980). The diverticula walls can additionally contain cells of smooth muscle tissue and clusters of adipose cells (Duncker 1971; Maina 2005). Pneumatic diverticula in the neck of extant birds are enwrapped in connective tissue and connected with each other via tiny ducts. The diverticula around the vertebrae can anastomose with one another (O'Connor 2006), forming larger hose-like diverticula units along the vertebral column. The units of pneumatic diverticula mechanically resemble pneumatic cushions, which can take over loads by using the compressibility of gasses: only part of the load is transmitted to the membrane, the other part increases gas pressure. In the experiment, the complex diverticular system was reduced to its mechanical properties. Therefore, tube-shaped inflated party balloons were used for the simulation. Similar to the pneumatic diverticula, these balloons can take loads by the compressibility of their air filling. The balloons were fixed along the chain beam using a gauze bandage. Such a fixation is necessary to maintain the coherence between the pneumatic system and the chain beam. As was demonstrated above, pneumatic diverticula in tetrapods show a variety of fixing systems, amongst them sheaths of connective tissue.

## RESULTS

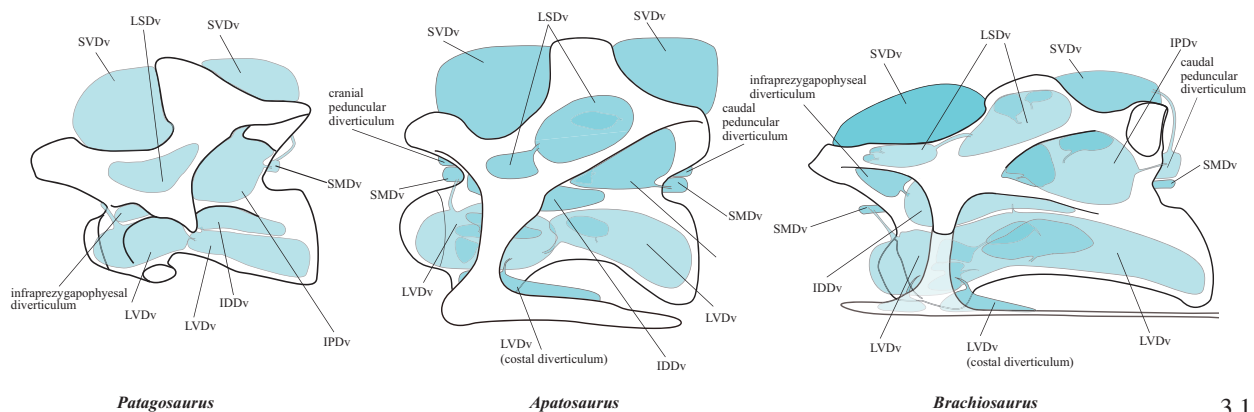
### Reconstructed topography of pneumatic diverticula in sauropod necks

The distribution of pneumatic diverticula in sauropod necks has been reconstructed in detail for *Sauroposeidon*, *Brachiosaurus*, diplodocids and dicraeosaurids (Wedel et al. 2000; Wedel and Cifelli 2005; Schwarz and Fritsch 2006; Schwarz et al. 2007). The topography of osteological correlates for pneumatic diverticula is similar in these and other sauropods, suggesting a similar distribution of pneumatic diverticula. The following pneumatic diverticula subsystems are likely to have been present in all eusauropods (Figure 3): lateral vertebral diverticula (LVDv) laterally adjacent to the vertebral bodies, infradiapophyseal diverticula (IDDv) ventral to the diapophyses, infrapostzygapophyseal diverticula (IPDv) ventral to the postzygapophyses, lateral spinal diverticula (LSDv) lateral to the neural arch and neural spine, supravertebral diverticula (SVDv) cranial and caudal to

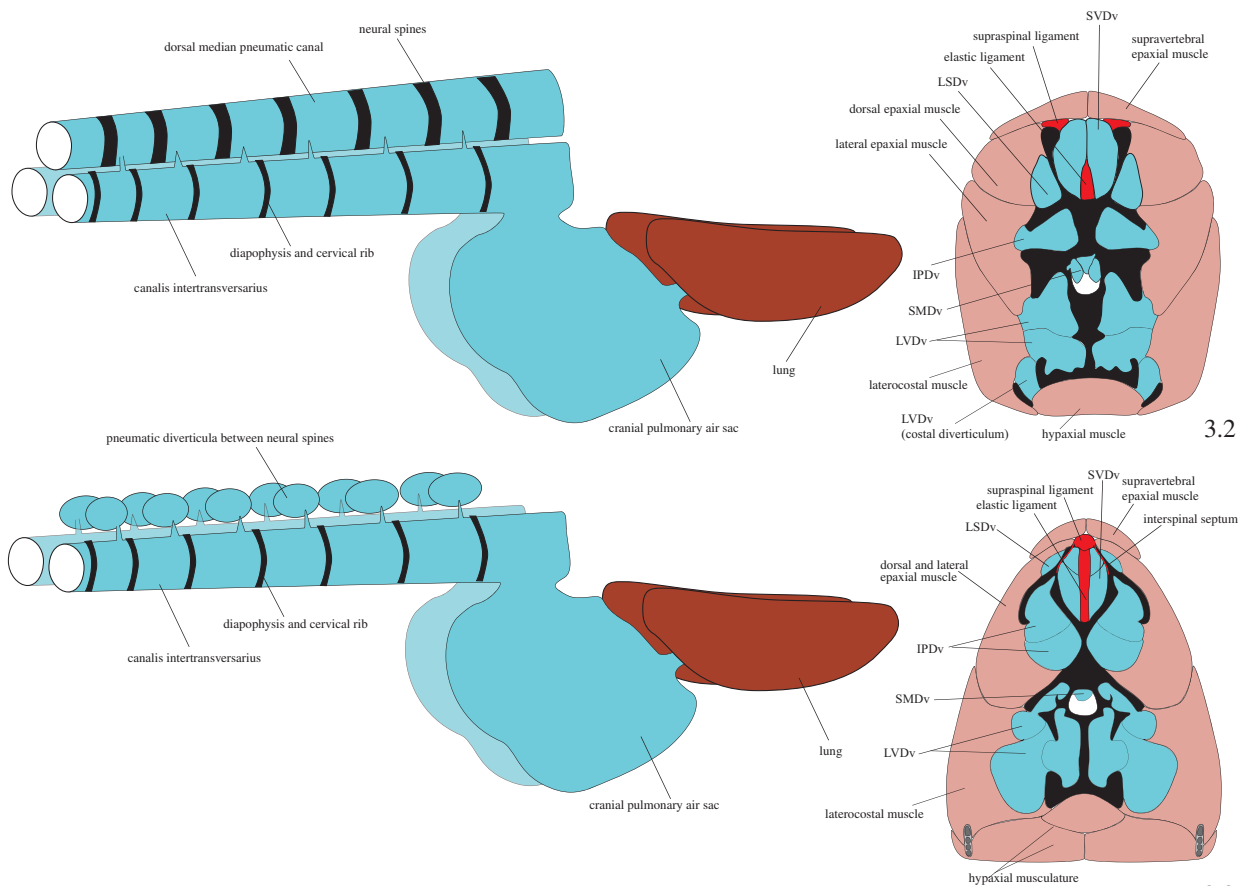
the neural spines, and supramedullary diverticula (SMDv) within the neural canal (Wedel et al. 2000; Wedel 2005; Schwarz and Fritsch 2006; Schwarz et al. 2007).

Size and depth of the pneumatic fossae and foramina in the lateral surface of the vertebral bodies, and comparisons with extant birds indicate large LVDv along the entire lateral surface of the cervical centra (Figure 3). The LVDv passed through the intertransversal foramina, forming a lateral vertebral pneumatic diverticula system similar to the canalis intertransversarius in birds (Müller 1908; Landolt and Zweers 1985). The lumen of the intertransversal foramina was most likely completely occupied by pneumatic diverticula, therefore the diameters of these foramina hint to the cross-section of the whole unit of LVDv. The LVDv were laterally bounded by the cervical ribs, connective tissue, and lateral epaxial and laterocostal cervical muscles, which inserted on the diapophyses and cervical ribs (Wedel and Sanders 2002; Schwarz et al. 2007). Like in birds (Müller 1908; Duncker 1971; O'Connor 2006), the pneumatic diverticula of sauropods were most probably connected with each other by a network of pneumatic ducts, although fossil evidence for pneumatic ducts is rare (Wedel et al. 2000). Pneumatic fossae in the external vertebral surface of many sauropod taxa, such as *Diplodocus*, *Apatosaurus*, *Barosaurus*, *Camarasaurus* or *Brachiosaurus*, are internally divided into subfossae, which indicates a segmentation of the respective pneumatic diverticula into subunits (Wilson 1999; Wedel 2005). Most likely, these diverticula anastomosed at least occasionally with one another, similar to birds (O'Connor 2006). It is likely that corresponding to extant birds, adjacent pneumatic diverticula were bundled together to "aggregates of narrow tubes rather than large, simple sacs" (Wedel 2003a, Figure 5 caption).

Rare pneumatic foramina and depressions on the medial surface of the metapophyses and within the postspinal cavity of the cervical vertebrae indicate that SVDv filled the gap between these metapophyses and the postspinal cavity, respectively (Figure 3.2-3.3) (Schwarz and Fritsch 2006; Schwarz et al. 2007). In sauropods with single neural spines in the neck, pneumatic diverticula formed large evulsions in the interarticular gaps, as is seen in extant birds (Müller 1908; Britt 1993; O'Connor 2001; Wedel 2003a; O'Connor 2006). Median tuberosities within the postspinal cavity and between the metapophyses of bifurcate neural spines provide osteological evidence for large elas-



3.1



3.2

3.3

**Figure 3.** Reconstruction of pneumatic diverticula around the cervical vertebrae of different sauropods. 3.1. Lateral view of cervical vertebrae of *Patagosaurus*, *Apatosaurus* and *Brachiosaurus*, with similar distribution of main pneumatic diverticula (for abbreviations, see “Results”). Possible distribution of pneumatic diverticula throughout the neck of sauropods, provided that pneumatic diverticula extended beyond their bony boundaries at the vertebral surface, 3.2. Tripartite configuration with schematic cross-section as in *Apatosaurus*, note that large SVDv are in contact with dorsal ligaments of the neck, 3.3. Dual configuration with schematic cross-section as in *Brachiosaurus*, note that SVDv are small and separate, but also in contact with dorsal ligaments of the neck. Not to scale.



tic ligaments inserting cranially and caudally on the neural spines of sauropods (Tsuihiji 2004; Schwarz et al. 2007). Therefore, pneumatic diverticula between the metapophyses and within the postspinal cavity must have been medially in direct contact with these elastic ligaments, proliferating around the latter (Figure 3.2-3.3). Additionally, thin laminae on the cranial and caudal margin of the metapophyses, and the well-developed postzygapophyseal laminae suggest the presence of a paired interspinal septum like in extant Crocodylia (Frey 1988a; Schwarz et al. 2007). Between single neural spines, the left and right sheet of the interspinal septum probably enclosed the elastic ligament and the SVDv, which both filled also the postspinal fossa (Schwarz and Fritsch 2006; Schwarz et al. 2007). In bifurcate neural spines, the interspinal septum probably adjoined the SVDv around the elastic ligaments and dorsally contacted the supraspinal ligament. Such an arrangement of spinal ligament sheaths would have provided a hose-like envelope for the dorsal pneumatic diverticula. The width of the area between the metapophyses indicates the volume of the SVDv including their ligamentary envelope.

