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RESEARCH ARTICLE

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Neural canal ridges: A novel osteological correlate of postcranial neuroanatomy in dinosaurs

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Abstract

In this article, we document the widespread presence of bony ridges in the neural canals of non-avian dinosaurs, including a wide diversity of sauropods, two theropods, a thyreophoran, and a hadrosaur. These structures are present only in the caudal vertebrae. They are anteroposteriorly elongate, found on the lateral walls of the canal, and vary in size and position both taxonomically and serially. Similar bony projections into the neural canal have been identified in extant teleosts, dipnoans, and urodelans, in which they are recognized as bony spinal cord supports. In most non-mammals, the dura mater that surrounds the spinal cord is fused to the periosteum of the neural canal, and the denticulate ligaments that support the spinal cord can pass through the dura and periosteum to anchor directly to bone. The function of these structures in dinosaurs remains uncertain, but in sauropods they might have stabilized the spinal cord during bilateral movement of the tail and use of the tail as a weapon. Of broader significance, this study emphasizes that important new discoveries at the gross anatomical level can continue to be made in part by closely examining previously overlooked features of known specimens.

KEYWORDS

bony spinal cord supports, dinosaur, neuroanatomy, osteological correlate, paleontology, sauropod

1 | INTRODUCTION

The vertebrate spinal cord passes through a tube known as the neural canal, which is formed by the vertebral foramina of successive vertebrae. In life, the bony components of the neural canal are bound together by various ligaments and lining membranes, uniting soft and hard tissue in a protective yet flexible cradle for the spinal cord

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and the roots of the spinal nerves. Throughout tetrapod evolutionary history, the spinal cord itself has remained largely morphologically conserved (Butler & Hodos, 2005; Hodos, 2009). In contrast, the neural canal may house expansions, cavities, channels, and foramina related to numerous body systems, including the neural tissue of the spinal cord, glial tissue, the meninges, vasculature, and even, in birds, pneumatic diverticula of the respiratory system (see review in Wedel et al., 2021). Non-pathological bony projections into the neural canal are less well understood, despite their presence in many extant fishes and amphibians (Skutschas, 2009; Skutschas & Baleeva, 2012) and in at least some fossil amniotes (Averianov & Lopatin, 2020). Aside from clinical symptoms caused by pathological spinal stenosis, the neural canals of vertebrates are generally under-studied. This is doubly true in extinct taxa—the neural canals of fossilized vertebrae are often not completely prepared (i.e., they are left full of rock matrix). We have therefore been opportunistic in our investigation, comparing extinct and extant taxa as we are able, to test hypotheses about the soft tissues associated with specific osteological correlates.

Relatively little is known about the anatomy of the postcranial nervous system and associated structures (such as the meninges) in dinosaurs. However, the subject has been extensively discussed in extant groups, and we start here as a basis for making inferences in fossil taxa. Sakka et al. (2016) recently reviewed the anatomy and evolution of the spinal cord meninges in vertebrates. Other useful descriptions of the meninges and their specializations in various vertebrate groups include Palay (1944) for amphibians, and Streeter (1904), Hansen-Pruss (1923), and Azcoitia et al. (1987) for birds. Two key points from previous work are relevant here.

The first is that all vertebrates, including cyclostomes, have a system of connective tissues ("ligaments" sensu lato) derived from the innermost meningeal layer (pia mater) that project laterally from the spinal cord and anchor the cord to the outer meningeal envelope (dura mater; Ariëns Kappers et al., 1936; Sakka et al., 2016). These connective tissues are alternatively referred to as "lateral ligaments" (Necker, 2006; Sakka et al., 2016) or "denticulate ligaments" (Azcoitia et al., 1987; Ceylan et al., 2012; Elvan et al., 2020; Streeter, 1904; Tubbs et al., 2001); in Nomina Anatomica Avium (Baumel, 1993) each one is "*Ligamentum denticulatum*". For simplicity and consistency, we will refer to them as "denticulate ligaments" herein. The denticulate ligaments form part of a deeply conserved mechanosensory system of intraspinal stretch receptors in the lateral portion of the spinal cord in vertebrates (Anadón et al., 1995; Necker, 2006; Picton et al., 2021; Schroeder, 1986).

A more elaborate system of supporting ligaments is present in birds (Baumel, 1993; Dingler, 1965; Hansen-Pruss, 1923; Necker, 2006; Streeter, 1904). The presacral denticulate ligaments are similar to those of other vertebrates, but the lumbosacral enlargement of the spinal cord is supported by a much stronger and more complex arrangement of ligaments. At each vertebral level, the lumbosacral spinal cord is supported by an arrangement of three ligaments (two lateral and one ventral) that is T-shaped in transverse section. The ligaments are all formed of pia mater and are continuous with each other, but for nomenclatural purposes they are divided into three groups based on their positions. The bilaterally paired, horizontal portion (the crossbar of the 'T' shape) is made up of a continuous band that stretches across the entire neural canal, ventral to the spinal cord. The portions of this band lateral to the spinal cord are called denticulate ligaments, and the portions ventral to the spinal cord are called transverse suspensory ligaments (*Ligamenta suspensoria transversa*, Baumel, 1993). The midsagittal, vertical portion (the upright of the 'T' shape) consists of an unpaired median ligament (*Ligamentum ventromedianum*, Baumel, 1993) that anchors the cord to the dura on the ventral midline. This arrangement of ligaments at each vertebral level is connected craniocaudally by a ventral longitudinal ligament, and by parasagittal connections between serially-adjacent denticulate ligaments, forming a double-ladder shape (Dingler, 1965: pp. 81–82 and figure 12). The entire system is substantial and can often be recognized in transverse sections of the avian spinal cord even when it is not labeled (e.g., Watterson, 1949: plate 5; compare to Streeter, 1904: figure 5 and Necker, 2006: figure 1).

The second point is that in non-mammalian vertebrates, the dura mater (or the homologous pachymeninx, in basal vertebrates) is typically attached or even fused to the periosteum that lines the inner walls of the neural canal (Hansen-Pruss, 1923; Sakka et al., 2016). An epidural space between the dura mater and the periosteum is only variably present in extant reptiles, sometimes as a potential space rather than an actual one (Sakka et al., 2016). In birds, the potential space between the dura mater and the periosteum can house an internal vertebral venous plexus (Baumel, 1993), and, in many lineages, air-filled paramedullary diverticula of the respiratory system (Atterholt & Wedel, 2022; Müller, 1908). In mammals, the epidural space is typically present in postcervical portions of the vertebral canal, and it is filled with loose connective tissue, adipose tissue, and a venous plexus (Gray, 1918). Even in mammals, the dura mater is in direct contact with the periosteum in the cervical region (Sakka et al., 2016: p. 14). Other attachments of the dura mater to the periosteum or to the dorsal longitudinal ligament in mammals include durovertebral attachments, the ligament of Trolard, the filum terminale

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externum, and fusion of the dura mater to the periosteum at each intervertebral foramen (Sakka et al., 2016: p. 8).

The extension of the denticulate ligaments to the dura mater, and the attachment or fusion of the dura mater to the periosteum, creates the possibility for the lateral attachments of the denticulate ligaments to become ossified. Bony spines or ridges that project medially from the lateral wall of the neural canal and anchor the denticulate ligaments were first described by Wake and Lawson (1973) in the extant salamander *Aneides*. Wake and Lawson (1973: p. 263 and figures 35 and 36) referred to these medially-projecting bony processes as "nerve cord supporters" or "nerve cord supports". Skutschas (2009) identified a pair of "small, bony thickenings" located along the lateroventral margins of the neural canal and described these as "neural cord supports" in the atlantes of the Cretaceous salamanders *Nesovtriton mynbulakensis* and *Eoscapherpeton asiaticum*.

Skutschas and Baleeva (2012) provided the first comprehensive review of ossified spinal cord supports in vertebrates. They reported that these structures are present in both extant and fossil salamanders, as well as teleost and dipnoan fishes. In contrast, they did not observe bony spinal cord supports in chondrichthyans, chondrosteans, or in frogs. This phylogenetic distribution led Skutschas and Baleeva to conclude that bony spinal cord supports are a synapomorphy of salamanders, independently derived from their occurrence in osteichthyans. Among amniotes, Skutschas and Baleeva (2012) only found rudimentary spinal cord supports in a hatchling lizard *Lacerta agilis* but reported them absent in adult *L. agilis*, and absent in the lizard *Laudakia caucasia*, snakes *Macrovipera lebetinus* and *Python regius*, tortoise *Testudo graeca*, pigeon *Columba livia*, and rat *Rattus norvegicus*. On this basis, they concluded that ossified spinal cord supports are absent in amniotes. The phylogenetic distribution of ossified spinal cord supports is at least partly explained by the presence or absence of three prerequisites for ossified spinal cord supports: a bony skeleton, without which the septal bundles that form the denticulate ligaments have no chance to become ossified (hence their absence in elasmobranchs and chondrosteans); septal bundles that protrude into the vertebral canal to reach the spinal cord, hence their absence in anurans (Skutschas & Baleeva, 2012: p. 8); and having the dura mater fused to the periosteum of the neural canal, allowing for the possibility of meningeal structures to attach to bone (hence their absence in mammals).

The following conclusions can be drawn from previous work on spinal cord supports in non-dinosaurian vertebrates. Ossified spinal cord supports are morphologically variable among taxa in mediolateral length, dorsoventral position within the neural canal, and orientation (Skutschas & Baleeva, 2012: pp. 2, 5; Figure 1, this article). They also vary serially within individuals (Skutschas & Baleeva, 2012). Large body size may make the spinal cord supports easier to detect, as in *Thunnus* (Figure 1a), but it is not a prerequisite for their presence, since they were first identified by Wake and Lawson (1973) in a larval salamander less than 2 cm long. Finally, ossified spinal cord supports are phylogenetically labile among major vertebrate clades.

