

Pneumaticity and soft-tissue reconstructions in the neck of diplodocid and dicraeosaurid sauropods

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The axial soft-tissue system in the neck of Dicraeosauridae and Diplodocidae, including pneumatic diverticula, ligaments, and muscles, is reconstructed on the basis of phylogenetic and functional morphological comparisons with extant crocodylians and birds and compared with other soft-tissue reconstructions for sauropods. Bifurcation of the neural spines separated the paired supraspinal ligament into two sheets. A paired interspinal septum was attached to the cranial and caudal margins of the neural spines. The dorsal and the lateral portions of the cervical musculature must have been strongly segmented, whereas the laterocostal portion was divided with one myoseptum per vertebral segment. The hypaxial cervical muscle was most probably small and only poorly segmented. In Diplodocidae and Dicraeosauridae, the distribution of external pneumatic structures is similar, whereas only Diplodocidae possess intraosseous pneumatic structures. Supravertebral pneumatic diverticula are reconstructed for both groups, which, together with dorsal ligaments filled the gap between the metapophyses of bifurcate neural spines. Comparisons between the vertebrae of juvenile and adult diplodocids strongly indicate that pneumatisation proceeded from the supramedullary diverticula into the neural arch and the neural spine. The regular branching pattern of the pneumatic cavities as well as the vertical I-beam construction of the vertebral corpora is interpreted as a consequence of the biomechanical constraints of the vertebral corpora in diplodocids. These reconstructions form the ground for functional morphological considerations in Diplodocidae and Dicraeosauridae while addressing the possible mechanical consequences of pneumatic structures for the integrity of the support system of the neck.

Key words: Diplodocidae; Dicraeosauridae, vertebral pneumaticity; cervical ligaments; cervical musculature; functional morphology; ontogeny; tomography.

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Introduction

With body lengths exceeding 30 m and masses presumably reaching more than 26 tons (Henderson 2004), sauropods were the largest terrestrial vertebrates that ever existed (Upchurch et al. 2004a). Their presacral vertebrae bear external laminae and are in most cases hollowed out by a complex pattern of cavities. These structures have been explained as the osteological traces of a pneumatic system similar to that of extant birds (Seeley 1870; Janensch 1947; Britt 1997; Britt et al. 1998; Wedel et al. 2000a; O'Connor 2006). Pneumaticity of the sauropod axial skeleton in sauropods was recognized early (Seeley 1870; Cope 1877; Marsh 1877), signalled by presence of large pneumatic foramina and fossae in the presacral vertebrae. The most comprehensive description of pneumatic structures and a first detailed outline nomenclature of laminae in sauropods was published by Janensch (1950). Since non-invasive techniques such as computed tomography became available for analyzing the detailed internal morphology of sauropod vertebrae in detail, research on the pneumaticity of sauropod bones has come under renewed scrutiny

(Britt 1993, 1997; Wedel et al. 2000a, b; Wedel 2003a, b). The distribution and general pattern of pneumatic structures in sauropod presacral vertebrae ranges from simple external pneumatic fossae (e.g., *Haplocanthosaurus*, *Dicraeosaurus*, *Amargasaurus*; Janensch 1947; Salgado and Bonaparte 1991; Britt 1993; Wedel 2003a) to large internal pneumatic chambers (e.g., *Diplodocus*, *Camarasaurus*, *Apatosaurus*; Britt 1993; Wedel et al. 2000a; Wedel 2003a) or a densely spaced meshwork of many small camellae (e.g., *Austrosaurus*, *Sauroposeidon*, *Saltasaurus*; *Mamenchisaurus*; Longman 1933; Young and Zhao 1972; Wilson and Sereno 1998; Wedel et al. 2000b). Pneumatic structures in sauropods are highly variable within species and individuals (Britt 1993; Curtice 1998; Wedel et al. 2000a; Wedel 2003a), but some of their osteological traces, such as the laminae (Wilson 1999) or the structure and position of pneumatic fossae, can be used for taxonomy (see characters in Upchurch 1995; Salgado et al. 1997; Upchurch 1998; Wilson and Sereno 1998; Wilson 2002; Upchurch et al. 2004a).

Hypotheses on the possible functions of vertebral pneumaticity in sauropods have included mostly weight reduction,

but also other possibilities such as body cooling (Janensch 1947; Coombs 1978; Britt 1993, 1997; Wedel et al. 2000a; Wedel 2005; O'Connor 2006). Vertebral pneumaticity in sauropods indicates the presence of lung dilatations or air sacs in the trunk, which could have had an impact on mechanisms of their respiratory apparatus (Perry and Reuter 1999; Wedel 2003b; O'Connor 2006). A possible biomechanical role of pneumatic structures in the sauropod axial skeleton as stiffening device was suggested by Akersten and Trost (2000, 2001, 2004). However, there is general agreement on the fact that the main function of vertebral pneumaticity in sauropods was to reduce the density of the skeleton, making the attainment of such large body sizes possible at all (Britt 1993, 1997; Wedel 2003b, a, 2004, 2005; O'Connor 2006).

A rationale for the distribution, amount, and possible biological roles of pneumatic diverticula in the axial skeletons of eusauropods is difficult to explain without detailed reconstructions of the distribution of the pneumatic diverticula, in context with the tendinomuscular bracing system. Reconstructions of the distribution of pneumatic diverticula in the neck of sauropods are provided by Wedel (2005) and Wedel et al. (2000a), but overall soft-part reconstructions are restricted to isolated muscle portions and ligaments (see e.g., Tsuihiji 2004) or muscles and ligaments depicted only by their assumed force vectors (Wedel et al. 2000a; Wedel and Sanders 2002). An integrative functional morphological analysis of the cervical vertebral column of different sauropods, including both soft-tissue reconstructions and evaluations of neck mobility, could be used to understand better how the long sauropod necks were supported. The results of such an analysis could then be taken as basis for the understanding of feeding ranges and locomotor options of sauropods, therefore for niche partitioning amongst sauropods or their settlement in different ecosystems.

Because birds are the phylogenetically closest extant relatives of sauropods, the reconstruction of sauropod soft-tissues hitherto was mainly based on the anatomy of ratites like *Struthio* or *Rhea* (Wedel et al. 2000a; Wedel and Sanders 2002; Tsuihiji 2004). Extant crocodylians form the other pole of the extant phylogenetic bracket of sauropods (Witmer 1995, 1997), but topological similarities of crocodylian and sauropod cervical vertebrae have been generally neglected. Here, we present soft-tissue reconstructions for the necks of diplodocid and dicraeosaurid sauropods by using both crocodylians and birds, and discuss differences between our and other reconstructions. We have chosen diplodocid and dicraeosaurid sauropods for different reasons. The diplodocids *Diplodocus* Marsh, 1878 and *Apatosaurus* Marsh, 1877 and the dicraeosaurids *Dicraeosaurus* Janensch, 1914 and *Amargasaurus* Salgado and Bonaparte, 1991 are known from well-preserved, near-complete skeletons and therefore provide a good data basis for soft-tissue reconstructions. Existing CT scans of diplodocids (Britt 1993; Wedel et al. 2000a; Wedel 2003a, 2005) could be supplemented by further CT scans of *Diplodocus* and *Dicraeosaurus* material, providing again a good data basis for soft-tissue recon-

structions. From a phylogenetic viewpoint, diplodocid and dicraeosaurid sauropods comprise well-defined and most probably monophyletic sauropod clades (Upchurch 1995, 1998; Wilson 2002, 2005; Rauhut et al. 2005). Both clades have a rather unique morphology of their cervical vertebral column in terms of the bifurcation of neural spines, vertebral pneumaticity and cervical ribs in comparison with other sauropods, and they have been studied in terms of their neck mobility (Stevens and Parrish 1999, 2005b, a). Therefore, reconstructions of soft-tissues in the neck of diplodocids and dicraeosaurids will provide a basis for investigating possible biological roles of pneumatic structures in the neck, for devising models of the bracing system of extremely long necks in sauropods, and with some restrictions also for reconstructions of soft-tissues in other eusauropods.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CM, Carnegie Museum of Natural History, Pittsburgh, USA; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; NMB, Naturhistorisches Museum Basel, Switzerland; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Germany; SMA, Saurier-Museum Aathal, Switzerland; SNM, Naturmuseum Senckenberg, Frankfurt, Germany; USNM, National Museum of Natural History, Smithsonian Institution, Washington, USA; YPM, Yale Peabody Museum, New Haven, USA; ZMB, Museum für Naturkunde der Humboldt-Universität Berlin, Berlin, Germany.

Other abbreviations.—ASP, Airspace Proportion; CT, computed tomography; m., musculus (muscle); sprl, spinoprezygapophyseal lamina; spol, spinopostzygapophyseal lamina.

Materials and methods

Material and techniques.—Postcranial material of *Amargasaurus*, *Apatosaurus*, *Barosaurus*, *Dicraeosaurus*, *Diplodocus*, and *Tornieria* was examined (DS) at AMNH, CM, MACN, NMB, SMA, SNM, USNM, YPM, and ZMB. Only taxa with well-preserved cervical vertebrae were used, in particular the diplodocids *Apatosaurus* (Gilmore 1936; Upchurch et al. 2004b), *Barosaurus lentus* (Marsh 1890; Lull 1919; McIntosh 2005), *Diplodocus* (Hatcher 1901, 1903; Holland 1906), and *Suuwassea* (Harris and Dodson 2004; Harris 2006a, b), and the dicraeosaurids *Amargasaurus* (Salgado and Bonaparte 1991; Salgado 1999) and *Dicraeosaurus hansemani* (Janensch 1914, 1929).

Four cervical vertebrae and a cervical rib of juvenile specimens of an undetermined diplodocid from the Howe Stephens Quarry of the Late Jurassic (Kimmeridgian) Morrison Formation (SMA D15-2, 4th cervical; SMA H25-1, axis; SMA H25-2, 3rd cervical; SMA I34-1, 5th cervical; SMA D15-6, cervical rib) as well as the 8th cervical vertebra of an adult specimen of *Diplodocus* (SMA L25-3, 8th cervical), were scanned with X-ray computed tomography at the Department of Medical Radiology of the University Hospital

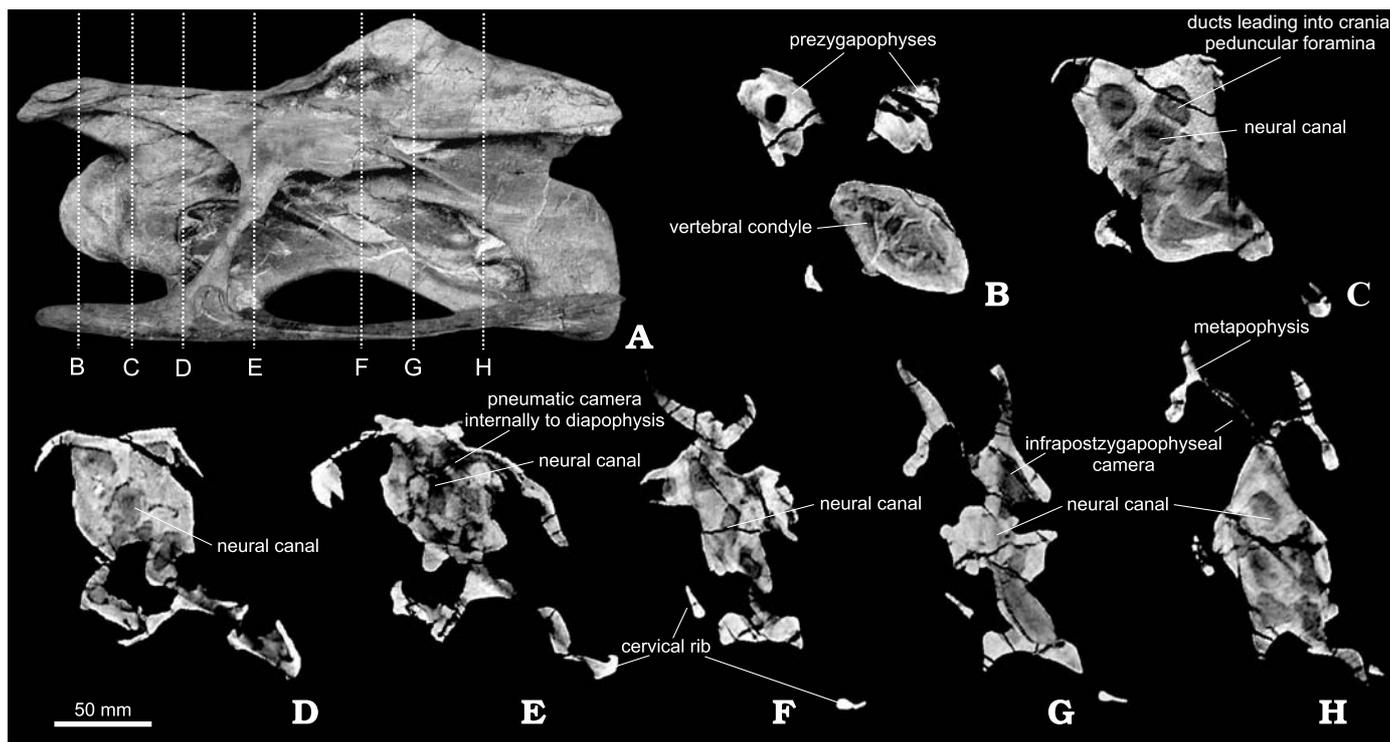


Fig. 1. Photograph of 8th cervical vertebra (SMA L25-3) of subadult *Diplodocus* sp., Howe Stephens Quarry, Wyoming, USA, Morrison Formation, Kimmeridgian, Late Jurassic (A) showing location of transverse sections (B–H) obtained from X-ray computed tomography.

