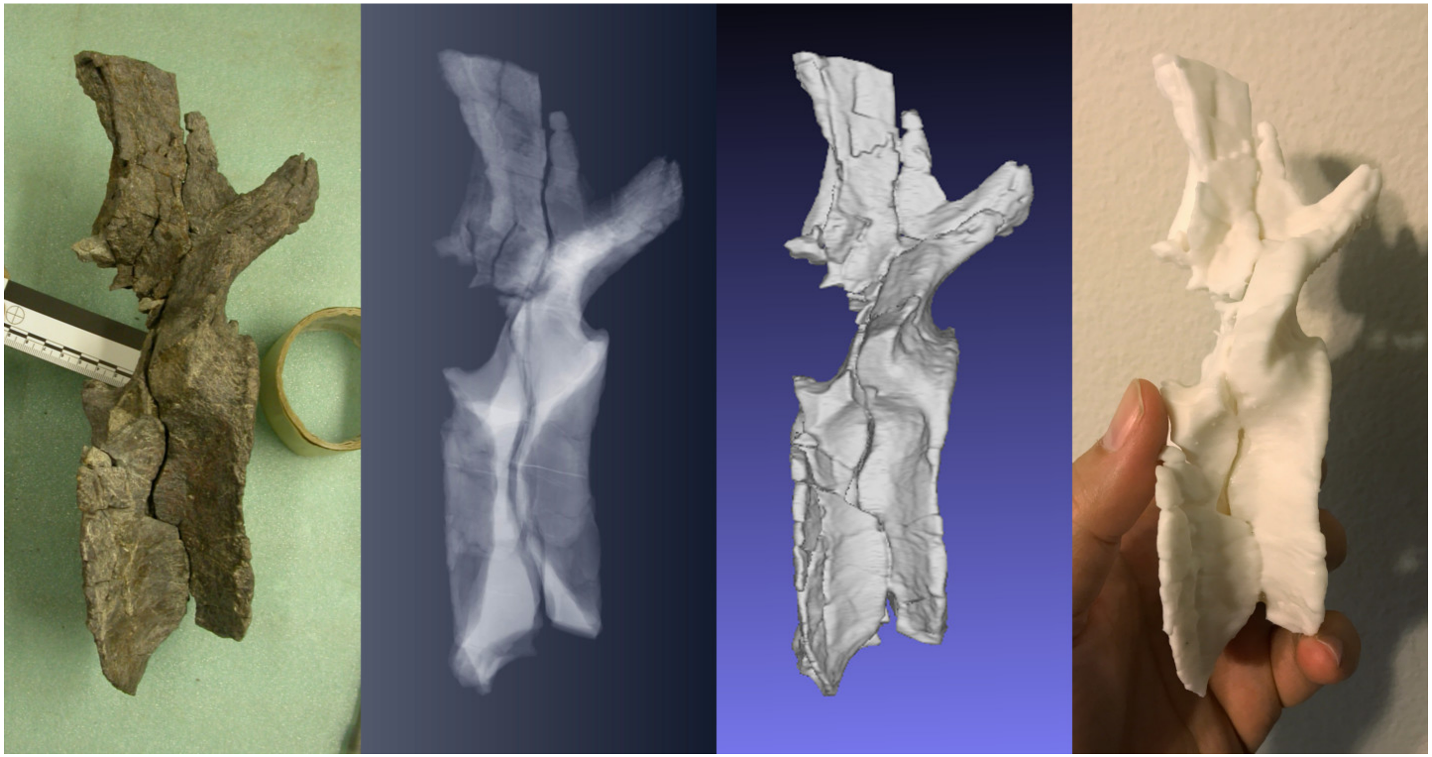
Reconstructing an unusual specimen of *Haplocanthosaurus* using a blend of physical and digital techniques



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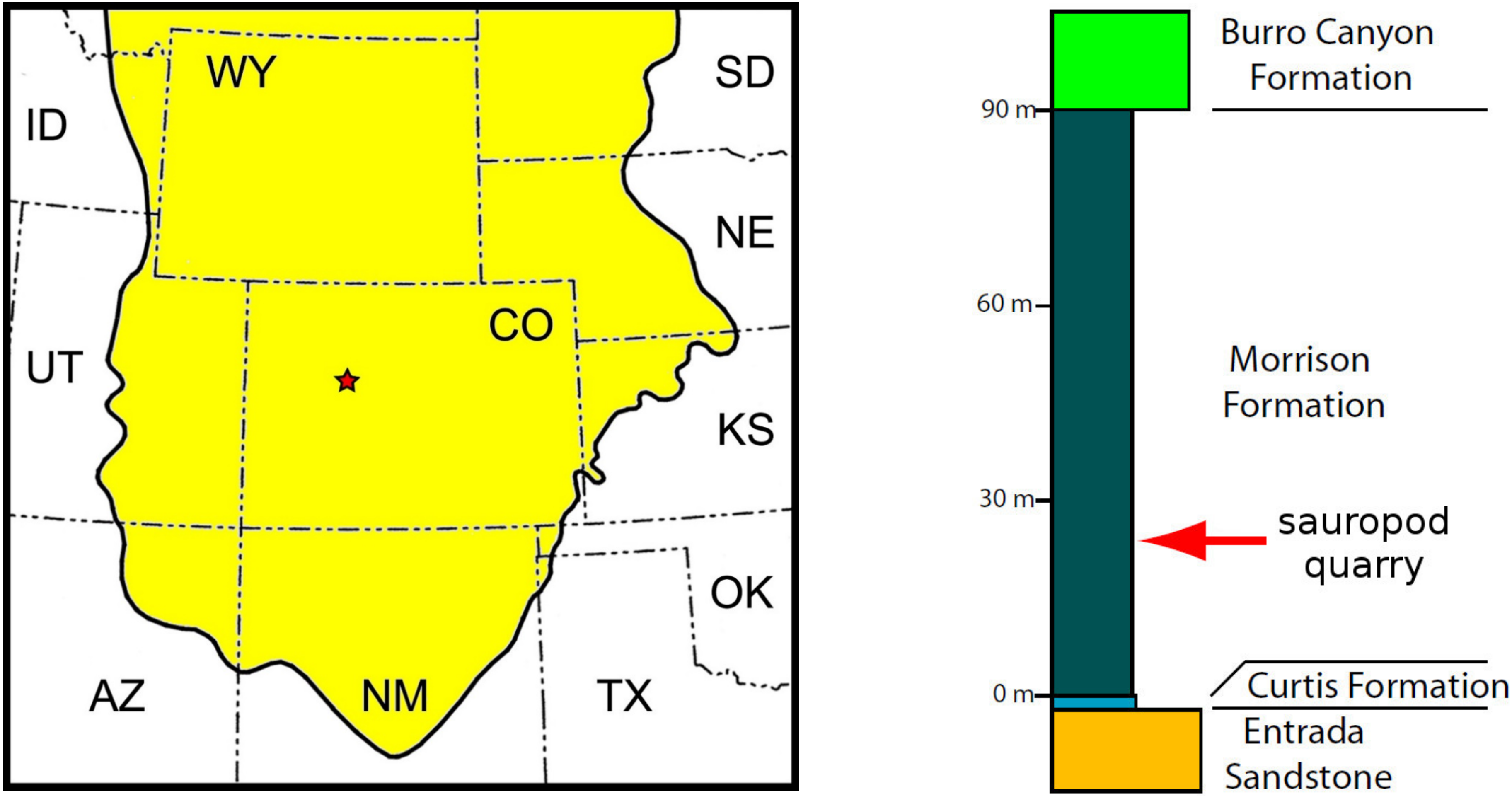
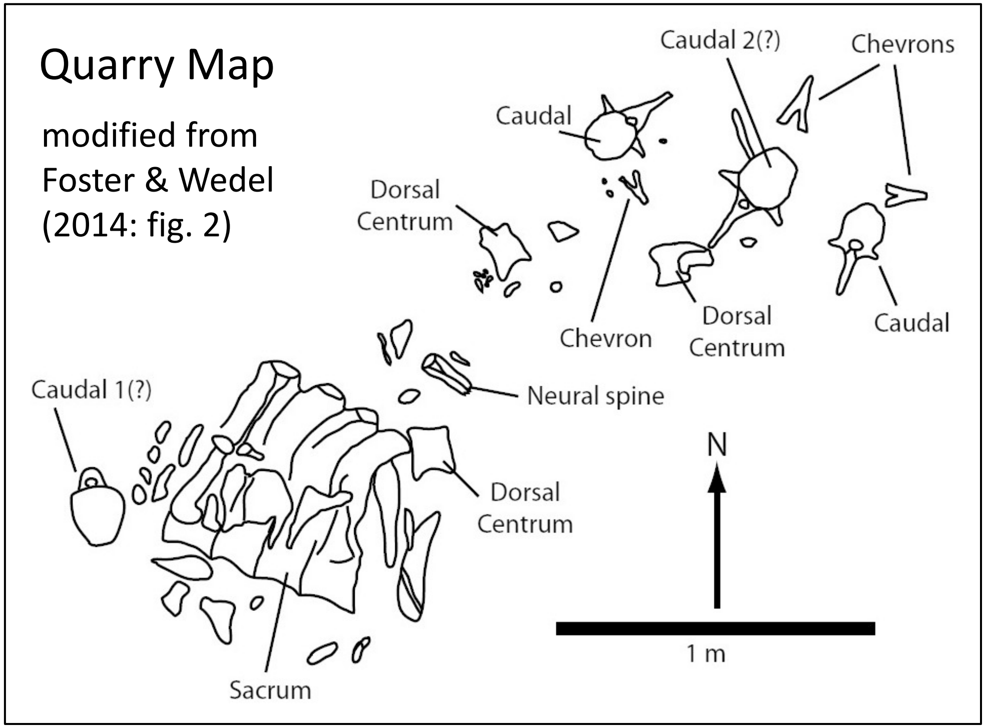
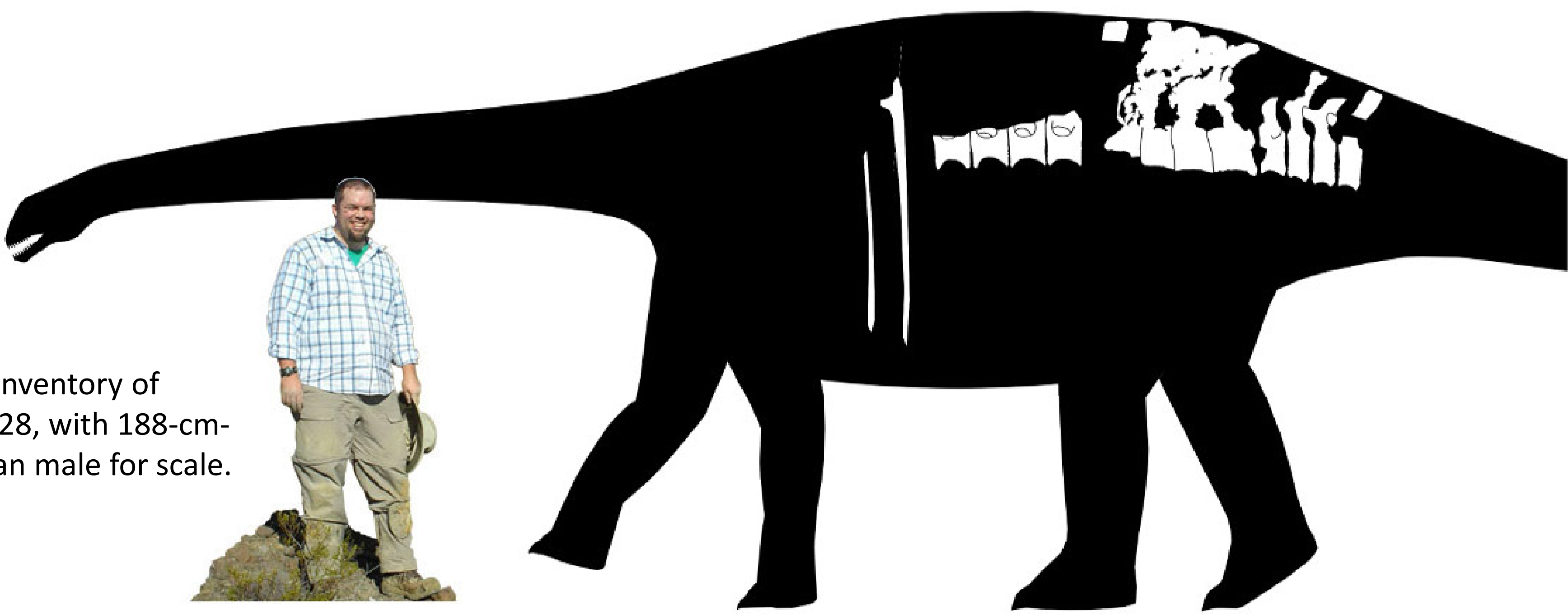


Left: Location of the quarry (red star) in the Morrison Formation of the western U.S. (yellow), modified from Bonnan and Wedel (2004: fig. 2). Right: Stratigraphic position of the quarry, modified from Foster and Wedel (2014: fig. 2).

In 2009, college student Mike Gordon discovered dinosaur bones on his grandfather's land in western Colorado. Over the next four years, crews from the Museum of Western Colorado (MWC) excavated the partial skeleton of sauropod dinosaur from the site, which lies in the lower part of the Upper Jurassic Morrison Formation.