Averianov and Lopatin (2020) described a new macronarian sauropod, *Abdarainurus barsboldi*, from the Upper Cretaceous Alagteeg Formation in the northern Gobi Desert of Mongolia, and identified neural canal ridges in the caudal vertebrae. Their description of these features is brief, apt, and worth quoting in full (Averianov & Lopatin, 2020: p. 16):

> In the anterior caudals of *Abdarainurus*, there are longitudinal ridges on the medial side of the neural arch pedicels forming the wall of the neural canal, approximately at the mid-height of the neural canal. These ridges are present in caudals A1 and A3–A7 (the neural arch is not preserved in caudals A2 and A8) and absent in the middle caudal, A10. These ridges have not been reported previously for any sauropod. By analogy with some fishes and amphibians, these ridges may have served as spinal cord supports.
>
> (Skutschas & Baleeva, 2012)

Working independently and concurrently, we discovered similar neural canal ridges in numerous sauropod genera, representing most of the major lineages of sauropods (Figure 2). Although our search was originally limited to sauropods, in time we found examples of other non-avian dinosaurs with neural canal ridges. We agree with Averianov and Lopatin (2020) that the neural canal ridges of non-avian dinosaurs may have served as spinal cord supports, as in fishes and amphibians, but that hypothesis will be on sturdier footing if alternative hypotheses are evaluated. Our goals in this article are to describe the neural canal ridges in the taxa we examined, to summarize all known instances of neural canal ridges in vertebrates (Figure 3), and to consider alternative hypotheses to explain the soft tissue correlates and possible functions of neural canal ridges in non-avian dinosaurs.

2 | MATERIALS AND METHODS

We examined the inner surface of the neural canals from a wide range of sauropod and other dinosaur specimens.

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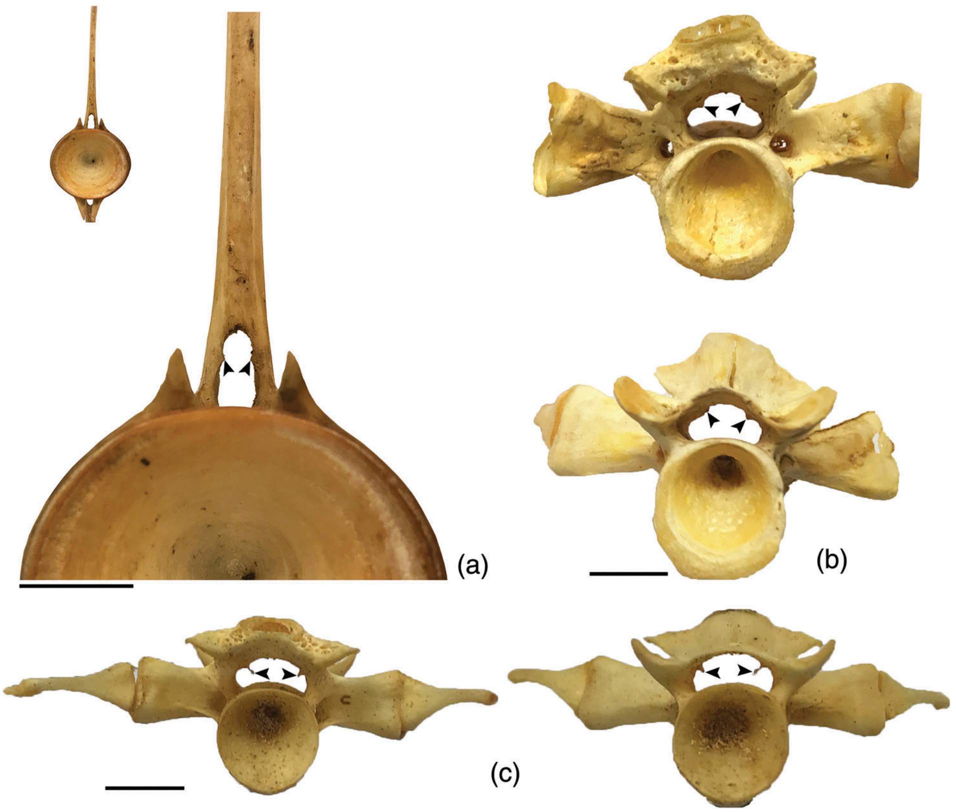

FIGURE 1 Bony spinal cord supports in extant vertebrates. (a) *Thunnus* sp. vertebra (OMNH RE 0042), anterior view. Scale bar = 1 cm. (b) Dorsal vertebra with supports in *Andrias japonicus* (LACM 162481) in posterior view (top) and anterior view (bottom). Scale bar = 0.5 cm. (c) Dorsal vertebra with supports in *Andrias davidianus* (LACM 162475) in posterior view (left) and anterior view (right). Scale bar = 0.5 cm.

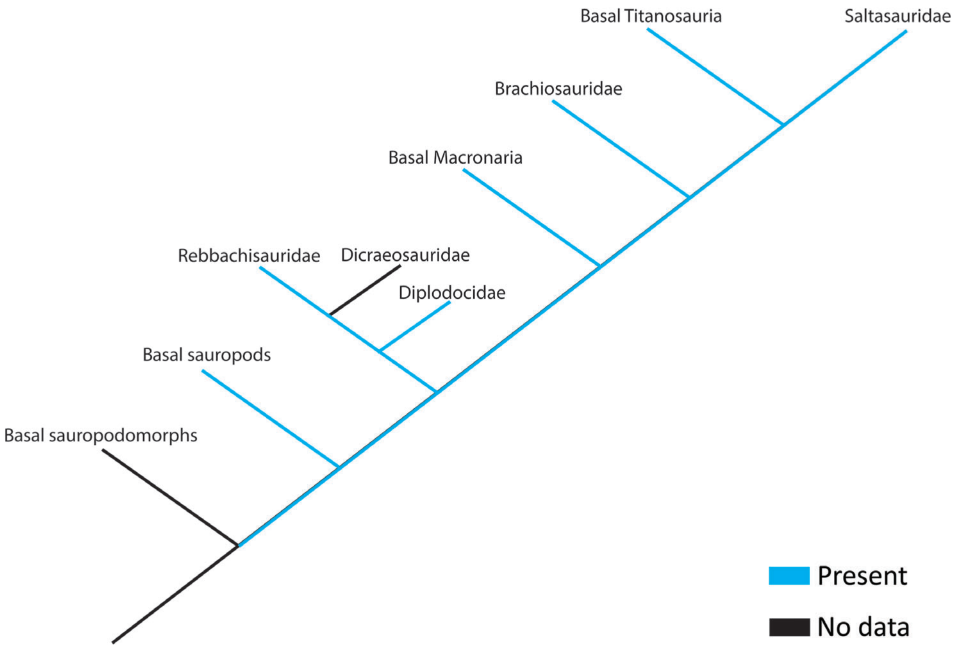

FIGURE 2 Phylogeny showing sauropod groups in which bony spinal cord supports have been observed. Blue = present, black = no data. Spinal cord supports are indicated as present if at least one individual in a given group exhibits them, but does not imply that these structures are ubiquitously present across individuals or genera within a group. The presence of bony spinal cord supports in rebbachisaurids is based on observations of uncatalogued specimens from the Isle of Wight.

For a given specimen, all available vertebrae were observed; however, we only found neural canal ridges in the caudal vertebrae. For comparative purposes, we also documented neural canal ridges in prepared dry skeletal specimens of several extant taxa from collections at the Natural History Museum of Los Angeles County and the Oklahoma Museum of Natural History.

In addition to documenting neural canal ridges in specimens that we were able to personally examine, we also found some instances in which neural canal ridges were visible in photographs in previously published works, although not commented on by those authors. This is analogous to pre-discovery or "precovery" images in astronomy, in which asteroids, comets, and Kuiper

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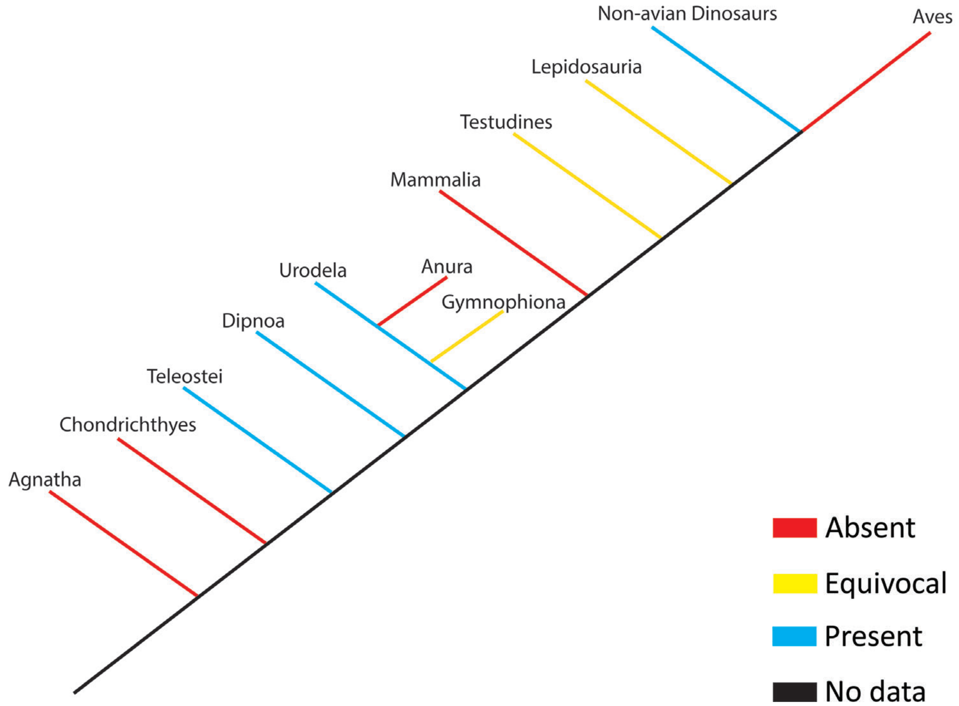

FIGURE 3 Phylogeny showing vertebrate clades in which bony spinal cord supports have been observed. Blue = present; red = absent; yellow = equivocal, more data needed. Figure shows current known presence and absence of these structures, but does not attempt to infer ancestral states.

