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Cervical ligament systems in sauropod dinosaurs: what support is there?

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Abstract: Sauropod dinosaurs, such as *Diplodocus* and *Dicraeosaurus*, have been the subject of numerous hypotheses about what ligamentous structures could have aided in lifting and supporting their long necks. Because the supportive tissues rarely fossilize, palaeontologists historically have relied on assumptions and on presumed osteological correlates, such as rugosities, on cervical vertebrae to infer their nature. Based on comparisons with extant animals, options for supportive cervical ligaments in sauropods include mammal-style nuchal ligaments, avian-style interlaminar elastic ligaments, reptilian-style supraspinal ligaments, or some combination thereof. This study tested for the presence of a mammal-style nuchal ligament using histology and micro-computed tomography of cervical hemispinous processes of *Apatosaurus* and *Diplodocus*, as well as the examination of gross morphological features of the cervical vertebrae of *Apatosaurus*, *Diplodocus*, and *Camarasaurus*. A non-uniform bone orientation in the thin sections from a hemispinous processes of *Diplodocus* and from micro-CT imaging of a hemispinous process of *Apatosaurus* suggests that a dorsally or dorsolaterally positioned supraspinal ligament, rather than a mammal-like nuchal ligament, attached to the distal tips of the spines. Additionally, initial observations of pseudospinous tubercula in *Diplodocus* and *Apatosaurus* suggests that they also possessed interlaminar elastic ligaments in at least portions of their necks. Whether or not such ligaments were the sole means of cervical support and whether or not such ligaments were capable of providing entirely passive (non- or minimally muscle aided) neck support remain unclear. These findings could be incorporated into future models of sauropod neck mobility and further the understanding of sauropod feeding styles and mechanics.

INTRODUCTION

Sauropod dinosaurs have intrigued palaeontologists ever since their initial discoveries. As the largest known terrestrial animals, understanding various aspects of their anatomies and physiologies is instrumental to understanding how they evolved and thrived. Unfortunately, no extant animals are entirely suitable analogs for sauropods, which has complicated previous attempts to reconstruct their anatomies and physiologies using comparative anatomy and uniformitarian principles.

While great advances nevertheless have been made toward understanding various aspects of sauropod anatomy and physiology (e.g., Klein et al. 2011; Sander et al. 2011; Christian et al. 2013), one structure that has received little direct study is the nature of sauropod sagittal and parasagittal epaxial cervical ligaments. The purpose of such ligaments in extant quadrupeds is to support the neck, ideally passively (non- or minimally muscle aided), thus preventing excess energy expenditure while countering the force of gravity (Gellman and Bertram 2002).

The functional morphology of cervical ligament(s) in sauropod necks has been a topic of interest because no extant animals possess cervical vertebrae similar to those of sauropods (Woodruff 2014), especially those with bifurcate cervical hemispinous processes. The presence of bifurcate cervical vertebrae, in which the spinous process divides into two hemispinous processes (sensu Harris 2006), is not limited to sauropod dinosaurs; this feature appears, to varying degrees, in many different tetrapod species, including within Aves and Primates, in which they assist in supporting horizontal weight (Woodruff 2014). Many sauropods exhibit spinal bifurcation, including *Mamenchisaurus*

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(Young and Zhao 1972; Ouyang and Ye 2002) and *Camarasaurus* (Osborn and Mook 1921; Holland 1924). However, spinal bifurcation attains an extreme state in members of the sauropod clade Flagellicaudata, in which deep spinal bifurcation typically extends from cranial- or mid-cervical vertebrae to the cranial- or mid-thoracic vertebrae. The clade primarily spans the Late Jurassic through the Early Cretaceous (Leanza et al. 2004; Whitlock 2011; Van der Linden et al. 2025); Middle Jurassic sauropod taxa also have been attributed to the clade (Charig 1980; Xu et al. 2018; Bajpai et al. 2023), but the accuracy of these and other attributions remains uncertain (Whitlock 2011; Mannion and Moore 2025; Van der Linden et al. 2025).