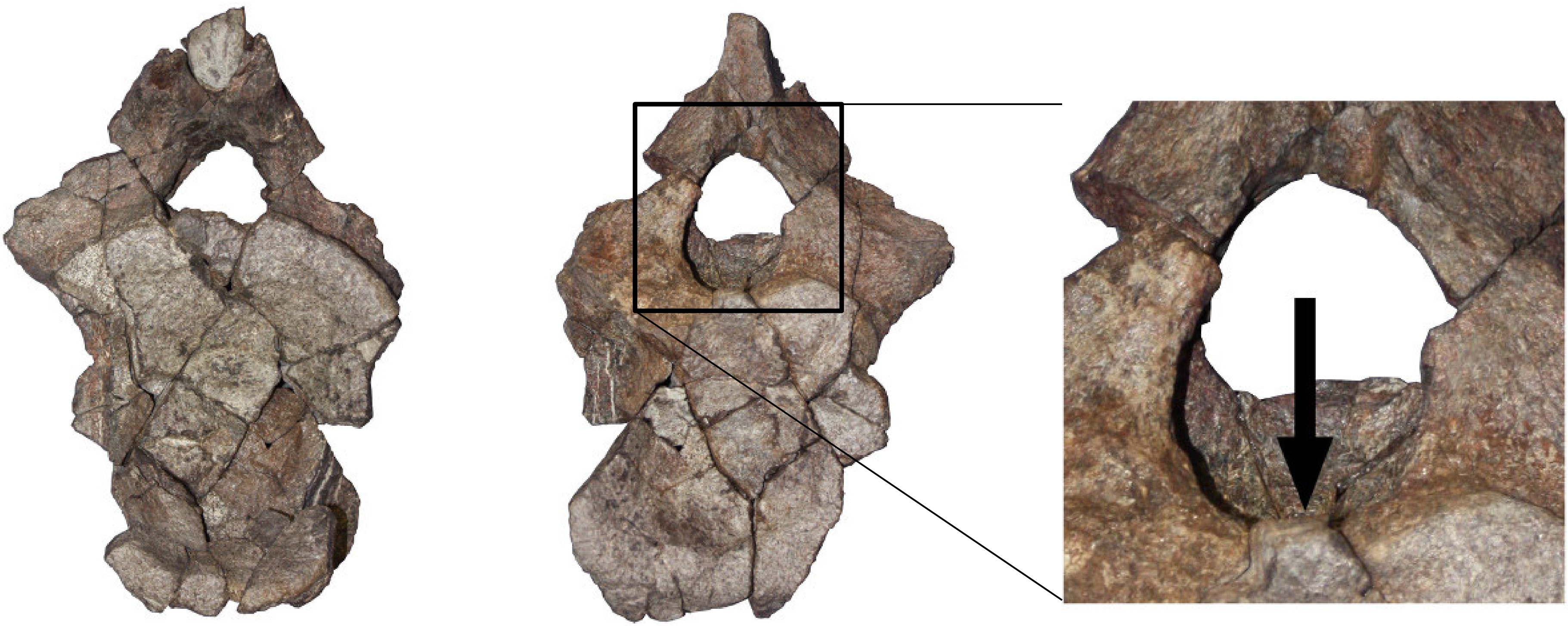
The skeleton consists of a sacrum, several partial dorsal and caudal vertebrae, a chevron, and several partial ribs. In 2014, Foster and Wedel described the specimen, MWC 8028, and referred it to *Haplocanthosaurus*. *Haplocanthosaurus* is a rare Morrison sauropod that is frequently recovered as the most basal diplodocoid in phylogenetic analyses.





Skeletal inventory of MWC 8028, with 188-cm-tall human male for scale.

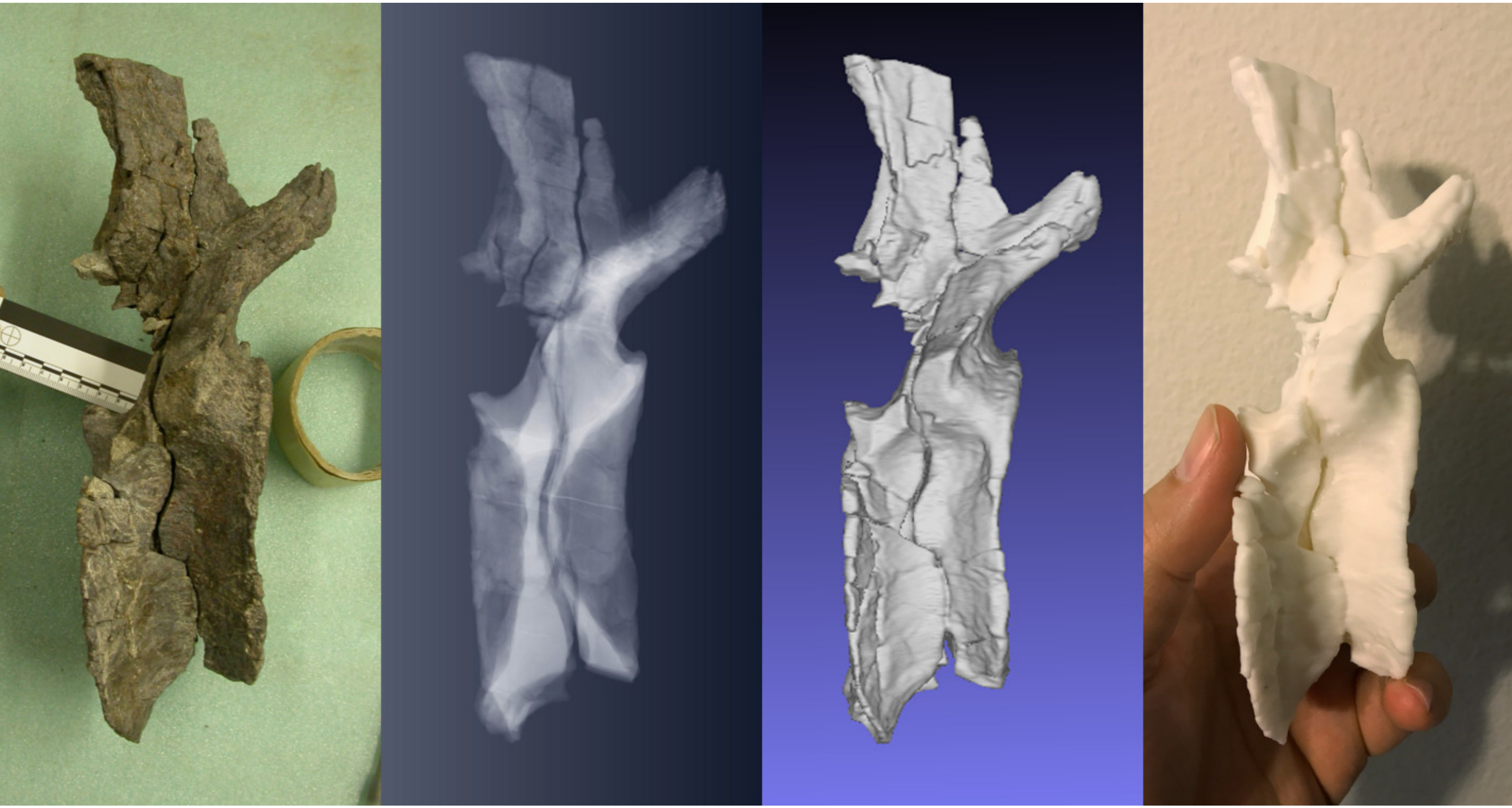
In most aspects of its morphology, MWC 8028 is a close match for previously-described specimens of *Haplocanthosaurus*, including the holotype, Carnegie Museum (CM) 572.



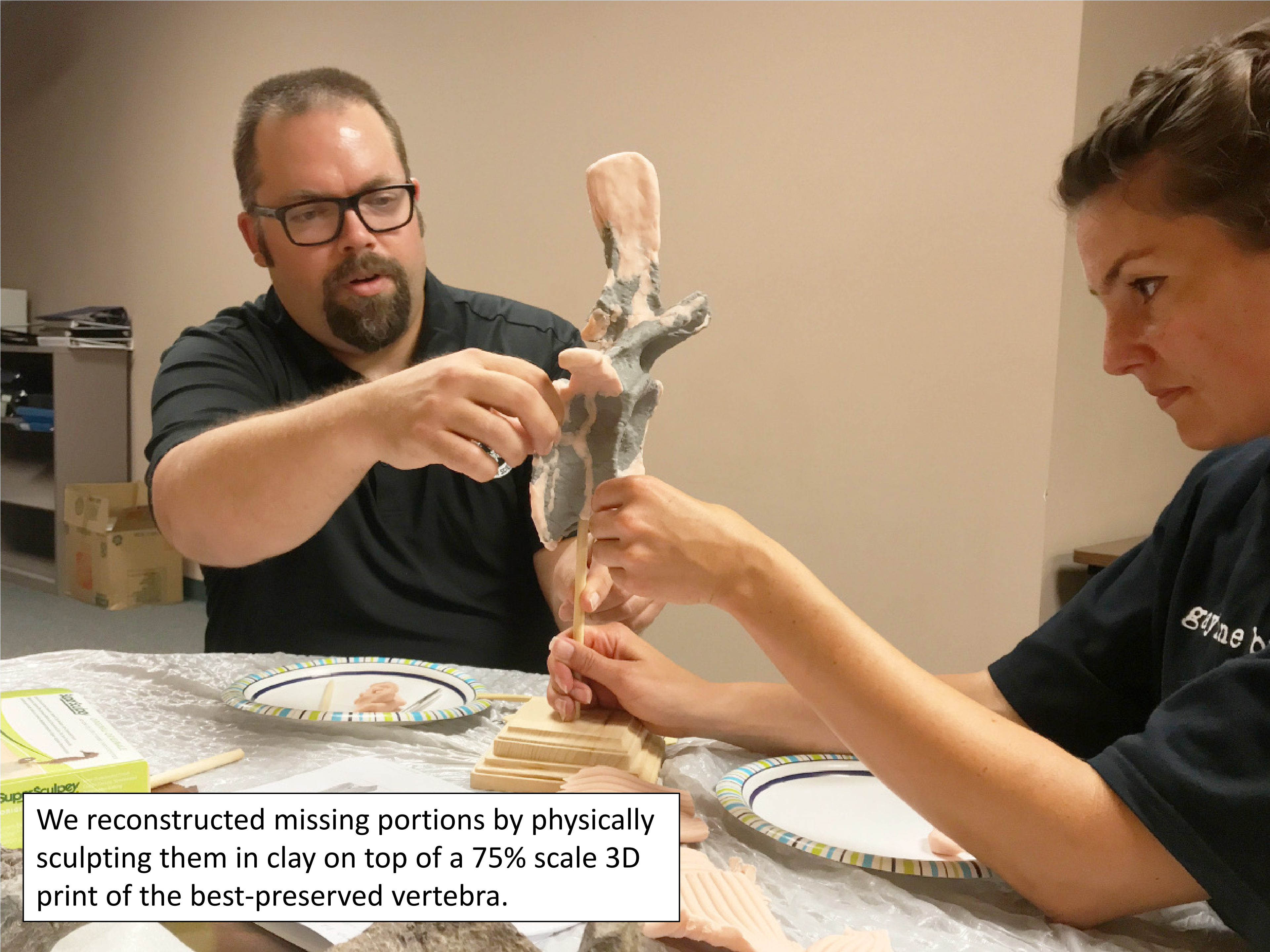
Caudal 1 of MWC 8028, in anterior (left) and posterior (middle) views. Close-up on right shows expanded neural canal (black arrow). Modified from Foster & Wedel (2014: fig. 5).

One exception is that the neural canals of the caudal vertebrae are bizarrely expanded, making dish-like impressions in the dorsal surfaces of the caudal centra, as shown above.

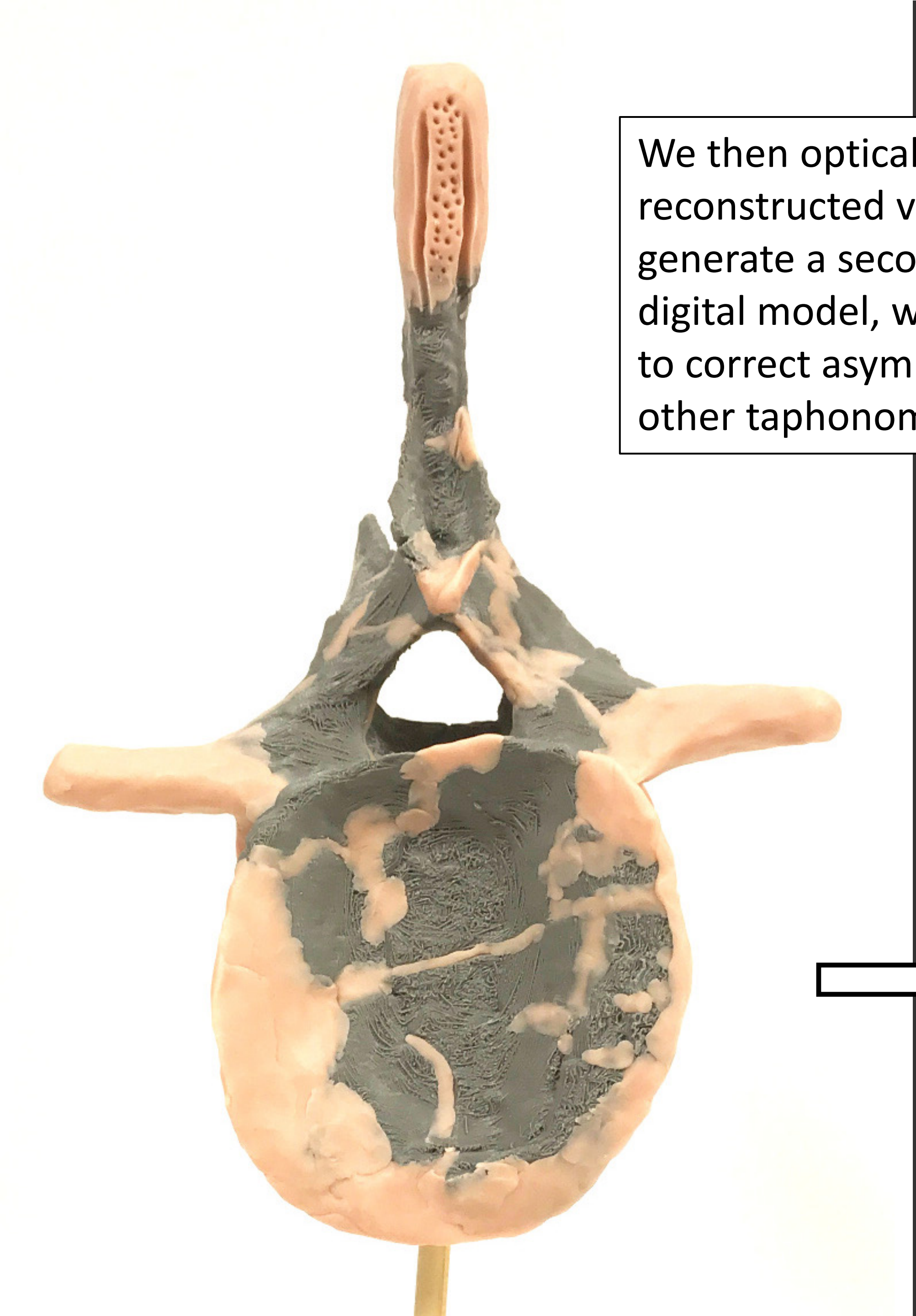
To further investigate the unusual morphology of this specimen, we CT scanned the posterior sacral and anterior caudal vertebrae, and generated and printed 3D models.