Basel. The scans were performed with a Multidetector CT-scanner (Sensation 16, Siemens, Erlangen; Germany). The vertebrae were scanned along their long axis with a parameter setting of 140 keV and 350 mA and a primary collimation of 16×0.75 mm. The raw data were reconstructed applying a standard algorithm for human osseous structures using the standard CT imaging processor with the imaging software version VA 70C. The data were reconstructed in all orthogonal planes at 3 mm thickness and additionally along designated planes along anatomical structures (Schwarz et al. 2005).

Two cervical vertebrae of *Dicraeosaurus* sp. (ZMB E14; ZMB E27) were scanned in the Clinic for Small Pets of the Free University of Berlin, using a high-resolution Multi-slice-CT scanner (GE Healthcare Light Speed advantage QXi). A spiral scan with a 0.6 mm interval was made, leading to a 383 images DICOM stack. The settings were 140 kV and 220 mA (Schwarz and Fritsch 2006).

The skeletons of *Crocodylus porosus* (FUB OS 13), *Tomistoma schlegeli* (NMB, no collection number), *Rhea americana* (NMB 2670), *Struthio camelus* (NMB 8180), *Dromaeus novaehollandiae* (NMB 2978), *Casuaris casuaris* (NMB 1829), *Sarcorhamphus gryphus* (NMB 3295), *Cygnus cygnus* (NMB 10588), *Varanus salvator* (NMB 2139), *Equus caballus* (NMB 7175) and *Camelus dromedarius* (NMB 1022) were examined for comparison. The necks of *Palaeosuchus palpebrosus*, *Meleagris gallopavo*, *Columba livia*, *Ardea cinerea*, and *Uromastyx acanthinurus* were dissected. For the

comparison of internal structures, CT scans of a crane (*Grus grus*) and a white-tailed eagle (*Haliaeetus albicilla*) were examined. Measurements were taken with a metric slide gauge, tape measure, and angle ruler.

Reconstruction method.—For soft-tissue reconstructions in extinct vertebrates, topographical similarities of tissue-attachment sites can be used in the context of an Extant-Phylogenetic-Bracket (EPB) approach (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 soft-tissue reconstructions according to extant phylogenetic bracketing (see for example Gauthier et al. 1988; Witmer 1997; Benton 2004). Axial muscles and ligaments often leave characteristic traces on the surface of the cervical vertebrae of avians and crocodylians, such as rugosities, crests or striations. If such osteological correlates are present at vertebrae of sauropods, similar muscles and ligaments are reconstructed. However, the derived osteology of sauropod necks and the presence of osteological correlates for vertebral pneumaticity only in extant avians hindered inference of many specific structures by extant phylogenetic bracketing. In these cases, soft structures were reconstructed by one-way phylogenetic comparison (e.g., for the reconstructions of pneumatic diverticula, or many aspects of the cervical musculature), extrapolatory inference by structural similarities (e.g., in case of the extremely high cervical neural spines of *Amargasaurus*), and mechanical considerations. Indeed, an integrated reconstruction can be

tested as morphologically feasible when it leads to a bio-mechanical functioning model of the organism (Weishampel 1995; Carrano and Hutchinson 2002; Gudo et al. 2002; Hutchinson 2004; Perry and Sander 2004), in concert with phylogenetic inferences. Such mechanical aspects of the sauropod neck construction can best be realistically reconstructed, if the soft-tissues and hard-parts are seen as a functionally coherent and operating entity (Frey et al. 1993; Herkner 1999; Salisbury 2001; Salisbury and Frey 2001), allowing the reconstruction and interpretation of mechanical aspects of organismic form and operation, in the context of the anatomy of a coherent bracing system.

Anatomical nomenclature.—Criteria for recognizing osteological correlates of pneumatic structures in sauropod vertebrae followed the work of Britt (1993), O'Connor (2003, 2004, 2006), Wedel (2000a, 2005), and Witmer (1990, 1997). The reconstructions of vertebral pneumaticity in the sauropod necks by a one-way phylogenetic comparison with extant birds induces the usage of a standard nomenclature of pneumatic structures for birds (Müller 1908; Duncker 1971; O'Connor 2003, 2006), which is supplemented by topographical descriptors for additional pneumatic structures. For the intraosseous pneumatic structures of the vertebrae, the terms already applied to sauropods (Britt 1993; Wedel et al. 2000a; Wedel 2003a, 2005) were used. No statements on a possible homology of the reconstructed muscles of sauropods with extant archosaurs are made in this study, therefore the used nomenclature for these soft-tissues is purely topographical. The nomenclature of the external laminae in sauropod vertebrae follows that of Wilson (1999).

Soft-tissue reconstructions in Diplodocidae and Dicraeosauridae

Pneumatic diverticula in the neck

Lateral vertebral diverticula.—In the cranial cervical vertebrae of Diplodocidae, approximately three fourths of the lateral surfaces of the vertebral corpora, are occupied by subdivided communicating pneumatic fossae (Appendix 1). In the caudal cervical vertebrae, the communicating pneumatic fossae are restricted to the cranial two thirds of the lateral surface (Figs. 1–3). In subadult to adult *Diplodocus* and *Apatosaurus*, the middle and caudal cervical vertebrae possess several pneumatic camerae inside the vertebral condyle, separated from each other by thin bony laminae (Figs 1, 2). The parapophyses and cervical ribs bear pneumatic foramina (Fig. 1), and are hollowed out by pneumatic camellae (Appendix 1). The vertebral body of the cranial cervical vertebrae of juvenile diplodocids including *Apatosaurus* is excavated by a left and right pneumatic camera, which is connected with the pneumatic fossa (Figs. 2, 3; Appendix 1).

In Diplodocidae, the presence of deep pneumatic fossae and large foramina is similar to the pneumatised vertebrae of extant birds (O'Connor 2004, 2006). This indicates unambiguously that the lateral surface of the cervical vertebral corpora was in contact with lateral vertebral diverticula, which deeply excavated their lateral surface (Fig. 4). The lateral vertebral diverticulum system probably contacted the infradiapophyseal diverticulum dorsally and the intracostal diverticulum ventrally (Fig. 4). The parapophyseal pneumatic fossa and the pneumatised cervical ribs suggest the presence of an intracostal pneumatic diverticulum filling the capitulotubercular incision (Fig. 4). Whether these diverticula expanded continuously over the entire lateral vertebral surface of the cervical vertebral corpora as in extant birds (Müller 1908; Cover 1953; O'Connor 2003, 2004), or whether they were segmented, as is indicated by the interfossal laminae at least in the adult specimens (Fig. 4), cannot be reconstructed with certainty. In any case, the extension of the communicating pneumatic fossae, the connection between them, and the adjacent ventral and dorsal pneumatic structures suggest a lateral vertebral pneumatic diverticula system similar to the canalis intertransversarius in birds (Müller 1908; Landolt and Zweers 1985). If this canal was present, then the lumen of the intertransversal foramina was most likely completely occupied by pneumatic diverticula in Diplodocidae. This compares well with the situation in birds, where the pneumatic intertransversal canal occupies at least one fourth of the intertransversal space (Müller 1908; Landolt and Zweers 1985).

In Dicraeosauridae, fossae of the vertebral corpora are noncommunicating (blind) and divided only into a cranial and a caudal part (Appendix 1, Fig. 3F). The fossae extend into the vertebral body, leaving a median bone strut, and the parapophysis bears a pneumatic foramen and is hollowed out (Appendix 1). The noncommunicating fossae of the vertebral corpora of Dicraeosauridae provide no unambiguous evidence for vertebral pneumaticity as such fossae can be associated with other tissues (e.g., muscles or adipose tissue) in extant vertebrates (O'Connor 2003, 2006). The occurrence of these fossae in similar places as at the vertebrae of diplodocids, and the presence of a pneumatic foramen at the parapophysis makes it probable that dicraeosaurids possessed indeed lateral vertebral diverticula.

Pneumatic diverticula around the prezygapophyses and the diapophyses.—An infraprezygapophyseal communicating pneumatic fossa, roofed by the prezygodiapophyseal lamina, and an infradiapophyseal communicating pneumatic fossa is present in Diplodocidae (Appendix 1, Fig. 3). Pneumatic foramina within the prezygapophyseal pneumatic fossa give way into pneumatic camellae hollowing out the prezygapophyses. The cranial part of the neural arch is hollowed out internally to the infradiapophyseal pneumatic fossa (Appendix 1, Fig. 2). In the cervical vertebrae of the juvenile diplodocids, around the pneumatic cavity in the neural arch small spongy areas of bone indicate a progressive resorption of

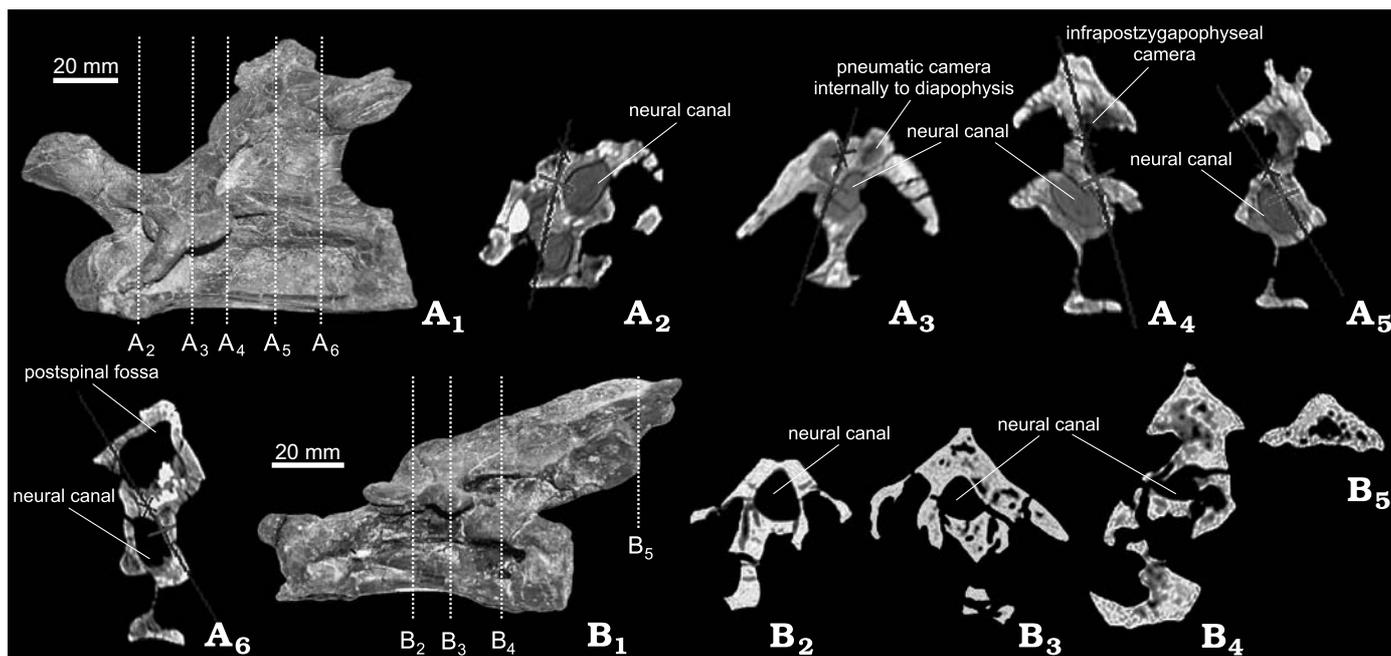


Fig. 2. Cervical vertebrae of juvenile, undetermined diplodocids from Howe Stephens Quarry, Wyoming, USA, Morrison Formation, Kimmeridgian, Late Jurassic. **A.** Photograph of 3rd cervical vertebra (SMA I34-1) (A₁) with location of transverse sections A₂–A₆ obtained from X-ray computed tomography. **B.** Photograph of axis (SMA D 25-1) (B₁) with location of transverse sections B₂–B₅ obtained from X-ray computed tomography.

bone material (Fig. 2B). Similar, but noncommunicating infrapostzygapophyseal and infradiapophyseal fossae are present in Dicraeosauridae. The infradiapophyseal fossa of *Dicraeosaurus* undermines the diapophysis and excavates slightly into the neural arch (Appendix 1; Schwarz and Fritsch 2006).

The infrapostzygapophyseal and infradiapophyseal pneumatic fossae with adjacent intraosseous pneumatic camerae in Diplodocidae allow, in accordance with extant birds (O'Connor 2006), an unambiguous reconstruction of pneumatic diverticula in this region of the vertebra. The infradiapophyseal pneumatic diverticula of Diplodocidae covered the lateral surface of the vertebrae ventral to the diapophysis and prezygapophysis (Fig. 4) and expanded inside the neural arch into larger and smaller camerae. Those branches of the infradiapophyseal diverticula of Diplodocidae lying within the neural arch appear to have opened into the neural canal (Fig. 4). The excavation of the neural arch by infrapostzygapophyseal and infradiapophyseal fossae makes it likely for Dicraeosauridae that these sauropods possessed likewise pneumatic diverticula in this area.

