

Expanded neural canals in the caudal vertebrae of a specimen of Haplocanthosaurus

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Museum of Western Colorado (MWC) 8028 is a recently-described specimen of the sauropod dinosaur *Haplocanthosaurus*, a rare taxon from the Upper Jurassic Morrison Formation of the American West (Foster and Wedel 2014). In most aspects of its morphology, MWC 8028 closely resembles previously-described specimens of *Haplocanthosaurus*. One exception is that the neural canals of the proximal caudal vertebrae are uniquely expanded, excavating both the centra and the neural arch pedicles (Figure 1). To investigate these unusual features, we scanned the fossils using computed tomography (CT), and generated and printed 3D models of the vertebrae and inferred soft tissues. Herein we describe our methods, and compare the expanded neural canals in MWC 8028 to similar features in other dinosaurs, including extant birds.

CT scans of the vertebrae of MWC 8028 were performed at Hemet Global Medical Center in Hemet, California, using a Toshiba Prime 80 CT scanner. Scout images were obtained in lateral projection at 120 kVp (kilovolt peak) and 150mA (milliamperes) and in coronal projection at 120KVp and 50mA. Coronal images were produced at 120 kVp and 100 mA, scanned at 0.5mm thickness and 0.3mm intervals. Data were reconstructed in the bone algorithm using

x86 architecture, a 64-bit parallel imaging processor, and the Toshiba V7.0SP0315E application imaging software.

To generate 3D models, the CT scan slices (DICOM files) of each vertebra were imported into the 3D visualization program Amira 6.2 and combined to produce a volume stack file (.am). Next, voxels were selected and assigned to the vertebral element. Voxel assignment was verified in all three orthogonal views, and *Generate Surface* was used to produce a *labels* file (.labels.am). A 3D surface model was then rendered from the labels file using an unconstrained smoothing setting of 5. Finally, a model of each vertebra was saved as a stereolithography (.stl) file.

We printed models of the vertebrae with a MakerBot Replicator at 75% scale. Using more complete and less-distorted specimens of *Haplocanthosaurus* as guides (see Hatcher 1903), we repaired breaks and sculpted missing features of the most complete vertebra, caudal 3, using modeling clay. We then digitized the repaired model using an HDI Advance R3 optical scanner and Polyga FlexScan3D and used Autodesk Meshmixer to generate a 2nd-generation 3D model. We used Autodesk Maya and Pixologic ZBrush to retrodeform the virtual model, producing a symmetrical version that approximated the in-vivo morphology of the vertebra.

We generated spinal cord and intervertebral disc models in Meshmixer. The retrodeformed third caudal vertebra was replicated, with the linear dimensions of successive replicants reduced by 10%, to roughly match the relative dimensions of the preserved proximal caudal vertebrae. The replicated vertebrae were digitally rearticulated using the centra and zygapophyses as alignment guides. The resulting negative spaces in the neural canal and between the centra were then converted into solid objects, generating endocasts for the neural canal and intervertebral joints respectively (Figure 2).

In each of the four preserved caudal vertebrae of MWC 8028, the neural canal is both laterally and ventrally expanded (Figure 3). Midsagittal sections show that the ventral expansions make dish-like depressions in the dorsal surfaces of the caudal centra. In contrast, the lateral expansions of the neural canals into the neural arch pedicles are much smaller, and the dorsal roofs of the neural canals are flat. The anterior sacral vertebrae are too poorly preserved to assess, but the neural canals of the dorsal and posterior sacral vertebrae of MWC 8028 are cylindrical, and not expanded. Collectively the neural canal expansions form a series of rounded vacuities like beads on a string, rather than a cylindrical tunnel as in most vertebrates.

Among birds, the closest extant relatives of sauropod dinosaurs, at least six different types of soft tissues can produce either neural canal expansions or bony cavities opening from the neural canal (Figure 4). Here we briefly describe these soft-tissue structures and their osteological correlates and compare them to the neural canal expansions present in MWC 8028.