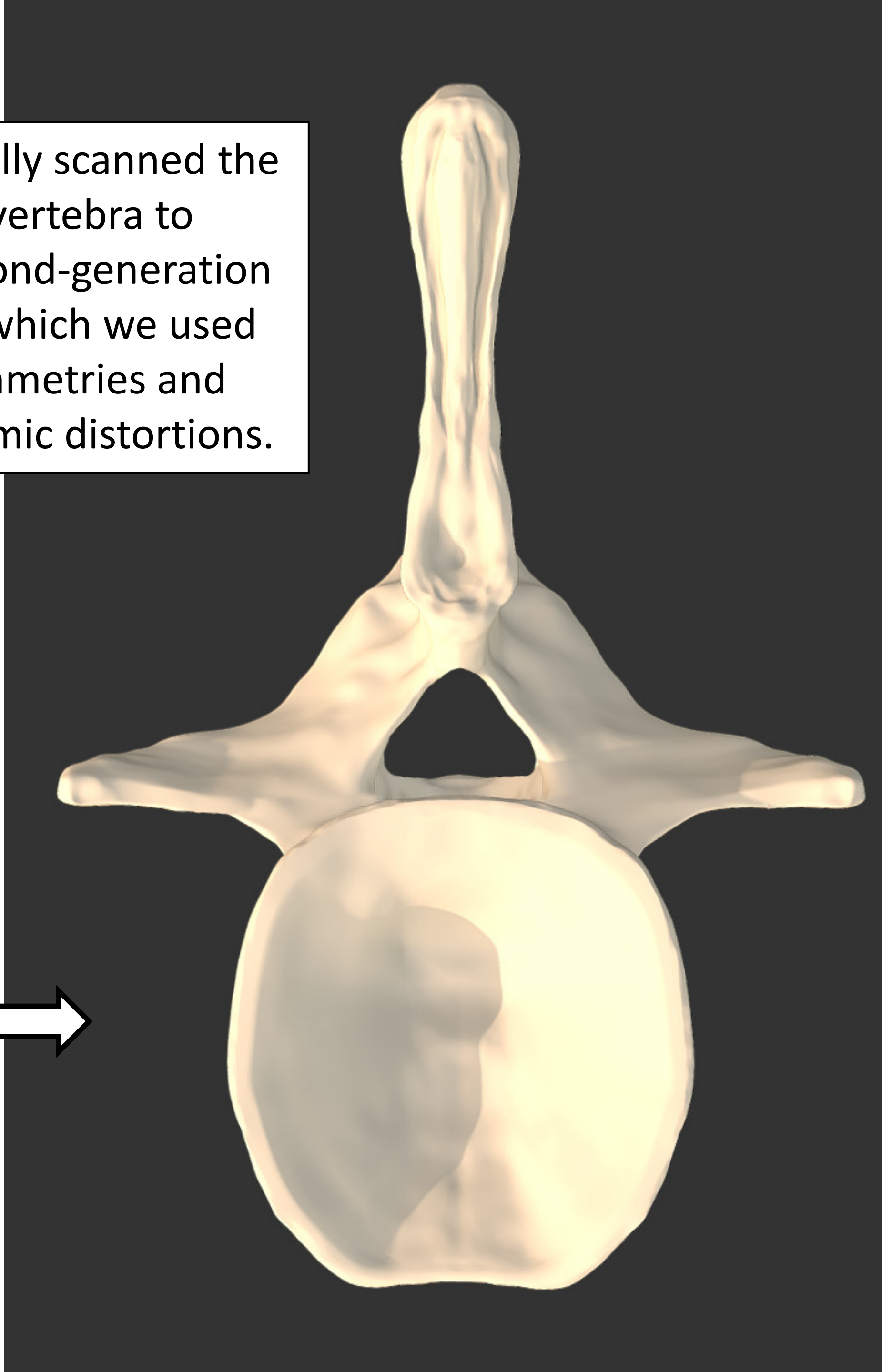
original fossil → CT scout → digital model → 3D print (50% scale)



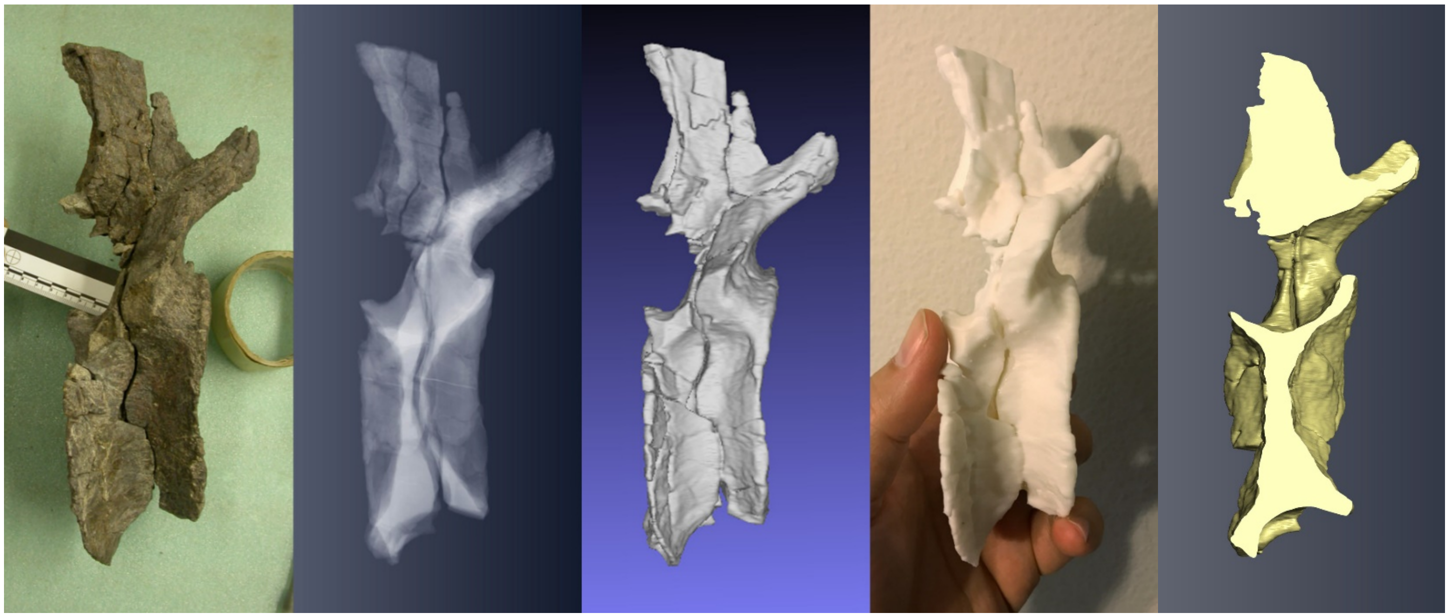
We reconstructed missing portions by physically sculpting them in clay on top of a 75% scale 3D print of the best-preserved vertebra.



We then optically scanned the reconstructed vertebra to generate a second-generation digital model, which we used to correct asymmetries and other taphonomic distortions.

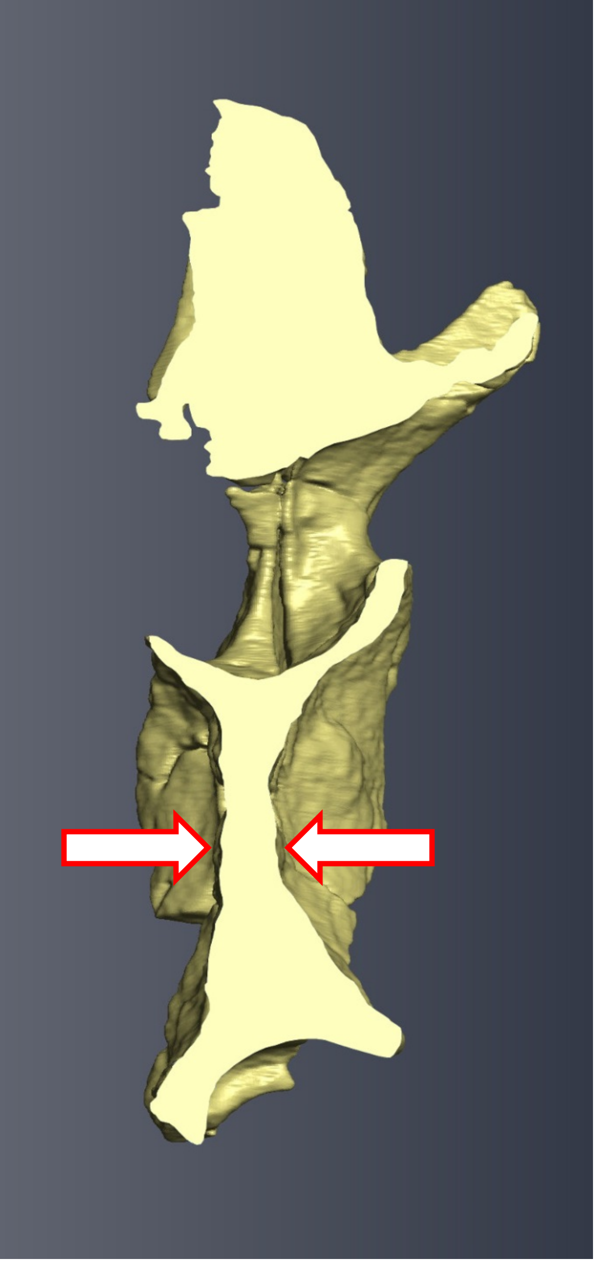


Our ultimate goal is to digitally rearticulate the sacrum and anterior caudal vertebrae of MWC 8028. This will allow us to reconstruct the soft tissues that were present in life, which influenced the unusual morphology of the vertebrae. The process of retrodeforming and digitally rearticulating the vertebrae is underway, but not yet complete.



Nevertheless, we can use the CT data and models already available to investigate the anatomy of MWC 8028. In the following slides we discuss three features in particular:

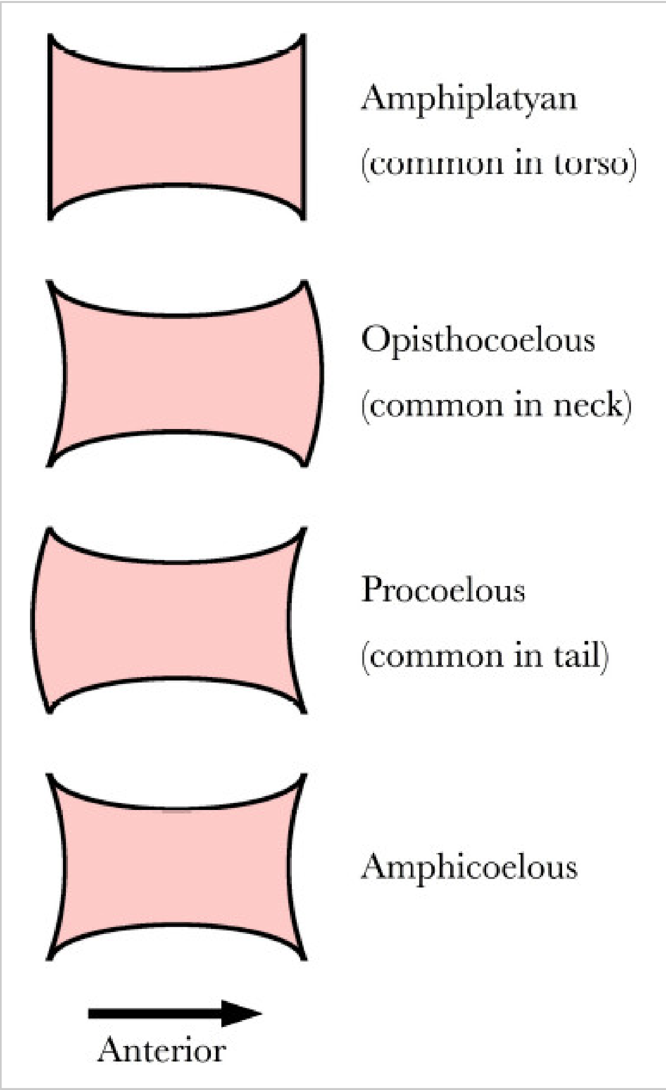
1. Deeply amphicoelous (biconcave) caudal centra
2. The angle of the neural canals relative to the centra
3. Expanded neural canals



Midsagittally hemisected 3D model of caudal 3 of MWC 8028. Anterior is to the right.