Pneumatic diverticula around the postzygapophyses.—An infrapostzygapophyseal fossa, deeply excavating the lateral face of the neural arch, lies ventral to the base of the postzygapophyses on the lateral surface of the cervical vertebrae of Diplodocidae and Dicraeosauridae (Appendix 1). The infrapostzygapophyseal fossa is bordered by the postzygodiapophyseal and the posterocentrodiaepophyseal lamina (Fig. 3A). In Diplodocidae, the infrapostzygapophyseal pneumatic fossa possesses pneumatic foramina leading into an infrapostzygapophyseal camera (Fig. 1).

The presence of an infrapostzygapophyseal pneumatic fossa with foramina and an infrapostzygapophyseal camera are correlations of vertebral pneumaticity similar to extant birds and provide evidence that in the cervical vertebrae of Diplodocidae, the space lateroventral to the postzygodiapophyseal lamina was occupied with pneumatic diverticula (Fig. 4). Those pneumatic diverticula extended cranially into the diapophysis and mediodorsally into the neural arch. Probably, a similar infrapostzygapophyseal pneumatic diverticulum was present in Dicraeosauridae.

Pneumatic diverticula lateral to the neural arch.—On the lateral face of the neural arch of the cervical vertebrae in Diplodocidae and Dicraeosauridae there are depressions and blind fossae, which vary in shape within the neck of different individuals (Appendix 1, Fig. 3). Pneumatic foramina that lead into pneumatic camerae of the neural arch are not present in this region. Without more extensive data, the surface texture within the fossae cannot be unambiguously correlated with any one soft tissue (O'Connor 2003, 2006), although the texture has been used as indicator for a contact of cortical bone with pneumatic epithelium (Britt 1993; Wedel et al. 2000a). Therefore, it is not certain that the impressions on the lateral face of the neural arches contained pneumatic diverticula. The partition and lamination of these fossae in diplodocids and *Amargasaurus* (Appendix 1) makes the presence of pneumatic diverticula at least possible (Fig. 4), but neither their exact extension nor possible connections to other pneumatic diverticula can be reconstructed. If present at all, then these pneumatic diverticula (from their topography) could have been connected with the internal pneumatic

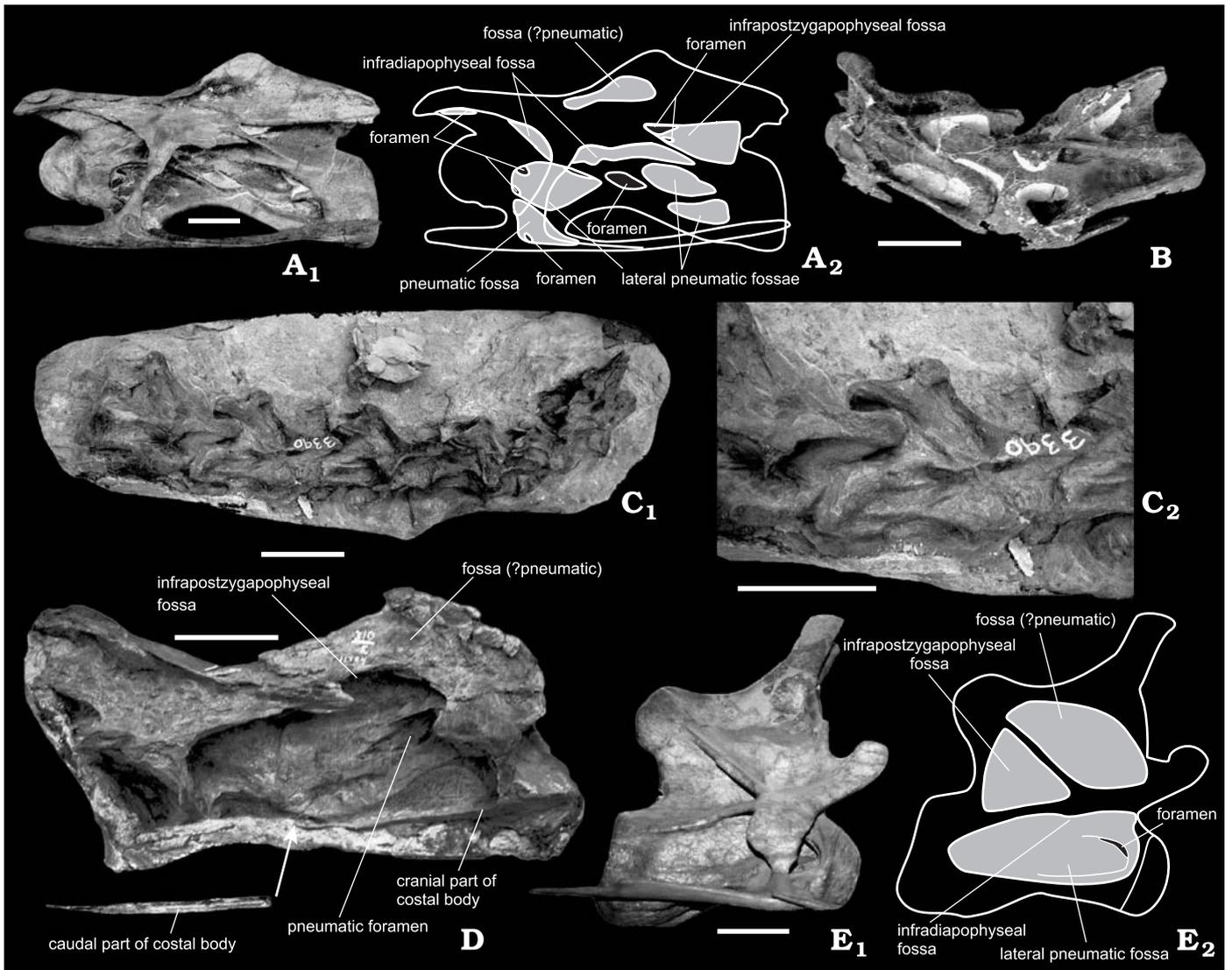


Fig. 3. Diplodocid and dicraeosaurid cervical vertebrae. **A.** 8th cervical vertebra (SMA L25-3) of subadult *Diplodocus* sp., Howe Stephens Quarry, Wyoming, USA, Morrison Formation, Kimmeridgian, Late Jurassic, in left lateral aspect (A₁) and as schematic drawing indicating external pneumatic structures (A₂). **B.** 7th and 8th cervical vertebra (SMA M34-1 and M34-2) of juvenile undetermined diplodocid, Howe Stephens Quarry, Wyoming, USA, Morrison Formation, Kimmeridgian, Late Jurassic, in left lateral aspect. **C.** Series of six cervical vertebrae of immature juvenile *Apatosaurus louisae* (CM 3390), Carnegie Museum Quarry at Dinosaur National Monument, Utah, USA, Morrison Formation, Late Jurassic, in right lateral aspect (C₁) and with single vertebra in a larger scale (C₂). **D.** Midcervical vertebrae of *Barosaurus lentus* (CM 1198), Carnegie Museum Quarry at Dinosaur National Monument, Utah, USA, Morrison Formation, Late Jurassic, in left lateral aspect, with broken distal half of cervical rib below. **E.** 8th cervical vertebra of *Dicraeosaurus hansemanni* (ZMB "skeleton m"), Middle Saurian Bed, Tanzania, Tendaguru Beds, Late Jurassic, in right lateral aspect (E₁) and with schematic drawing of external pneumatic structures (E₂). Scale bars 50 mm, except D, for which is 300 mm.

diverticula of the diapophysis, or the supravertebral pneumatic diverticula or both (Fig. 4).

Supravertebral pneumatic diverticula.—In the neck of adult Diplodocidae and Dicraeosauridae, the neural spines of most cervical vertebrae are bifurcate in their dorsal half or completely divided (Appendix 1). If the neural spines are not bifurcate, they possess a deep postspinal cavity. If they are partially bifurcate, the postspinal cavity laterally widens into a shallow fossa on the medial surface on each ramus of the neural spine (Fig. 4A–C). CT scans reveal internal pneumatic

ducts running from the metapophyses or the postspinal cavity into the caudal camera of the neural arch of Diplodocidae (Fig. 1A, B). Single neural spines and the metapophyses of bifurcate neural spines of Diplodocidae contain small pneumatic cavities (Appendix 1). In *Diplodocus*, the completely bifurcate neural spines can bear a large, longitudinally oval pneumatic foramen penetrating the medial wall of either the left or the right metapophysis (Appendix 2). In the axis of a juvenile diplodocid (SMA H25-1), the spongy structure inside the neural spine (Fig. 2B) marks the beginning of intrasosseous pneumatisation of this single neural spine.

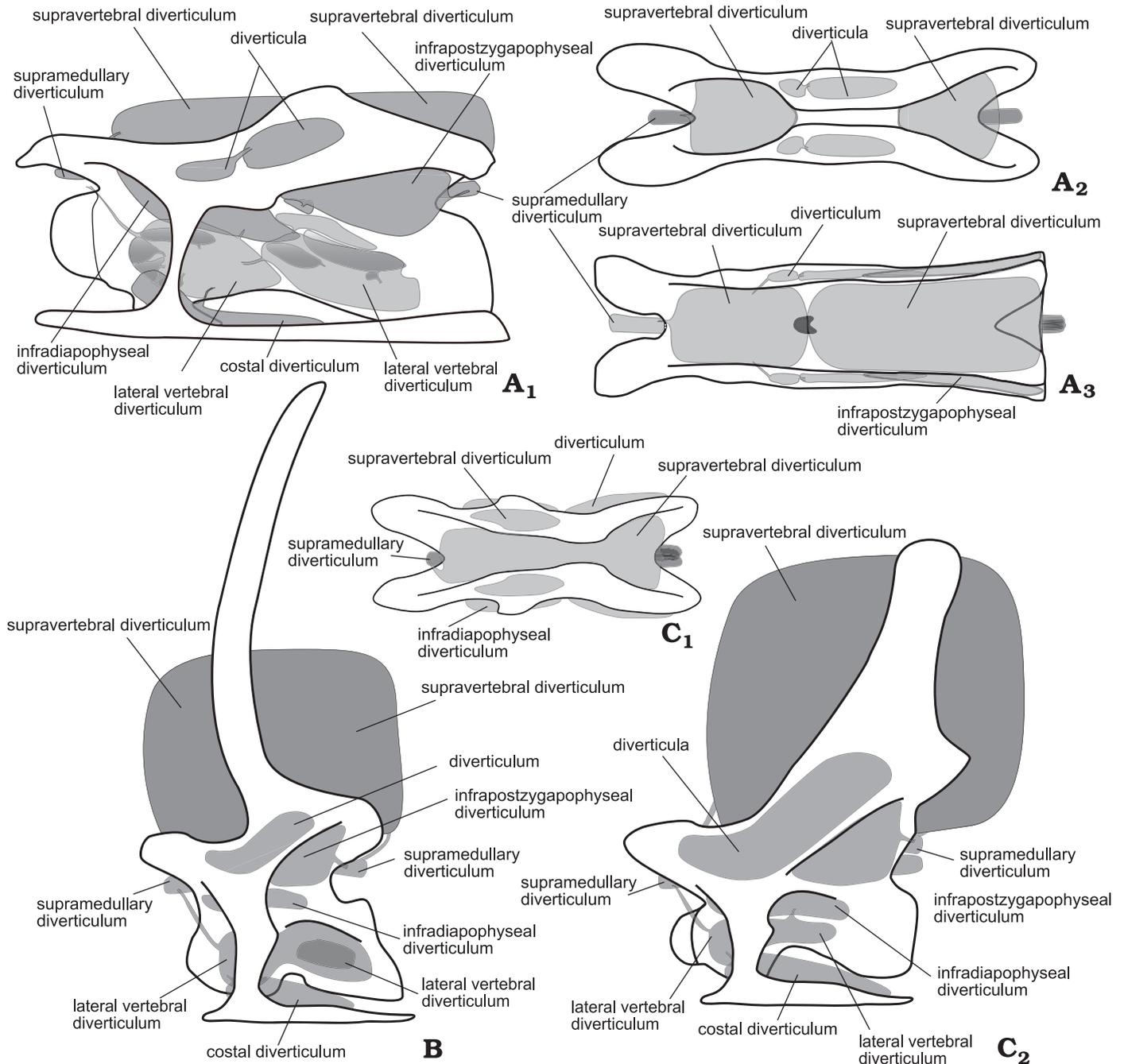


Fig. 4. Reconstruction of the distribution of pneumatic diverticula in diplodocids and dicraeosaurids. **A.** Schematic drawing of midcervical vertebra of *Diplodocus* in left lateral aspect (**A₁**), in dorsal aspect with single neural spine (**A₂**) and in dorsal aspect with bifurcate neural spine (**A₃**). The partitioning of pneumatic diverticula at the lateral surface of the vertebral corpus is hypothetical, based on the strongly divided pneumatic fossae. **B.** 10th cervical vertebra of *Amargasaurus cazau* in left lateral aspect. **C.** 8th cervical vertebra of *Dicraeosaurus hansemanni* in dorsal (**C₁**) and in left lateral (**C₂**) aspects. Not to scale.

The presence of pneumatic foramina and depressions on the medial surface of the metapophyses of the cervical vertebrae indicate that in Diplodocidae supravertebral pneumatic diverticula must have filled the gap between these metapophyses and the postspinal cavity, respectively (Fig. 4). Pneumatic ducts connecting the intraosseous pneumatic structures of the neural arch with the dorsal face of the neural spine support this reconstruction (Figs. 1, 2). These

supravertebral pneumatic diverticula were most probably extensions of the supramedullary diverticula, as in extant birds (Müller 1908; Wedel 2003a: fig. 4; O'Connor 2006).