Sauropods, and flagellicaudatans in particular, have been presumed to have had either a mammal-like nuchal ligament (e.g., Janensch 1929; Figs. 1A, 2A), a bird-like interlaminar elastic ligament system (e.g., Schwarz et al. 2007) (Figs. 1B, 2B), or simply a basal-reptile-like supraspinal ligament (Woodruff 2016; q.v., Harris 2024; Figs. 1C, 2C) in their necks. Additionally, sauropods could have had both a bird-like system of interlaminar elastic ligaments and a supraspinal ligament (Tsuihiji 2004; Fig. 2D) as in *Alligator* (Fig. 1C). Nuchal ligaments (*ligamenta nuchae*) sensu stricto (Harris 2024) are most commonly seen, but have variable morphologies, in euungulate mammals such as *Bos taurus* and *Equus caballus* (Dimery et al. 1985; Harris 2024) and consist of two components: a funiculus and usually one or more laminae (Harris 2024; Fig. 1A). The funiculus lies dorsal to the cervical spinous processes and originates as a continuation of the supraspinal ligament at the cervicothoracic region, typically on elongate spinous processes referred to collectively as 'withers' or a 'shoulder hump'. The funiculus extends to the external occipital protuberance or two fossae adjacent to a sagittal crest on the occiput in most mammals that possess one. The laminae, when present, are fibrous sheets that extend from the funiculus and attach to the apices of the spinous processes via a cartilaginous cap or sesamoid (Woodruff 2014; Harris 2024).

The avian interlaminar elastic ligament (ligamentum elasticum interlaminare) system is widespread within Aves and typically consists of a discontinuous set of ligaments that connect the bases of sequential spinous processes (Baumel and Raikow 1993; Tsuihiji 2004; Dzemski and Christian 2007; Böhmer et al. 2020; Fig. 1B). In the caudal cervical region of *Rhea americana*, an interspinal elastic ligament (ligamentum elasticum interspinale) has a unique morphology reminiscent of a euungulate-like nuchal ligament (Tsuihiji 2004). It functions similarly to a nuchal ligament, having a fascial or ligamentous sheath that extends from the interlaminar elastic ligament and attaches to bifurcate hemispinous processes in the middle and caudal portions of the neck (Tsuihiji 2004). This structure, referred to as an avian 'nuchal ligament', has been reported in *Gallus gallus domesticus*, *Rhea*, and *Piculus aurulentus* (Barkow 1856; Yasuda 2002; Tsuihiji 2004), although its extent varies. For example, in *Gallus* and *Rhea*, it extends as far cranially as the axis, but in *Piculus aurulentus*, the structure is restricted to the caudal region of the neck.

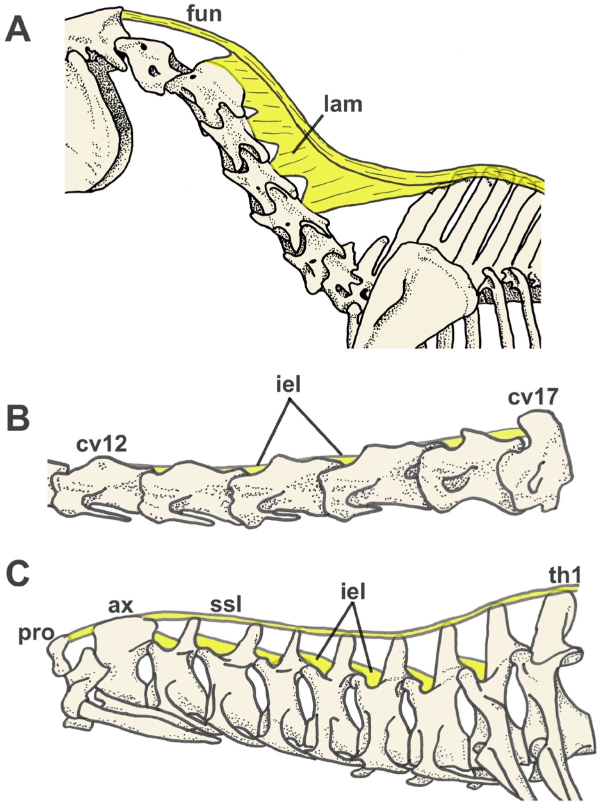


Figure 1. Comparative sagittal, dorsal epaxial cervical ligaments and the vertebrae to which they attach in select tetrapods in left lateral view. A, Mammalian-style nuchal ligament as seen in *Equus caballus* (horse; from Harris 2024). B, Avian-style interlaminar elastic ligament as seen in the caudal cervical vertebrae of *Struthio camelus* (ostrich; after Apostolaki et al. 2015). C, Crocodylian-style supraspinal ligament as seen in *Alligator mississippiensis* (alligator; after Frey 1988). Abbreviations: ax, axis; cv, cervical vertebra (position denoted by number); fun, funiculus of the nuchal ligament; iel, interlaminar elastic ligament; lam, lamina of the nuchal ligament; pro, proatlas; ssl, supraspinal ligament; th, thoracic vertebra (position denoted by number).