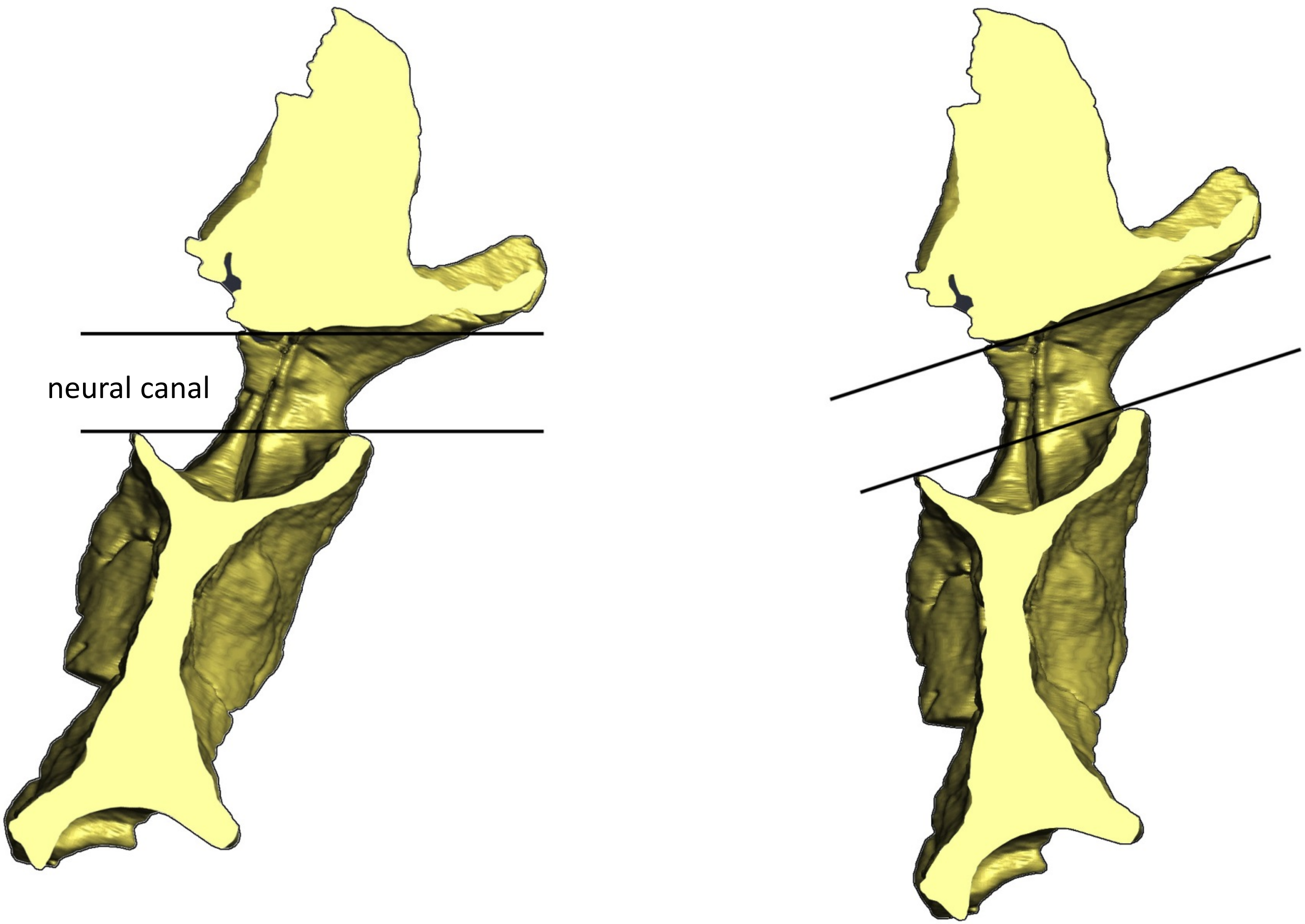
The caudal vertebrae of MWC 8028 are strongly amphicoelous, with deep, cup-shaped articular surfaces at both ends of each centrum (see arrows at left). The center of each caudal centrum is reduced to a thin vertical plate of bone.

This is in contrast to the caudal vertebrae of other sauropods, which are typically amphiplatyan (many taxa) or procoelous (some mamenchisaurs, diplodocoids, and titanosaurs).

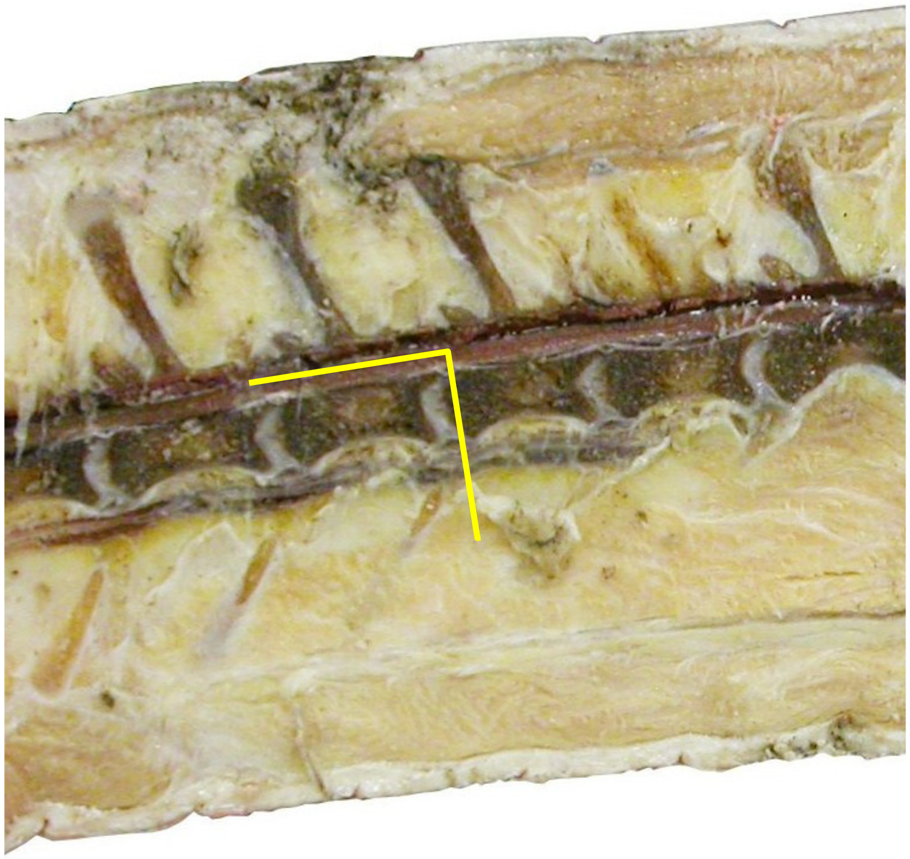


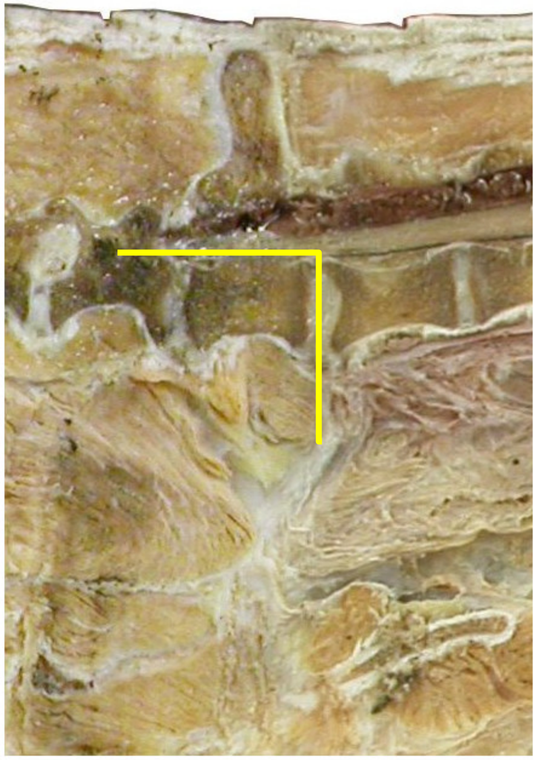
Articular shapes of sauropod vertebrae, from Taylor & Wedel (2017).

The neural canals of the proximal caudal vertebrae are not orthogonal to the centra. When the vertebrae are oriented with the neural canal horizontal (left), the centrum tilts forward at 18° from vertical. If the centrum is vertical (right), the neural canal is angled 18° above horizontal.

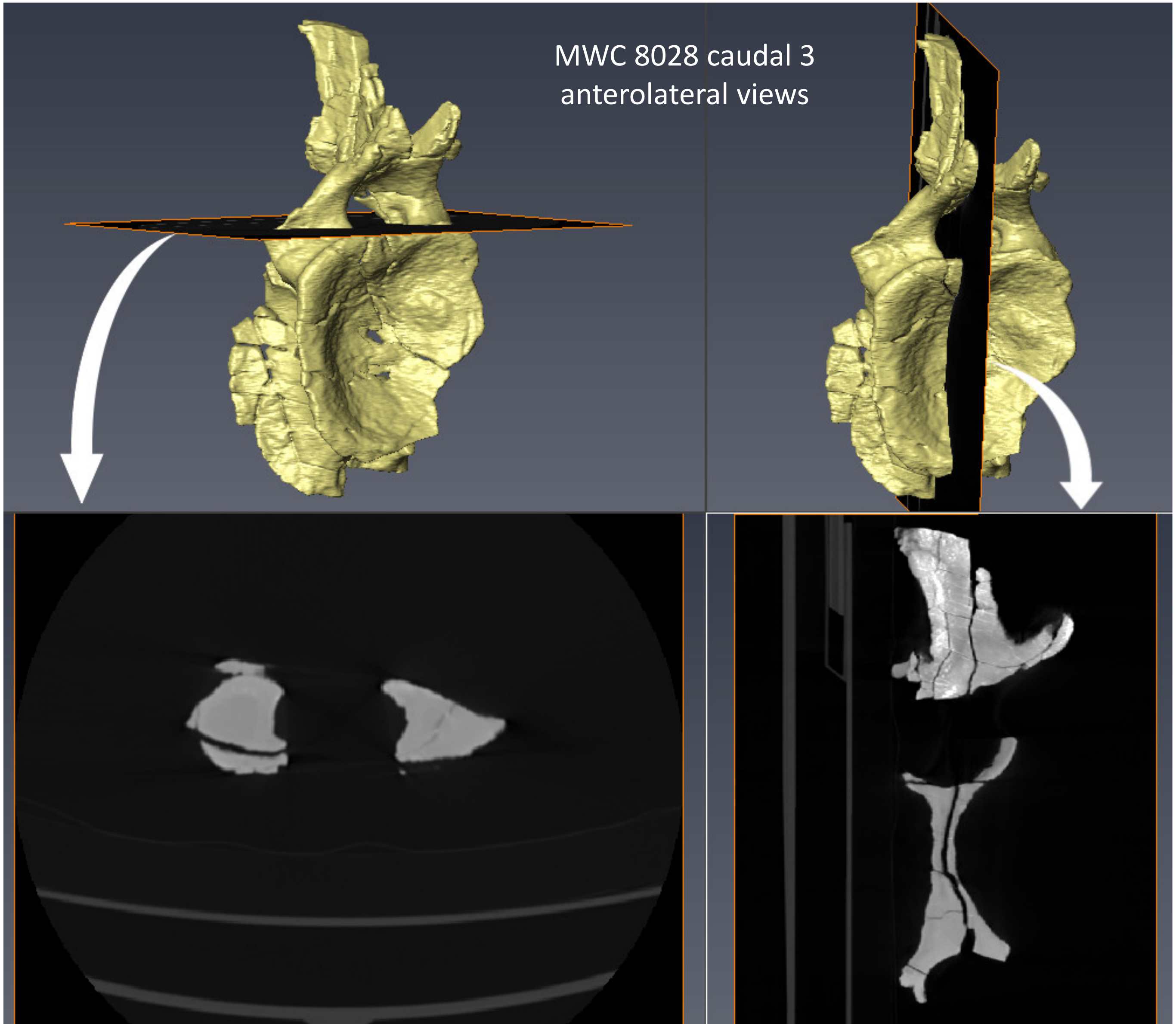


In most other vertebrates, such as this alligator, the neural canal of each vertebra is parallel to the long axis of the centrum, and perpendicular to the intervertebral joints.