Although there is no osteological correlate for supravertebral pneumatic diverticula in Dicraeosauridae, the possible reconstruction of supramedullary diverticula (see below) implies that they also possessed supravertebral diverticula, protruding from the supramedullary diverticula.

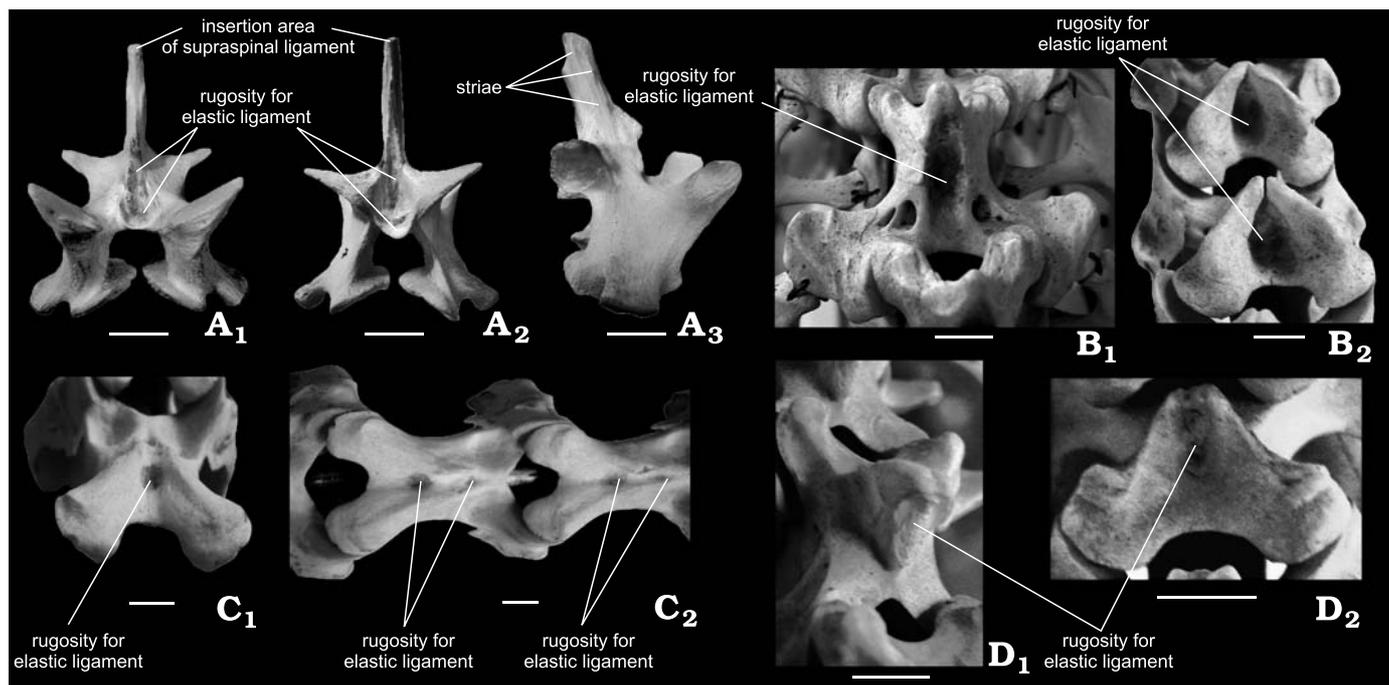


Fig. 5. Cervical vertebrae of extant crocodylians and birds exposing osteological correlates for soft-tissue. **A.** Neural spine of 7th cervical vertebra of *Crocodylus porosus* (FUB OS 13) in cranial (A₁), caudal (A₂) and lateral (A₃) aspects. Note subdivision of the rugosity for the interlamellar elastic ligament in A₁ and A₂. **B.** Neural spines of cervical vertebrae of *Casuarius casuarius* (NHM 1829) in craniodorsal (B₁) and caudal (B₂) aspects. Note bifurcate neural spine and distinct rugosity for the interlamellar elastic ligament in B₂. **C.** Neural spine of 14th cervical vertebra of *Rhea americana* (NHM 3534) in caudal (C₁) and dorsal (C₂) aspect, with rugosity for interspinal elastic ligament virtually not being distinguishable from rugosity for interlamellar elastic ligaments, as in B and D. **D.** Neural spines of *Sarcorhamphus gryphus* (NMB 3295) in craniolateral (D₁) and caudal (D₂) aspect. Scale bars 10 mm.

Because the neural spines in *Dicraeosaurus* are tall, and the medial faces of the metapophyses are smooth and their tips are medially inclined, the supravertebral pneumatic diverticula would have occupied the entire space between the rami and thus had more volume than in Diplodocidae (Fig. 4B).

In *Amargasaurus*, there is no structure that allows a reliable reconstruction of a distinct supraspinal ligament extending along the dorsal margins of consecutive cervical neural spines (see also below in “Supraspinal ligament”). In contrast, the ripple-and-striation pattern in the dorsal part of the cervical metapophyses of *Amargasaurus* (Table 2) is similar to that found at the surface of the bony cores of bovid horns (Bubenik and Bubenik 1990). Because it is also consistent with the shape of the dorsally tapering and slightly caudally curving metapophyses, the striation pattern in the dorsal two thirds of the neural spines therefore might indicate an integumental cover such as a keratinized horn sheath (see also Salgado 1999: fig. 9) or skin. In this case, the supravertebral pneumatic diverticula of *Amargasaurus* would have occupied the ventral third in the medial cervical vertebrae, and in the cranial and caudal cervical vertebrae the ventral half of the gap between the metapophyses (Fig. 4C).

It is probable that supravertebral pneumatic diverticula were also present cranial to the neural spines of Diplodocidae and Dicraeosauridae (Fig. 4A) as in extant birds.

Supramedullary diverticula.—A pneumatic meshwork connects the neural canal of the cervical vertebrae of *Diplodocus*, *Apatosaurus* and the undetermined juvenile diplodocids with adjacent pneumatic cavities, e.g., the infradiapophyseal or the infrapostzygapophyseal camerae (Appendix 1, Figs. 1, 2). Apparently, this system reaches maximum complexity level with the diapophysis and even more pneumatic cavities proliferate. From this osteological evidence and the comparison with extant birds, it appears evident that at least one supramedullary pneumatic diverticulum was present inside the neural canal of the cervical vertebrae of Diplodocidae (Figs. 3, 7; Britt 1993; Wedel 2003a). It is impossible to say, if these supramedullary diverticula formed supramedullary pneumatic canals, which ran continuously through the neural canal of the entire cervical column as in birds (Müller 1908; Cover 1953; Duncker 1971; O’Connor 2006) or if they were restricted to their respective vertebrae.

In contrast to diplodocids, the neural canal of the cervical vertebrae of *Dicraeosaurus* exhibits no pneumatic structures and the whole neural arch is unpneumatized (Schwarz and Fritsch 2006). In extant birds with pneumatized cervical vertebrae, the supramedullary diverticula system originates from the cervical air sacs and enters the vertebral canal at the cervico-thoracic junction (Müller 1908; O’Connor 2006). The supramedullary diverticula and the lateral vertebral diverticula communicate with each other by pneumatic ducts and small pneumatic diverticula (Müller 1908; Duncker

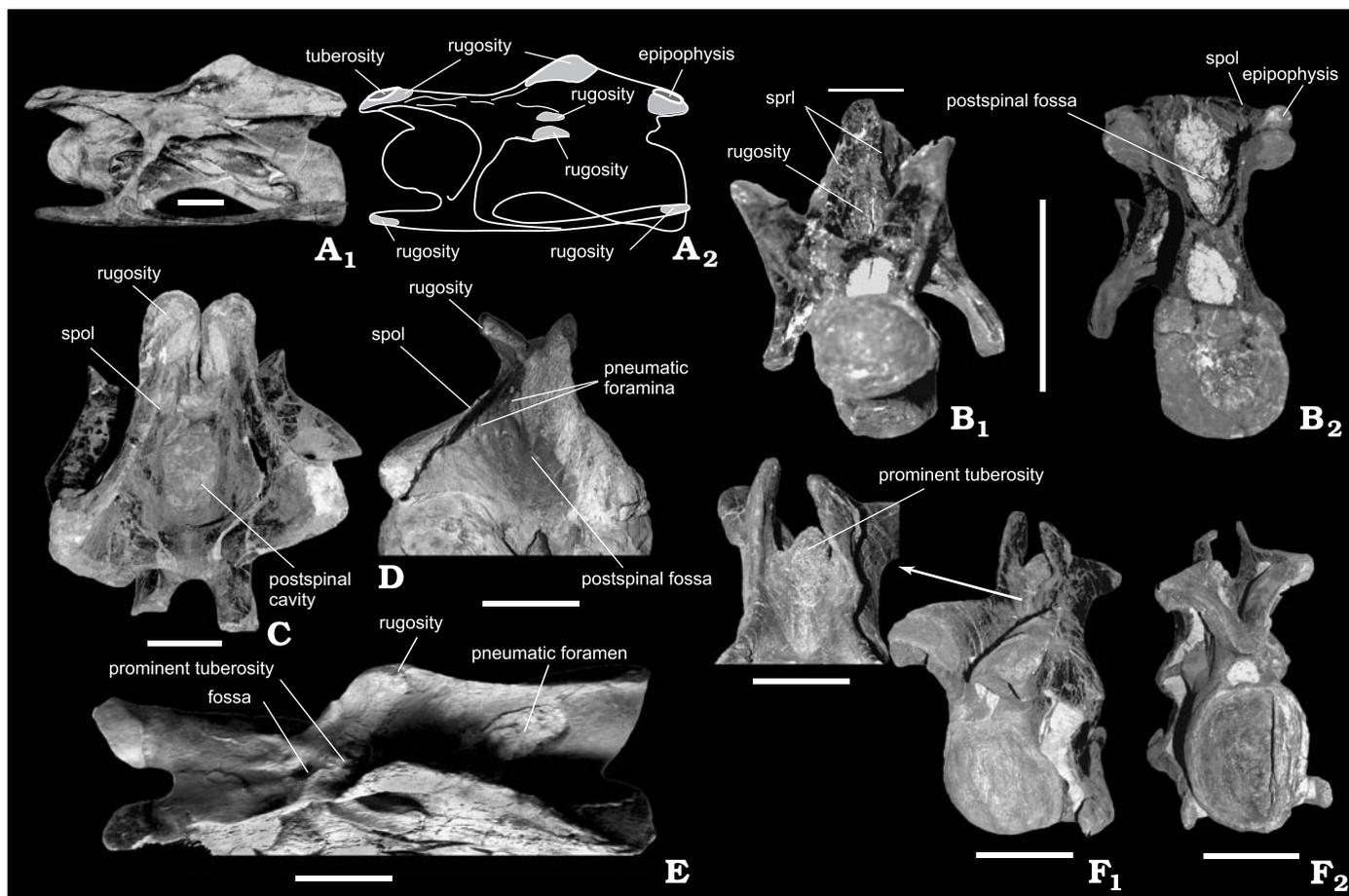


Fig. 6. Cervical vertebrae of diplodocids exposing osteological correlates for soft-tissue. **A.** Cervical vertebra of *Diplodocus* (SMA L25-3), Howe Stephens Quarry, Wyoming, USA, Morrison Formation, Kimmeridgian, Late Jurassic, in left lateral aspect (**A₁**) and as schematic drawing with insertion areas for tendinomuscular apparatus (**A₂**). **B.** 4th cervical vertebra (SMA D25-2) of undetermined juvenile diplodocid, Howe Stephens Quarry, Wyoming, USA, Morrison Formation, Kimmeridgian, Late Jurassic, in cranial (**B₁**) and caudal (**B₂**) aspects. **C.** Isolated neural spine of a cervical vertebra of *Apatosaurus excelsus* (CM 555), Quarry D (Sheep Creek), Wyoming, USA, Morrison Formation, Late Jurassic, in caudal aspect showing postspinal fossa. **D.** Cervical vertebra of *Barosaurus lentus* (CM 1198), Carnegie Museum Quarry at Dinosaur National Monument, Utah, USA, Morrison Formation, Late Jurassic, in caudal aspect showing postspinal fossa containing pneumatic foramina. **E.** Cervical vertebra of *Diplodocus* (SMA L25-3), Howe Stephens Quarry, Wyoming, USA, Morrison Formation, Kimmeridgian, Late Jurassic, in dorsolateral aspect showing large pneumatic foramen. **F.** Cervical vertebra of *Diplodocus* sp. (SMA, no collection number), Howe Stephens Quarry, Wyoming, USA, Morrison Formation, Kimmeridgian, Late Jurassic, in cranial aspect with close-up showing peduncle for interspinal elastic ligament (**F₁**) and in caudal aspect (**F₂**). Scale bars 50 mm.

1971; Wedel 2003a; O'Connor 2006). If pneumatic diverticula are reconstructed for the neck of Dicraeosauridae in general, they would have extended from a cervical air sac, making the presence of suprasedullary diverticula likely as well (Figs. 8, 9).