1. In most vertebrates, the floor of the neural canal is penetrated by vascular foramina

(Smuts 1975, Zippel et al. 2003). These foramina are sometimes situated in a narrow trough or fossa that runs longitudinally in the floor of the neural canal.

2. In all tetrapods with limbs, and in some fishes with sensitive fins, the spinal cord has expansions of gray and white matter in the spinal levels that serve the limbs (Streeter 1904, Giffin 1990). Although the spinal cord does not fill the volume of the neural canal, the neural canal expands radially, with an increased diameter, to accommodate the expansions of the spinal cord adjacent to the limbs. This expansion is gradual, occurring over several vertebral levels, and without discrete cavities or pockets.
3. The glycogen body is a mass of specialized, glycogen-rich glial cells of unknown function, which among extant animals occurs only in birds (Watterson 1949, Giffin 1991). The glycogen body occupies a trough, the sinus rhomboidalis, that separates the dorsal halves of the spinal cord. Glycogen bodies vary widely in size among taxa, from tiny (e.g., ostriches) to larger in cross-section than the spinal cord itself (e.g., chickens, pigeons). If the glycogen body is large, the neural canal will be dorsally expanded to accommodate it. Serially, this dorsal pocket of the neural canal expands and contracts rapidly, over just a few segments.
4. The lumbosacral organ of birds comprises a series of transverse, fluid-filled meningeal tubes that arch dorsally over the spinal cord, which function as semicircular-canal analogues for maintaining equilibrium (Necker 2006). The meningeal canals occupy dorsal expansions of the neural canal at former intervertebral joints in the synsacrum, which manifest as transverse ridges in neural canal endocasts (Necker 2006, Stanchak et al. 2020).
5. Ventral eminences are segmental bumps on the ventral surface of the spinal cord in some birds, especially ostriches (Streeter 1904). Ventral eminences are caused by the increased cross-sectional area of the ventral horn of the spinal cord (motor neurons). The resulting bumps fill rounded recesses in the ventral floor of the neural canal in the synsacrum.
6. Supramedullary diverticula are pneumatic diverticula (epithelium-lined air spaces that develop from the lungs and respiratory air sacs) that extend inside the neural canal to sit adjacent to the spinal cord in many birds (Müller 1908, Cover 1953, O'Connor, 2006). These diverticula can remodel the walls of the neural canal, producing a pocked or sculpted texture, and can induce bone resorption to produce pneumatic foramina. Pneumatic foramina are most commonly found in the dorsal surface of the neural canal,

but they can also occur in the lateral or even ventral surfaces of the canal (Atterholt and Wedel 2018).

To date, osteological correlates of four of these six systems have been found in sauropods and other extinct dinosaurs. Foramina for basivertebral blood vessels have been identified in the neural canals of some sauropods (Manning et al. 2015, Mannion et al. 2019). Lumbo-sacral expansions in dinosaurs and other extinct vertebrates are consistent in morphology with those of extant taxa and are inferred to have housed enlargements of the spinal cord to innervate the hindlimbs (Giffin 1990). Abrupt dorsal expansions of the neural canal over just a few segments occur in the sacral vertebrae of several genera of sauropods and stegosaurs (Marsh 1896, Janensch 1939). These are most similar to cavities for the glycogen body in extant birds (Giffin 1991). Finally, Schwarz and Fritsch (2006) identified pneumatic foramina in the neural canals in the presacral vertebrae of *Giraffatitan*, indicating that supramedullary diverticula were present. However, none of these four systems is a good match for the morphology of the neural canal expansions in MWC 8028.

Of all the specializations of the neural canal in birds, only three expand ventrally: ventral eminences of the spinal cord, vascular foramina, and some pneumatic foramina derived from supramedullary diverticula. All others expand the neural canal in other directions, or radially in all directions. Pneumatic diverticula and blood vessels may produce foramina in the walls or floor of the neural canal, but neither system produces regular, hemispherical, smooth-surfaced vacuities like those of MWC 8028.