Belt objects have often been photographically recorded before anyone recognized their existence as new and distinct objects (see, e.g., Boattini et al., 2001). An unusual case is that of the sauropod *Brontomerus*, in which a neural canal ridge is visible in a figure (Taylor et al., 2011: figure 6D) in an article coauthored by one of the authors of this work (MJW), but not recognized or mentioned in the original description. All novel observations of bony spinal cord supports are reported in Table 1. A summary of specimens with bony spinal cord supports from previously-published works (both pre-discovery and explicitly described) is found in Table 2.

The radiographic techniques discussed herein were performed at Hemet Valley Imaging Center in Hemet, California. Computed tomography (CT) scans of sauropod vertebrae were performed using a Philips Brilliance 64 slice CT scanner. Scout images were obtained in coronal projection with a technique setting of 120 kVp (kilovolt peak) and 30 mA (milliamperes). The coronal images were scanned at 0.67 mm slice thickness at the maximum technique setting of 140 kVp at 385 mA. Data were reconstructed in bone algorithm applied by a Philips Extended Brilliance Workstation and a Fuji Film Medical Systems Synapse PACS.

To remove remaining matrix and further analyze the individual vertebra, CT scans of MWC 10613 were processed to generate a virtual 3D surface model. We used the three-dimensional visualization program Amira 6.2$^{®}$ to segment the vertebra and produce a Polygon File Format (.PLY) for 3D visualization and printing. The PLY model of MWC 10613 is available on MorphoSource at https://www.morphosource.org/concern/media/000655927?locale=en.

Institutional abbreviations: BIBE, Big Bend National Park, Texas, USA; CM, Carnegie Museum of Natural History, Pittsburg, Pennsylvania, USA; DFMMh, Dinosaurier-Freilichtmuseum Münchehagen/Verein zur Förderung der Niedersächsischen Paläontologie (e. V.), Germany; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; G, Museum of Gloucester, Gloucester, UK; MWC, Museums of Western Colorado, Dinosaur Journey, Fruita, Colorado, USA; NHMUK, Natural History Museum, London, United Kingdom; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; RAM, Raymond M. Alf Museum of Paleontology, Claremont, California, USA. SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas, USA; SUSA, Southeastern Utah Society of Arts and Sciences, Moab Museum, Moab, Utah, USA.

3 | RESULTS

The descriptions below focus on the dinosaurian taxa in which neural canal ridges are described for the first time for most clades. Most are in sauropod dinosaurs (Figure 2), though we also document two occurrences in theropods, one in a thyreophoran, and one in a hadrosaur. The only previously described example in dinosaurs is the probable basal titanosaur *Abdarainurus* in

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TABLE 1 Novel observations of bony spinal cord supports.

Taxon	Specimen number	Vertebral region
Sauropods		
Cetiosaurus sp.†	G10005	Caudal
Haplocanthosaurus sp.†	CM 879	Caudal
Apatosaurus†	MWC 5019, MWC 2250, MWC 5270, MWC 5521, MWC 5653, MCW 7399, MWC 4016, MWC 3838, MWC 2724, MWC 2739, MWC 5005	Caudal
Diplodocus sp.†	MWC 10613, MWC 3797	Caudal
Camarasaurus sp.†	MWC 5496, MWC 2847, SUSA 515, CM 584	Caudal
Brachiosaurus altithorax†	FMNH P25107	Caudal
Brontomerus mcintoshi†	SMU 61732, OMNH 61248	Caudal
Astrophocaudia slaughteri†	SMU 61732	Caudal
Alamosaurus sanjuanensis†	BIBE 45885	Caudal
Rapetosaurus krausei†	FMNH PR 2209	Caudal
Sauropoda indet.†	MWC 7399, MWC 5915, MWC 8049, MWC 5077	Caudal
Non-sauropod dinosaurs		
Allosaurus sp.†	MWC 6703	Caudal
Hadrosauridae indet.†	RAM 23434	Caudal
Other vertebrates		
Thunnus	OMNH RE 0042	Caudal
Andrias japonicus	LACM 162481	Dorsal
Andrias davidianus	LACM 162475	Dorsal

Averianov and Lopatin (2020); as that example is already published, we have not redescribed it here. Also included are descriptions of bony spinal cord supports in a handful of extant taxa (the tuna *Thunnus* and giant salamanders *Andrias*), based on our first-hand observations of dry skeletal specimens in museum collections.

3.1 | *Thunnus* sp. (OMNH RE 0042)

Neural canal ridges are present in a tuna vertebra, located in a very dorsal position on the wall of the dorsoventrally elongate neural canal (approximately 2/3s of the way up; Figure 1a). In this taxon, the neural arch is quite short along its anteroposterior axis, thus the bony spinal cord supports are not elongate ridges, but rather anteroposteriorly abbreviated projections into the space of the neural canal.

3.2 | *Andrias japonicus* (LACM 162481)

In a dorsal vertebra of a Japanese giant salamander, the neural canal is ovoid in shape, with the mediolateral axis longer than the dorsoventral axis. Bony spinal cord supports present as distinct bumps projecting into the canal, located in a very dorsal position on the wall of the canal (Figure 1b).

3.3 | *Andrias davidianus* (LACM 162475)

In a dorsal vertebra of a Chinese giant salamander, bony spinal cord supports are very similar in position to those in the dorsal vertebra of a giant Japanese salamander; they are located in a very dorsal position on the lateral walls of the dorsoventrally-compressed neural canal (Figure 1c). However, they differ in that they present as sharp, elongate, spike-like projections which extend further into the space of the canal than those of the giant Japanese salamander.

3.4 | *Cetiosaurus* sp. (G10005)

G10005 is a non-neosauropodan sauropod anterior caudal vertebra from Bajocian-Bathonian of Gloucestershire, UK. The centrum lacks a keel or ventral hollow, pneumatic features, and ventrolateral ridges; there is no indication of wing-shaped transverse processes; and the neural arch only has simple lamination, unlike Callovian sauropod caudals from the UK (Holwerda et al., 2019). In the absence of those derived features, it is unlikely that this early Middle Jurassic caudal belonged to a neosauropod. It more likely represents a non-neosauropod eusauropod. The presence of a ‘lip’ on the ventral side of the articular surface, together with a boss and accompanying concavity on the anterior and posterior surface, is shared with *Cetiosaurus oxoniensis* and *Patagosaurus fariasi* from the early Middle Jurassic (Holwerda et al., 2021; Upchurch & Martin, 2003), making it likely this caudal belonged to a cetiosaurid eusauropod, and possibly *Cetiosaurus*.

The neural canal is oval in anterior view, elliptical in posterior view, and wider ventrally than dorsally. This specimen shows a sharp triangular protrusion internally on each lateral side, which are also visible in posterior view (Figure 4a). These protrusions continue along the lateral walls of the neural canal as elongated ridges.

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TABLE 2 Bony spinal cord supports from previous publications. In some cases, details such as a specimen number or vertebral region in which the supports were observed are not noted in the original publication. A question mark indicates uncertainty of the vertebral region in cases where it was not specified by the original publication.

Larger clade	Taxon	Specimen number	Vertebral region	Citation
New observations from previous publications (precovery images)				
Sauropoda	*Europasaurus holgeri*†	DFMMh/FV 553.1	Caudal	Carballido and Sander (2014)
	Camarasaurus sp.†	—	Sacral	Marsh (1896)
Theropoda	*Ceratosaurus* sp.†	UUVP 5960	Caudal	Madsen and Welles (2000)
Thyreophora	*Stegosaurus*	NHMUK PV R36730	Caudal	Maidment et al. (2015)
Teleostei	*Salmo salar*	—	Caudal?	Watt et al. (1997)
	Argentina silus	—	Dorsal?	Watt et al. (1997)
Reports from previous publications				
Sauropoda	*Abdarainurus barsboldi*†	PIN 5669/1	Caudal	Averianov and Lopatin (2020)
Urodela	*Eurycea bislineata*	—	Atlas and trunk	Wake and Lawson (1973)
	Nesovtriton mynbulakensis†	ZIN PH 1/85	Atlas	Skutschas (2009)
	Eoscapherpeton asiaticum†	ZIN PH 15/85	Atlas	Skutschas (2009)
	Salamandrella sp.	—	—	Skutschas (2009)
	Cryptobranchus sp.	—	—	Skutschas (2009)
	Andrias sp.	—	Atlas, trunk, and caudal	Skutschas (2009) Skutschas and Baleeva (2012)
	Ambystoma sp.	—	—	Skutschas (2009)
	Salamandra sp.	—	—	Skutschas (2009)
	Kiyatriton sp.†	—	—	Skutschas (2009)
	Scapherpeton sp.†	—	—	Skutschas (2009)
	Kokartus sp.†	—	—	Skutschas (2009)
	Salamandra salamandra	—	Trunk and caudal	Skutschas and Baleeva (2012)
	Salamandrella keyserlingii	—	—	Skutschas and Baleeva (2012)
	Lissotriton vulgaris	—	—	Skutschas and Baleeva (2012)
Teleostei	*Salmo salar*	—	Trunk and caudal	Skutschas and Baleeva (2012)
	Oncorhynchus mykiss	—	—	Skutschas and Baleeva (2012)
Dipnoa	*Protopterus* sp.	—	—	Skutschas and Baleeva (2012)

3.5 | *Haplocanthosaurus priscus* (CM 879)

CM 879 is a partial skeleton of *Haplocanthosaurus* from the Marsh-Felch Quarry in the Morrison Formation near Garden Park, Colorado. The skeleton is that of a subadult individual, in which most of the vertebral neural arches are not fused to the centra. The third caudal vertebra of CM 879 has paired neural canal ridges (Figure 4b). The right ridge is more pronounced and appears slightly ventral to the ridge on the left, but the proximal caudals of this specimen have some shearing distortion and this asymmetry is more likely taphonomic than congenital. None of the other caudal vertebrae of this specimen show neural canal ridges, but it is not possible to determine whether these absences are genuine or if the ridges could have been obscured or destroyed during preservation, excavation, or preparation of the fossils.