Reconstruction of major neck ligaments and musculature

Supraspinal ligament.—The rugosities at the dorsal margins of the neural spines of Diplodocidae and *Dicraeosaurus* (Appendix 2, Figs. 5, 6) are similar to attachment areas of supraspinal ligament elements in extant crocodylians (Frey 1988) and a homologous “ligamentum nuchae” system of ligaments in birds (Tsuihiji 2004), thus indicating a rope-shaped supraspinal ligament in Diplodocidae and *Dicraeosaurus* (Figs. 7, 8). As in extant Crocodylia (Frey 1988), the dorsal margin

of the supraoccipital of Diplodocidae and *Dicraeosaurus* is rugose and bears a median nuchal crest (Holland 1924; Janensch 1936; Berman and McIntosh 1978; Harris and Dodson 2004; Harris 2006a), most likely representing the occipital insertion area for the supraspinal ligament.

As in extant crocodylians (Frey 1988; Salisbury 2001), the heights of the neural spines in the neck of Diplodocidae gradually increase from cranial to caudal (Appendix 2, Fig. 7). In contrast, the cervical neural spines of extant birds are high in the cranial and caudal neck region, but very low in the middle cervical region (Appendix 2). For the neck of Diplodocidae, we therefore infer a configuration of the supraspinal ligament similar to that of extant crocodylians, connecting the apices of each neural spine with each other (Fig. 7, 8). In contrast, the shorter 9th and 10th cervical neural spine of *Dicraeosaurus* (Appendix 2, Fig. 8) make it possible that single fibres of the supraspinal ligament ex-

tended over more than one vertebral segment in the middle cervical region.

According to the size of the insertion areas along the tips of the neural spines, the diameter of the supraspinal ligament of Diplodocidae and *Dicraeosaurus* did not exceed one tenth of the height of a neural spine, and was smaller when the ligament was stretched (McGowan 1999). In bifurcate neural spines, the supraspinal ligament was split into two strings, each of them connecting the tips of one metapophysis (Figs. 7A, 8A). A rugosity continues from the dorsal margin to the medial surface of the metapophyses in bifurcate neural spines (Fig. 6C, E), indicating that the ligament was also inserted medioventrally.

The height and shape of the neural spines of the presacral vertebrae of *Amargasaurus* is unique among eusauro-pods (Appendix 2, Fig. 9A, B, E). Because in *Amargasaurus* there is no structure that allows a reliable reconstruction of a distinct supraspinal ligament, this ligament was either completely reduced or it was integrated in the interspinal elastic ligament system.

Elastic ligament system.—In Diplodocidae, cranial and caudal rugosities of single neural spines (Appendix 2, Fig. 6) are indicative for the presence of an elastic ligament system as in extant crocodylians and birds (Boas 1929; Frey 1988). Because the medial tuberosity of bifurcate neural spines (Appendix 2, Fig. 5) is positioned medially between the metapophyses, and thus is equivalent to the cranial and caudal rugosities of the single neural spines, this medial tuberosity at the base of bifurcate neural spines (Appendix 2, Fig. 6C, E) probably represents the mineralised attachment area for the elastic ligament in bifurcate neural spines.

Extant crocodylians and most extant birds possess an interlaminar elastic ligament (Boas 1929; Landolt and Zweers 1985; Frey 1988; Tsuihiji 2004), which connects the bases of the neural spines of adjacent vertebrae. In *Rhea*, a second, interspinal elastic ligament is present, branching out from a dorsal string to insert at the caudal aspect of each neural spine (Fig. 5C; Boas 1929; Tsuihiji 2004). The rugosities for the interspinal elastic ligament of *Rhea* and those for the interlaminar elastic ligament of other birds, such as *Sarcophamphus* or *Casuaris*, are similar (Appendix 2, Fig. 5B, D). In extant crocodylians, the rugosity for the elastic ligament can be distinctly divided, although the ligament itself is simple and not partitioned (Appendix 2, Fig. 5A). Applying the situation of the elastic ligament system and its osteological correlates in extant birds and crocodylians, we conclude that it is not possible to specify the kind of elastic ligament as a specific interspinal or interlaminar elastic ligament in Diplodocidae and Dicraeosauridae.

The differences between the height increase of the neural spines in extant birds and Diplodocidae and Dicraeosauridae (Appendix 2) make a similar configuration of the elastic ligament in those sauro-pods and extant birds unlikely. In contrast, the similarities in neural spine presence and height increase between extant Crocodylia (Frey 1988;

Salisbury 2001) and diplodocid and dicraeosaurid sauro-pods suggest that the elastic ligament of Diplodocidae and Dicraeosauridae ran, as in extant crocodylians, craniocaudally connecting the bases of successive neural spines. The height of the insertion scars for the elastic ligament in single neural spines (see above) makes it probable that the elastic ligament extended here at least along the ventral two-thirds of the neural spines (Figs. 7–9). The tuberosities between the metapophyses of bifurcate neural spines are restricted in height to the ventral fourth of the neural spines. Most likely these tuberosities coincide with the diameter of the elastic ligament.

Interspinal septum.—In *Alligator* and most likely all other extant crocodylians, the paired crests in the ventral two thirds of the cranial and caudal neural spine margins are the insertion areas for a pair of interspinal septa, which enclose the interlaminar elastic ligament (Appendix 2; Frey 1988). Dorsally, the interspinal septa merge with the supraspinal ligament. Applying the configuration of these ligaments to the topographically identical structures in Diplodocidae and Dicraeosauridae (Appendix 2, Fig. 6) a paired interspinal septum is inferable as present, which attached cranially and caudally to the lateral crests of the spine margins. Between single neural spines, the left and right sheet of the interspinal septum embedded the elastic ligament as well as supra-vertebral pneumatic diverticula within the postspinal fossa (Fig. 7). In bifurcate neural spines, the interspinal septum adjoined the supra-vertebral pneumatic diverticula around the elastic ligaments and dorsally contacted the supraspinal ligament (Fig. 7A, B).

Zygapophyseal articulation, interarticular ligament.—The articular surfaces of the pre- and postzygapophyses of the cervical vertebrae of Diplodocidae and Dicraeosauridae are surrounded by an annular rugosity (Fig. 3A), which indicates similar to extant birds and crocodylians the presence of a zygapophyseal articular capsule of fibrous connective tissue enclosing a synovial joint between the zygapophyses.

In the cervical vertebrae of Diplodocidae and Dicraeosauridae, a rugosity lies on the ventral part of the lateral surface of the prezygapophyseal peduncle adjacent to its articular surface. From its position, this rugosity represents most likely the insertion area of a lateral interarticular ligament, as in Aves and Crocodylia (Frey 1988; Baumel and Raikow 1993), which ran from the prezygapophysis cranioventrally to the caudoventral margin of the cranially following postzygapophysis and inserted on the slightly rugose lateral margin of the vertebral foramen. The fibres of the lateral interarticular ligament were probably connected with the articular capsule of the zygapophyses (Fig. 7).

Intercostal ligaments.—In Diplodocidae and Dicraeosauridae, only the caudalmost part of the costal corpus ventrolaterally overlaps the cranial process or cranial portion of the caudally following rib (Appendix 2). The morphology of the cervical ribs, the ventrolateral overlap of craniocaudally fol-

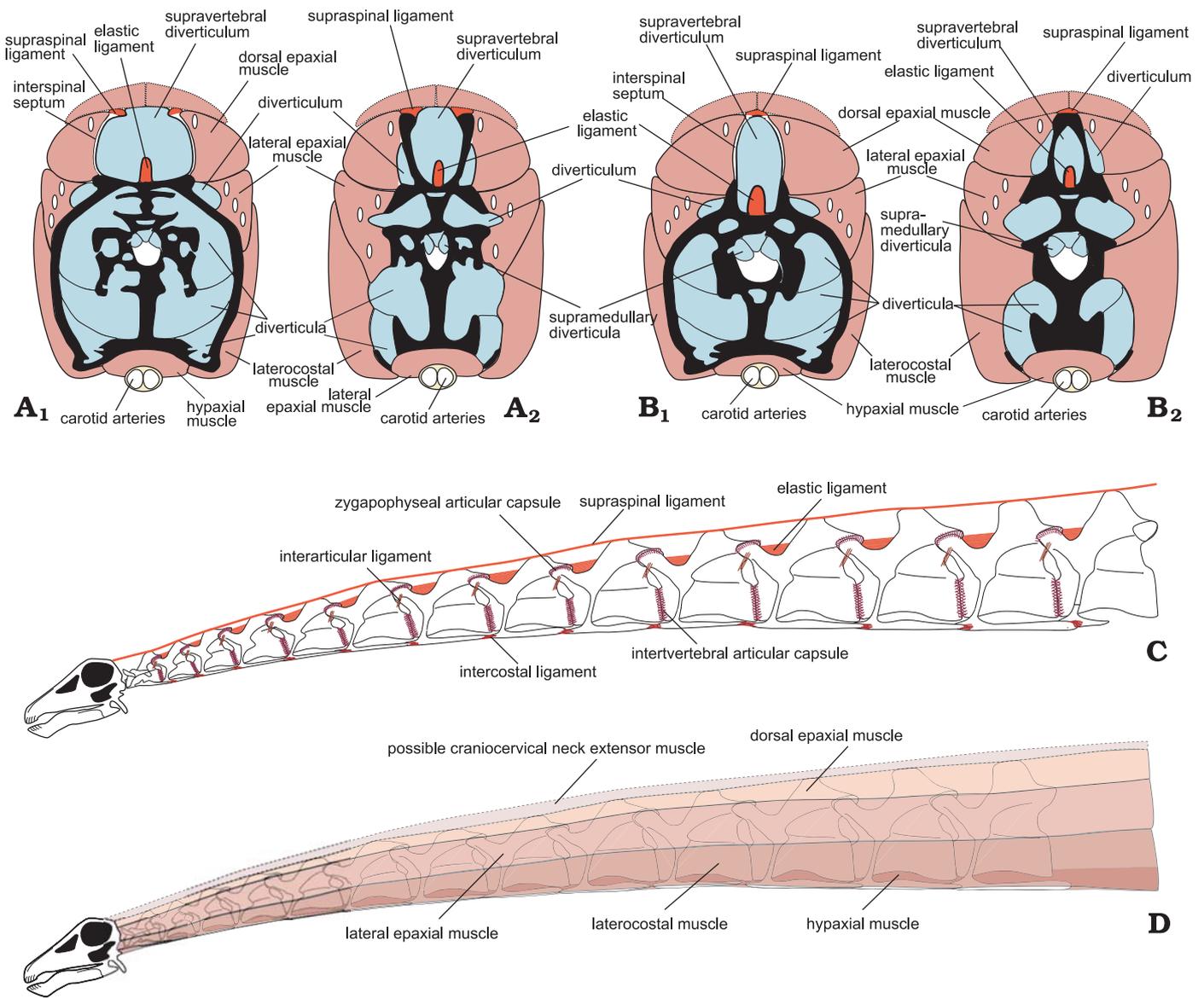


Fig. 7. Reconstruction of soft-tissues in the neck of *Diplodocus*. **A.** Transverse cross-sections through cervical vertebra with bifurcate neural spine in the diapophysis region (A₁) and in caudal third of vertebra (A₂). **B.** Transverse cross-sections through cervical vertebra with single neural spine in diapophysis region (B₁) and in caudal third of vertebra (B₂), dashed outlines representing possible craniocervical extensor muscle analogous to *m. biventer cervicis* of extant birds or *m. transversospinalis capitis* of extant crocodylians. **C.** Reconstruction of cervical ligaments in left lateral aspect. **D.** Reconstruction of cervical axial musculature in left lateral aspect. Vertebrae and skull for C and D from *Diplodocus carnegii* (Hatcher, 1901). Not to scale.

lowing cervical ribs, and the presence of a striation pattern at the cranial and caudal tips of the costal corpora in *Diplodocidae* and *Dicraeosauridae* (Fig. 9D) is more similar to the cervical ribs of extant crocodylians (Appendix 2; Frey 1988) than to those of extant birds. This indicates the presence of an intercostal ligament connecting two adjacent ribs with each other, similar to extant Crocodylia. If so, the intercostal ligament of *Diplodocidae* and *Dicraeosauridae* extended from the ventral and lateral surface of the costal corpora caudo-dorsally to the cranioventral and cranio-lateral surface of the cranial process of the caudally following cervical rib (Fig. 7). In the non-overlapping cervical ribs (i.e., in *Apatosaurus*),

the ligament fibres must have bridged the intercostal gap as a longitudinally oriented string, which ran in line with the costal corpora.

Intervertebral articulation.—The cervical vertebrae of *Diplodocidae* and *Dicraeosauridae* are opisthocoelous, with a cranial hemispherical vertebral condyle and a caudal bowl-shaped cotyla (Upchurch 1995, 1998; Wilson and Sereno 1998; Wilson 2002; Upchurch et al. 2004a). The cranial condyle and the caudal cotyla are both surrounded by a thin rugose rim (Fig. 6B, E). At its cranial and caudal margins adjacent to the articular surfaces of the vertebral corpora, the

lateral surface is covered with strong, longitudinally oriented striae. The vertebral condyle bears a central high-oval fovea. The overall morphology of these intervertebral articular surfaces is different to the heterocoelous articular condyles of extant avians (Landolt and Zweers 1985; Baumel and Witmer 1993), but strikingly similar to the intervertebral articulations of the procoelous vertebrae of recent crocodylians. Additionally, the intervertebral articulation is not perfectly matching as seen for example in the procoelous vertebrae of monitor lizards (*Varanus*; Goette 1897; Salisbury and Frey 2001), but shows an intervertebral gap as in extant Crocodylia (Goette 1897; Higgins 2005; Wettstein 1937; Frey 1988; Salisbury 2001; Salisbury and Frey 2001). Therefore, it appears most likely that the intervertebral articulation of Diplodocidae and Dicraeosauridae must have been similar to that of extant Crocodylia.