This leaves ventral eminences of the spinal cord as the only soft tissue system of birds—or of extant vertebrates in general—that produces traces similar to the neural canal expansions in this specimen of *Haplocanthosaurus*. The osteological traces of ventral eminences in birds are not identical to those in MWC 8028—the ventral eminences of ostriches occupy bilaterally paired troughs in the floor of the canal, not a single midline depression, and they occur in the synsacrum, not in the free caudal vertebrae. Still, ventral eminences show that at least some extant dinosaurs have segmented ventral expansions of the spinal cord created by ‘extra’ motor neurons that innervate large groups of muscles.

Possibly the expanded neural canals of MWC 8028 accommodated expansions of the spinal cord to innervate the large muscle groups of the pelvis and tail. It is not clear, however, why such spinal swellings would be present in this specimen of *Haplocanthosaurus*, a relatively small-bodied and small-tailed sauropod, but not in others, nor why they would be absent in larger-bodied and proportionally larger-tailed taxa such as *Apatosaurus*. It is also unclear why the neural canals of MWC 8028 are only expanded in the caudal series, and not in the dorsal or posterior sacral vertebrae. Nevertheless, ventral eminences of the spinal cord are the best explanation we have found for the expanded neural canals in this specimen.

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References

- Atterholt, J., and Wedel, M. 2018. A CT-based survey of supramedullary diverticula in extant birds. 66th Symposium on Vertebrate Palaeontology and Comparative Anatomy, Programme and Abstracts, p. 30 / PeerJ Preprints 6:e27201v1.
- Cover, M.S. 1953. Gross and microscopic anatomy of the respiratory system of the turkey. III. The air sacs. *American Journal of Veterinary Research* 14:239-245.
- Foster, J.R., and Wedel, M.J. 2014. *Haplocanthosaurus* (Saurischia: Sauropoda) from the lower Morrison Formation (Upper Jurassic) near Snowmass, Colorado. *Volumina Jurassica* 12(2): 197– 210.
- Giffin, E.B. 1990. Gross spinal anatomy and limb use in living and fossil reptiles. *Paleobiology* 16(4): 448-458.
- Giffin, E.B., 1991. Endosacral enlargements in dinosaurs. *Modern Geology* 16: 101-112.
- Hatcher, J.B. 1903. Osteology of *Haplocanthosaurus* with description of a new species, and remarks on the probable habits of the Sauropoda and the age and origin of the *Atlantosaurus* beds; additional remarks on *Diplodocus*. *Memoirs of the Carnegie Museum* 2: 1-75.
- Janensch, W. 1939. Der sakrale Neuralkanal einiger Sauropoden und anderer Dinosaurier. *Paläontologische Zeitschrift* 21(3): 171-193.
- Manning, P.L., Egerton, V.M., and Romano, M. 2015. A new sauropod dinosaur from the Middle Jurassic of the United Kingdom. *PLoS ONE* 10: e0128107.
- Mannion, P.D., Upchurch, P., Schwarz, D. and Wings, O. 2019. Taxonomic affinities of the putative titanosaurs from the Late Jurassic Tendaguru Formation of Tanzania: phylogenetic and biogeographic implications for eusauropod dinosaur evolution. *Zoological Journal of the Linnean Society* 185(3): 784-909.