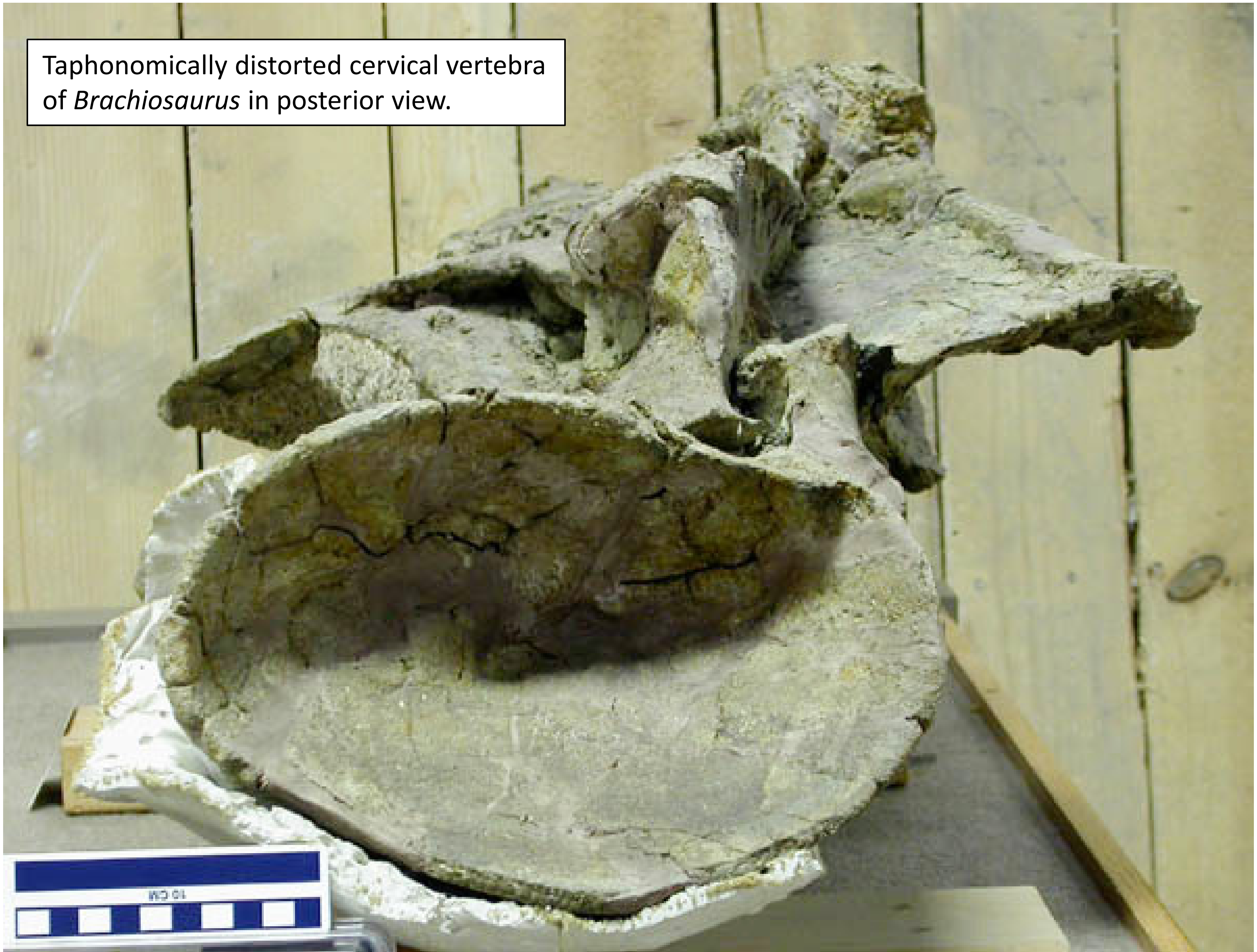




The neural canal of each proximal caudal vertebra is expanded both laterally (below left) and ventrally (below right), forming a roughly hemispherical vacuity, instead of a cylindrical tunnel as in most vertebrates.

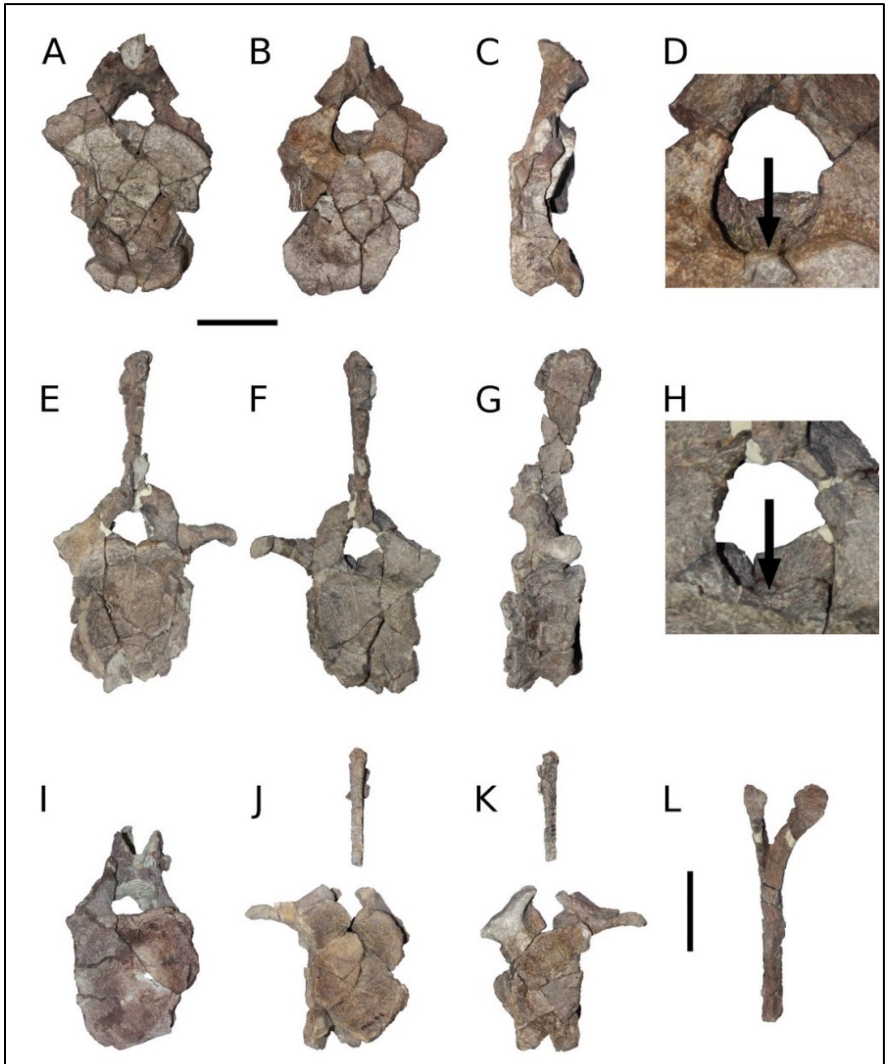


One possibility we must consider: could the unusual morphological features of MWC 8028 be artifacts caused by taphonomic distortion?



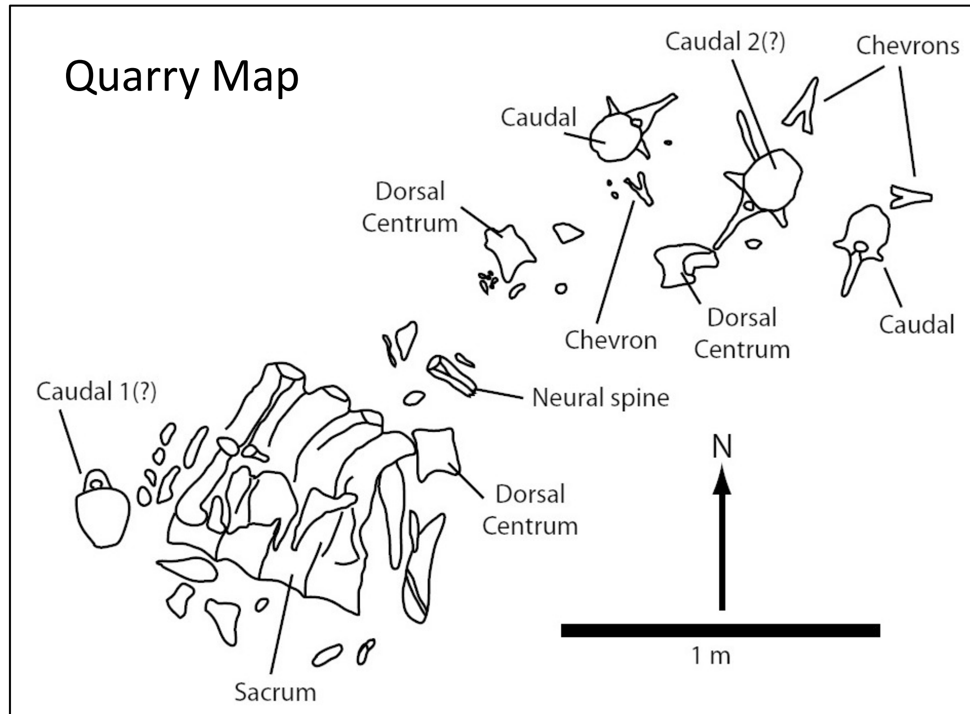
Taphonomically distorted cervical vertebra of *Brachiosaurus* in posterior view.

We think it is unlikely that the three features of interest (pronounced amphicoely, 'sloped' and expanded neural canals) could be taphonomic artifacts, for several reasons.



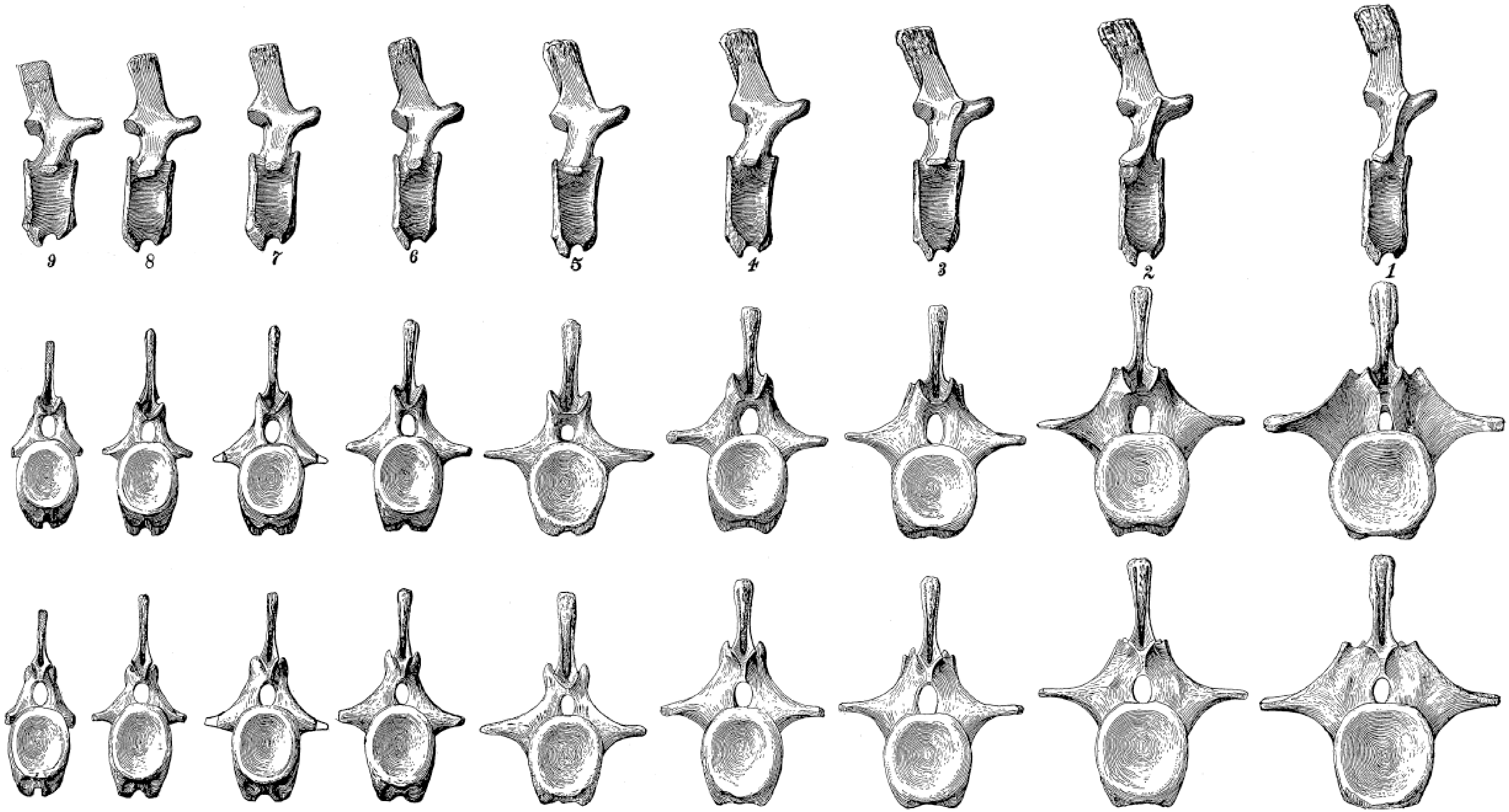
Caudal vertebrae 1 (A-D), 2 (E-H), 3 (I), and 4 (J-K) of MWC 8028, from Foster & Wedel (2014: fig. 5).

For one thing, these characters are consistent in all four of the recovered caudal vertebrae. The vertebrae were scattered across the quarry in different orientations, and would not have deformed in the same ways.



Modified from Foster & Wedel (2014: fig. 5).

Also, the overall proportions of the vertebrae of MWC 8028 are a good match for those of other specimens of *Haplocanthosaurus*, which have anteroposteriorly short centra, neural arches angled slightly forward, and neural spines angled back.



Proximal caudal vertebrae of *Haplocanthosaurus priscus* CM 572 in right lateral (top), anterior (middle), and posterior (bottom) views, from Hatcher (1903: plate 3).

Finally, each of the features of interest has a precedent: similar characters in other dinosaurs.

Deeply amphicoelous vertebral centra have also been reported in AMNH FARB 291, a series of articulated dorsal vertebrae of an unidentified sauropod from the Morrison Formation.

AMNH FARB 291 in right lateral view, from Taylor & Wedel (2017).
Note the deep, cup-shaped articular surface (red arrow).

Enlarged neural canals are known from the sacral vertebrae of several genera of sauropods and stegosaurs. These endosacral cavities differ from the expanded neural canals of MWC 8028 in two important ways, however: (1) they occur in the sacral vertebrae rather than the caudal vertebrae, and (2) they expand dorsally and laterally rather than ventrally.

Giffin (1991) reviewed the anatomy and proposed functions of endosacral enlargements in Mesozoic dinosaurs and concluded that they were most similar to cavities for the glycogen body in extant birds (discussed later in this presentation).