3.6 | *Apatosaurus louisae* (MWC 5019)

MWC 5019 is an isolated partial caudal from the Mygatt-Moore Quarry in the Morrison Formation near Fruita, Colorado. The neural spine, zygapophyses, and transverse processes are missing, but the heart-shaped centrum and overall proportions show that the specimen is a proximal caudal of an apatosaurine sauropod. The only apatosaurine known from the Mygatt-Moore Quarry is *Apatosaurus louisae* (Foster et al., 2018), so we infer that MWC 5019 belongs to that taxon. The neural canal is oval, and

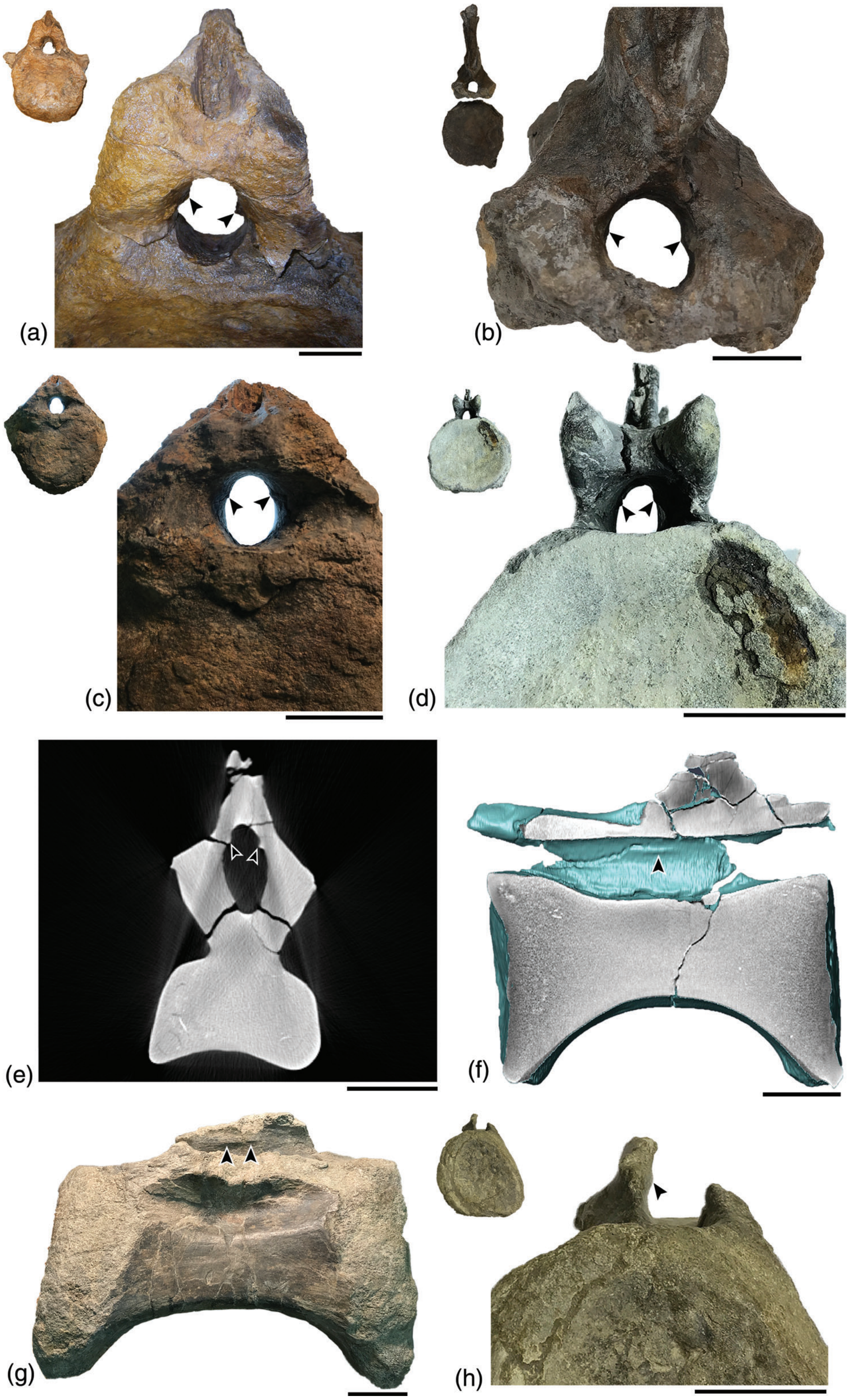

FIGURE 4 Bony spinal cord supports (arrows) in the caudal vertebrae of non-macronarian sauropods. (a) *Cetiosaurus* (G10005) showing posterior view of the neural canal. (b) *Haplocanthosaurus* (CM 879) showing posterior view of the neural canal. (c) *Apatosaurus* (MWC 5019) showing posterior view of the neural canal. (d–f) *Diplodocus* (MWC 10613) with the neural canal and bony spinal cord supports shown in anterior view, left lateral view (of a 3D model of the specimen), and a mid-sagittal transverse section (from a CT scan of the specimen) respectively. (g, h) Diplocodine (MWC 3797) with neural canal and bony spinal cord supports shown in right lateral and posterior views, respectively. In both diplodocine specimens, the elongate neural canal makes it difficult to visualize the spinal cord supports in anteroposterior view, as these structures are located deep in the canal at approximately the antero-posterior midpoint. All scale bars = 5 cm.

taller than wide. Relative to the size of the body of the vertebra, this foramen is small. The neural canal ridges are less sharply defined than in most other specimens described here, and grade into the walls of the canal to which they attached (Figure 4c). The ridges are present on the lateral sides of the canal and are closer to the dorsal surface than to the ventral surface.

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3.7 | *Diplodocus* sp. (MWC 10613)

MWC 10613 is one of an associated series of mid-caudal vertebrae from Bone Cabin Quarry in the Morrison Formation of Wyoming. The morphology of the vertebrae is a good match for those of AMNH 223, a partial skeleton which was originally referred to *D. longus* by Osborn (1899), but which Tschopp et al. (2015) recovered as *D. hallorum* (see Foster, 2020 for a review of historical and recent fieldwork at Bone Cabin Quarry). In MWC 10613, the neural canal is strongly ovate, and much taller than wide. The neural canal ridges are located high in the canal, nearly 3/4 of the way up the lateral wall and near the dorsal portion of the canal (Figure 4d–f). They are also relatively abbreviated in terms of length, occupying only about 20% of the lateral walls of the neural canal. The ridges are located just behind the anteroposterior midpoint of the canal.

3.8 | Diplodocinae indet. (MWC 3797)

MWC 3797 is an isolated partial caudal vertebra of an indeterminate diplodocine from the Mygatt-Moore Quarry (Foster et al., 2018: figure 19 [mistakenly referenced as MWC 3707]). The form and proportions of the centrum suggest an approximate serial position near caudal 20, by comparison with more complete specimens (Hatcher, 1901; Osborn, 1899). The right half of the neural arch and the entire neural spine above the neural canal are missing. Enough material remains to show that the neural canal was taller than wide, and an elongate ridge is situated at least halfway up the lateral wall on the left side of the canal (Figure 4g,h). The ridge is very similar to that of *Diplodocus* sp. MWC 10613, but situated a little farther anteriorly, near the anteroposterior midpoint of the canal.

3.9 | *Camarasaurus* sp. (MWC 5496)

MWC 5496 is from Hups Quarry 3A in the Morrison Formation near Delta, Colorado. In MWC 5496, the neural arch is incomplete, with the neural spine and dorsal portion missing. The bony spinal cord support has been lost from one side because the break was asymmetrical and occurred just below the bony ridge. However, this provides a clear view of the structure on the opposite side. This bony ridge is located on the lateral wall just dorsal to the midline of the dorsoventral axis (Figure 5a). Anteroposteriorly it occupies approximately the middle 1/3 of the neural canal. The ridge has a distinct edge that projects into the space of the canal, though the very anterior and posterior margins are slightly tapered and grade into the wall of the canal.

3.10 | *Camarasaurus* sp. (SUSA 515)

SUSA 515 is a partial skeleton of *Camarasaurus* from the Brushy Basin Member of the Morrison Formation on the slopes of the La Sal Mountains near Moab, Utah (Foster, 2005). It consists of posterior dorsal vertebrae, sacral vertebrae, anterior caudal vertebrae, and some fragments of the pelvis. The neural arch of the third caudal vertebra is incomplete, providing an excellent view of the lateral wall of the left side, where a prominent, sharp bony ridge is present along the ventral portion of the wall, just dorsal to the neurocentral joint (Figure 5b). This ridge extends anteroposteriorly along the middle half of the canal. The fifth caudal vertebral preserves something similar, but it is missing the left half of the neural arch. A distinct bony ridge is visible on the preserved right side of the neural canal (Figure 5c). This ridge is present near the ventral portion of the canal, similar to the position in caudal 3. The anteroposterior length of this ridge is approximately 1/3 the length of the canal.

3.11 | *Camarasaurus* sp. (CM 584)

CM 584 was collected from Sheep Creek Quarry D in the Morrison Formation of Wyoming, USA. It consists of a partial skeleton, including many vertebral elements (2 cervicals, 8 dorsals, and 31 caudals), all largely uncrushed and intact (McIntosh, 1981). In this specimen, neural canal ridges were observed in a middle caudal vertebra (Figure 5d). The ridges are located along the midpoint of the lateral walls of the neural canal, and are sharply defined but very small, projecting only slightly into the space of the foramen.