The striae on the lateral surface cranially and caudally of the articular rims of the vertebral corpora represent parts of the annular rugosity, where the articular capsule inserted. The flat, sub-horizontal circumference around the articular surfaces would then be the medial part of the annular rugosity and most likely housed the annulus fibrosus, from which a cranial and caudal sheet of a fibrous intercorporal septum emerged that lined the articular cavity. The cranial sheet of the intercorporal septum was probably medially attached to the vertebral condylus with a binding ligament. As in extant crocodylians (Salisbury 2001; Salisbury and Frey 2001), this ligament inserted in the central fovea on the condylus of Diplodocidae and Dicraeosauridae. The gap between the intercorporal septae was most likely filled with a synovial liquid, which was pumped around with the movement of the joints and kept the intercorporal septae under tension. Therefore we assume that the intervertebral joint of Diplodocidae and Dicraeosauridae was a synovial joint.

Dorsal epaxial muscle group.—In extant crocodylians, the cervical neural spines are plate-like in lateral view and bear a few vertical striae (Fig. 5A, Appendix 2). The main dorsal epaxial muscle of Crocodylia (*m. transversospinalis cervicis I–III*) is poorly segmented and inserts by fleshy fibres on the lateral face of the cervical neural spines (Appendix 2; Frey 1988; Salisbury 2001). In extant avians, the neural spines can be reduced to a slender median crest in the middle of the neck, whereas they increase in height cranially and caudally and bear in their dorsal half a lateral rugosity (Appendix 2). The main dorsal epaxial muscle of birds (*m. longus colli dorsalis*) inserts with a tripartite system of muscle slips laterally and laterodorsally at the cervical neural spines (Zusi and Storer 1969; Landolt and Zweers 1985; Tsuihiji 2005). The neural spines in the neck of Diplodocidae and Dicraeosauridae are, concerning their morphology, neither similar to extant birds nor to extant crocodylians (Appendix 2). It is therefore difficult to reconstruct the detailed configuration of the dorsal epaxial muscle group. However, for Diplodocidae and *Dicraeosaurus*, the rugosity at the lateral face of the cervical neural spines (Appendix 2, Fig. 6) suggests the presence of Sharpey's

fibres, indicating that a dorsal part of the epaxial muscle mass was present, inserting tendinous on the rugose lateral surface of the neural spines and fleshy on the interspinal septum between the neural spines (Fig. 7). If so, a strongly segmented dorsal epaxial muscle mass, such as suggested by Wedel and Sanders (2002), would have inserted along the dorsal half of the lateral surface of the neural spines in Diplodocidae, and at least along their dorsal fifth in *Dicraeosaurus*. The striation pattern at the lateral face of the cervical neural spines of *Dicraeosaurus* makes it possible, that the dorsal epaxial muscle contained a poorly segmented ventral portion, similar to *m. transversospinalis cervicis II* and *III* of extant crocodylians. The diameter of the dorsal epaxial muscle mass must have gradually increased caudally together with the height of the neural arches (Figs. 7, 8). Due to the higher cervical neural spines, the dorsal epaxial muscle mass in *Dicraeosaurus* was most probably about three times as large as in Diplodocidae. In both Diplodocidae and Dicraeosauridae, the supraoccipital at the skull shows a pair of bowl-shaped depressions lateral to its median vertical crest (Holland 1924; Janensch 1936; Berman and McIntosh 1978; Harris and Dodson 2004; Harris 2006a). Probably these depressions served as an attachment area of the dorsal epaxial muscle group.

The lack of any rugosities at the lateral face of the cervical metapophyses in *Amargasaurus* (Appendix 2) argues against the presence of a strongly segmented dorsal epaxial muscle group. According to the reconstruction of a keratinized horn sheath covering the dorsal two thirds of the cervical neural spines and the presence of only a fine vertical striation ventrally to the sheath, the dorsal epaxial muscle group in *Amargasaurus* was most probably poorly segmented and did not exceed the ventral third of the height of the neural spine (Fig. 9).

Lateral epaxial muscle group.—The morphological change at the bases of the lateral face of the neural spine from striations towards pneumatic fossae, which occurs level with the epipophyses, might indicate a separation of the dorsal and lateral epaxial muscle mass by a border fascia in Diplodocidae and Dicraeosauridae. The lateral epaxial muscle mass would have extended ventrally adjacent to the latter (Fig. 8). If there were pneumatic diverticula laterally at the base of the neural arch, the lateral epaxial muscle portion must have been dorsally interweaved by the latter (Fig. 7). The lateral epaxial muscle mass would have inserted in the shallowly concave, rugose surface of the exoccipital dorsally and laterally to the foramen magnum. The muscle extended from the exoccipital caudally and inserted along the lateral faces of the neural arches and the diapophyses. Its diameter must have gradually increased caudally together with the expansion of the cervical diapophyses (Figs. 7, 8).

The presence of structures as epipophyses, rugosities and crests at the lateral face of the neural arches, diapophyses and zygapophyses at the cervical vertebrae of Diplodocidae and Dicraeosauridae corresponds to extant birds (Appendix 2; Landolt and Zweers 1985, Tsuihiji 2005), but differs from the cervical neural arches of extant Crocodylia (Appendix 2).

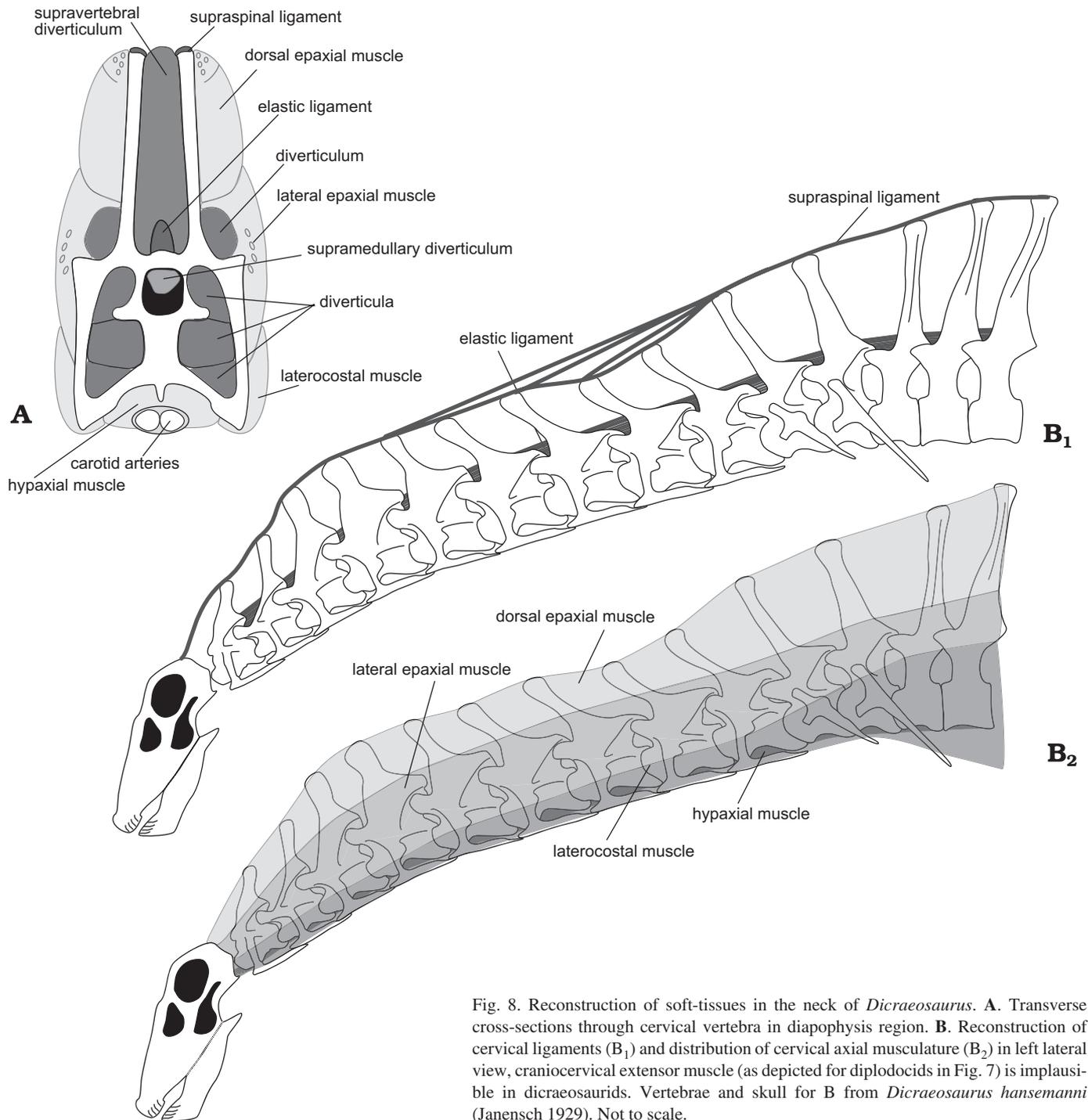


Fig. 8. Reconstruction of soft-tissues in the neck of *Dicraeosaurus*. **A**. Transverse cross-sections through cervical vertebra in diapophysis region. **B**. Reconstruction of cervical ligaments (**B₁**) and distribution of cervical axial musculature (**B₂**) in left lateral view, craniocervical extensor muscle (as depicted for diplodocids in Fig. 7) is implausible in dicraeosaurids. Vertebrae and skull for **B** from *Dicraeosaurus hansemanni* (Janensch 1929). Not to scale.

Apparently, the lateral epaxial muscle group of Diplodocidae and Dicraeosauridae was, as in extant birds, a complex tendinomuscular system with segmental arranged insertion tendons and aponeuroses, as suggested for sauropods by Wedel and Sanders (2002). However, the lack of a complex system of crests laterally at the lateral face of the diapophyses (the area is mainly rugose here) and a less complex pattern of crests in Diplodocidae and Dicraeosauridae indicates that the arrangement of the tendinomuscular system was not identical to that of birds, but could have been arranged as follows: The

postzygapophyseal epiphyses and ventral tuberosities at the prezygapophyses were probably the insertion areas for craniolaterally directed subcircular tendons. The longitudinally oriented crests at the lateral surface of the neural arches (Fig. 3A) could be explained by mineralised insertions of a system of interstitial aponeuroses from which muscle fibres emerge. The caudal, roughened flanges or knobs at the diapophyses appear to represent an insertion area of a caudally directed aponeurosis and with the distal margin of the flanges into the postzygodiapophyseal lamina probably formed a

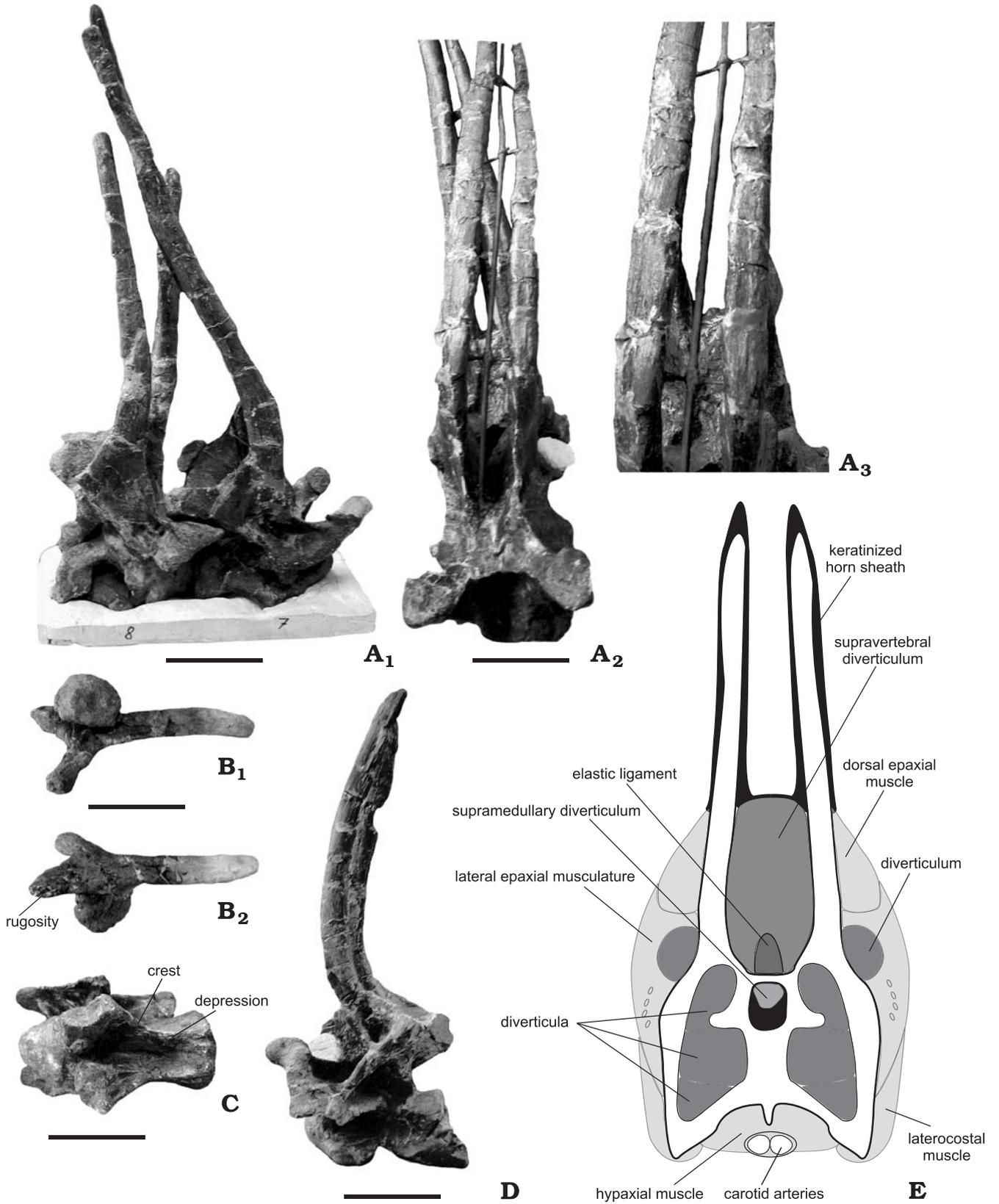


Fig. 9. Photographs and reconstructions of soft-tissues in the neck of *Amargasaurus cazau* (MACN-N-15), La Amarga, Neuquén, Argentina, La Amarga Formation, Hauterivian, Early Cretaceous. **A.** 7th and 8th cervical vertebra in left lateral (**A₁**) and in cranial aspects (**A₂**) and with close-up cranial view showing crests at the cranial face of neural spines (**A₃**). **B.** Isolated cervical rib in dorsal (**B₁**) and ventral (**B₂**) aspects. **C.** Vertebral corpus of 5th cervical vertebra in ventral aspect. **D.** 10th cervical vertebral in left lateral aspect. **E.** Transverse cross-sections through cervical vertebra in the diapophysis region, with internal extension of pneumatic cavities basing on *Dicraeosaurus hansemanni* (see also Fig. 8). Scale bars 60 mm, E is not to scale.