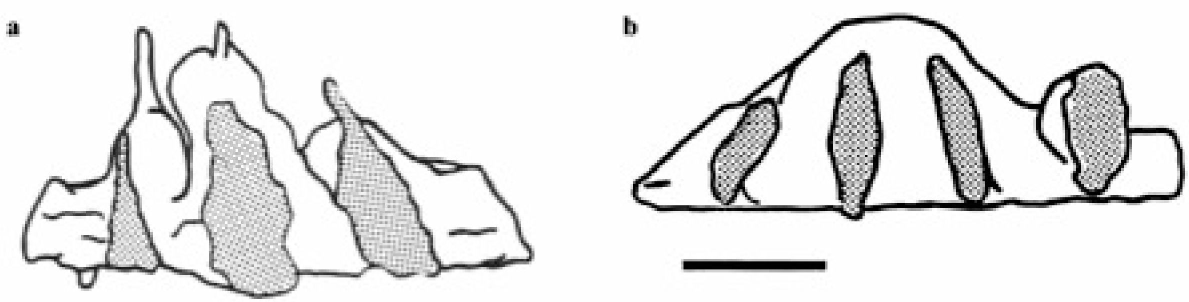
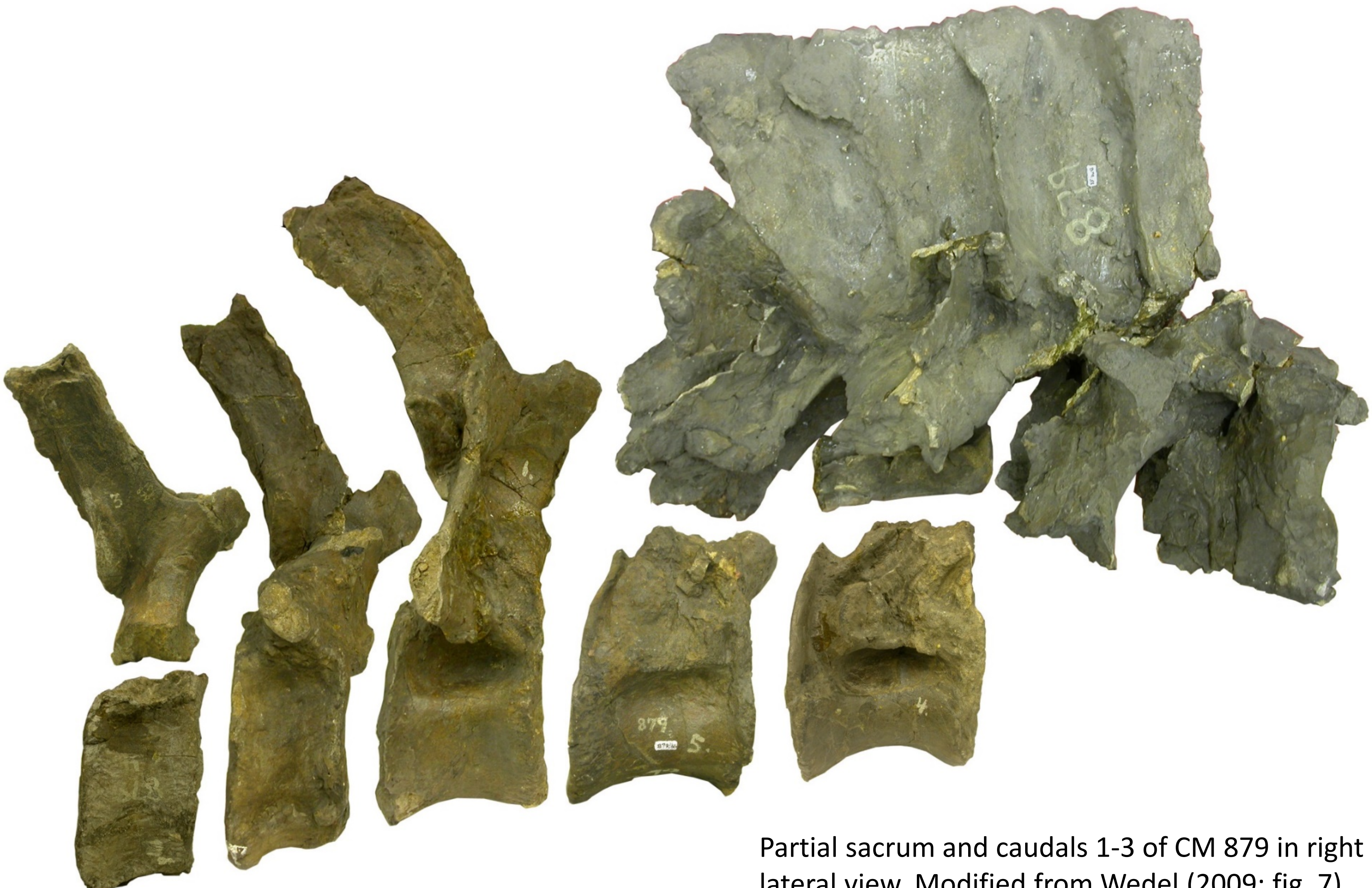


Figure 1 Endosacral casts. (a) *Barosaurus* (after Janensch, 1939). (b) *Kentrosaurus* (after Hennig, 1915). Scale bar = approximately 10 cm; stippled areas = intersegmental openings; left = anterior.

From Giffin (1991).

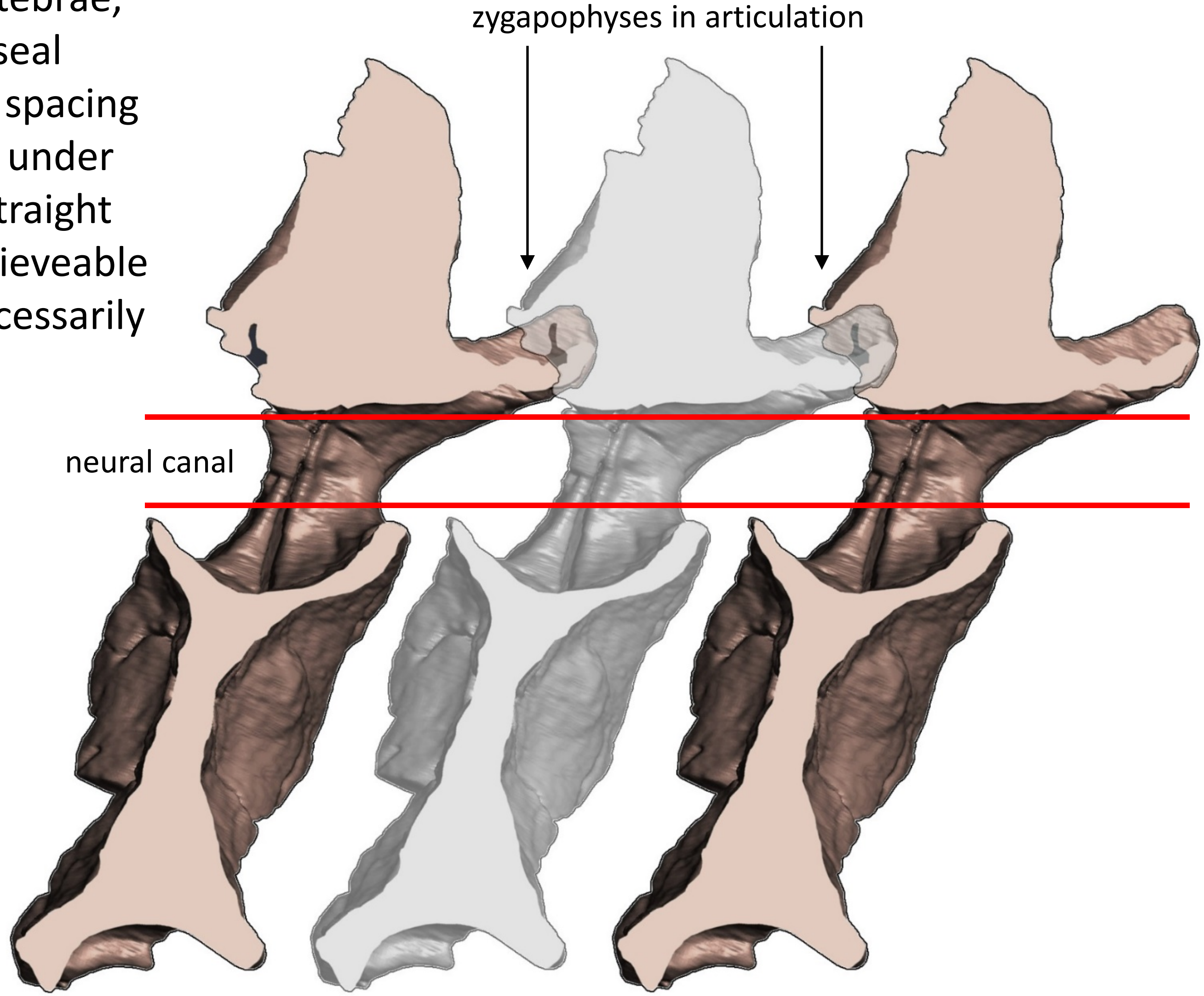
Neural canals sloped relative to the centra are also present in the proximal caudals of other specimens of *Haplocanthosaurus*, albeit to a lesser extent. The slope is roughly 14° in CM 879, shown here, versus 18° in MWC 8028.



Partial sacrum and caudals 1-3 of CM 879 in right lateral view. Modified from Wedel (2009: fig. 7).

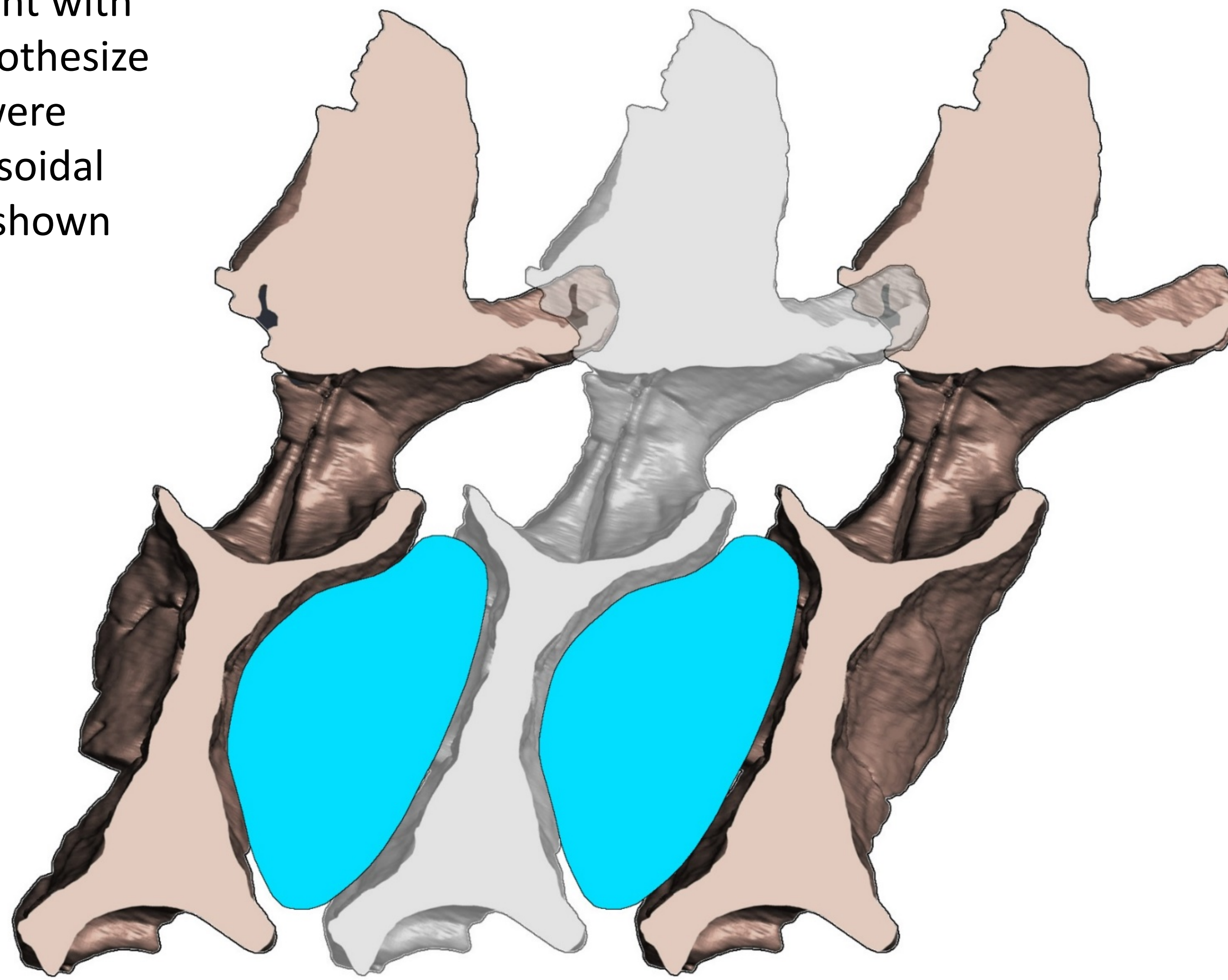
With the digital rearticulation still in progress, we cloned caudal 3 of MWC 8028, the only vertebra that preserves both sets of zygapophyses, to get a rough estimate of the sizes and shapes of the soft tissues that filled the intervertebral spaces and neural canal.

In rearticulating the vertebrae, we used the zygapophyseal facets to determine the spacing between the vertebrae, under the assumption that a straight neural canal was an achieveable posture in life (if not necessarily the default).



The deeply amphicoelous centra would have enclosed large intervertebral joint spaces. The total volume of the soft tissues that filled the joint spaces probably exceeded the volume of the vertebral centra.