According to the distribution of pneumatic diverticula along the neck of sauropods, a tripartite arrangement can be distinguished from a dual one (Figure 3). Sauropods with a tripartite arrangement of pneumatic diverticula have bifurcate neural spines in at least half the cervical vertebrae, such as *Apatosaurus*, *Diplodocus*, *Dicraeosaurus* or *Amargasaurus*. In the area of bifurcate neural spines, the entity of SVDv formed a dorsal median pneumatic canal around the elastic ligaments (Figure 3.2). Additionally, a pair of LVDv units at the vertebral centra, assembled in an intertransversar canal, would have been present. In sauropods with a dual arrangement of pneumatic diverticula, bifurcate neural spines occurred in less than half of the cervical vertebrae, like in *Camarasaurus*, or were completely missing like in *Mamenchisaurus* or *Euhelopus*. In the first case, single SVDv formed a dorsal pneumatic canal in the caudal region of the neck only (Figure 3.3). In the second case, SVDv filled the interarticular space and the postspinal cavity. Similar to the tripartite arrangement, the LVDv formed a paired, voluminous, hose-like intertransversar canal.

### Results of the Experiment - Pneumatic Stabilization of a Chain Beam

The experiment was carried out with those configurations of balloons corresponding to the

arrangement of pneumatic diverticula reconstructed for sauropod necks. Each experimental approach (E1-E8) followed a specific question that is outlined below. In the following description, proximal refers to the end of the chain fixed at the pivot board, whereas distal refers to the opposite end bearing the plastic cup with iron powder. The *sagging index* ( $si$ ; in mm) indicates the holding point of the distal end of the chain beam aboveground in a vertical plane. The *bending index* ( $bi$ ; in mm) is the dislocation of the distal end of the chain beam from the straight line in a horizontal plane.

#### E1: Calibration of the unbraced chain beam.

Objective: What is the maximum  $si$  of the system without pneumatic bodies and with other bracing elements?

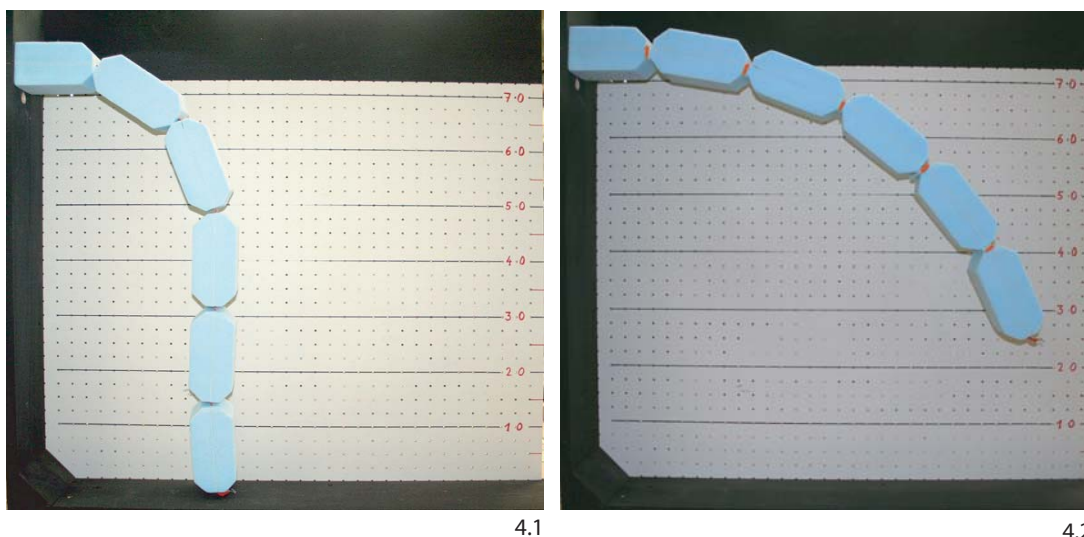
As a calibration base for all following experiments, the intrinsic curvature of the system with and without a bracing element was determined. The chain beam was fixed with its proximalmost segment at the pivot board and loaded by its own weight in the absence of any bracing structure. The chain beam hung vertically down in its basal joint (Figure 4.1). A small intersegmental wedge of Styrodur™ was then placed in the gap between each segment. This arrangement yielded an intrinsic curvature  $siE1$  of the chain beam, which was 265 mm above-ground (Figure 4.2). For all following experiments,  $siE1$  represents the intrinsic reference curvature of the plain coil chain with a bracing element.

#### E2: One median ventral pneumatic tube

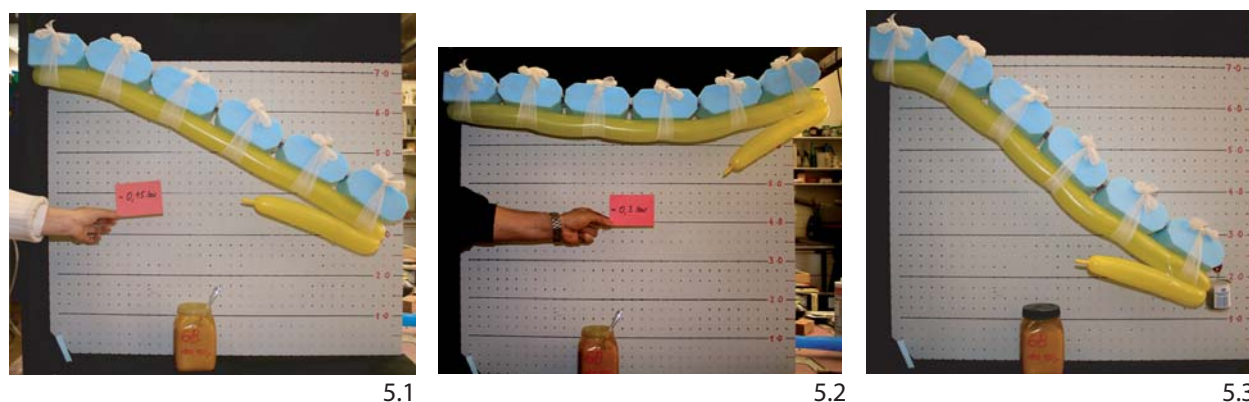
Objective 1: What is the bracing and deformation effect of one median ventral pneumatic tube?

One inflated balloon with a pressure of 0.15 bar was tied with gauze bandages ventral to the chain beam. The  $si$  of the chain beam with this arrangement was 370 mm. The curvature of the beam was strongest between both proximalmost segments, whereas the other segments formed nearly a straight line (Figure 5.1). At an increase of the pressure to 0.3 bar, the chain beam curved slightly dorsally (Figure 5.2). In contrast, the decrease of the pressure to 0.1 bar resulted in a sagging of the chain beam with the balloon buckling up between the two proximal segments. The insertion of a ventral intersegmental wedge between both proximalmost segments resulted in the curvature  $siE1$  at a pressure of 0.1 bar.

Objective 2: How does the median ventral pneumatic tube influence the load capacity of the chain



**Figure 4.** Experiment E1. The intrinsic curvature of the system with and without ventral bracing elements was determined. The chain beam was fixed at the pivot board and  $s_i$  was determined under its own weight and with the insertion of intersegmental blocks. 4.1. The chain beam without any bracing structures hangs vertically down in its basal joint. 4.2. The inserting of intersegmental wedges (marked in red) between the segments of the chain beam yields the intrinsic curvature  $s/E1 = 265$  mm aboveground.



**Figure 5.** Experiment E2. The support effect with one median ventral pneumatic body was tested. One inflated balloon was tied with gauze bandages ventral to the segments and filled with air until a specific pressure was reached. 5.1. With a pressure of 0.15 bar, the curvature  $s_i = 370$  mm and was strongest between the two proximalmost segments, whereas the other segments formed a straight line. 5.2. The increase of pressure to 0.3 bar caused the chain beam to curve dorsally. 5.3. With a pressure of the balloon of 0.15 bar, 45 g iron powder were necessary to achieve  $s/E1$ .

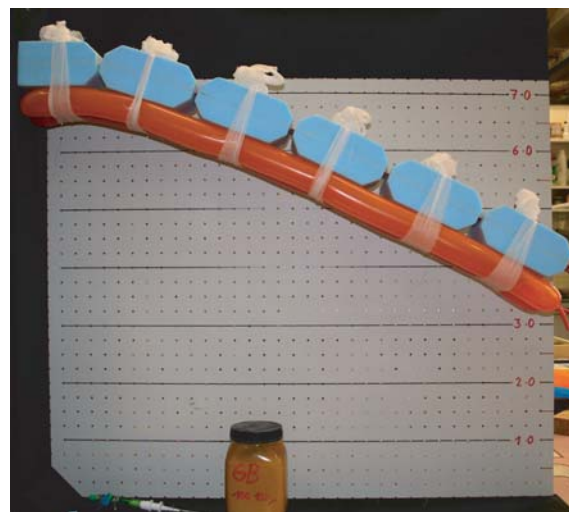
beam and what effect has a pressure increase to the load capacity?

An empty cup was attached to the distal end of the chain beam and filled with iron powder until  $s/E1$  was reached. No ventral intersegmental wedges were used. At a pressure of 0.15 bar, 45 g of iron powder was necessary to produce  $s/E1$ , which is 122.5% of the weight of the chain beam

itself. At a pressure of 0.25 bar, 230 g of iron powder was necessary to deflect the chain to  $s/E1$  (Figure 5.3). This corresponds to 215% of the weight of the chain beam. As a result, a pressure increase of 0.1 bar only increased the load capacity of the system by five times. In both load cases, the chain beam tended to twist around its long axis due to torque moments.



6.1



6.2

**Figure 6.** Experiment E3. The support effect of one pair of pneumatic bodies, positioned laterally or ventrally on the chain beam, was studied. 6.1. A pair of balloons tied laterally to the chain beam yielded zero bracing effect. 6.2. A pair of balloons tied ventrally to the chain beam yielded an *si* of 410 mm.

### E3: One pair of ventral or lateral pneumatic tubes

Objective 1: What is the bracing effect with a pair of lateral or ventral pneumatic bodies respectively?

Two inflated balloons were tied with gauze bandage lateral to each side of the chain beam. The lateral arrangement of the balloons yielded no support effect for the chain beam, which sagged completely (Figure 6.1). The two inflated balloons were then tied ventral to the chain beam. This configuration yielded a *si* of 410 mm (Figure 6.2), which is 10% less than with one ventral balloon. With the ventral pair of balloons, the chain beam was stable with respect to torque.

Objective 2: How does the configuration influence the load capacity of the chain beam?

An empty cup was attached to the distal end of the chain beam and filled with iron powder until the curvature *s/E1* was reached. At a pressure of 0.15 bar, 80g of iron powder were needed to reach *s/E1*, corresponding to 140% of the weight of the chain beam.

### E4: One pair of ventral and a median dorsal pneumatic tube

Objective 1: What is the bracing effect with two ventral and one dorsal pneumatic body?

Two inflated balloons were tied ventral and one dorsal to the chain beam with gauze bandages. The pressure in all balloons was 0.15 bar. The tripartite arrangement of pneumatic bodies led to a *si* of 435 mm aboveground. The dorsally posi-

tioned balloon was under tension, whereas the two ventral balloons were under pressure and pushed proximally towards the pivot board (Figure 7.1). When an intersegmental wedge was inserted ventrally between the two proximal segments (Figure 7.2), the *si* decreased to 475 mm.