3.12 | *Brachiosaurus altithorax* (FMNH P25107)

The holotype partial skeleton of *Brachiosaurus* was recovered from the Brushy Basin member of the Morrison Formation in the Colorado River Valley west of Grand Junction, Colorado (Riggs, 1903, 1904). The first caudal vertebra of the specimen is essentially complete, and neural canal ridges are present (Figure 6a). The second caudal vertebra is missing the entire neural arch, including the portions that might have had neural canal ridges, and no other caudal vertebrae were recovered. The neural canal of the first caudal vertebra is small and roughly circular. Low bony ridges are present in a very dorsal position along the lateral walls of the canal.

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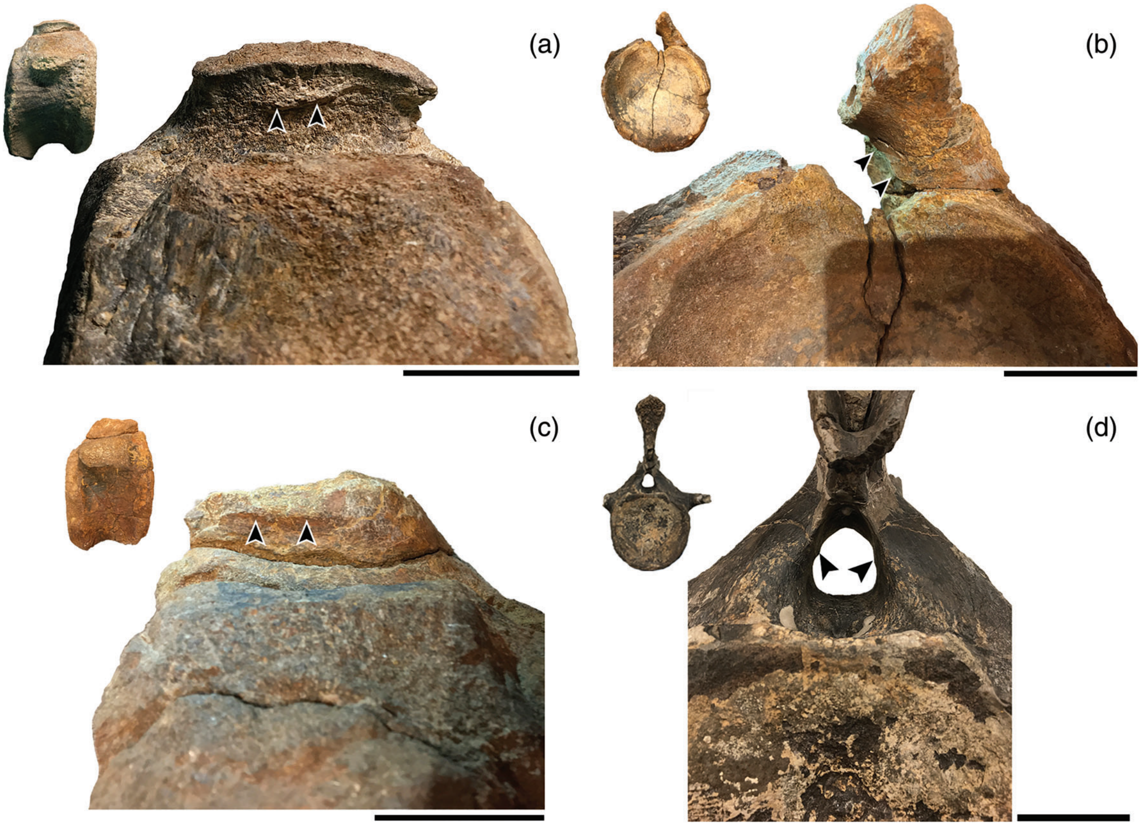

FIGURE 5 Bony spinal cord supports (arrows) in caudal vertebrae of several specimens of *Camarasaurus*. (a) Right lateral view of neural canal with broken vertebral arch, clearly exposing a bony spinal cord support (MWC 5496). (b) Anterolateral oblique view of the neural canal of the third caudal vertebra (SUSA 515) with a broken vertebral arch displaying a bony spinal cord support. (c) Right lateral view into the neural canal of the fifth caudal vertebra of SUSA 515, also with a broken arch allowing clear visualization of a bony spinal cord support. (d) Posterior view showing bony spinal cord supports in profile (CM 584). All scale bars = 5 cm.

3.13 | *Brontomerus mcintoshi* (OMNH 61248)

OMNH 61248 is from the Hotel Mesa Quarry, OMNH locality V857, in the Ruby Ranch Member of the Lower Cretaceous Burro Canyon Formation (laterally equivalent to the Cedar Mountain Formation) of southeastern Utah (Taylor et al., 2011). Sauropod material from the Hotel Mesa Quarry is all consistent with a single macronarian species, and Taylor et al. (2011) referred all the material, including OMNH 61248, to a single taxon, *Brontomerus mcintoshi*. In this specimen, identified as a distal caudal vertebra, the neural canal is circular in shape and small relative to the body of the vertebra. Neural canal ridges are located on the lateral walls, just dorsal to the midline of the canal (Figure 6b). They are slightly asymmetrical; the right ridge is more prominently formed with a sharper edge, and the left is more rounded and slightly more dorsal in the canal. With respect to the anteroposterior length of the canal, the ridges are abbreviated and restricted only to the middle portion.

3.14 | *Astrophocaudia slaughteri* (SMU 61732)

This specimen is the holotype for this taxon, from the Walnut Creek sauropod site in the Paluxy Formation (lower Albian) of Wise County, Texas (D'Emic, 2013). It consists of a partial skeleton, including 25 caudal vertebrae, partial pectoral and pelvic girdles, and other fragments. Neural canal ridges are present in all caudal vertebrae figured in the original description of this specimen (D'Emic, 2013).

The best-preserved neural canal ridges are present in the putative caudal 14 (Figure 6c). The vertebral foramen is dorsoventrally oblong, with a round dorsal margin and a squared-off ventral margin. The neural canal ridges are located asymmetrically approximately 2/3 of the way up the lateral walls of the canal, more dorsal than ventral. They also have an anteroposterior asymmetry; the ridges are shifted back, nearly reaching the posterior border of the neural canal. Both ridges project most strongly into the canal at the midpoint of the opening, and gradually become

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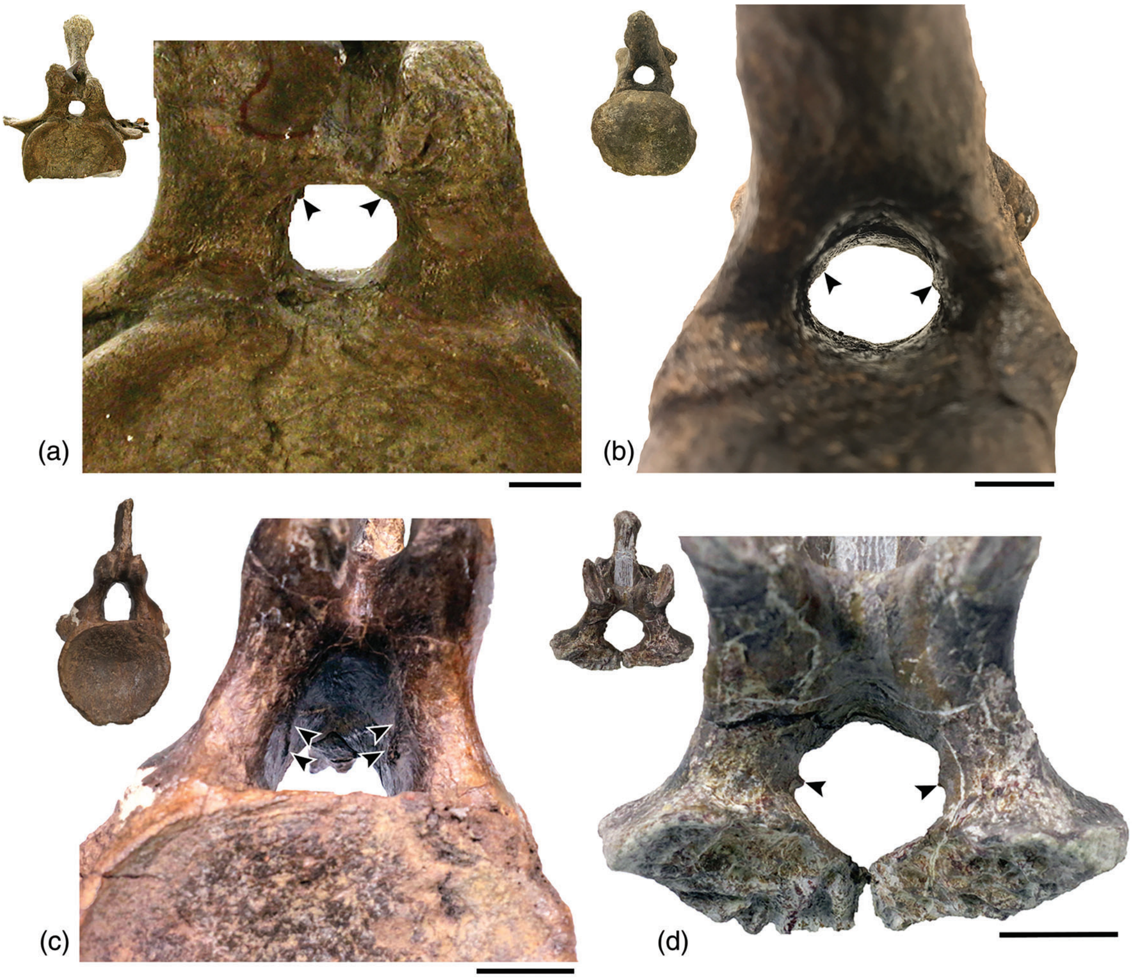

FIGURE 6 Bony spinal cord supports (arrows) in caudal vertebrae of titanosauriforms. (a) Anterior view of caudal 1 of *Brachiosaurus* (FMNH P25107). (b) Posterior view of a distal caudal in *Brontomerus mcintoshi* (OMNH 61248). (c) Anterior view of caudal 14 in *Astrophocaudia slaughteri* (SMU 61732). (d) Anterior view of the neural arch of an unfused caudal vertebra from a juvenile specimen of *Alamosaurus sanjuanensis* (BIBE 45885). All scale bars = 2 cm.

smaller moving posteriorly. The left bony ridge is larger than the right.