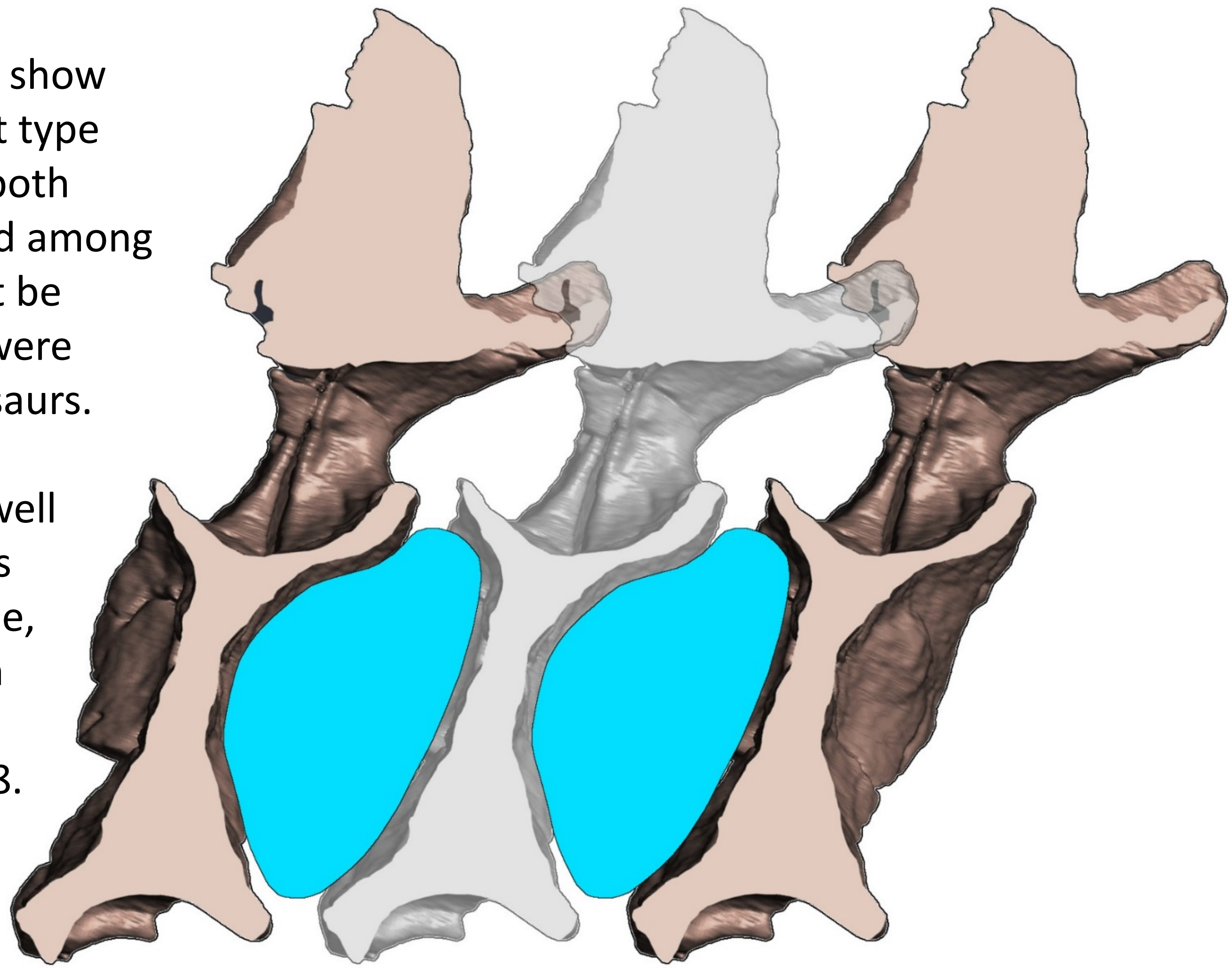
Such large intervertebral joint spaces are not consistent with synovial joints. We hypothesize that the joint cavities were occupied by thick, ellipsoidal discs of fibrocartilage, shown here in blue.



There is a widespread misapprehension in vertebrate paleontology that all non-mammalian amniotes have synovial intervertebral joints. In fact, some lizards have amphiarthrodial (fibrocartilaginous) joints throughout their vertebral columns (Winchester and Bellairs 1977, Winchester 1978), and birds have fibrocartilaginous joints between their free caudal vertebrae (Baumel 1993).

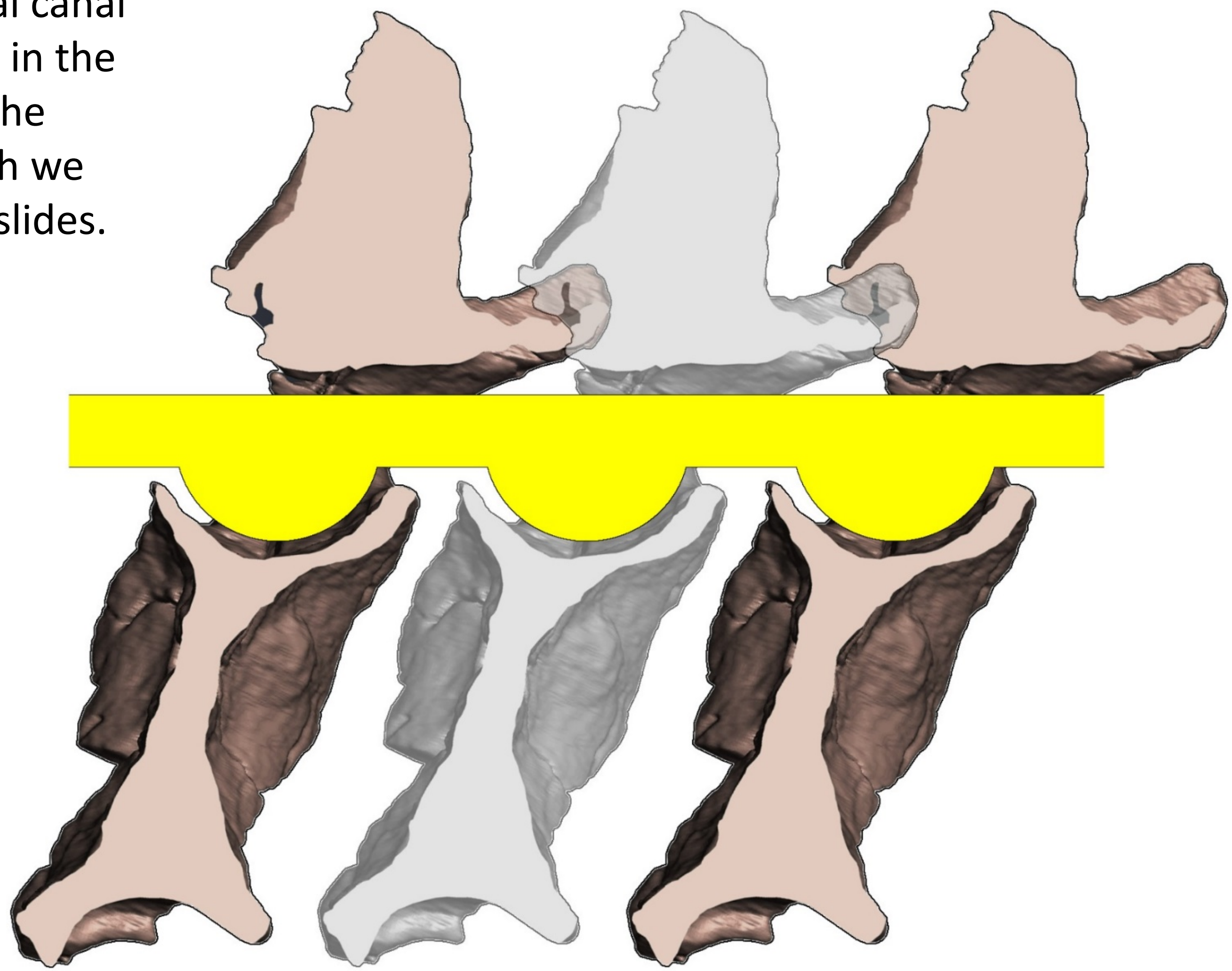
Extant birds and lizards show that intervertebral joint type can be highly variable both within an individual and among species, so it would not be surprising if the same were true of non-avian dinosaurs.

Other sauropods may well have had synovial joints between their vertebrae, but that does not seem to have been the case in the tail of MWC 8028.



The tissues that filled the expanded neural canals are more mysterious. Here we have illustrated one hypothesis, that the expanded neural canals accommodated expansions of the spinal cord, as seen in extant ostriches.

In extant birds, at least four different types of neural canal expansions are present in the lumbosacral region of the vertebral column, which we review in the next few slides.



Streeter 1904: fig 1

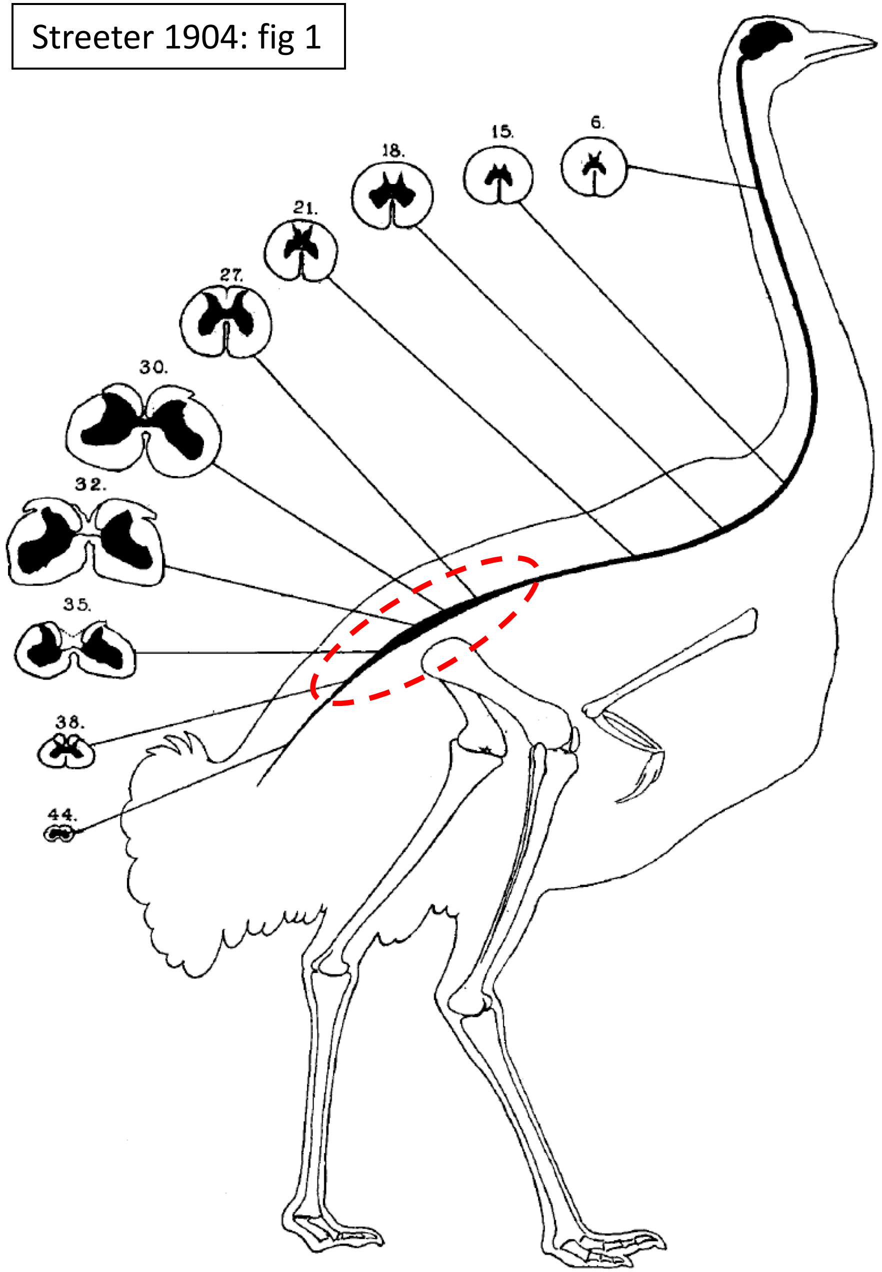


FIG. 3. Topography of the spinal cord of the ostrich. The transverse sections are all made on the same scale of enlargement and their proper levels are indicated on the drawing.

1. **Lumbosacral expansion** of gray and white matter of the cord in the spinal levels that serve the hindlimbs.

- Present in all limbed tetrapods, and in some fishes with sensitive fins.

- Cord expands and contracts gradually, over many segments.

- Even though the cord does not fill the volume of the neural canal, the swellings adjacent to the limbs are reflected in increased neural canal diameter at those levels (Giffin 1990).