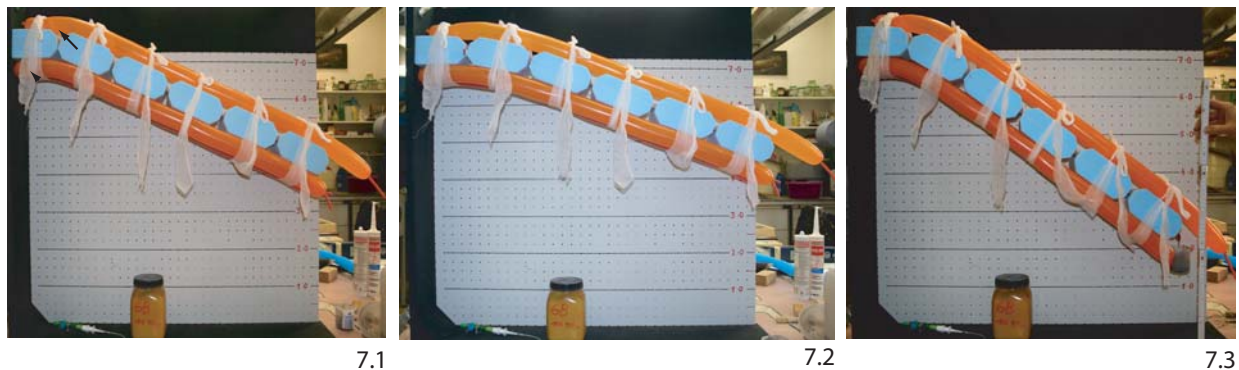
Objective 2: How does the configuration influence the load capacity of the chain beam?

An empty cup was attached to the distal end of the chain beam and filled with iron powder until *s/E1* was reached. The pressure of the balloons was 0.15 bar, and no intersegmental wedge was inserted. With this arrangement, 54 g of iron powder were necessary to achieve *s/E1* (Figure 7.3), corresponding to 127% of the inertial weight of the chain beam. Inserting an intersegmental wedge ventrally between the two proximal segments increased the load capacity to bear 136 g until reaching *s/E1*, which is 168% of the inertial weight of the chain beam.

### E5: One median dorsal pneumatic tube

Objective 1: What is the bracing effect with one dorsal pneumatic body?

One balloon was tied to the dorsal side of the chain beam with gauze bandages, but not fixed at its proximal end. The unfixed balloon generated no bracing effect, instead, the chain beam sagged (Figure 8.1), and the balloon was drawn in a distal direction (Figure 8.2). The balloon was then fixed at its proximal end with a clothespin (8.3). With this arrangement, the chain beam exposed a *si* of 265



**Figure 7.** Experiment E4. The support effect of a tripartite pneumatic system with one pair of ventral and a median dorsal pneumatic tube was studied. 7.1.  $si$  was 435 mm aboveground at a pressure of 0.15 bar, with the dorsal balloon being under tension (arrow) and ventral balloons and segments under pressure and pushing proximally towards the pivot board. 7.2.  $si$  reached 475 mm as one intersegmental wedge (marked in red) was inserted ventrally between the two proximalmost segments. 7.3. At a pressure of 0.15 bar and with the absence of intersegmental wedges, 54 g of iron powder were necessary to achieve  $siE1$ .

mm (Figure 8.4), similar to  $s/E1$ . The dorsal balloon was tensed proximally, but distally kept the segmented chain in a straight line. Following, the combination of a ventral intersegmental wedge and a proximal fixation of the balloon yielded an  $si$  of 405 mm (Figures 8.5, 8.6). The combination of an unfixed dorsal balloon, but a ventral intersegmental wedge yielded a  $si$  of 320 mm aboveground.

Objective 2: How does the configuration influence the load capacity of the chain beam and what influence has the basal pivot?

An empty cup was attached to the distal end of the chain beam and filled with iron powder until  $siE1$  was reached. In the arrangement with one ventral intersegmental wedge and the proximally unfixed balloon with a pressure 0.15 bar, 34 g of iron powder were necessary to achieve  $siE1$ . This corresponds to 117% of the intrinsic weight of the chain beam. In the arrangement with one ventral intersegmental wedge and an additional proximal fixation of the balloon, 54 g of iron powder were necessary to achieve  $siE1$ . This was 127% of the intrinsic weight of the chain beam. At this load, the balloon buckled proximally.

#### **E6: One median dorsal or ventral pneumatic tube fixed to the segments**

Objective: What is the influence of a segmentally fixed median pneumatic body on the bracing of the chain beam?

A party balloon was tied to the dorsal side of the chain beam with gauze bandages and fixed to the segments by a patch of double-sided tape (Fig-

ures 9.1, 9.2). The achieved curvature of the chain beam with this arrangement and a pressure of 0.15 bar was  $si=405$  mm (Figure 9.1). Both proximalmost segments approached each other (Figure 9.2), and the dorsal balloon bulged at the articulation between two segments (Figure 9.3).

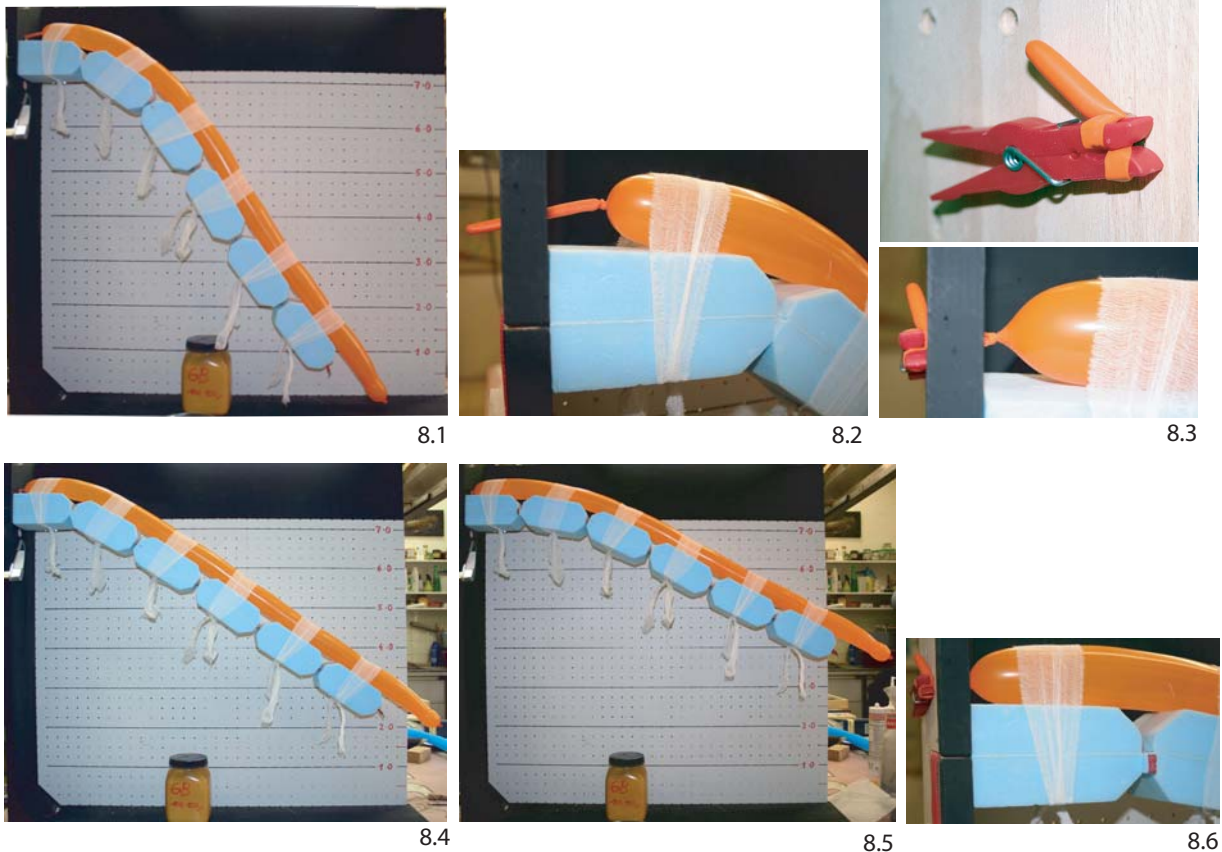
In a second test, one balloon was tied to the ventral side of the chain beam with gauze bandages and fixed to the segments by a patch of double-sided tape. At a pressure of 0.15 bar, the  $si$  was 420 mm aboveground (Figure 9.4). The ventral balloon was compressed, and the chain beam exposed a deflection at its base only. Distally, the chain beam formed a nearly straight line. Applying extra load to this system, 115 g of iron powder were necessary to achieve  $siE1$ . This is 157.5% of the weight of the chain beam.

For the third test, the gauze bandages were removed, the balloon being held only by double-sided tape. This resulted in an  $si$  of 350 mm, and 22 g of iron powder were necessary to produce  $siE1$ .

#### **E7: Segmented dorsal pneumatic tube**

Objective: How do pneumatic segments connected with each other influence the bracing of a chain beam?

A balloon was segmented by twisting it according to the distances of the segments of the chain beam. The balloon was tied to the dorsal side of the chain beam with a gauze bandage. When the intersegmental parts of the pneumatic tube were positioned level with the intersegmental



**Figure 8.** Experiment E5. The bracing effect with one dorsal pneumatic tube was studied. 8.1. When the balloon was tied dorsally to the chain beam and proximally not fixed, there was no bracing effect. 8.2. The offset of the balloon from the proximal end of the chain beam demonstrates that the balloon is drawn in a distal direction. 8.3. The balloon was fixed proximally to the pivot board. 8.4. The fixation of the balloon yielded an *si* of 265 mm with the dorsal balloon being tensed proximally and continuing distally in a straight line. 8.5. Adding an intersegmental wedge to the chain beam with the fixed dorsal balloon resulted in an *si* of 405 mm. 8.6. The balloon is under full tension.

gaps of the chain beam, no bracing effect occurred. When the intersegmental parts of the pneumatic tube were positioned mediodorsally to the Styrodur™ segments and thus bridged the intersegmental gaps of the chain beam, the achieved *si* was 125 mm. By placing ventral intersegmental wedges between the proximal three segments, the *si* of the chain beam increased to 270 mm (Figure 9.5).

### **E8: Mobility by asymmetrical pressure changes**

**Objective:** Is there an option to move the chain beam pressure increase in one pneumatic tube in a triple system of pneumatic bodies?

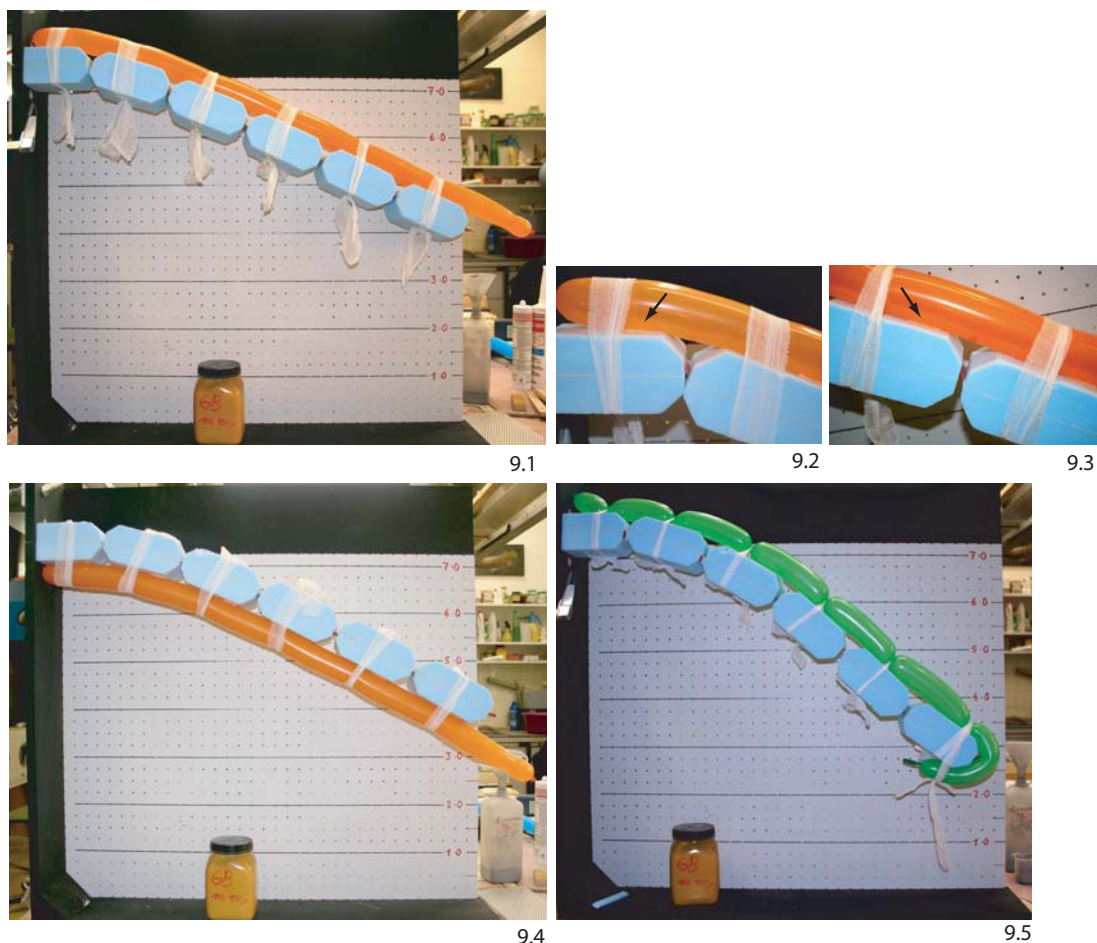
The chain beam was positioned with the belt joints standing vertically to allow lateral movements. One pair of balloons was tied ventrally and one balloon dorsally to the chain beam with a