horizontally extended system of caudolaterally directed aponeuroses. As the rugose dorsal surface of the diapophyses indicates, deep parts of the lateral epaxial muscle mass inserted fleshy on the diapophyses. The interdigitating tendinoaponeurotical meshwork of the lateral epaxial muscle group in Diplodocidae and Dicraeosauridae was probably interwoven by a system of fascicular muscle fibres.

Laterocostal cervical muscle.—The morphological change between the diapophysis and the rib tuberculum of Diplodocidae and Dicraeosauridae indicates a separation of the tendinomuscular lateral epaxial muscle group from a laterocostal muscle by a border fascia. The topographical similarities between the cervical ribs of extant crocodylians and these of Diplodocidae and Dicraeosauridae (Appendix 2), especially the slender and pillar-like costal tuberculum, make it likely that the laterocostal cervical muscle was segmented as in Crocodylia (Frey 1988) with a myoseptum per vertebral segment, the myoseptum inserting at the laterocaudal surface of the costal tuberculum. In contrast, there is no morphological change between the diapophysis and the costal process of modern birds, both being fused with each other, longitudinally expanded and bearing longitudinal crests serving as insertion points for muscle slips of *m. intertransversarius* (Appendix 2; Boas 1929; Zusi and Storer 1969; Landolt and Zweers 1985).

The occiput of Diplodocidae and Dicraeosauridae bears a sharp crest separating the dorsal and ventral half of the paroccipital process (Holland 1924; Janensch 1936; Berman and McIntosh 1978; Harris and Dodson 2004; Harris 2006a). It is likely that the laterocostal cervical muscle of these sauropods originated as in extant crocodylians (Frey 1988), from the ventral half of the paroccipital process, lateral to the occipital condyle. From there, the muscle ran caudally, inserting on the cervical ribs and on the lateral face of the vertebral corpora of the cervical vertebrae (Figs. 7, 8).

Hypaxial cervical muscle portion.—In extant crocodylians, *m. longus colli* is unsegmented and inserts by fleshy fibres at the lateral faces of the hypapophyses, the ventral face of the cervical vertebral corpora and the medial face of the cervical ribs (Appendix 2; Frey 1988). In extant birds, the hypapophyses and carotid processes serve as attachment points for the complex tendon system of *m. longus colli ventralis* (e.g., Boas 1929; Landolt and Zweers 1985), which inserts also tendinous at the roughened spina processus costalis (Appendix 2). In contrast to the situation in extant crocodylians and birds, there are neither distinct hypapophyses nor carotid processes at the ventral surface of the vertebral corpora of Diplodocidae and Dicraeosauridae (Appendix 2; Wedel et al. 2000b), and the cervical ribs do not possess a spina processus costalis. It is therefore unlikely, that the hypaxial muscle of Diplodocidae and Dicraeosauridae was as strongly segmented as in extant birds. Similarly, the osteological correlates for a crocodylian-like hypaxial muscle (i.e., distinct hypapophyses) are not developed in Diplodocidae and Dicraeosauridae, making a cro-

codylian-like hypaxial muscle in these sauropods implausible. Instead, the hypaxial muscle mass of Diplodocidae and Dicraeosauridae could have been an impair medial muscle mass with long external fibres and a poor segmentation, the segments of which inserted at the ridges and crests of the ventral face of the vertebral bodies (Figs. 7–9). If so, then the basioccipital tubera of Diplodocidae and Dicraeosauridae formed the area of origin for the hypaxial cervical muscle mass, from which it ran caudally along the ventral surface of the cervical vertebral corpora (Fig. 9B).

Position of the carotid arteries.—The strongly concave ventral face of the cervical vertebral corpora of Diplodocidae and Dicraeosauridae (Fig. 9D) resembles the sulcus or canalis caroticus of extant birds (Boas 1929; Baumel and Witmer 1993). In birds, the paired carotid artery lies within this depression between the hypaxial cervical muscles *m. inclusus* and *m. longus colli ventralis* (Crowe and Crowe 1979; Landolt and Zweers 1985; Baumel 1993). However, in extant crocodylians, the vertebral corpus is ventrally not concave and the carotid arteries lie ventrally to the hypaxial muscle *m. longus colli* and the neck muscle *m. capitisternalis* (Wettstein 1937). Due to the similarities in vertebral morphology, it is probable that the position of the carotid arteries in Diplodocidae and Dicraeosauridae was similar to extant birds within the ventral concavity formed by the vertebral corpus and cervical ribs (Figs. 7–9).

Discussion

Comparison with other soft-tissue reconstructions for sauropods

Dorsal ligament system.—A strong dorsal ligament system, either developed as a ligamentum nuchae like in artiodactyl mammals, or as a large, multisegmental interspinal elastic ligament has been reconstructed for sauropods (Janensch 1929; Alexander 1985, 1989; Frey and Martin 1997; Martin et al. 1998; Wilson and Sereno 1998; Stevens and Parrish 1999; Tsuihiji 2004). In artiodactyls, the cervical neural spines are low, but increase rapidly in height in the cranial thoracic region, and a strong nuchal ligament arises from the high neural spines of the cranialmost dorsal vertebrae to attach with several branches to the low neural spines of the cervical vertebrae (Dimery et al. 1985; Gellman et al. 2002). In contrast to artiodactyls, the gradual height increase of the cervical neural spines of Diplodocidae and Dicraeosauridae (Appendix 2) makes a nuchal ligament unlikely.

The ligament topography in the sauropod neck with bifurcate neural spines was previously reconstructed based on that of *Rhea*, where the interspinal elastic ligament inserts in branches dorsal to the interlaminar elastic ligament along the caudal margins of the neural spines (Tsuihiji 2004). We found similar osteological correlates for an elastic ligament system as described by Tsuihiji (2004) in diplodocids and dicraeo-

saurids (Appendix 2), but we disagree in the reconstruction of the configuration of this ligament. First, we found it difficult to distinguish between an interlaminar and an interspinal elastic ligament on the basis of ligament insertion scars in extant crocodylians and birds (see Appendix 2 and above). Second, in all birds, neural spines are only present in the cranialmost and caudalmost cervical vertebrae (Boas 1929), whereas Diplodocidae and Dicraeosauridae possess distinct neural spines in all cervical vertebrae (Appendix 2). Third, Dodson and Harris (2001) did a biomechanical analysis of such an arrangement and pointed out that a multibranching ligament inserting medially between the metapophyses and/or at the summits of the neural spines would have a very low mechanical advantage. These differences make a dorsally expanded interspinal elastic ligament, as in *Rhea*, unlikely for Diplodocidae and Dicraeosauridae. In contrast to *Rhea*, modern crocodylians can, due to the similarities in heights of the cervical neural spines, give valuable hints for reconstructing the configuration of supraspinal and elastic ligaments in diplodocids and dicraeosaurid sauropods.

Tsuihiji (2004) discussed an interesting aspect for soft-tissue reconstructions. He described that in *Rhea*, the interspinal elastic ligament is enclosed by a "... ligamentous or fascial sheath, which attaches to the tip of the bifurcated neural spine as well as to the lamina connecting the neural spine and the postzygapophysis..." (Tsuihiji 2004: 166), and which is interpreted as a derivate of the supraspinal ligament. The described topography of the "ligamentous sheath", in particular its insertion at the cranial and caudal laminae of the neural spines makes it likely, that it represents the equivalent to the interspinal septum in extant crocodylians (Frey 1988). Therefore, the reconstruction of such an interspinal septum in the neck of Diplodocidae and Dicraeosauridae would be justified by equivalent structures in both modern crocodylians and birds.

Axial neck musculature.—A profound system of intersegmental muscle slips identical to that of extant birds has been reconstructed for sauropods on the base of partially similar insertion scars (Appendix 2; Wedel et al. 2000a; Wedel and Sanders 2002). In extant birds, who hold their neck in an S-shaped loop, the cervical muscles form three segment systems (from cranial to caudal), interconnecting multiple vertebrae by muscular slips (Zweers et al. 1987; Bout 1997). The overall construction of the neck of a bird functions for intra- and intersegmental mobility of a strongly S-curved structure, which is evidenced by this multisegmental muscle and ligament system, allowing the movement of neck segments against each other (Elshoud and Zweers 1987). This is effective in birds because acute curvatures, dorsally concave caudally and convex cranially, allow individual slips to span several vertebrae and flex the curvature between them (mm. splenii colli and mm. cervicales ascendentes: Vanden Berge and Zweers 1993), or even coalesce into larger muscle bellies, as with slips from caudal cervical vertebrae running craniodorsally to join the belly of m. longus colli dorsalis

cranialis (Vanden Berge and Zweers 1993). Only some of the osteological correlates of a bird-like cervical musculature can be found in diplodocids and dicraeosaurids, whereas other structures are more similar to extant crocodylians (see Appendix 2 and above). Without a strong caudal neck curvature, multiple long slips coursing to join with an m. longus colli dorsalis analogue could not extend the caudal part of the sauropod neck to the same degree as in birds, although the neck extensor muscles may have been of similar complexity to those of birds. Furthermore, a strictly bird-like neck mobility is contraindicated for sauropods (Stevens and Parrish 1999; Christian 2002; Stevens and Parrish 2005a, b). We therefore conclude that for sauropods like Diplodocidae and Dicraeosauridae, the reconstruction of a longitudinally tripartite cervical muscular system identical to that of birds is not justified. Proportional and topological comparisons with modern birds and crocodylians reveal that, although a strong segmentation of the dorsal and lateral epaxial muscle mass is likely for Diplodocidae and Dicraeosauridae, a bird-like topology of the laterocostal and hypaxial cervical muscle mass in these sauropods seems unlikely.

Soft-tissues between bifurcate neural spines in the neck.—

Most hypotheses about the soft-part anatomy between the bifurcate neural spines favour nuchal or interspinal ligaments (Janensch 1929; Alexander 1985, 1989; Wilson and Sereno 1998), a medial axial muscle string (Osborn and Mook 1921; McIntosh 1990; Wedel et al. 2000a), or a combination of both (Tsuihiji 2004: fig. 5A). There is no osteological correlate for a cervical muscle portion dorsal or dorsomedially to the dorsal epaxial muscle group in Diplodocidae and Dicraeosauridae as suggested by Tsuihiji (2004) and Wedel and Sanders (2002), although such a muscle is present in both modern crocodylians (m. transversospinalis capitis, Frey 1988) and birds (Landolt and Zweers 1985; Vanden Berge and Zweers 1993). From an anatomical point of view (i.e., applying Extant Phylogenetic Bracketing), the presence of a craniocervical muscle, running dorsally above the neural spines can therefore not be excluded for Diplodocidae (Fig. 7) and Dicraeosauridae. However, it is unlikely that the evolution of neural spines probably protruding through the dermis like reconstructed for *Amargasaurus* (see above) could have evolved out of a preconstruction, in which a supraspinal tendinomuscular system used the neural spines as a lever or was included into the bracing system.

The diameter of the notch between bifurcate neural spines in Diplodocidae and Dicraeosauridae allows together with the reconstructed cervical muscles (Figs. 7–9) a rough estimation of the cross-sectional area that would have been occupied by a muscle filling the notch between bifurcate neural spines completely. According to these reconstructions, such a muscle would take at least 15% of the total cross-section of the neck vertebrae, thereby increasing the weight of the neck by approximately 15%. Although this assumed increase in neck weight makes it implausible that a muscle filled the space between the bifurcate neural spines, it might have been compensated by the weight-saving effect of vertebral pneu-

maticity: The magnitude of bone reduction by pneumatic structures can be quantified by calculations from the CT sections of the bones (Airspace Proportion, or ASP, of Wedel 2004, 2005) to have reached a maximum of 69% in some regions of the vertebral corpus of *Apatosaurus* (Wedel 2005). According to the CT sections presented in this work, and if muscles and ligaments throughout the whole neck are taken into account, the neck of *Dicraeosaurus* (ca. 2.4 m in length) would have been lightened for at least 6% (Schwarz and Fritsch 2006), that of a sub-adult diplodocid (ca. 4 m in length) for at least 14% and that of an adult *Diplodocus* (ca. 7 m in length) for at least 25% by their total of pneumatic structures. A compensation of the additional neck weight by such a dorsal epaxial muscle filling the gap between bifurcate neural spines therefore would only be likely in diplodocids, but not in dicraeosaurids.