The plesiomorphic reptilian supraspinal (or supraspinous) ligament (ligamentum supraspinale) is a thin, continuous, strap-like ligament that attaches directly to the dorsal edges of the tips of sequential spinous processes in diapsids such as *Alligator mississippiensis* and *Iguana iguana*. In the neck, the ligament spans from the cervicothoracic junction to either the axis or proatlas (Frey 1988: fig. 14; Fig. 1C) or the occiput (Tsuihiji 2004). However, R. Wilhite (pers. comm. 2025) has been unable to confirm the presence of a supraspinal ligament in *Alligator* in multiple dissections of individuals of different sizes. *Alligator*, and possibly other crocodylians, additionally have a bird-like system of interlaminar elastic ligaments (Frey 1988; Fig. 1B, C). Homology between what Frey (1988) called interlaminar elastic ligaments in *Alligator* and interspinal ligaments is unclear; the interspinal ligaments lie dorsal to the interlaminar ligaments (q.v., Cong et al. 1998: fig. 148).

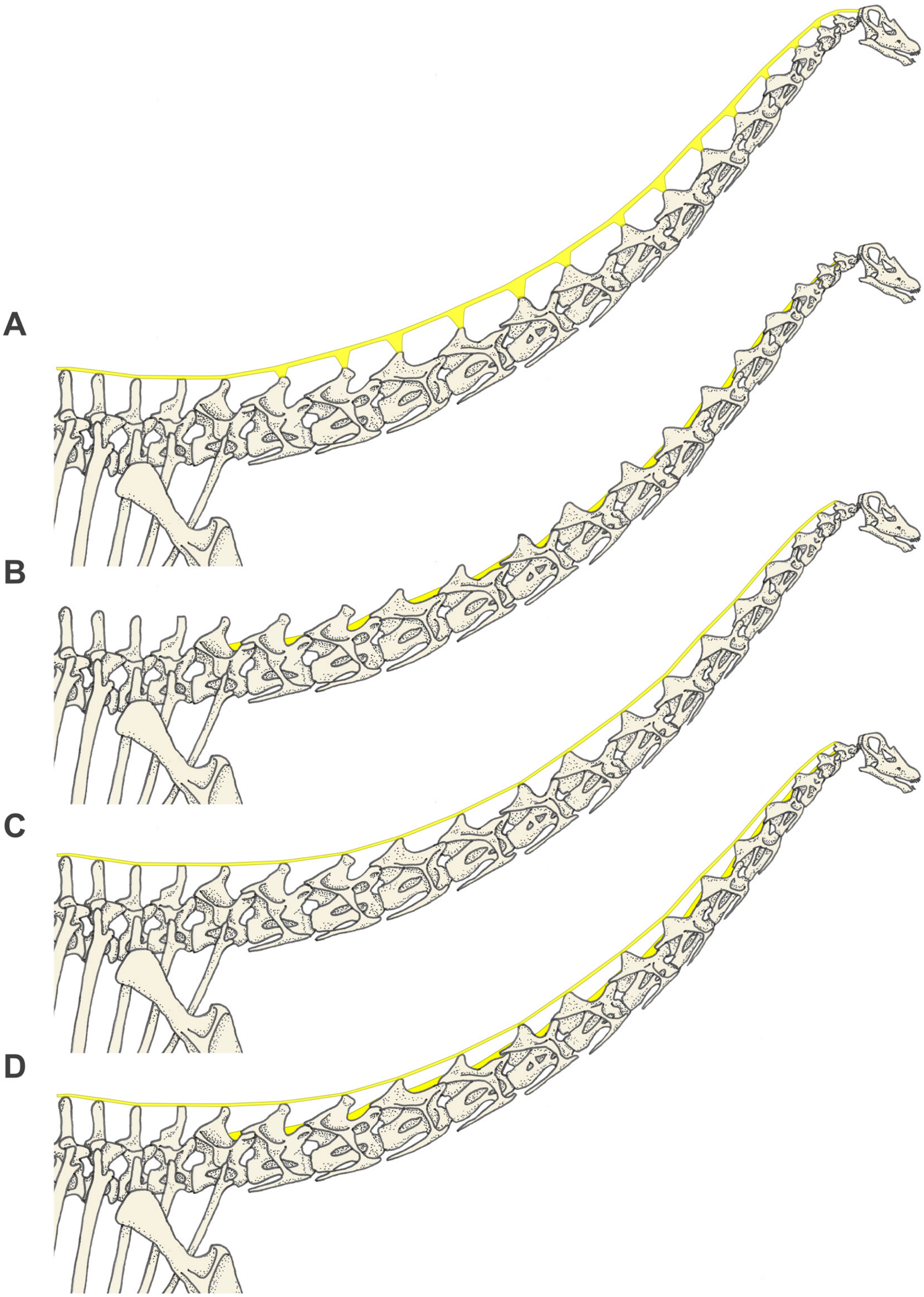


Figure 2. Reconstructions of different possible epaxial cervical ligaments in *Diplodocus* in right lateral view. A, Mammalian-style nuchal ligament. B, Avian-style interlaminar elastic ligament system. C, Crocodylian-style supraspinal ligament. D, Combination of interlaminar elastic and supraspinal ligaments. Skeletal elements traced from the digital model by Matt Dempsey at https://www.artstation.com/artwork/qeo4W2.