gauze bandage. At a pressure of 0.15 bar in all balloons, the chain beam formed a straight line (Figure 10.1). If the pressure in the right ventral balloon was increased to 0.25 bar, this resulted in a *bi* of 405 mm to the right side (Figures 10.2, 10.3).

## **DISCUSSION**

### **Implications of the Experiment for Pneumatic Support of a Chain Beam**

As can be seen from the experiment, already one ventral pneumatic body on a chain beam has a bracing and support effect even under low pressure. An additional bracing element at the base of the chain beam, represented in the experiment by a ventral compressive bracing element), is crucial to hold the entire beam. The higher the internal



**Figure 9.** Experiment E6. The influence of fixation of one median dorsal or ventral pneumatic tube on the bracing capacity of the chain beam was studied. 9.1. A balloon tied dorsally to the chain beam and additionally fixed to the segments with double-sided tape yielded an  $s_i=405$  mm of the chain beam. 9.2. The two proximalmost segments approached each other, see also position of double-sided tape between segment and balloon (arrow). 9.3. The dorsal balloon slightly bulged at the articulation between two adjacent segments (here the 3<sup>rd</sup> and 4<sup>th</sup> segment counted from proximal). 9.4. A balloon tied ventrally to the chain beam and additionally fixed to the segments with double-sided tape yielded a  $s_i = 420$  mm. Experiment E7. Segmentation of the dorsal pneumatic tube was tested. 9.5. A segmented balloon was tied to the dorsal side of the chain beam, so that the segments bridged the intersegmental gap, and two proximal intersegmental blocks were inserted, yielding an  $s_i$  of 270 mm.

pressure of the balloon, the better is the support effect.

A ventral pneumatic body increases the load capacity of a chain beam. Even a slight increase of pressure results in an over-proportional increase of load capacity, which is aligned with longitudinal torque problems. With two ventral pneumatic systems these torque problems vanish, however, the increase of the support effect and loading capacity is not doubled at the same time. Laterally placed pneumatic bodies have no support effect to a chain beam.

The introduction of a dorsal pneumatic body additionally to the pair of ventral tubes increases

the support effect further and decreases the sagging of the distal part of the chain beam. However, a single dorsal pneumatic system needs to be connected with the pivot segments. The support quality of a segmented beam with a dorsal pneumatic system depends on the quality of its fixation at the base: stabilizing the pivot point of the chain beam increases the load capacity of the dorsally pneumatically stabilized chain beam.

In all arrangements of pneumatic systems tested here, pneumatic stabilization occurs already at low pressures and increases with increasing pressure. The mobility of the segments against each other is restricted, if the pneumatic system is



**Figure 10.** Experiment E8. The possible option to move the chain beam by unilateral pressure increase of one pneumatic body in a triple system of pneumatic bodies was studied. 10.1. At a pressure of 0.15 bar, the chain beam lay with its panel in a horizontal plane, so that the belt joints stood vertical. 10.2. and 10.3. Increasing the pressure in the right balloon to 0.25 bar resulted in a curvature  $bi$  of 405 mm of the whole beam to the right side.

firmly fixed to the segments, and the load capacity increases at the same time. Segmentation of the pneumatic tube decreases the support effect drastically even with proximal suspension. The intersegmental constriction of the balloons reduces the support effect to zero. There is some support effect, if the constrictions between the pneumatic subunits lie level with the middle of the chain beam segments. In general, the increase of pneumatic segmentation results in a decrease of the support effect. A unilateral increase of pressure results in curvature of the chain beam towards the low-pressure side. The pressure difference determines the degree of curvature.

The support effect of the investigated pneumatic structures is also influenced by other bracing elements. Adding proximoventral intersegmental wedges in all experiments demonstrates that ventral compressive structures provide an essential bracing effect in a chain beam. One single dorsal pneumatic system only works together with a dorsal tensile bracing element attached to the pivot, which suspends the pneumatically braced chain beam as a whole. Ventral compressive and dorsal tensile structures both work independently, but a maximum support effect is achieved when both are present at the same time.

#### **The Reconstructed Distribution of Pneumatic Diverticula in the Neck of Sauropods and Their Influence on a Hypothesized Pneumatic Support**

Based on osteological correlates of vertebral pneumaticity, the reconstruction of pneumatic diverticula in sauropods can only mirror their minimum hypothetical extension, determined from their bony boundaries on the vertebrae. The relationship

between vertebral pneumaticity and its osteological correlates in extant birds shows that the diverticula can be much larger than suggested by osteology (Müller 1908; O'Connor 2006). For sauropods, it cannot be excluded that pneumatic diverticula formed similar large segmented air chambers extending all along the neck, and in between the extremes of a minimum and a maximum hypothetical extension of the pneumatic diverticula, everything is possible. However, the reconstructed extension of pneumatic diverticula determines the possibility of the diverticula system to contribute to neck support in sauropods. Laminae-bounded deep fossae and/or foramina on the surface of the cervical vertebrae of sauropods are similar to the characteristic traces that pneumatic diverticula leave on the cervical vertebrae of extant avians (Britt 1993; Wedel et al. 2000; O'Connor 2001; Wedel 2005; O'Connor 2006). Although it has been proposed that deep fossae in the presacral vertebrae of sauropods would represent muscle attachment pits (e.g., Bonaparte 1999), there are no muscles in extant Sauria that produce such deep insertion pits along the vertebral column (Britt 1993; O'Connor 2006). The general absence of Sharpey's fibres in these fossae, which would be indicative for muscle or tendon insertions, also argues for a pneumatic origin of these structures. The presacral vertebrae of many sauropods are also hollowed out by a cavity system like in extant birds (Britt 1993; Wedel et al. 2000; Wedel 2003a; Upchurch et al. 2004; O'Connor 2006). In birds, these cavities are the result of bone resorption caused by bone-penetrating pneumatic epithelium (Bremer 1940; Witmer 1997). The presacral intra-vertebral cavity system of sauropods is most probably the result of a similar process (Janensch

1947; Britt 1993; Wedel et al. 2000; Wedel 2003a). The assumption that the intravertebral cavities could have been filled with blood or lymph is highly unlikely, because pneumatic epithelium is the only material known among vertebrates that can actively produce such cavities. Furthermore, a liquid infill would reasonably increase the weight of the vertebrae and thus the load of the neck. Vertebral pneumaticity therefore is the most plausible explanation for the intravertebral system of caverns in sauropods. The direct comparison with extant birds suggests that the combination of fossae and foramina connecting to an intravertebral cavity system is indicative for vertebral pneumaticity in Eu- and Neosauropoda.

1. **The Minimum Expansion Model.** Assuming that the pneumatic diverticula were strictly restricted to the fossae and foramina in the vertebrae, these pneumatic diverticula would be small and strictly segmentally organized (Figure 11.3). The interarticular joints of the vertebral column would be free of pneumatic diverticula. In this case the pneumatic system of the sauropod neck mechanically would not support the neck. The bracing would be restricted to the tendinomuscular system and bone-ligament locks, e.g. by overlapping cervical ribs. A pneumatic cushioning effect might be possible during a maximum lateral flexion of the neck, due to compression of the segmental diverticula. The weight saving factor of the pneumatic diverticula due to bone replacement would likely facilitate neck support and movements by other bracing structures.
2. **The Intermediate Expansion Model.** The pneumatic diverticula in this reconstruction extended along the cervical vertebrae according to their osteological correlates. However, the diverticula were larger than their osteological correlates, overlapping each other distally and bridging the interarticular gaps (Figure 11.4, Figure 12). The segmented pneumatic diverticula would have been fixed to the vertebral segments by connective tissue, the lateral bony arc formed by the tuberculum and diapophysis of the cervical rib, the laterally adjacent axial musculature, as well as the interspinous septum and supraspinal ligaments (Figures 3, 11). There is an actualistic support for this reconstruction from the cervical anatomy of birds, where large pneumatic diverticula can grow around the cervical vertebrae without

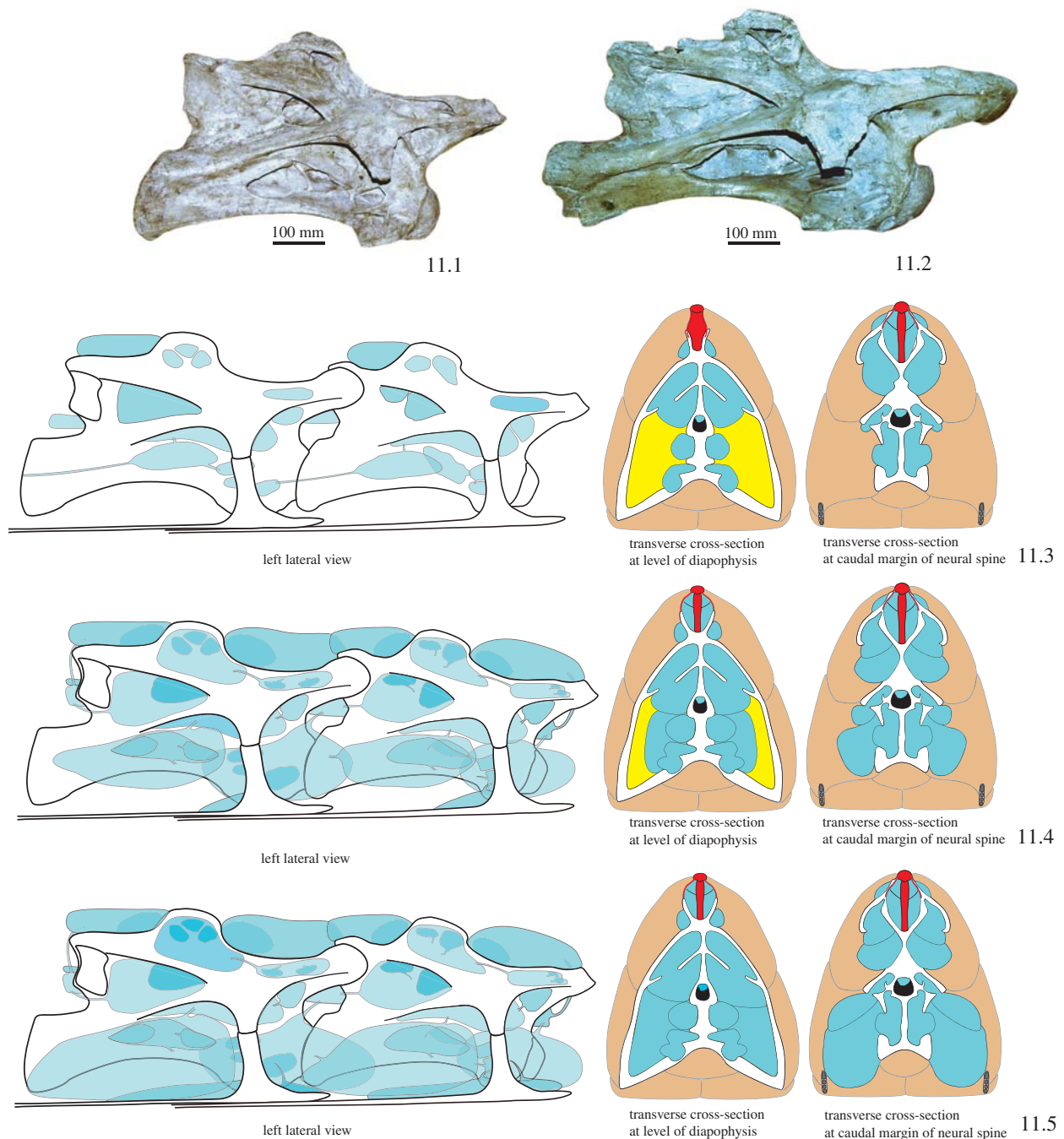
leaving osteological traces (Duncker 1971; Britt 1993; O'Connor 2006).