3.15 | *Alamosaurus sanjuanensis* (BIBE 45885)

This specimen is one of multiple, disarticulated elements representing parts of at least three small, relatively immature individuals, including multiple unfused neural arches and centra of vertebrae. The specimens come from a single site in the lower Black Peaks Formation (Maastrichtian) in Tornillo Flat, Big Bend National Park, Texas. Currently, all titanosaur material from the upper Javelina and lowermost Black Peaks Formations of Big Bend National Park is referred to *Alamosaurus sanjuanensis* (Lehman & Coulson, 2002; Tykoski & Fiorillo, 2016).

The neural canal of BIBE 45885 is roughly circular. The neural canal ridges are located slightly dorsal to midline of the lateral walls of the canal (Figure 6d). They form sharp ridges projecting prominently into the vertebral foramen. They are long relative to the length of the canal, extending nearly to the anterior and posterior margins.

3.16 | *Rapetosaurus krausei* (FMNH PR 2209)

FMNH PR 2209 is an associated and mostly complete skeleton of a juvenile titanosaur from the Maevarano Formation (Maastrichtian) of the Mahajanga Basin in northwestern Madagascar. It was referred to *Rapetosaurus* and described in detail by Curry Rogers (2009). None of the neural arches are fused to their respective

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vertebral centra in this specimen. The neural canals of the caudal vertebrae are slightly taller than wide. In both proximal and distal caudal vertebrae, prominent ridges are visible near the mid-point of the lateral walls of the neural canals (Curry Rogers, 2009: figures 27a and 29b).

Of note, we first observed these structures in photos of a caudal vertebra figured in Curry Rogers (2009: figures 27A and 29B). Subsequently, we were able to make observations from the actual specimen, mounted and on display at the Field Museum of Natural History in Chicago, Illinois. This is an important point, as it confirms that these features can indeed be accurately identified from photos.

In this specimen, neural canal ridges were observed serially, in every caudal vertebra with a well-preserved vertebral arch, and vertebral canal large enough such that observation was possible in the mounted skeleton. In total, they were observed in four caudal vertebrae across the tail, ranging from proximal, mid-caudal, and distal (Figure 7). In all four vertebrae, the neural canal ridges present as a thin, elongate ridge of bone that extends bilaterally along nearly the entire length of the lateral wall of the neural canal. The length of these ridges is proportional to the anteroposterior size of the arch; in the more proximal caudals (with an anteroposteriorly longer arch) they are longer, and in the more distal caudals (with an anteroposteriorly shorter arch) they are shorter. Otherwise, they are serially very similar in morphology and appearance. In all of these vertebrae, the neural canal ridges are angled and slightly curved, with the anterior end slightly higher than the posterior end.

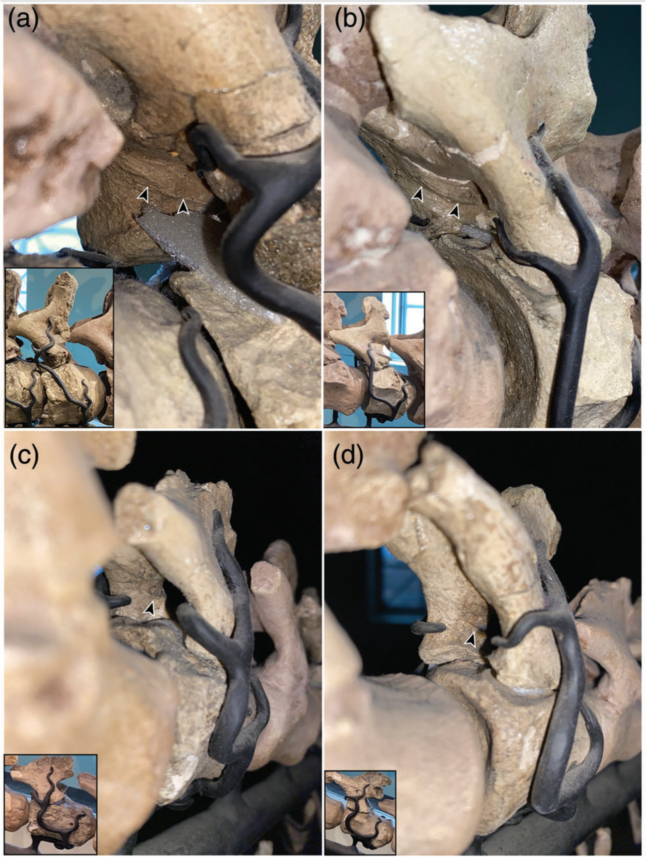

FIGURE 7 Bony spinal cord supports (arrows) in serial caudal vertebrae of *Rapetosaurus* (FMNH PR 2209). They were observed in one proximal (a), two mid-caudal (b, c), and one distal (d) caudal vertebra. Photos were taken from the mounted specimen on display at the Field Museum of Natural History; insets show each vertebra in left lateral view.

3.17 | *Allosaurus* sp. (MWC 5492)

MWC 5492 is a partial proximal caudal vertebra of a large theropod from the Mygatt-Moore Quarry (same locality as *Apatosaurus louisae* MWC 5019 and Diplodocinae indet. MWC 3797 described above). Both *Allosaurus* and *Ceratosaurus* are known from the Mygatt-Moore Quarry (Foster et al., 2018). The centrum of MWC 5492 is much taller than wide, with a narrow ventral margin, which is more consistent with the morphology of the proximal caudals of *Allosaurus* than those of *Ceratosaurus* (see Madsen, 1976: figure 26). The neural canal is rounded dorsally but narrows ventrally, giving it a rough teardrop shape in cross-section. The neural canal ridges are located high on the lateral walls, about 80% of the way up from the floor of the canal (Figure 8a). The right ridge is more distinct, and takes the form of a rounded shelf of bone that projects into the canal by slightly more than 1 mm. The left ridge is only preserved as a low, rounded bulge on the wall of the canal, but it may have been damaged taphonomically or during preparation.

3.18 | Hadrosauridae indet. (RAM 23434)

This specimen is an isolated caudal vertebra of a hadrosaur from the Kaiparowits Formation (Campanian) of Garfield County, Utah. It has undergone considerable taphonomic deformation, which has distorted the vertebra and vertebral canal. However, a pair of ridges is clearly visible protruding into the neural canal from the lateral walls (Figure 8b). They are located approximately at the vertical mid-point of the neural canal.

3.19 | Observations from published figures

In addition to specimens we examined in person, we have also found neural canal ridges in the figures of previously published articles. These observations are important because they expand the phylogenetic and

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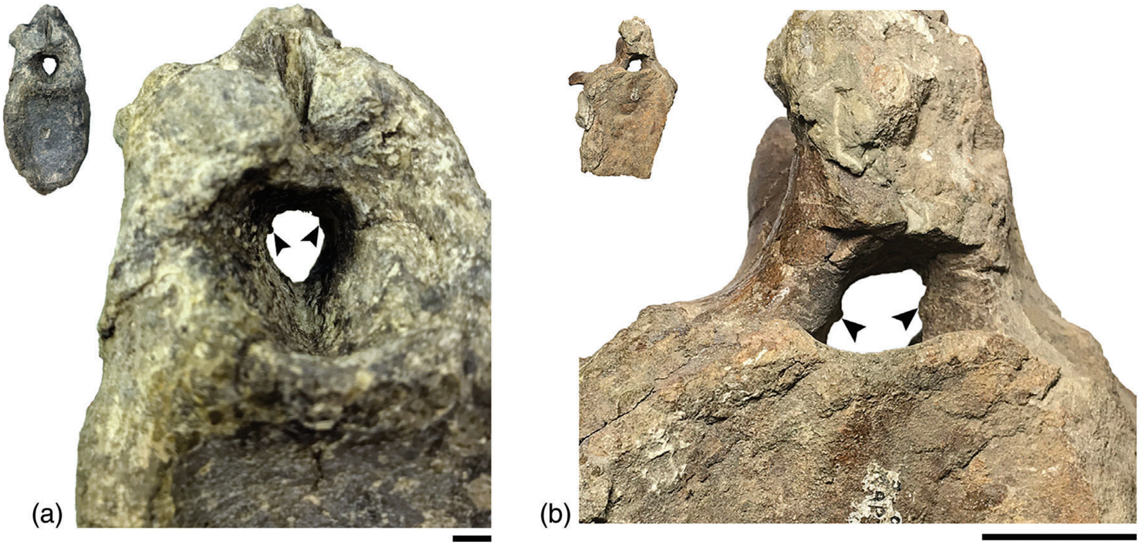

FIGURE 8 (a) Anterior view of the caudal vertebra of an *Allosaurus* (MWC 5492) with bony spinal cord supports (arrows). Scale bar = 1 cm. (b) Bony spinal cord supports (arrows) in a caudal vertebra of an indeterminate hadrosaurid (RAM 23434). Scale bar = 5 cm.

paleobiogeographic occurrences of neural canal ridges in non-avian dinosaurs. However, because our observations for these specimens are based only on published figures, our descriptions are less detailed.