Although multiple extant taxa possess nuchal ligaments (mammals) or interlaminar elastic ligaments (crocodylians and birds), the presence and degree of development of the structures varies both between and within species, and even across the cervical vertebral column (Tsuihiji 2004; Harris 2024). For example, among mammals, *Giraffa camelopardalis* and *Tragulus napu* both possess a nuchal ligament, but they differ in the number of laminae connecting the funiculus to cervical spinous processes (Harris 2024). Likewise, most, if not all, birds possess interlaminar elastic ligaments (Baumel and Raikow 1993), which are robust in the caudal portion of the neck but, in many taxa, absent in the middle portion of the neck (Boas 1929; Zweers et al. 1994; Tsuihiji 2004). Extinct taxa likely also had variable expressions of whichever types of dorsal ligaments their respective clades possessed. A morphological reconstruction of such a ligament in a single species (extant or extinct), therefore, may not necessarily model what the morphology was for every member of the higher clade(s) to which that species belongs.

In contrast to the understood diversity of epaxial cervical ligaments in extant animals, unambiguous evidence for the presence of such ligaments in extinct animals has yet to be identified (Harris 2024). Research to address which type(s) of epaxial cervical ligaments extinct taxa possessed could follow one of two paths: (1) using gross morphological features of the vertebrae, or (2) using osteohistological features of ligament attachment sites. Correlations between any gross osteological features with the presence of one or another ligament type have yet to be firmly established in either extant or extinct animals (Harris 2024), but several hypotheses along this line have been proposed. For example, some scars, striations, rugosities, and crests have been suggested to demonstrate attachments of nuchal, supraspinal, and elastic ligaments on the cervical vertebrae of mammals, crocodylians, and birds (Tsuihiji 2004; Schwarz et al. 2007; Harris 2024). Additionally, possession of 'withers'—tall cranial thoracic spinous processes immediately caudal to short caudal cervical spinous processes—to provide maximal mechanical advantage as the attachment site for nuchal ligaments (Dodson and Harris 2001; Harris 2024) has been hypothesized as a correlate specifically of a nuchal ligament. Currently known sauropods do not exhibit anything demonstrably resembling 'withers', although they have been presumed in *Giraffatitan brancai* (Paul 1988). Known material of flagellicaudatans shows that they lack 'withers'; instead, their gradual, cranial-to-caudal increase in cervical hemispinous process heights more closely resembles the pattern in extant crocodylians (Frey 1988; Schwarz et al. 2007; see below). However, a nuchal ligament that anchored farther caudally in the thorax, where the spinous processes cease to be bifurcate (Janensch, 1929; Preuschoft and Klein 2013), cannot be ruled out a priori. As another example, cervical spinous processes in birds tend to be tall in the cranial and caudal regions, where interlaminar elastic ligaments are present, but short in the middle region (Schwarz et al. 2007), so spine height may correlate with the presence of interlaminar elastic ligaments. The cervical hemispinous processes of flagellicaudatans gradually increase in height from cranial to caudal, a pattern unlike that of *Rhea* (Tsuihiji 2004; Schwarz et al. 2007), making it difficult to determine whether or not diplodocid necks possessed either interspinal or interlaminar (or both) elastic ligaments based solely on spine heights. Ultimately, until firm correlations between any osteological features and the presence of a specific type of epaxial, cervical ligament are discovered, other methods of determining the presence of a particular ligament type must be used.

The second path, osteohistology, has potential to elucidate the presence of one or another type of ligament (Harris 2024), but to date, few attempts have been made to ascertain if microscopic features in bones suggest the presence of a specific ligament type. Cerda et al. (2015) used histology to support the presence of a supraspinal ligament in the sacra of *Epachthosaurus sciuttoi* and another, unattributed titanosaurian sauropod, both from the Cretaceous of Argentina. Woodruff et al. (2016) similarly used histology to identify a supraspinal ligament in the dorsal and sacral regions of a titanosaurian (?*Alamosaurus*) from the Upper Cretaceous Javelina Formation of Texas. Woodruff (2016) additionally used osteohistology to demonstrate the presence of a supraspinal ligament [although called a 'nuchal ligament'—see discussion in Harris (2024)] in the Late Jurassic flagellicaudatan sauropod *Diplodocus*. His study ostensibly determined its presence in the cervical region, but the vertebra used for the study (part of MOR 592) was the same one studied by Horner et al. (2016), who specified that this element is a caudal vertebra.