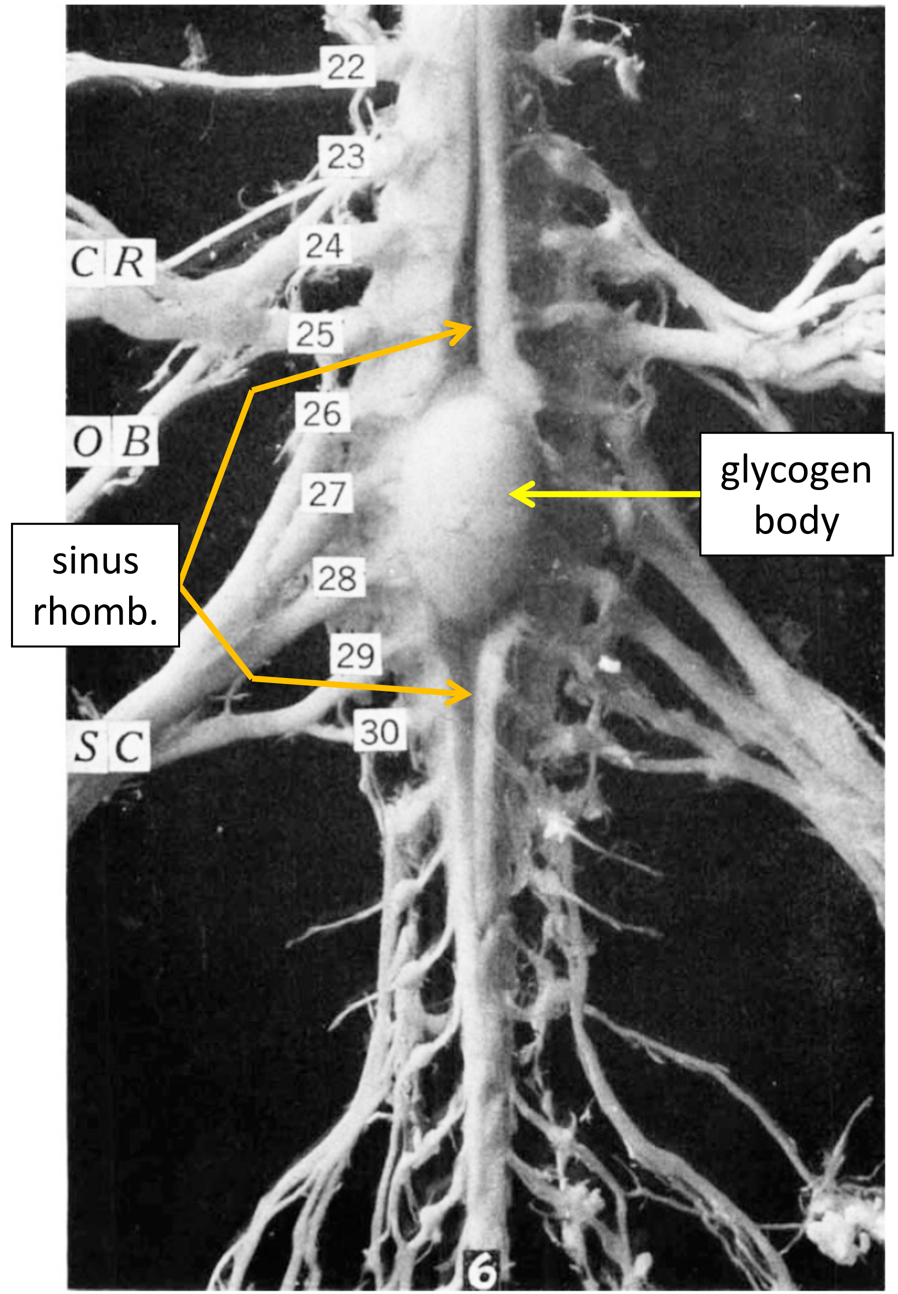
2. **Glycogen body**: a mass of specialized, glycogen-rich glial cells that occurs only in birds.

- Occupies a trough, the *sinus rhomboidalis*, that separates the dorsal halves of the spinal cord.

- Varies widely in size among taxa, from tiny (e.g., ostriches) to larger in cross-section than the spinal cord itself (e.g., chickens, pigeons).

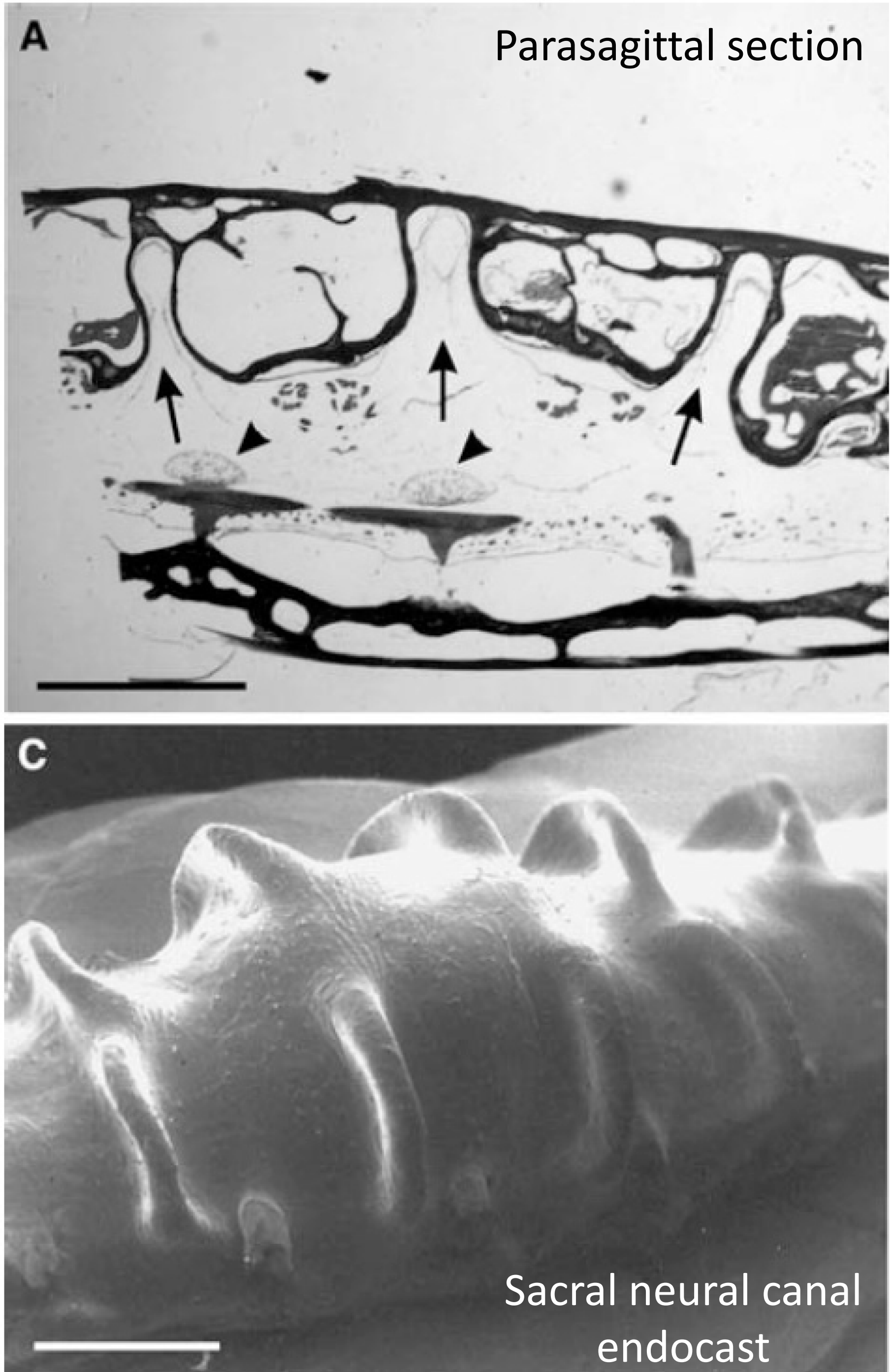
- Serially, it expands and contracts rapidly, over just a few segments.

- If the glycogen body is large, the neural canal will be noticeably expanded to accommodate it.



3-week-old chick, Watterson 1949: pl. 1

6 Dissection of the vertebral column and meninges of a chick three weeks post-hatching. CR = nervus cruralis; OB = obturator nerve; SC = sciatic (ischiadicus) nerve. × 5.



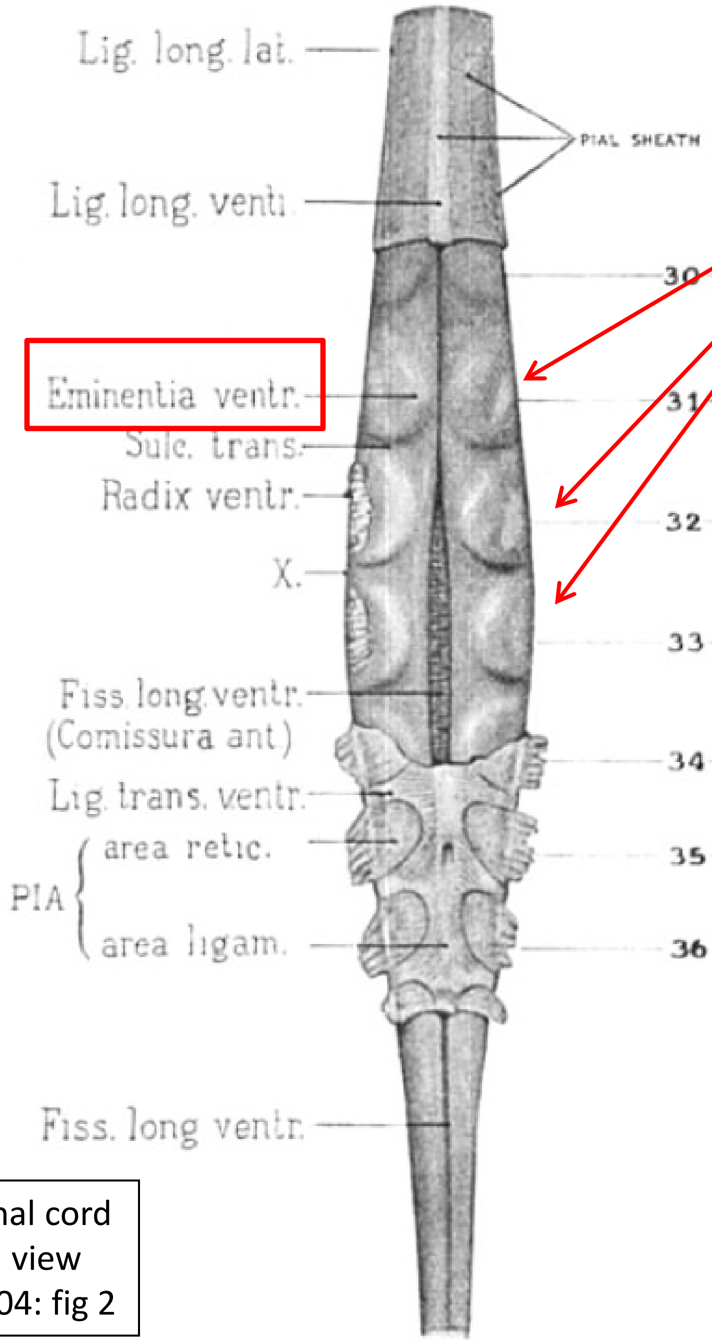
3. **Lumbosacral canals**: transverse, fluid-filled meningeal tubes that arch dorsally over the spinal cord.

- Present in most (all?) birds, larger and earlier-developing in weak fliers and flightless taxa.

- These canals occupy expansions of the neural canal at former intervertebral joints in the synsacrum.

- Many lines of evidence point to function as semicircular-canal analogues for maintaining equilibrium—see Necker (2005).

Necker 2005: fig 3



Ostrich spinal cord
in ventral view
Streeter 1904: fig 2

4. **Ventral eminences**: segmental bumps on the ventral surface of the spinal cord.

- Caused by increased cross-sectional area of spinal cord ventral horn (motor neurons) adjacent to ventral roots of spinal nerves.

- Ventral roots emerge from the ventral eminences.

- Only lumbosacral specialization that projects ventrally instead of dorsally or laterally.

- Osteological correlates: these bumps fill troughs in the floor of the neural canal in the synsacrum.

Type	Made of	Occurs in	Segmental or continuous	Anatomical direction	Osteological correlate?
Lumbosacral enlargement	White and gray matter	Limbed tetrapods	Continuous, many segments	All directions (radially)	Neural canal expansion
Glycogen body	Glycogen cells (glia)	Birds	Continuous, few segments	Dorsal	Neural canal expansion
Lumbosacral canals	Meninges	Birds	Segmental	Dorsolateral	Neural canal expansion
Ventral eminences	Gray matter	Ostriches, other birds?	Segmental	**Ventral**	Neural canal expansion

Of all the specializations of the spinal cord in birds, only the ventral eminences of ostriches expand ventrally. All others expand the neural canal in other directions, or in all directions at once. And the osteological trace is not the same as in MWC 8028—the ventral eminences of ostriches occupy bilaterally paired troughs in the floor of the canal, not a single midline depression. Still, ventral eminences show that some dinosaurs have ventrally-expanded neural canals to house 'extra' motor neurons that innervate large groups of muscles.

Possibly the expanded neural canals of MWC 8028 accommodated expansions of the spinal cord to help innervate the large muscle groups of the pelvis and tail, including the caudofemoralis, which provided most of the hindlimb power stroke for walking.

It is not clear, however, why such spinal swellings would be present in *Haplocanthosaurus*, a relatively small-bodied and small-tailed sauropod, but absent in larger-bodied and 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 dorsals or sacrals.

Ventral eminences of the spinal cord were not *definitely* present in MWC 8028; that is merely the least bad hypothesis we have yet found to explain the expanded neural canals.

An adult *Apatosaurus* (left) to scale with *Haplocanthosaurus* CM 879 (right).
Apatosaurus sculpture by Jorge Blanco and Steve Riojas, photo by M. Wedel.

Conclusions

MWC 8028 is characterized by three unusual morphological features:

- Deeply amphicoelous caudal vertebrae. Biconcave centra are rare in dinosaurs, and the caudal centra of other specimens of *Haplocanthosaurus* are only shallowly amphicoelous. The large intervertebral joint spaces are inconsistent with synovial joints, and were probably occupied by large fibrocartilaginous discs in life, as in the intervertebral joints of some extant lizards and the unfused caudal vertebrae of extant birds.
- Neural canals in caudal vertebrae strongly sloped relative to the centra. This character is present in other specimens of *Haplocanthosaurus* and in some other sauropod taxa, but not to the same degree as in MWC 8028. The implications of this character for function or habitual posture in life are not yet known.
- Ventrally-expanded neural canals in the proximal caudal vertebrae. Although birds have several types of neural canal expansions in the lumbosacral region, only the ventral eminences of ostriches, which accommodate extra motor neurons for the large hindlimb muscles, expand the neural canal ventrally. Still, it is not clear why the small-bodied and small-tailed *Haplocanthosaurus* would need such expansions, which have not been reported in any other sauropod.

Closing thought: this research is ongoing, and we welcome your input. If there are facts or hypotheses we haven’t considered but should, please let us know!

Acknowledgments

We thank John Foster for initiating research on MWC 8028 and for numerous conversations since, Julia McHugh at the Museum of Western Colorado – Dinosaur Journey for access to the specimen, and many colleagues for sharing their thoughts on the specimen, especially Mike Taylor and Anne Weil.

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