Furthermore, although these discoveries may seem to indicate that a large-scale search for neural canal ridges in dinosaurs and other extinct vertebrates could be undertaken as a library project, canvassing the published literature for examples, in our experience this is surprisingly difficult. There are three reasons for this: (1) the rock matrix must be fully prepped out of the neural canals of the vertebrae of interest, (2) those vertebrae must be illustrated in anterior or posterior view, and (3) the illustrations must be of sufficient scale, detail, and fidelity that the neural canal ridges are clearly visible. *Haplocanthosaurus priscus* is a good example. In the genoholotype specimen, CM 572, only the neural canal of caudal vertebra 2 is fully prepared, and it is not sufficiently well-preserved for us to say definitively whether neural canal ridges were present. Neural canal ridges are present in at least one vertebra of the referred specimen CM 879 (fig. 4b), but we had to examine the vertebrae ourselves to make this determination, because the neural canal ridges are not visible in the illustrations in the original descriptive monograph (Hatcher, 1903). Although we have had some success identifying neural canal ridges from previously-published sources (see below), we found many more examples by the simple expedient of looking inside the neural canals of as many vertebrae as possible during museum collections visits, and we expect that this will continue to be the dominant mode of discovery going forward.

3.19.1 | *Europasaurus holgeri* (DFMMh/FV 553.1)

Europasaurus is known from several disarticulated partial skeletons from Langenberg Quarry (Kimmeridgian) in the Lower Saxony basin of northern Germany (Sander et al., 2006). Neural canal ridges are visible in published photos of a middle caudal vertebra (Carballido & Sander, 2014: figure 27). The neural canal is ovate with the long axis in the dorsoventral plane and a flattened ventral margin. Bony ridges are present approximately at the dorsoventral mid-point of the lateral walls. The ridges appear sharply defined near the posterior margin of the canal, but diminish and grade into the lateral wall as they continue anteriorly.

3.19.2 | *Ceratosaurus* sp. (UUVP 5960)

UUVP 5960 is a hemisected distal caudal vertebra of *Ceratosaurus* from the Cleveland-Lloyd Quarry in the Morrison Formation of central Utah (Madsen & Welles, 2000: figure 6). The neural canal resembles a squat numeral 8 in cross section. This appearance is produced by paired bony protuberances midway up the lateral walls of the neural canal. Although these bony projections are more rounded than pointed, we tentatively infer that they are neural canal ridges, homologous with similar structures described herein for other taxa.

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3.19.3 | *Stegosaurus stenops* (NHMUK PV R36730)

This specimen is one of the most complete *Stegosaurus* skeletons found to date, preserving elements representative of essentially the entire post-cranial specimen. It is from Morrison Formation deposits at the Red Canyon Ranch quarry near Shell, Wyoming, USA. In their thorough monograph describing NHMUK PV R36730, Maidment et al. (2015) provide photos of numerous vertebrae, including many with the neural canal prepped out. From the images included in the figures of this article, we identify neural canal ridges in caudal vertebrae 32 (figure 47A,B) and 34 (figure 49A,B). Although harder to discern in the photos and more equivocal due to diagenetic deformation, other caudal vertebrae appear to have structures highly suggestive of neural canal ridges: caudal 33 (figure 48A,B), caudal 36 (figure 51A,B), caudal 37 (figure 52A,B), and caudal 41 (figure 55A,B). In all of these vertebrae, the ridges (or purported ridges) are subtle yet distinct projections present 2/3 to 3/4 of the way up the lateral walls of the canal.

4 | DISCUSSION

We have documented that bony ridges projecting medially from the walls of the neural canal are present in the caudal vertebrae of many sauropod dinosaurs, and at least some theropods, thyreophorans, and hadrosaurs. In our attempts to identify the soft tissues related to the bony neural canal ridges in non-avian dinosaurs, we considered several alternative hypotheses. Below, we detail these alternative hypotheses, and explain why neural canal ridges are best interpreted as bony spinal cord supports.

4.1 | Alternative hypotheses

4.1.1 | Neurocentral joints

In ontogeny, each vertebra develops from the fusion of two major portions: a neural arch and a centrum (Schaefer et al., 2009; Williston & Gregory, 1925). Each forms from separate centers of ossification, which in juveniles are connected by cartilage. Only later in development do the two components fuse together. We considered that the ridges in the neural canals of dinosaurs might be remnants of the neurocentral joints. However, we find that neurocentral joints are present as separate structures, ventral to the neural canal ridges (Figure 6d [juvenile *Alamosaurus*]) and occasionally entirely ventral to the neural canal (Wedel & Atterholt, 2023). Neurocentral fusion lines are present in *Brontomerus* and *Astrophocaudia*, and in both cases the lines of fusion are ventral to the spinal cord supports. In the juvenile specimens of *Rapetosaurus* and *Alamosaurus*, distinct lateral ridges are present in the neural canal even though the centrum and arch were unfused at time of death.

4.1.2 | Ligamentum flavum scars

In extant taxa, various ligaments connect consecutive vertebrae to one another to support the vertebral column. One such ligament is the ligamentum flavum of mammals. The ligamentum flavum attaches to the dorsal portion of the neural arch of consecutive vertebrae (the 'lamina' in mammalian and human anatomical terms, e.g., White & Folkens, 2000: 143, not to be confused with the numerous vertebral laminae of sauropods and other dinosaurs, Wilson, 1999: 639), thereby forming a continuous 'roof' of tissue (formed of bone and ligament) over the spinal canal and its contents. We considered the possibility that the attachment for this ligament may extend into the neural canal. However, examination of human thoracic vertebrae revealed that the rugosities representing attachment sites of this structure are restricted to the anterior and posterior ends of the canals (they do not extend far within the space), and only to the dorsal part of the canal and not the lateral wall (Figure 9a).

4.1.3 | Vascular traces

In Aves, there is a large venous sinus located dorsal to the spinal cord, between the dura mater and the periosteum (Baumel, 1993; Lob, 1967). This internal vertebral sinus (Baumel, 1993) affects the geometry of the vertebral canal in some avian taxa (e.g., *Phalacrocorax penicillatus* and *Phoebastria nigripes*, personal observation) causing it to have a figure-8 shape in anterior and posterior view (Figure 9b). Similarly, in crocodilians, a large dorsal spinal vein shares space in the vertebra canal with the spinal cord (Zippel et al., 2003). Often, the two structures are slightly separated from each other by bilateral bony ridges on the lateral walls of the vertebral canal (Figure 9c). Similarly, snakes have a pair of ventral spinal veins of substantial size (Zippel et al., 1998, 2001), which also may be partially separated from the cord itself by a pair of bony ridges on the ventral part of the lateral canal walls.

Although these superficially are very similar to the bony ridges observed in sauropod caudal vertebrae, there are subtle, yet significant, differences. Large spinal veins

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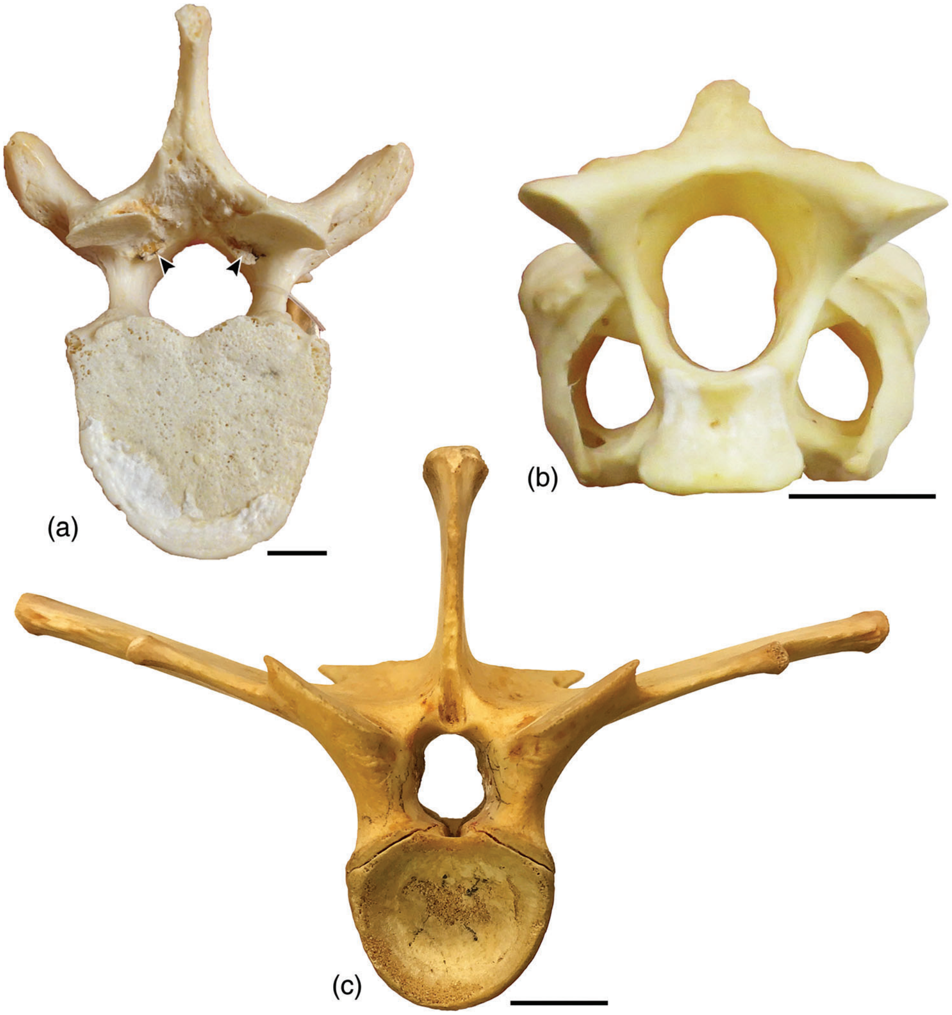

FIGURE 9 Examples of other bony structures associated with the vertebral canal but ruled out as possible explanations for the ridges observed in dinosaurs (see text for details). (a) *Homo sapiens* thoracic vertebra in posterior showing the scar for the ligamentum flavum (arrows) located at the roof/entrance of the neural canal. (b) Cervical vertebra of *Phoebastria nigripes* (LACM 115139) in posterior view showing bilobed geometry of the neural canal. (c) Alligator dorsal vertebra in anterior view showing bilobed geometry of the neural canal. All scale bares = 1 cm.

cause the neural canal to have a variant shape, typically bilobed like a numeral 8 (in birds and crocodilians) or trilobed and having a trefoil shape (in snakes), along its entire length. In contrast, neural canal ridges in sauropods do not extend all the way to the anterior and posterior margins of the canal, and therefore do not change the overall geometry of the neural canal. Rather, they appear as discrete structures that project into the canal but do not alter its overall shape. Furthermore, in crocodilians and birds with bilobed neural canals, the corpus of bone on either side of the neural canal that separates the canal into dorsal and ventral regions is typically dorsoventrally rounded and extends completely through the neural canal, so that the anterior and posterior apertures of the canal are themselves bilobed. In contrast, neural canal ridges arise inside the canal—they do not extend to the ends of the canal—and they are sharply delimited with clear dorsal and ventral margins. This is true of the spinal cord supports in fishes and salamanders (Figure 1) as well as the neural canal ridges in sauropods, as shown by *Diplodocus* MWC 10613 (Figure 4e–g) and by *Camarasaurus* SUSA 515 (Figure 5c,d).