The experimental data suggest that the pneumatic diverticula despite their longitudinal intersegmental expansion could have supported the sauropod neck. Compression loads normally exerted onto the intervertebral articulations would be partially transmitted to the intersegmental diverticula. The resulting increase of pressure inside these diverticula would reduce the loading of the vertebrae and the intervertebral articulations in the neck. However, tendinomuscular bracing would still be crucial for the stabilization of the sauropod neck, especially against torsion. Like in the Minimum Expansion Model, the weight saving factor of the diverticula system would facilitate neck support by the tendinomuscular systems.

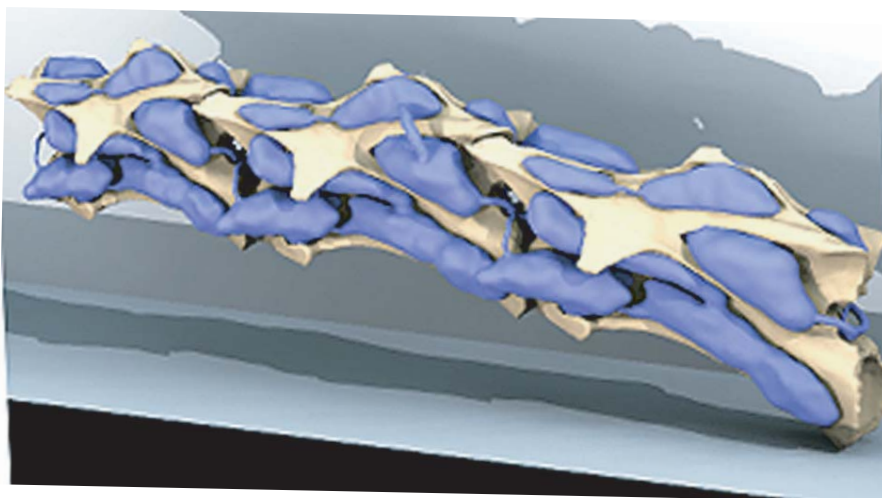
3. **The Maximum Expansion Model.** For this model, the pneumatic diverticula in the neck of sauropods are reconstructed to be bundled in large, densely packed diverticula systems, forming large hose-like canales intertransversarii and supraspinal diverticula units (Figure 11.5). Osteological structures on the cervical vertebrae of sauropods indicate the contact area of the diverticula with the vertebral surface, as well as the presence of interspinous septa and ligaments and muscles, which could, together with connective tissue, have wrapped expanded diverticula systems at least partially (see above). Both the presence of large hose-like canales intertransversarii and supraspinal diverticula units can only be reconstructed indirectly by comparison with extant birds. Thus, the reconstruction of the pneumatic diverticula to the maximum extent must remain partly speculative, hence not more likely or unlikely than the previous two options.

The maximum extension reconstruction would result in a significant support effect of the pneumatic diverticula system as demonstrated in the experiment. This pneumatic support would have allowed a partial reduction of the tendinomuscular bracing system, and together with weight reduction by the pneumatic diverticula, a minimum of muscle mass would be needed to move the neck. The experiment also showed that the dorsal pneumatic diverticula would have needed to extend into the trunk to provide stable abutment for this diverticula group.

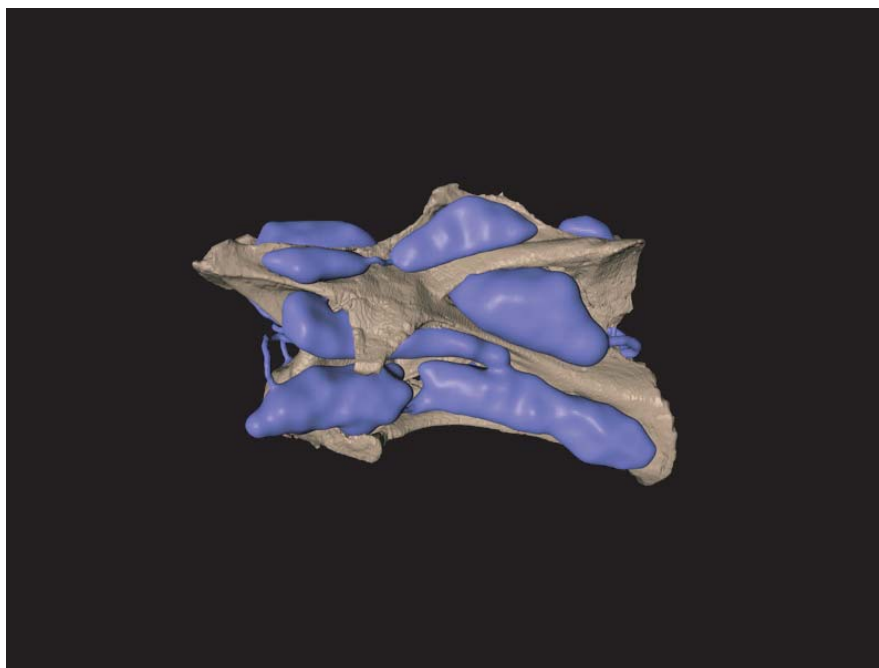




**Figure 11.** Reconstruction hypotheses for pneumatic diverticula in sauropod vertebrae, demonstrated at 4<sup>th</sup> and 5<sup>th</sup> cervical vertebra of *Brachiosaurus brancai*, all in right lateral view. Photographs of right lateral view of 11.1. 4<sup>th</sup> cervical vertebra (MB.R. 2180.25), and 11.2. 5<sup>th</sup> cervical vertebra (MB.R.2180.26). Schematic drawing of 4<sup>th</sup> and 5<sup>th</sup> cervical vertebra in lateral view and in transverse cross-sections, 11.3. Minimum expansion of pneumatic diverticula based on osteological evidence, reconstructed pneumatic ducts are hypothetical, based on the assumption that the diverticula are linked to each other and grow in the neck from the neck base in headward direction, 11.4. Intermediate expansion of pneumatic diverticula, based on osteological evidence and in analogy with extant birds, pneumatic ducts are again hypothetical, 11.5. Maximum expansion of pneumatic diverticula, which cannot be reconstructed by osteological evidence. Blue = pneumatic diverticula; orange = axial muscles; red = dorsal neck ligaments; yellow = connective tissue. With exception of 11.1 and 11.2 not to scale.



12.1



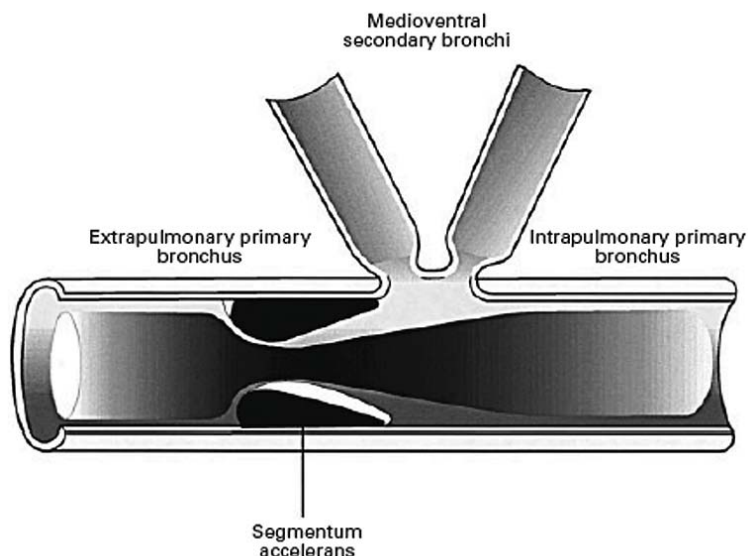
12.2

**Figure 12.** 3D reconstruction of intermediate expansion of pneumatic diverticula around some cranial cervical vertebrae of *Brachiosaurus*, pneumatic diverticula are simplified and without subdivisions, pneumatic ducts connecting the diverticula are purely hypothetical. Note that around the pneumatic diverticula, there is space on the neural spines for the insertion of large ligaments. 12.1. 3 cervical vertebrae of *Brachiosaurus* in left lateral view; 12.2. animated movie of 4<sup>th</sup> cervical vertebra of *Brachiosaurus*.

**Respiration, Regulation Mechanisms and Pressures in the Cervical Pneumatic System of Sauropods**

If the pneumatic diverticula in the neck of sauropods are reconstructed according to an intermediate or maximum expansion model, they could have contributed to neck support. Such a supporting pneumatic system would require a minimum

amount of pressure in the air sacs and diverticula, which supposedly would have been already necessary to warrant the open lumen. Pressure regulating mechanisms could have been present, but mechanically would not be necessary for support and bracing. None of these mechanisms leave osteological traces, and their presence can only be discussed in comparison with birds as the only



**Figure 13.** Schematic drawing of the *segmentum accelerans* in extant birds, taken from Maina (2002).

extant vertebrates possessing pulmonary pneumaticity.

The lung air sac system of modern birds differs from the respiratory system of other amniotes by its small incompressible lungs connected to nine air sacs. The avian lung is positioned ventrally adjacent to the vertebral column of the trunk and the arcades of the vertebral ribs. The pulmonary air sacs, positioned cranially and caudally to the lungs, change in volume and ventilate the lungs back-to-front in a manner of bellows. The gas exchange is conducted in the unidirectionally ventilated lung pipes, but not in the pulmonary air sacs (Duncker 1971; Schmidt-Nielsen 1971; Maina 2005). In modern birds, controlled pressure and volume changes of the cranial (interclavicular, cervical and cranial thoracic) and caudal (caudal thoracic and abdominal) pulmonary air sacs and between them are crucial for the unidirectional ventilation of the lungs (Brackenbury 1971; Duncker 1971; Schmidt-Nielsen 1971; Duncker 1974; Brown et al. 1995; Boggs et al. 1998; Fedde 1998). Starting from a normal pressure of zero, pressure differences comprise a positive and negative spectrum around 0.05 kPa (=0.0005 bar), and the pressure drop from the caudal thoracic air sac to the cranial intrapulmonary bronchus has been determined to be about 4.9 kPa (= 0.049bar) (Banzett et al. 1991; Brown et al. 1995).