- Marsh, O.C. 1896. Dinosaurs of North America. US Geological Survey Annual Report 16: 142– 230.
- Müller, B. 1908. The air-sacs of the pigeon. Smithsonian Miscellaneous Collections 50: 365-420.
- Necker, R. 2006. Specializations in the lumbosacral vertebral canal and spinal cord of birds: evidence of a function as a sense organ which is involved in the control of walking. *Journal of Comparative Physiology A* 192(5): 439-448.
- O'Connor, P.M. 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.
- Schwarz, D., and Fritsch, G. 2006. Pneumatic structures in the cervical vertebrae of the Late Jurassic Tendaguru sauropods *Brachiosaurus brancai* and *Dicraeosaurus*. *Eclogae Geologicae Helvetiae* 99: 65–78.
- Smuts, M.M.S. 1975. The foramina of the cervical vertebrae of the ox. Part II: cervical vertebrae 3-7. *Anatomia, Histologia, Embryologia* 4(1): 24-37.
- Stanchak, K.E., French, C., Perkel, D.J., and Brunton, B.W. 2020. The balance hypothesis for the avian lumbosacral organ and an exploration of its morphological variation. *Integrative Organismal Biology* 2(1): obaa024. <https://doi.org/10.1093/iob/obaa024>.
- Streeter, G.L. 1904. The structure of the spinal cord of the ostrich. *American Journal of Anatomy* 3(1): 1-27.
- Watterson, R.L. 1949. Development of the glycogen body of the chick spinal cord. I. Normal morphogenesis, vasculogenesis and anatomical relationships. *Journal of Morphology* 85(2): 337- 389.
- Zippel, K.C., Lillywhite, H.B., and Mladinich, C.R. 2003. Anatomy of the crocodylian spinal vein. *Journal of Morphology* 258(3): 327-335.