The presence of ligaments in the area between bifurcate neural spines is supported by osteological correlates in Diplodocidae and Dicraeosauridae (Tsuihiji 2004), as is, at least for Diplodocidae, the presence of supravertebral pneumatic diverticula between bifurcate neural spines and in the postspinal cavity (see “Supravertebral pneumatic diverticula”). The hypothesis of pneumatic diverticula surrounding these ligaments provides a reasonable model for the filling of this gap, as it is based on osteological correlates and does not lead to weight increase of the neck. Since supravertebral diverticula in extant birds fill the interarticular foramen between following cervical vertebrae (Müller 1908; O’Connor 2003; Wedel 2003a; O’Connor 2006), such supravertebral pneumatic diverticula in Diplodocidae and Dicraeosauridae could have risen from the supramedullary diverticula, and extended between the sheets of the interspinal septum.

Development, distribution and biomechanical implications of pneumatic structures

The extent of vertebral pneumatic structures in the neck of Diplodocidae and Dicraeosauridae reaches a maximum in the caudalmost cervical vertebrae. This corresponds to extant birds (Hogg 1984a, b; O’Connor 2003, 2004) and supports the suggestion of Wedel (2003b) for a possible position of a cervical air sac at the base of the neck. From there, pneumatic diverticula invaded the cervical vertebrae progressively from caudally to cranially during ontogeny (Müller 1908; King 1966; Hogg 1984a; O’Connor 2003; Wedel 2003a; O’Connor 2006).

The distribution of structures associated with vertebral pneumaticity around the cervical vertebrae of Diplodocidae and Dicraeosauridae is similar to that generally found in other sauropods, differing in the amount of subdivisions (Appendix 1, Fig. 3; Britt 1993; Carpenter and McIntosh 1994; Wedel et al. 2000a, b; Wedel 2003a, b; Schwarz and Fritsch 2006). This indicates a common pattern of pneumatic structures in sauropod cervical vertebrae. Judging by the osteology of the cervical column in juveniles and adult diplodocids (Fig. 3; Carpenter and McIntosh 1994; Wedel 2003a), these systems

must have developed at early ontogenetic stages. During ontogeny, pneumatic diverticula progressively expanded to produce the camerate and polycamerate pneumaticity pattern characteristic for adult diplodocids (Figs. 1, 2; Britt 1993; Wedel et al. 2000a; Wedel 2003a).

Dicraeosauridae have no intraosseous pneumatisation, and external structures indicating vertebral pneumaticity are restricted mostly to fossae, which can extend deeply into the vertebrae. From a strict, comparative anatomical viewpoint, the presence of vertebral pneumaticity in the neck of Dicraeosauridae remains uncertain. The position of pneumatic fossae in similar places as in Diplodocidae, their depth and obviously invasive nature, the presence of at least a parapophyseal pneumatic foramen, and the bracketing of Dicraeosauridae with sauropod taxa that possess pneumatic diverticula make the presence of pneumatic diverticula in the neck of Dicraeosauridae highly probable. Dicraeosauridae possess short necks with not more than 12 cervical vertebrae (Bonaparte 1999; Rauhut et al. 2005) and a relatively small overall size. Histological studies (Sander 1999, 2000) show that *Dicraeosaurus* grew fast and continuously, but reached sexual maturity with 80% of its maximum size at a relatively larger size than other sauropods. Taken this together, there seems to be an earlier growth arrest in Dicraeosauridae, which may have been accompanied with a shortened pneumatisation of the postcranial skeleton (Schwarz and Fritsch 2006).

If the reconstruction of supramedullary pneumatic diverticula in Diplodocidae and Dicraeosauridae holds, a pneumatisation centre inside the neural arch can be postulated to have extended from the cervical air sacs as in modern birds (Müller 1908; O’Connor 2006). In the cervical vertebrae of the juvenile diplodocids, the early presence of pneumatic structures connected with the neural canal makes it plausible that the supramedullary diverticula formed prior to or parallel with the beginning of internal pneumatisation of the neural arch. A connection between the neural canal and the surrounding pneumatic structures by pneumatic ducts was found in the cervical vertebrae of juvenile diplodocids and other sauropods (Britt 1993; Wedel 2003a; Schwarz and Fritsch 2006). Without the inclusion of the neural canal, no internal pneumatisation of the neural arch has been documented in sauropods. Internal pneumatisation of the neural arch was therefore most likely triggered by supramedullary diverticula, the latter being a major factor for pneumatising the neural arch. On the other hand, the case of Dicraeosauridae shows that supramedullary diverticula might have persisted without further internal pneumatisation of the neural arch. The function of the supramedullary pneumatic diverticula within the neural canal of recent birds is not known yet, and the same holds true for sauropods.

Although it has not been tested yet by mechanical approaches, the distribution of intraosseous pneumatic structures in juvenile and adult diplodocids might suggest the following biomechanical explanations: Reducing the cervical vertebral corpora and the ventral half of the neural arches to a vertical I-beam construction could indicate a

main stabilisation of the cervical vertebral column against load in the vertical plane. As visible from the comparison between the CT sections of juvenile and adult diplodocids, additional bony struts appeared on the lateral surface of the I-beam together with the increase of the absolute size of the vertebrae. The bone struts might have prevented local buckling of the median vertical lamella. If so, then the progressive structural complexity of the cervical vertebrae in Diplodocidae might be explained as a consequence of increased mechanical demands in the context of a mass increase. Pneumatic cavities in the neural arch in Diplodocidae are distributed irregularly, with secondary pneumatic cavities randomly arranged around existing cavities, which indicates load differences between the neural arch and the vertebral corpus.

The maximum size of the camerae could also be subject to physiological constraints, probably in context with the respiratory apparatus. A paired cervical air sac, which can be reconstructed by the presence of vertebral pneumaticity in diplodocids and dicraeosaurids, would have been part of the respiratory systems as in birds (Duncker 1971; Schmidt-Nielsen 1971). In sauropods, cervical air sacs could have acted as air reservoirs and could have contributed to ventilating the gas exchanged tissue in the lungs (Perry and Reuter 1999; Perry and Sander 2004). Surely, the ongoing research (Codd and Perry 2005; Perry 2006) on the functional morphology of the respiratory apparatus in sauropods will give much more valuable information on this issue. It cannot be excluded that pneumatic diverticula in the neck of diplodocids and dicraeosaurids did also contribute to respiration by acting as additional air reservoirs. However, the uncertainties in reconstructing the extension of the cervical pneumatic diverticula, and the multiple and small connections between individual pneumatic diverticula probably hindering rapid exchange of air, make this assumption highly speculative. Possible biological roles of vertebral pneumaticity in the neck of sauropods that can be better evaluated at the moment are a weight reduction and possibly a contribution to neck support (see below).

Biomechanical implications for neck support by the reconstructed soft-tissue apparatus

The sauropod neck can be modelled as a segmented beam anchored at the trunk and loaded by the weight of the skull (Martin et al. 1998). The neutral position of the necks of Diplodocidae and Dicraeosauridae is reconstructed to have formed a slightly ventrally sloping curve, with the short cervical ribs overlapping only in a short area or not at all (Salgado 1999; Stevens and Parrish 1999; Christian 2002).

In Diplodocidae and Dicraeosauridae, the double supraspinal and the large elastic ligaments were well developed, yet they were not extraordinarily large. Bifurcation of the neural spines improved the dorsal ligament support system of the neck, since it forced the supraspinal ligament to divide into two parts, therefore to form a dorsal double-string. Dor-

sal ligaments surely were one important support mechanism in the neck of Diplodocidae and Dicraeosauridae: During flexion and extension, elastic energy was stored in the dorsal ligament apparatus and launched an elastic recoil, as it has been described for extant vertebrates (Alexander and Bennet-Clark 1977; Dimery et al. 1985; Bennett and Alexander 1987). The intercostal ligament apparatus around the cervical ribs probably provided elastic recoil when the neck was extended. Another factor in bracing the neck must have been the strongly segmented dorsal and lateral epaxial muscles, which could have stiffened the neck as a whole during simultaneous contraction. Axial neck muscles did also achieve neck mobility. In contrast to these dorsal bracing mechanisms, cervical ribs as ventral bracing elements were reduced and did most probably not contribute to bracing of the neck of Diplodocidae and Dicraeosauridae.

The reconstructed arrangement of pneumatic diverticula around the cervical vertebrae and in the notch between bifurcate neural spines suggests that the cervical pneumatic system in sauropods might have contributed to neck support as passive support structures (Akersten and Trost 2000, 2001, 2004; Schwarz and Frey 2006; Schwarz et al. 2006). There is no indication that vertebral pneumaticity in Diplodocidae and Dicraeosauridae was a separate system from the respiratory apparatus, so that most likely, pneumatic diverticula in these sauropods were linked as dead space to cervical air sacs. If it is assumed, that these pneumatic diverticula, like in birds, were brimming with air, the large pneumatic systems in the neck could theoretically have passively supported the neck, but only together with its ligaments and muscles. However, this would also require the presence of regulation mechanisms for the volume and pressure of the pneumatic diverticula system of the neck of sauropods, which cannot be reconstructed by osteological evidence. Pressure and volume of air sacs of birds is connected with a complicated array of regulating mechanisms for respiration, such as control units for the bronchial diameters (Brown et al. 1995) or the regulation of muscle activity for driving air sac ventilation (Beckers et al. 2003). In chickens, the ostia width can be controlled to regulate the amount of air passing through the lungs to a certain degree (Cook et al. 1986). The presence of vertebral pneumaticity in the neck of Diplodocidae and Dicraeosauridae as in extant birds makes it likely, that air sacs could possibly be regulated in the same way as in birds.

In the case that the pneumatic diverticula systems in the neck of diplodocid and dicraeosaurid sauropods did contribute to neck support, the combination of pneumatic and ligamental support of the neck would have made a large physiological cross-section of the axial muscle obsolete, therefore reducing the weight of the neck. It would be consistent with the reconstruction of non-multibranching and not outstandingly large dorsal ligaments in the neck of Diplodocidae and Dicraeosauridae, and might explain the lack of effective ventral bracing structures such as long, overlapping cervical ribs, in their necks. In Dicraeosauridae, the presence of large supravertebral pneumatic diverticula systems would be an

explanation for the enormous height increase in neural spines and the possibility of a reduction of the supraspinal ligament in *Amargosaurus*.

Conclusions

The reconstructions of the configuration of the elastic ligaments and the axial cervical muscles in the neck of Diplodocidae and Dicraeosauridae differ partly from those postulated by other authors for sauropods. Differences in the soft-tissue reconstructions cannot be taxonomically biased, as many of the osteological structures observed in Diplodocidae and Dicraeosauridae and discussed in this paper are also found in other sauropods. They are interpreted here as the result of a reconstruction method acting purely on the basis of birds, which have very specialized necks. In contrast, inclusion of extant Crocodylia into soft-tissue reconstructions of sauropods helps to understand their soft-part anatomy better and is consistent with functional morphological models for the sauropod neck support. The special neck morphology of diplodocid and dicraeosaurid sauropods does often allow only a one way phylogenetic comparison with either birds or crocodylians (Level II inference, Witmer 1995, 1997), which leads to uncertainties in the reliability of these reconstructions.

Taking into account different ontogenetic stages shows details of the development of pneumatic structures in sauropod necks and allows some conclusions for the development and biomechanical importance of these pneumatic structures. The presence of suprasedullary pneumatic diverticula was important for further pneumatisation of the neural arch. The pattern of internal pneumatic structures and their ontogenetic change in Diplodocidae might be explained having been induced by the increasing mass during growth. In contrast, the lack of internal pneumatisation and the simple pattern of pneumatic fossae in Dicraeosauridae prohibit an unambiguous reconstruction of vertebral pneumaticity in the neck of this sauropod group in a strict comparative anatomical approach. Nevertheless, the similarly distributed pneumatic fossae in Dicraeosauridae and in Diplodocidae, and the bracketing of Dicraeosauridae with sauropod taxa possessing pneumatised necks make the presence of vertebral pneumaticity in the neck of Dicraeosauridae highly probable.

With the inclusion of all osteological evidence, a model for the filling of the gap between the metapophyses of bifurcate neural spines by ligaments and supravertebral pneumatic diverticula is represented. If so, then it is even possible that growth and interseptal segmentation of supravertebral diverticula in sauropods influenced or triggered bifurcation of neural spines during ontogeny. Bifurcation of the neural spines improved the dorsal ligamentous support system of the neck by forcing the supraspinal ligament to divide into two parts. Our soft-tissue reconstructions, in particular the reconstructed array of pneumatic diverticula around the cervical vertebrae lead to a biomechanical consistent model for the bracing of the neck of Diplodocidae and Dicraeosauri-

dae. It is plausible that dorsal ligaments and epaxial muscles contributed to neck bracing, whereas ventral cervical ribs as ventral bracing elements were reduced. Within this dorsally dominated bracing systems, it is possible that the pneumatic system was an additional, passively stabilising and shape-controlling mechanism in the neck.

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