Pressure and volume of the different pulmonary air sacs are also influenced by locomotion (Schorger 1947; Kooyman 1971; Tucker 1972; Banzett et al. 1992; Boggs et al. 1997; Boggs et al. 1998; Boggs et al. 2001). Pressure differences between cranial and caudal air sacs during locomotion in different birds reach values between 0.12 kPa and 0.5 kPa (=0.0012 to 0.005 bar), pressure changes within the air sacs are around 0.35 kPa (= 0.0035 bar) (Boggs et al. 2001). Other muscle activities, singing or defecation lead to further pressure changes in the air sacs (Gaunt et al. 1973; Gaunt et al. 1976; Smith 1977; Brackenbury 1978; Suthers et al. 2002; Beckers et al. 2003; Franz and Goller 2003; Mindlin et al. 2003).

The regulation of pressure and volume in the air sacs of birds is connected with a complicated and only partially understood array of mechanisms for controlling the air flow (Maina 2005). These are intrapulmonary chemoreceptors for the detection of CO<sub>2</sub> concentrations (Burger et al. 1974; Burger et al. 1976; Molony et al. 1976; Scheid 1979), sensitivity of the intrapulmonary smooth muscle to changes in the concentration of CO<sub>2</sub> (Barnas et al. 1978), control units for the bronchial diameters (Brown et al. 1995), or regulation of muscle activity for driving air sac ventilation (Beckers et al. 2003). An investigation of chickens yielded a sphincter-like muscle on the internal surface of the ostia,

which controls the width of the ostia by ciliar cells reacting to pressure changes in the air sacs (Cook et al. 1986). A swelling or constriction narrowing the lumen of the extrapulmonary primary bronchus, the *segmentum accelerans*, was reported in the domestic fowl (Wang et al. 1992; Maina and Africa 2000; Maina 2002, 2005) (Figure 13). The *segmentum accelerans* changes in size with respiratory rate to make this passage either wide or narrow (Wang et al. 1992). The aerodynamic shape of the *segmentum accelerans* accelerates the air flow to be driven past the medioventral secondary bronchi and into the intrapulmonary primary bronchus (Maina and Africa 2000; Maina 2002, 2005). However, no mechanisms are reported regulating the air flow between cervical pulmonary air sacs and the pneumatic diverticula system of the neck of birds.

Even if the respiratory system of sauropods did incorporate unidirectional ventilation of the lungs by pulmonary air sacs, the rigidity of the sauropod trunk dictates completely different pumping mechanisms of these air sacs from that of birds. Together with the sheer dimensions of the respiratory apparatus, this would necessarily have required active regulation mechanisms, pressure and air flow control combined with a much slower breathing frequency. The presence of air sacs both in sauropods and in birds, the hypothesized similarities in the respiration mechanism between both groups, and the close phylogenetic relationship between sauropods and birds make bird-like regulation mechanisms for air sac volume and pressure possible for sauropods. The large variety in regulation mechanisms of birds shows that such a bird-like respiration system bears a great potential for the development of structures regulating air flow and pressure properties of the air sacs. However, it remains unknown, which of these is crucial for the maintenance of extended air sac systems in general. What can be reconstructed is that in sauropods at least the contraction of some muscles inserting ventrally on the scapulocoracoid and running to the neck, e.g., *m. levator scapulae* and *m. capitisternalis*, and of muscles running from the sternum to the skull, like *m. episternobranchiotendineus* and *m. episternobranchialis* would have resulted in a pressure increase of the cranial pulmonary air sacs. It is also possible that sauropods had developed their own, unique regulation and ventilation mechanisms, such as dynamic valves or constrictor muscles. Sauropod lungs were most likely as in birds positioned ventrally adjacent to the vertebral column of the trunk and the vertebral ribs

and possessed large, sac-like dilatations (pulmonary air sacs) in the cranial and probably also caudal trunk region (Britt 1993, 1997; Perry and Reuter 1999; Wedel et al. 2000; Wedel 2003b). The pneumatic diverticula in the cervical vertebral column of sauropods can be most plausibly explained as derivatives of pulmonary air sacs in the cranial trunk region (Wedel et al. 2000; Wedel 2003b, 2005). Assuming similar histology and properties of the pneumatic epithelium of sauropods as in birds, the air sacs and their continuation of cervical pneumatic diverticula were non-respiratory and connected to the respiratory apparatus as dead space. The presence of extraordinarily long necks in sauropods is combined with exceedingly long tracheas. If a bidirectional breathing mechanism would be assumed, much of the tracheal air pillar would just be moved forth and back without any respiration effect. This dead air pumping could have been avoided with a unidirectional ventilation of the lungs similar to birds. The incorporation of pulmonary air sacs into the respiration process for ventilation of the lungs would have made a cross-current gas exchange possible (Daniels and Pratt 1992; Perry and Sander 2004). Physiological considerations demonstrate that a bird-like model of a cross-current gas exchange, with a unidirectional ventilation of the lungs, would have yielded an optimum breathing efficiency in sauropods compared to other breathing mechanisms (Daniels and Pratt 1992; Perry and Sander 2004).

No data are available about pressures in the cervical pneumatic system of extant birds. The pressure in the air sacs of birds is very low, and varies only slightly during breathing (e.g., Boggs et al. 1997; Boggs et al. 1998). Akerssen and Trost (2004) described experimental inflation of air sacs and pneumatic diverticula of the neck of extant birds, which revealed a support effect already at 0.6 +/-0.2 psi (= 4.137 +/-1.379 kPa). These values are similar to the pressure differences between parts of the lung air sac system in extant birds (see above), making it possible that similar pressures can be reached in the pneumatic diverticula system. Even if stabilizing pressures of around 4 kPa would have occurred in their cervical diverticula system, regulation of the pressure or the possibility to disconnect the cervical system from the pulmonary air sacs were necessary preconditions for pneumatic stabilization in sauropods. Because the air sac system of sauropods was most likely non-respiratory, the cervical system could be easily disconnected from the rest of the respiratory apparatus without a negative influence to the respiration

process. The small size of the connections between the cervical pneumatic diverticula of sauropods must have made gas exchange between these diverticula slow, and certainly decreased the influence of inspiration- or expiration-induced pressure and volume changes of the pulmonary air sacs. It is therefore likely, that even without a possibility to shut the cervical diverticula system off, the pressure within the cervical pneumatic system remained more or less constant.

During movements of the sauropod neck (i.e. flexion, extension and lateral movements), pneumatic diverticula on the flexed part of the neck would be compressed. This could result in a partial deflation of these diverticula, with air exhausting into the opposite diverticula systems through pneumatic commissures, and/or into the cranial pulmonary air sacs. Alternatively, the small size of the pneumatic ducts could hinder such partial air flow, in which case air in these pneumatic diverticula would be compressed. In any case, the presumably small pressures in the air sac system of the neck would not lead to a failure of the system or the membrane. If regulation mechanisms were present in the diverticula system, this would make the system adjustable, leveling the compression effect during neck movement.

### **The Bracing System of Sauropod Necks and Pneumatic Support**

With a few exceptions (i.e., *Brachytrachelopan*, Rauhut et al. 2005), sauropod dinosaurs possessed enormously long necks, which could exceed 9 m in length (e.g., *Brachiosaurus*, Janensch 1950; or *Mamenchisaurus*, Young et al. 1972). With the enormous body sizes of sauropods, such long necks needed to be sustained by a combination of different bracing elements. Simplified to the mechanical model of a segmented cantilever (see above), the model sauropod neck would have to accommodate tensile forces dorsally and compression forces ventrally by dorsal and ventral bracing structures.

Sauropods show deep insertion scars for supraspinal and elastic ligaments (Tsuihiji 2004). The supraspinal ligaments connected the apices of each neural spine with each other, and were separated into two sheets in the case of bifurcate neural spines evidenced by cranial and caudal ridges on the neural spines. The elastic ligament system of sauropods extended craniocaudally connecting the bases of successive neural spines (Schwarz et al. 2007). The large dorsal ligament systems of sauropods most probably transmitted dorsal tensile

forces into the vertebral chain, stabilizing the neck from the dorsal side. The ligament system was most probably supported by the tendinous system of the strongly segmented epaxial musculature (Wedel and Sanders 2002; Schwarz et al. 2007).

The cervical ribs of most sauropods overlap ventral to the caudal following intervertebral gap and were connected with each other by short, intercostal ligament fibers (Schwarz et al. 2007). The cervical ribs can form overlapping bundles of up to five costal bodies like in *Mamenchisaurus*. Less overlapping is seen in *Brachiosaurus* or *Camarasaurus*. In other cases, the cervical ribs are approximately 1.5 times as long as the vertebrae with segment-to-segment overlap and have a stout, dorsomedially slightly concave costal body (e.g., in *Malawisaurus*, *Jobaria* or *Shunosaurus*). Along the cervical ribs, the compressive forces acting in longitudinal direction on the costal bodies probably transformed into a tensile load of the intercostal ligaments (Martin et al. 1998). Therefore, the elastic fixation of the overlapping costal bodies by ligaments allowed the rib apparatus along the neck to accommodate a part of the loading of the neck beam. Among extant animals, such a ventral costal bracing of the neck occurs in crocodylians only (Frey 1988b; Salisbury and Frey 2001).

Based on the mechanisms described above, the neck of sauropods was suspended by dorsal ligaments in combination with strongly segmented epaxial muscles. Ventrally, it was supported by the paired parallel line of cervical ribs. This dorsoventral combination of bracing elements corresponds mechanically to a segmented truss, where the dorsal, tensile element is conducted along the hard parts of the beam and thereby separated from the compression member. As in other vertebrates, the cervical vertebrae of sauropods were also stabilized by the zygapophyseal articulations especially against torsion (see above).

The presence of these bracing structures in sauropods shows that the pneumatic diverticula system in the neck of sauropods could only have contributed to neck support as a mechanically coherent part of the bracing system. If so, the diverticula system must have been compatible with the other bracing structures. Like in the experiment, the dorsal spinal ligaments and cervical ribs could have functioned as basal pivot supports, buffered by pneumatic diverticula as compression transmitting structures. There is a correlation between the development of the cervical pneumatic system and the other bracing elements in

specific sauropod neck constructions, which will be discussed here.

**Dual Pneumatic Systems.** Sauropods for which a dual pneumatic system in the neck is reconstructed (a pair of intertransversal diverticula units and a segmented chain of dorsal diverticula) have generally cervical ribs, which are longer than the adjacent vertebral segment. In *Mamenchisaurus* and *Omeisaurus*, the extremely low neural spines indicate a drastic reduction of the dorsal tensile elements due to the low spinal lever, which is combined with an extreme elongation of the cervical ribs, which span as much as seven vertebral segments (Young et al. 1972; Young and Zhao 1972; Russell and Zheng 1993; Tang et al. 2001). Probably, the twin chain of cervical ribs could in these cases support the neck beam nearly alone. If pneumatic diverticula in sauropod necks have a support function, the well-developed paired ventral pneumatic diverticula unit could have contributed to the ventral cervical support, increasing the efficiency of the intercostal bracing system due to pneumatic stabilizing effects. In contrast, the dorsal pneumatic structures in these sauropods were diminutive and mechanically could not contribute to the bracing of the neck. Regardless of the role of pneumatic diverticula, the focusing on ventral bracing elements in these sauropods is on the cost of overall mobility of the neck, because the long cervical ribs could slide along each other only to a small amount.

In other taxa with a dual pneumatic system (such as in *Brachiosaurus*, *Camarasaurus*, *Malawisaurus*, *Jobaria* or *Shunosaurus*), the presence of well-developed cervical neural spines and large insertion areas for dorsal ligaments indicate the existence of a dual ligamentocostal bracing. If pneumatic diverticula supported the neck of these sauropods, then the paired ventral pneumatic diverticula could have contributed to their cervical bracing system. Additionally, the bifurcation of the neural spines in the neck base and the cranial part of the thorax of these sauropods indicates the existence of pneumatic diverticula, which were transient from neck to trunk. Thus, these diverticula systems could have additionally reinforced the neck from dorsally, but only in context with the strong ligament system. The extension of the dorsal diverticula units into the trunk is consistent with the experimental data showing a need for an abutment of the dorsal diverticula system at the pivot plate.