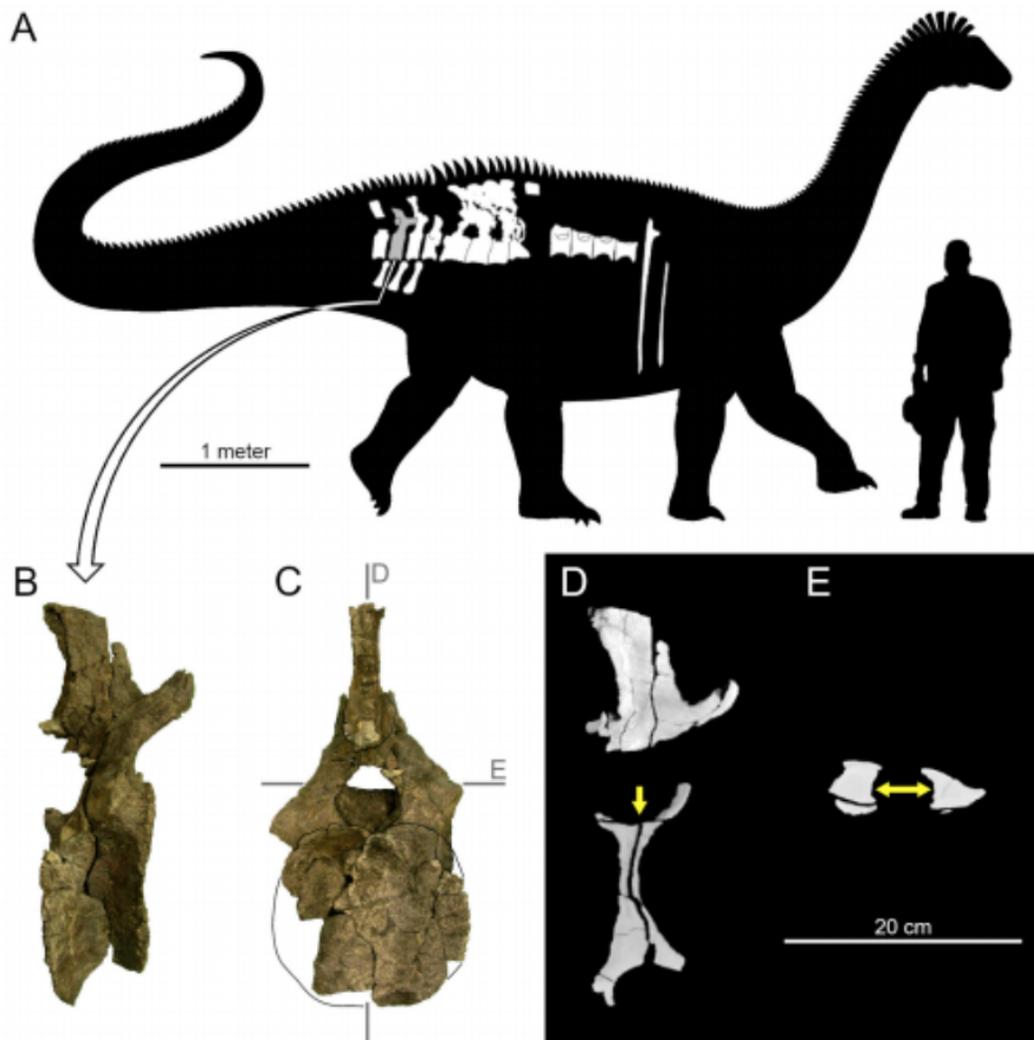


Figure 1. A. Recovered skeletal elements of *Haplocanthosaurus* specimen MWC 8028. B. Caudal vertebra 3 in right lateral view. C. The same vertebra in posterior view. Lines show the location of sections for D and E. D. Midsagittal CT slice. The arrow indicates the ventral expansion of the neural canal into the centrum. E. Horizontal CT slice at the level of the neural arch pedicles, with anterior toward the top. Arrows indicate the lateral expansions of the neural canal into the pedicles. B-E are shown at the same scale.

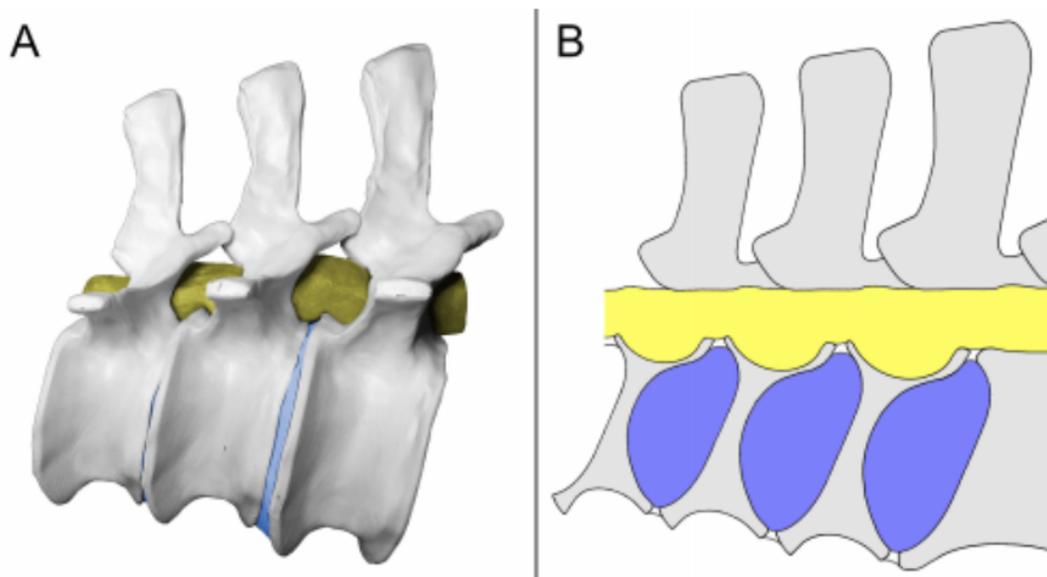


Figure 2. A. Photograph of a 3D-printed model of the first three caudal vertebrae of *Haplocanthosaurus* specimen MWC 8028, including endocasts of the neural canal (yellow) and intervertebral joints (blue), in right lateral view, and with the neural canal horizontal. **B.** Diagram of the same vertebrae in midsagittal section, emphasizing the volumes of the neural canal (yellow) and intervertebral joint spaces (blue). Anterior is to the right.