4.1.4 | Bony spinal cord supports

Skutschas and Baleeva (2012) identified bony spinal cord supports in teleosts, dipnoans, salamanders, and transiently in a juvenile lizard. Using their work as a guide, we identified similar structures in other fishes and salamanders (see Table 1). The morphology of the bony spinal cord supports varies among clades. In the teleosts we examined, the spinal cord supports typically manifest as sharp bony spikes extending medially from the lateral walls of the neural canal. In salamanders, they form as narrow tongue-shaped bony shelves that project some distance into the neural canal. The neural canal ridges in dinosaurs manifest as low ridges of bone. They are similar to the bony spinal cord supports of extant vertebrates in being discrete bony eminences that project into the neural canal near its craniocaudal midpoint, but which do not extend to the ends of the neural canal.

In sum, neural canal ridges in sauropods and other dinosaurs cannot be explained as epiphenomena of the neurocentral joints, which are too ventral; as ligamentum flavum scars, which are too dorsal; or as correlates of

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FIGURE 10 Hypothetical soft-tissue reconstruction showing the relationship of the spinal cord and spinal dura to the bony spinal cord supports. Red = dura mater (fused to periosteum of neural canal). Blue = pia mater and denticulate ligaments. Yellow = spinal cord. Posterior view of caudal 14 in *Astrophocaudia slaughteri* (SMU 61732).

large spinal veins, which change the entire geometry of the neural canal from end to end, in contrast to the discrete bony ridges that project into the neural canal only at its craniocaudal midpoint. The only hypothesis we cannot rule out is that neural canal ridges in dinosaurs were osteological correlates of enlarged denticulate ligaments that anchored the spinal cord to the bony walls of the neural canal. We therefore agree with Averianov and Lopatin (2020) that neural canal ridges in sauropods and other dinosaurs functioned as bony spinal cord supports, like those identified by Skutschas and Baleeva (2012) in teleosts, dipnoans, and salamanders, and we present a hypothetical reconstruction of the spinal cord, denticulate ligaments, and associate soft tissue structures in a sauropod caudal vertebra (Figure 10).

4.2 | Functional implications

In the course of this research, we examined cervical, dorsal, and sacral vertebrae of sauropods, but we found no examples of neural canal ridges in any precaudal vertebrae. The repeated presence of neural canal ridges in the caudal region, together with the consistent lack of such structures in any other vertebral region, suggests a functional explanation. Initially we considered that bony spinal cord supports might have anchored the spinal cord during tail sweeping, possibly for defense as in lizards (Murphy & Mitchell, 1974) or for social display or signaling (Conti et al., 2022; Myhrvold & Currie, 1997). Although intuitively appealing, that hypothesis does not explain the presence of neural canal ridges in caudal vertebrae of *Allosaurus*, *Ceratosaurus*, *Stegosaurus*, and a hadrosaur. In particular, the tails of hadrosaurs were reinforced by a lattice of ossified tendons (Adams & Organ, 2005). The ossified tendons probably stiffened the vertebral column in the sagittal plane, but they may have still allowed considerable lateral motion of the tail (Organ, 2006). Hadrosaurs were predominantly terrestrial animals, so their dorsoventrally deep but craniocaudally modest tails were probably not adapted for swimming, nor do their tails have any morphological elaborations that would suggest a role in defense.

Even if use of the tail in defense, social signaling, or swimming might explain the need for ossified spinal cord supports in one lineage of dinosaurs, none of those functions would have applied equally across clades as diverse in size and tail morphology as sauropods, theropods, thyreophorans, and hadrosaurs. All four clades do share one aspect of tail function, however: the tails of non-avian dinosaurs anchored the paired caudofemoralis muscles that retracted the femora during walking and running (Gatesy, 1990; Hone et al., 2021; Persons & Currie, 2017). Perhaps the stresses applied to the tail by locomotion were sufficient to make ossified spinal cord supports functionally advantageous in large dinosaurs. This hypothesis does not rule out the possibility that neural canal ridges are so prevalent in sauropods because they were sweeping their tails frequently for defense or social signaling.

4.3 | Directions for future work

We stumbled on neural canal ridges in sauropods serendipitously, while surveying sauropod neural canals for evidence of paramedullary diverticula (Atterholt & Wedel, 2022) and dorsoventral shifts in the position of the neurocentral joints (Wedel & Atterholt, 2023). We launched this project to document neural canal ridges in as many sauropods as possible. Late in the project we also found neural canal ridges in two theropods, in a thyreophoran, and in a hadrosaur, but we have not conducted a comprehensive survey of all dinosaurs, nor looked at non-dinosaurian amniotes. Crocodilians, snakes, monitor lizards, and mosasaurs seem like particularly promising taxa to investigate.

As discussed above, extant crocodilians and snakes often have neural canals that are bilobed or trefoil-shaped in cross-section, with long, large bony eminences

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TABLE 3 Summary of various structures found within the neural canal.

Type of structure	Associated soft tissue	Taxa where present	Citation
Reductive structures			
Neurovascular foramina	Nerves, arteries, veins	Vertebrata	Amato et al. (1959), Crock et al. (1973), Smuts (1975), Wintrich et al. (2017)
Pneumatic fossae	Respiratory diverticula	Aves, Sauropoda, Theropoda	Atterholt and Wedel (2022)
Pneumatic foramina	Respiratory diverticula	Aves, Sauropoda, Theropoda	Atterholt and Wedel (2022), O'Connor (2006), Schwarz and Fristsch (2006)
Neural fossae	Glycogen body, lumbosacral organ, ventral eminences	Aves	Huber (1936), Necker (2000, 2005, 2006), Schroeder and Murray (1987), Stanchak et al. (2020), Streeter (1904), Watterson (1949)
Additive structures			
Bony spinal cord supports	Pia mater	Teleostei, Dipnoa, Urodela, Sauropoda	Averianov and Lopatin (2020), Skutschas (2009), Skutschas and Baleeva (2012), Wake and Lawson (1973)
Spandrels			
Bi-lobed geometry	Spinal vein	Crocodylia, Aves	Zippel et al. (2003)
Trefoil geometry	Vertebral venous plexus	Ophidia	Zippel et al. (2001)

that partially separate the vascular channels from the portion of the neural canal that houses the spinal cord. Those bony eminences do not closely resemble the neural canal ridges found in fish, salamanders, and dinosaurs, but they might nevertheless anchor enlarged denticulate ligaments. That possibility should be straightforward to investigate through dissection or histological analysis.

In *Austrophocaudia slaughteri* SMU 61732 and *Rapetosaurus krausei* FMNH PR 2209, neural canal ridges are present in every preserved caudal vertebra. Virtually all our other sampled specimens are isolated vertebrae. Documenting serial variation within the vertebral column of an individual dinosaur would be a useful contribution, as would tracing the development of neural canal ridges in an ontogenetic series.

The possible functions of neural canal ridges in dinosaurs are not well constrained, but the presence of bony spinal cord supports in many extant teleost fishes and salamanders opens the door to potential biomechanical testing. Are enlarged denticulate ligaments and ossified spinal cord supports correlated with body size, or with specific behaviors? Even simple tug-tests like those done by Baumel (1985) on the suspensory ligaments of the brachial plexus in the pigeon could be illuminating.

The neural canals of archosaurs are host to a veritable zoo of morphological specializations (Table 3). Dilations of the neural canal occur in many archosaurian lineages, for many reasons: to accommodate large vascular pathways in crocodilians (Zippel et al., 2003) and in birds (Baumel, 1993; Lob, 1967), enlargements of the spinal cord in sauropods, stegosaurs, and birds (Giffin, 1991; Janensch, 1939; Wedel et al., 2021), and the lumbosacral balance organ in birds (Necker, 2006; Stanchak et al., 2020). Neurocentral joint surfaces are expanded and elaborated in many sauropods, presumably to better resist biomechanical stresses in large, fast-growing animals that fused their skeletons late in ontogeny (Fronimos & Wilson, 2017; Wedel & Atterholt, 2023). Neural canal ridges in sauropods and other non-avian dinosaurs are the latest additions to this array of anatomical novelties, which involve numerous body systems, and which have mostly been recognized only in the 21st century. In general, we find that structures in the neural canals of tetrapods are under-documented and that they present numerous opportunities for future discovery, in extinct and extant taxa, both at the dissecting table and in museum collections.

AUTHOR CONTRIBUTIONS

Jessie Atterholt: Investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; data curation; project administration. **Mathew J. Wedel:** Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; project administration. **Ron Tykoski:** Resources; methodology; writing – review and editing; validation. **Anthony R. Fiorillo:** Methodology; validation; writing – review and

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editing; resources. **Femke Holwerda:** Methodology; validation; writing – review and editing; resources. **Thierra K. Nalley:** Methodology; validation; visualization; software; formal analysis; resources. **Taormina Lepore:** Investigation; writing – review and editing. **John Yasmer:** Software; formal analysis; resources.

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