**Tripartite Pneumatic System.** Sauropods with a tripartite pneumatic system (a paired ventral inter-

transversal diverticula unit and a dorsal unit of pneumatic diverticula, which continues onto the trunk), such as dicraeosaurids, *Apatosaurus*, and *Diplodocus*, possess high neural spines indicating large dorsal ligaments (Tsuihiji 2004; Schwarz et al. 2007) and high epaxial muscles acting on long spinal levers. The diameter of the ligaments, however, was equal or less than in those taxa with a dual system of pneumatic diverticula like *Camarasaurus*. The cervical ribs do not reach more than the length of the adjacent vertebral segment and thus do not overlap. As a consequence, bracing of the neck must have been achieved mainly by the dorsal ligaments and the epaxial tendinomuscular systems. If it had a support function, the tripartite system of pneumatic diverticula would have reinforced the dorsal bracing structures. The pneumatic diverticula lying between the metapophyses of the bifurcate neural spines in the trunk were very likely connected to the vertebrae of neck and trunk. Due to this and its transient nature from neck to body, the cranial half of the dorsal pneumatic system of the trunk might have been part of the cervical bracing system, providing stable abutment for the dorsal unit of cervical diverticula at the trunk. A reduction of the cervical rib apparatus in these sauropods increased the overall mobility of the neck beam in comparison to other sauropods. An additionally pneumatic support might have triggered the reduction of the cervical costal chain.

## CONCLUSIONS

The presence of vertebral pneumaticity in the neck of sauropods can be reconstructed based on osteological evidence and by comparison with extant birds. Depending on the overall size and distribution of pneumatic diverticula, there are sauropods with a dual pneumatic system and sauropods with a tripartite pneumatic system. Whereas the osteological evidence for the size of the cervical pneumatic diverticula is restricted to pneumatic fossae and foramina on the cervical vertebrae, the comparison with extant birds suggests an expansion of diverticula systems beyond their bony frame. Different extensions of the pneumatic diverticula in the sauropod neck can be reconstructed, ranging from a minimum to a maximum expansion model. These differences in the reconstructed size of the cervical diverticula systems influence a possible pneumatic support function of the cervical pneumatic apparatus in sauropods.

Integrating vertebral pneumaticity in a model of neck support for sauropods shows that pneumatic diverticula could not achieve bracing of the

neck alone. However, pneumatic support mechanically coherent with other bracing structures yields a model for the neck support in sauropods that is consistent with anatomical development of non-pneumatic bracing structures. As shown in the experiment, the interaction of pneumatic support with other bracing elements increases the support effect of the whole system, but only if all systems are coherent. Thus, integrating pneumaticity into neck support might explain, why sauropods could develop such elongate necks for their large body size. Judging from a functional basis, pneumatic support in sauropod necks therefore would be an option to stabilize a long neck effectively at low weight. Experimental data with a simplified chain beam model show that a support function of pneumatic systems, with a configuration modelled after sauropod constructions, would be possible. Pre-conditions for such a pneumatic support are (1) that pneumatic diverticula extended beyond their bony boundaries, and (2) that regulation mechanisms for pressure maintenance and control in the air sac systems were present. Because of those preconditions neither the exact expansion of the cervical pneumatic system, nor regulatory mechanisms and the height of pressure in these pneumatic systems can be demonstrated on osteological evidence, the pneumatic support of sauropod necks remains hypothetical. With osteological evidence as a measure, the question of a mechanism of pneumatic support of sauropod necks must therefore remain unresolved at the moment, which holds true for any physiological assumptions concerning the respiratory system.

#### ACKNOWLEDGEMENTS

We thank the following individuals for providing access to museum collections and assistance to DS during visits of the collections: B. Herkner (Senckenbergmuseum Frankfurt a.M.), W.-D. Heinrich and D. Unwin (Museum für Naturkunde der HU Berlin), W. Joyce and D. Brinkman (Yale Peabody Museum, New Haven), C. Mehling and I. Rutzky (American Museum of Natural History), A. Henrici and D. Berman (Carnegie Museum for Natural History, Pittsburgh), M. Brett-Surman (Smithsonian Institution, Washington DC), J.F. Bonaparte and A. Kramarz (Museo Argentino de Ciencias Naturales, Buenos Aires) and J., Y. and M. Siber (Sauriermuseum Aathal). R. Kastner (SMNK) is thanked for helping us with the chain model, and R. Schumacher (FHNW) kindly provided the 3D models. For discussions on the problems of pneumaticity

we thank M. Wedel and M.P. O'Connor. The mechanical aspects of pneumatic neck support in sauropods were discussed with R. Luchsinger (EMPA, Dübendorf). We thank two anonymous reviewers for their hints and comments for improvement of an earlier version of this paper. Two further anonymous reviewers are thanked for their corrections and suggestions concerning the manuscript. We wish to also thank editors D. Polly, M. Purnell and W. Hagadorn for their continued support and suggestions concerning the improvement of the manuscript. This study was part of a project on the role of pneumatization in sauropods funded by the Swiss National Science Foundation (SNF No. 200021-101494/1 and No. 200020-109131/1).

#### REFERENCES

- Akersten, W., and Trost, C.H. 2000. Function of avian air sac diverticula, implications for sauropod cervical biomechanics. *Journal of Vertebrate Paleontology*, 20(Suppl. 3):25A.
- Akersten, W., and Trost, C.H. 2001. Studies on the function of avian air sac diverticula and possible comparisons with saurischian vertebral biomechanics II. *Journal of Vertebrate Paleontology*, 21(Suppl. 3):27A.
- Akersten, W., and Trost, C.H. 2004. Air sac diverticula as passive support devices in birds and saurischian dinosaurs: an overlooked biomechanical system. *Journal of Morphology*, 260(3):275.
- Alexander, R.M. 1989. *Dynamics of dinosaurs and other extinct giants*. Columbia University Press, New York.
- Alexander, R.M. 2002. Tendon elasticity and muscle function. *Comparative Biochemistry and Physiology*, A, 133:1001-1011.
- Banzett, R.B. 1976. Chemoreceptors in the paleopulmonic lung of the emu: discharge patterns during cyclic ventilation. *Respiration Physiology*, 28:249-259.
- Banzett, R.B., Nations, C.S., Wang, N., Butler, J.P., and Lehr, J.L. 1992. Mechanical independence of wing-beat and breathing in starlings. *Respiration Physiology*, 89:27-36.
- Banzett, R.B., Nations, C.S., Wang, N., Fredberg, J. J., and Butler, J.P. 1991. Pressure profiles show features essential to aerodynamic valving in geese. *Respiration Physiology*, 84:295-309.
- Barnas, G.M., Mather, F.B., and Fedde, M.R. 1978. Response of avian intrapulmonary smooth muscle to changes in carbon dioxide concentration. *Poultry Science*, 57:1400-1407.
- Beckers, G.J.L., Suthers, R.A., and ten Cate, C. 2003. Mechanisms of frequency and amplitude modulation in ring dove song. *The Journal of Experimental Biology*, 206:1833-1843.

- Bennett, M.B., and Alexander, R.M. 1987. Properties and function of extensible ligaments in the necks of turkeys (*Meleagris gallopavo*) and other birds. *Journal of Zoology*, London, 212:275-281.
- Benton, M.J. 2004. Origin and relationships of Dinosauria, p. 7-19. In Weishampel, D.B., Dodson, P., and Osmólska, H. (eds.), *The Dinosauria*. 2nd edition, University of California Press, Berkeley.
- Boas, J.E.V. 1929. Biologisch-Anatomische Studien über den Hals der Vögel. *Det Kongelige Danske Videnskabsbernes Selskabs Skrifter, Naturvidenskabelig og Mathematisk Afdeling*, 9(1):10-222.
- Boggs, D.F., Baudinette, R.V., Frappell, F.P., and Butler, J.P. 2001. The influence of locomotion on air-sac pressures in little penguins. *The Journal of Experimental Biology*, 204:3581-3586.
- Boggs, D.F., Butler, P.J., and Wallace, S.E. 1998. Differential air sac pressures in diving tufted ducks *Aythya fuligula*. *The Journal of Experimental Biology*, 201:2665-2668.
- Boggs, D.F., Jenkins, F.A.J., and Dial, K.P. 1997. The effects of the wingbeat cycle on respiration in black-billed magpies (*Pica pica*). *The Journal of Experimental Biology*, 200:1403-1412.
- Bonaparte, J.F. 1999. Evolución de las vértebras presacras en Sauropodomorpha. *Ameghiniana*, 36(2):115-187.
- Brackenbury, J.H. 1971. Airflow dynamics in the avian lung as determined by direct and indirect methods. *Respiration Physiology*, 13:319-329.
- Brackenbury, J.H. 1978. Respiratory mechanics of sound production in chicken and geese. *The Journal of Experimental Biology*, 72:229-250.
- Bremer, J.L. 1940. The pneumatization of the humerus in the common fowl and the associated activity of theelin. *Anatomical Record*, 77:197-211.
- Britt, B.B. 1993. *Pneumatic postcranial bones in dinosaurs and other archosaurs*. PhD Thesis, University of Calgary (Canada), Alberta.
- Britt, B.B. 1997. Postcranial pneumaticity, p. 590-593. In Currie, P.J., and Padian, K. (eds.), *Encyclopedia of dinosaurs*. Academic Press, San Diego, California.
- Brown, R.E., Kovacs, C.E., Butler, J.P., Wang, N., Lehr, J., and Banzett, R.B. 1995. The avian lung: is there an aerodynamic expiratory valve? *Journal of Experimental Biology*, 198:2349-2357.
- Bryant, H.N., and Russell, A.P. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philosophical Transactions of the Royal Society of London, B*, 337:405-418.
- Burger, R.E., Coleridge, C.G., Coleridge, H.M., Nye, P.C.G., Powell, F.L., Ehlers, C., and Burger, R.E., Osborne, J.L., and Banzett, R.B. 1974. Intrapulmonary chemoreceptors in *Gallus domesticus*: adequate stimulus and functional localization. *Respiration Physiology*, 22:87-97.
- Burger, R.E., Coleridge, C.G., Coleridge, H.M., Nye, P.C.G., Powell, F.L., Ehlers, C., and Banzett, R.B. 1976. Chemoreceptors in the paleopulmonic lung of the emu: discharge patterns during cyclic ventilation. *Respiration Physiology*, 28:249-259.
- Carlson, H.C., and Beggs, E.C. 1973. Ultrastructure of the abdominal air sac of the fowl. *Research in Veterinary Sciences*, 14:148-150.
- Carrano, M.T., and Hutchinson, J.R. 2002. Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). *Journal of Morphology*, 253:207-228.
- Cook, R.D., Vaillant, C.R., and King, A.S. 1986. The abdominal air sac ostium of the domestic fowl: a sphincter regulated by neuro-epithelial cells? *Journal of Anatomy*, 149:101-111.
- Coombs, W.P.J. 1975. Sauropod habits and habitats. *Palaeogeography Palaeoclimatology Palaeoecology*, 17:1-33.
- Currey, J.D. 1987. The evolution of the mechanical properties of amniote bone. *Journal of Biomechanics*, 21(11/12):1035-1044.
- Currey, J.D. 1999. The design of mineralized hard tissues for their mechanical functions. *Journal of Experimental Biology*, 202:3285-3294.
- Daniels, C.B., and Pratt, J. 1992. Breathing in long-necked dinosaurs: did the sauropods have bird lungs? *Comparative Biochemistry and Physiology, A*, 101:43-46.
- Duncker, H.-R. 1971. The lung air sac system of birds. *Advances in Anatomy, Embryology, and Cell Biology*, 45:1-171.
- Duncker, H.-R. 1974. Structure of the avian respiratory tract. *Respiration Physiology*, 22:1-19.
- Fedde, M.R. 1998. Relationship of structure and function of the avian respiratory system to disease susceptibility. *Poultry Science*, 77:1130-1138.
- Fletcher, O.J. 1980. Pathology of the avian respiratory system. *Poultry Science*, 59:2666-2679.
- Franz, M., and Goller, F. 2003. Respiratory pattern and oxygen consumption in singing zebra finches. *The Journal of Experimental Biology*, 206:967-978.
- Frey, E. 1988a. Anatomie des Körperstammes von *Alligator mississippiensis* Daudin. *Stuttgarter Beiträge zur Naturkunde, A*, 24:1-106.
- Frey, E. 1988b. Das Tragsystem der Krokodile - eine biomechanische und phylogenetische Analyse. *Stuttgarter Beiträge zur Naturkunde, A*, 26:1-60.
- Frey, E., and Martin, J. 1997. Long necks in sauropods, p. 406-409. In Currie, P.D., and Padian, K. (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.
- Gaunt, A.S., Gaunt, S.L.L., and Hector, D.H. 1976. Mechanics of the syrinx in *Gallus gallus*. I. A comparison of pressure events in chickens to those in oscines. *The Condor*, 78:208-223.