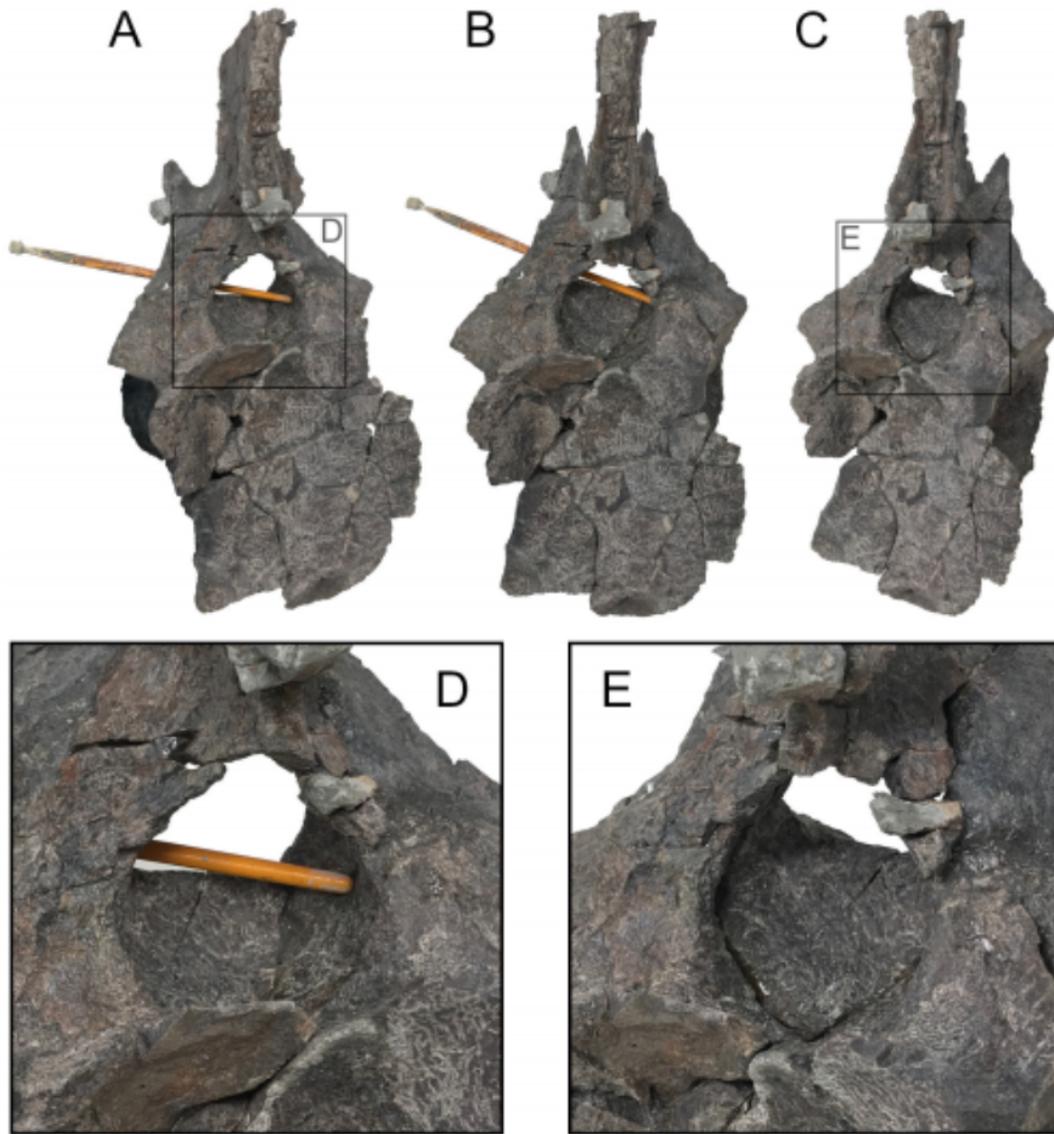


Figure 3. Caudal vertebra 3 of *Haplocanthosaurus* specimen MWC 8028 in left posterolateral (A), posterior (B), and right posterolateral (C) views, with close-ups (D and E). In A and B, a paintbrush is inserted into one of the lateral recesses, showing that the neural canal is wider internally than at either end.