- Gaunt, A.S., Stein, R.C., and Gaunt, L.L. 1973. Pressure and air flow during distress calls of the Starling, *Sturnus vulgaris* (Aves; Passeriformes). *The Journal of Experimental Biology*, 183:241-261.
- Gauthier, J.A., Kluge, A.G., and Rowe, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics*, 4:105-209.
- Gray, J. 1944. Studies in the mechanics of the tetrapod skeleton. *Journal of Experimental Zoology*, 20:88-116.
- Hildebrand, M., and Goslow, G.E.J. 2001. *Analysis of vertebrate structure*. John Wiley and Sons, New York.
- Janensch, W. 1947. Pneumatizität bei Wirbeln von Sauropoden und anderen Saurischiern. *Palaeontographica, Supplement 7*, 1(3):1-25.
- Janensch, W. 1950. Die Wirbelsäule von *Brachiosaurus brancai*. *Palaeontographica, Supplement 7*(3):27-92.
- Koch, J.C. 1917. The laws of bone architecture. *American Journal of Anatomy*, 21:177-298.
- Kooyman, G.L. 1971. Diving behaviour of the emperor penguin, *Apenodytes forsteri*. *The Auk*, 88:775-795.
- Kummer, B. 1959. *Bauprinzipien des Säugerskeletts*. Georg-Thieme-Verlag, Stuttgart.
- Landolt, R., and Zweers, G. 1985. Anatomy of the muscle-bone apparatus of the cervical system in the mallard (*Anas platyrhynchos* L.). *Netherlands Journal of Zoology*, 35(4):611-670.
- Maina, J.N. 2002. Some recent advances on the study and understanding of the functional design of the avian lung: morphological and morphometric perspectives. *Biological Reviews*, 77:97-152.
- Maina, J.N. 2005. *The Lung-Air Sac System of Birds*. Springer, Berlin.
- Maina, J.N., and Africa, M. 2000. Inspiratory aerodynamic valving in the avian lung: functional morphology of the extrapulmonary primary bronchus. *Journal of Experimental Biology*, 203:2865-2876.
- Martin, J., Martin-Rolland, V., and Frey, E. 1998. Not cranes or masts, but beams: The biomechanics of sauropod necks. *Oryctos*, 1:113-120.
- Mindlin, G.B., Gardner, T.J., Goller, F., and Suther, R. 2003. Experimental support for a model of birdsong production. *Physical Review E*, 68:041908-1-041908-5.
- Molony, V., Graf, W., and Scheid, P. 1976. Effects of CO<sub>2</sub> on pulmonary flow resistance in the duck. *Respiration Physiology*, 26:333-349.
- Müller, B. 1908. The air sacs of the pigeon. *Smithsonian Miscellaneous Collections*, 50:365-414.
- O'Connor, M.P. 2001. Postcranial pneumaticity in extant avians: distinguishing pulmonary from nonpulmonary pneumaticity. *Journal of Morphology*, 248(3):268.
- O'Connor, M.P. 2004. Pulmonary pneumaticity in the postcranial skeleton of extant aves: a case study examining Anseriformes. *Journal of Morphology*, 261:141-161.
- O'Connor, M.P. 2006. Postcranial pneumaticity: An evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *Journal of Morphology*, 267:1199-1226.
- O'Connor, M.P., and Claessens, L.P.A.M. 2005. Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. *Nature*, 436:253-256.
- Perry, S.F., and Reuter, C. 1999. Hypothetical lung structure of *Brachiosaurus* (Dinosauria: Sauropoda) based on functional constraints. *Mitteilungen aus dem Museum für Naturkunde Berlin, Geowissenschaftliche Reihe*, 2:75-79.
- Perry, S.F., and Sander, P.M. 2004. Reconstruction of the evolution of the respiratory apparatus in tetrapods. *Respiration Physiology & Neurobiology*, 144:125-139.
- Rauhut, O.W.M., Remes, K., Fechner, R., Cladera, G., and Puerta, P. 2005. Discovery of a short-necked sauropod dinosaur from the Late Jurassic period of Patagonia. *Nature*, 435:670-672.
- Russell, D.A., and Zheng, Z. 1993. A large mamenchisaurid from the Junggar Basin, Xinjiang, people's Republic of China. *Canadian Journal of Earth Sciences*, 30:2082-2095.
- Salisbury, S.W., and Frey, E. 2001. A biomechanical transformation model for the evolution of semi-spheroidal articulations between adjoining vertebral bodies in crocodylians, p. 85-134. In Grigg, G.C., Seebacher, F., and Franklin, C.E. (eds.), *Crocodylian Biology and Evolution*. Surry Beatty & Sons, Chipping Norton, Australia.
- Scheid, P. 1979. Respiration and control of breathing in birds. *Physiologist*, 22(5):60-64.
- Schmidt-Nielsen, K. 1971. How birds breathe. *Scientific American*, 225(6):72-79.
- Schorger, A.W. 1947. The deep diving of the loon and old-squaw and its mechanism. *The Wilson Bulletin*, 59(3):151-159.
- Schwarz, D., Frey, E., and Meyer, C.A. 2007. Pneumaticity and soft-tissue reconstructions in the neck of diplodocid and dicraeosaurid sauropods. *Acta Palaeontologica Polonica*, 52(1):167-188.
- Schwarz, D., and Fritsch, G. 2006. Pneumatic structures in the cervical vertebrae of the Late Jurassic (Kimmerigian-Tithonian) Tendaguru sauropods *Brachiosaurus brancai* and *Dicraeosaurus*. *Eclogae geologicae Helvetiae*, 99:65-78.
- Slijper, E.J. 1946. Comparative biologic-anatomical investigation on the vertebral column and spinal musculature of mammals. *Verhandelingen Der Koninklijke Ned. Akademie Van Wetenschappen, Afdeling Natuurkunde, Tweede Sectie*, 42(5):1-128.
- Smith, D.G. 1977. The role of the sternotrachealis muscle in bird song production. *The Auk*, 94:152-155.
- Stevens, K.A. 2002. DinoMorph: Parametric modeling of skeletal structures. *Senckenbergiana lethaea*, 82(1):23-34.

- Stevens, K.A., and Parrish, M.J. 1999. The posture and feeding habits of two Jurassic sauropod dinosaurs. *Science*, 284:798-800.
- Stevens, K.A., and Parrish, M.J. 2005. Digital reconstructions of sauropod dinosaurs and implications for feeding, p. 178-200. In Curry Rogers, K.A., and Wilson, J.A. (eds.), *The Sauropods: Evolution and Paleobiology*. California University Press, Berkeley.
- Suthers, R.A., Goller, F., and Wild, J.M. 2002. Somatosensory feedback modulates the respiratory motor program of crystallized birdsong. *PNAS*, 99(8):5680-5685.
- Tang, F., Jin, X., Kang, X., and Zhang, G. 2001. *Omeisaurus maoianus. A complete Sauropoda from Jingyan, Sichuan. Research Works of Natural Museum of Zhejiang*. China Ocean Press.
- Tsuihiji, T. 2004. The ligament system in the neck of *Rhea americana* and its implications for the bifurcated neural spines of sauropod dinosaurs. *Journal of Vertebrate Paleontology*, 24(1):165-172.
- Tucker, V.A. 1972. Respiration during flight in birds. *Respiration Physiology*, 14:75-82.
- Upchurch, P., Barrett, P.M., and Dodson, P. 2004. Sauropoda, p. 259-322. In Weishampel, D.B., Dodson, P., and Osmólska, H. (eds.), *The Dinosauria (2nd ed.)*. University of California Press, Berkeley.
- Wang, N., Banzett, R.B., Nations, C.S., and Jenkins, E.A. 1992. An aerodynamic valve in the avian primary bronchus. *Journal of Experimental Zoology*, 262:441-445.
- Wedel, M.J. 2003a. The evolution of vertebral pneumaticity in sauropod dinosaurs. *Journal of Vertebrate Paleontology*, 23(2):344-357.
- Wedel, M.J. 2003b. Vertebral pneumaticity, air sacs, and the physiology of sauropod dinosaurs. *Paleobiology*, 29(2):243-255.
- Wedel, M.J. 2005. Postcranial skeletal pneumaticity in sauropods and its implications for mass estimates, p. 201-228. In Curry Rogers, K.A., and Wilson, J.A. (eds.), *The Sauropods: Evolution and Paleobiology*. University of California Press, Berkeley.
- Wedel, M.J., Cifelli, R.I., and Sanders, R.K. 2000. Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*. *Acta Palaeontologica Polonica*, 45:343-388.
- Wedel, M.J., and Cifelli, R.L. 2005. *Sauroposeidon*: Oklahoma's native giant. *Oklahoma Geology Notes*, 65(2):40-57.
- Wedel, M.J., and Sanders, R.K. 2002. Osteological correlates of cervical musculature in Aves and Sauropoda (Dinosauria: Saurischia), with comments on the cervical ribs of *Apatosaurus*. *PaleoBios*, 22(3):1-6.
- Wettstein, O.v. 1937. Crocodilia, p. 236-424. In Kükenthal, W. (ed.), *Handbuch der Zoologie*. Fischer-Verlag, Jena.
- Wilson, J.A. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology*, 19(4):639-653.
- Witmer, L.M. 1990. The craniofacial air sac system of mesozoic birds (Aves). *Zoological Journal of the Linnean Society*, 100:327-378.
- Witmer, L.M. 1995. The Extant Phylogenetic Bracket and the importance of reconstructing soft tissues in fossils, p. 19-33. In Thomason, J. (ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, Cambridge.
- Witmer, L.M. 1997. The evolution of the antorbital cavity in archosaurs: a study in soft-tissue reconstruction in the fossil record with analysis of the function of pneumaticity. *Journal of Vertebrate Paleontology, Memoir* 3, 17:1-73.
- Young, C.C., Bien, M.N., and Mi, T.H. 1972. *Mamenchisaurus* from Ho Chuan. *Chinese Science Institute for Vertebrate Paleontology and Paleoanthropology, Monograph Series A*, 8:1-30.
- Young, C.C., and Zhao, X.-J. 1972. *Mamenchisaurus hochuanensis* sp. nov. [in Chinese with English abstract]. *Institute of Vertebrate Paleontology and Paleoanthropology Monographs, A*, 8:1-30.