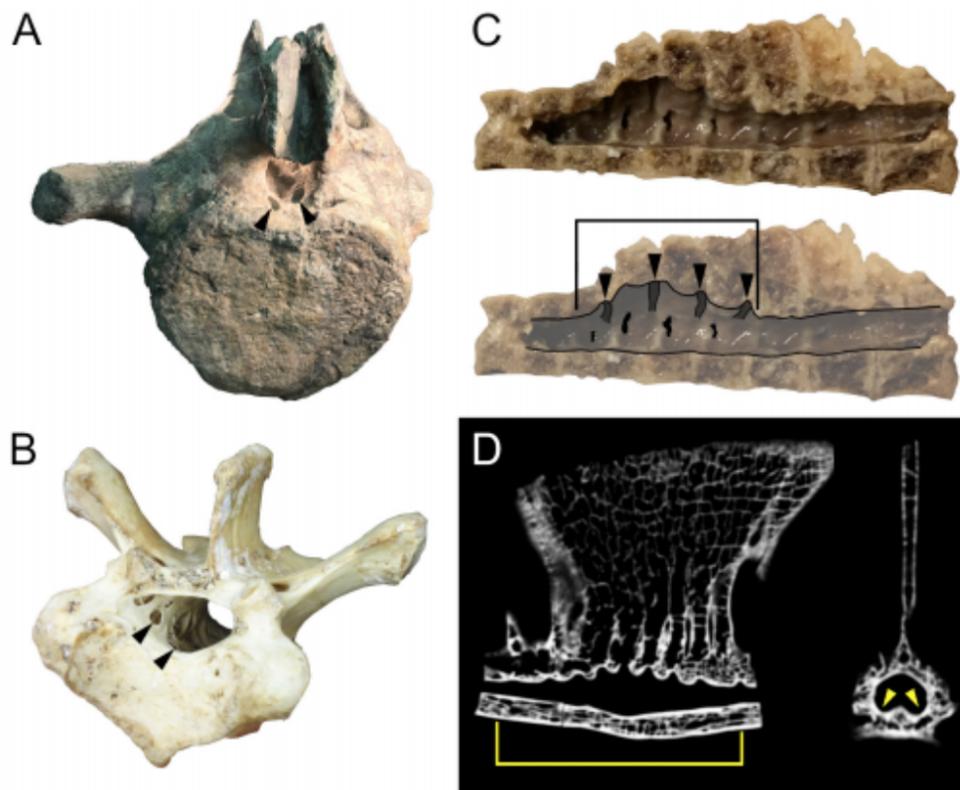


Figure 4. Anatomical features of the neural canal in birds and other dinosaurs. **A.** MWC 9698, a mid caudal vertebra of *Apatosaurus* in posterodorsal view. Arrows highlight probable vascular foramina in the ventral floor of the neural canal. **B.** LACM 97479, a dorsal vertebra of *Rhea americana* in left anterolateral view. Arrows highlight pneumatic foramina inside the neural canal. **C.** A hemisected partial synsacrum of a chicken, *Gallus domesticus*, obtained from a grocery store. Anterior is to the right. The bracket shows the extent of the dorsal recess for the glycogen body, which only spans four vertebrae. Arrows highlight the transverse grooves in the roof of the neural canal for the lumbosacral organ. **D.** Sagittal (left) and transverse (right) CT slices through the sacrum of a juvenile ostrich, *Struthio camelus*. The bracket shows the extent of the lumbosacral expansion of the spinal cord. Indentations in the roof of the neural canal house the lumbosacral organ. In contrast to the chicken, the ostrich has a small glycogen body that does not leave a distinct osteological trace. Yellow arrows show the longitudinal troughs in the ventral floor of the neural canal that house the ventral eminences of the spinal cord.