Thus, evidence supports that a variety of sauropods had supraspinal ligaments in the dorsal, sacral, and caudal regions, but the specific type(s) of epaxial, sagittal or parasagittal ligament(s) in the cervical region of a sauropod has yet to be determined. The problem of reconstructing dorsal, epaxial ligaments is compounded in sauropod taxa with bifurcate spinous processes because of their virtually unique morphology among known vertebrates. If such sauropods had mammal-like nuchal ligaments, they may have possessed (uniquely among vertebrates) a pair of parasagittal ligaments that inserted on the tips of both hemispinous processes (Fig. 3A), or they may have had a single, sagittal ligament that inserted on the midline, possibly on pseudospinous tubercula (sensu Harris 2006; Fig. 3B), as hypothesized by Janensch (1929). Likewise, a bird-like system of interlaminar elastic ligaments may have

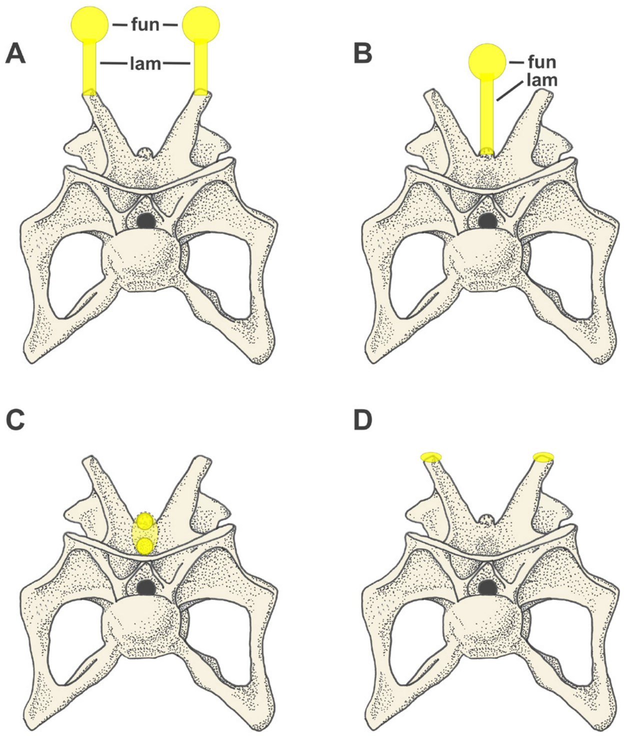


Figure 3. Schematic diagram of *Apatosaurus louisae* cervical vertebra 12 (traced from Gilmore [1936] and with median pseudospinous tubercula added) in cranial view showing different possible epaxial cervical ligament types (yellow) in coronal section and their presumed attachment sites. A, Paired, mammalian-style nuchal ligaments attaching in a vertical orientation on the distal ends of the hemispinous processes. B, Single (closely appressed or fused funiculi), mammalian-style nuchal ligament attaching on the pseudospinous tuberculum. C, Avian-style interlaminar elastic ligament inserting on the pseudospinous tuberculum (upper circle), a fossa between the tuberculum and the neural canal (lower circle), or both (oval). D, Paired, reptilian-style supraspinal ligaments attaching directly to the distal ends of each hemispinous process. Abbreviations: fun, funiculus of the nuchal ligament; lam, lamina of the nuchal ligament.

inserted on pseudospinous tubercula and/or fossae ventral to them (Fig. 3C), though at angles orthogonal to the laminae of a hypothetical, sagittal nuchal ligament. A pair of supraspinal ligaments would also insert at the tips of the spinous or hemispinous processes (Fig. 3D).

Cerda et al. (2015) conducted histological studies of ossified structures in two titanosaurians, and Woodruff et al. (2016) studied a non-ossified but taphonomically mineralized structure in a titanosaurian. In contrast, Woodruff (2016) made the first known attempt to determine the presence of an epaxial, sagittal ligament by examining the microstructure of the bone (a distal spinous process) to which an epaxial, sagittal ligament hypothetically attached. This novel approach established the vast potential for this technique to elucidate what type(s) of ligament(s) sauropods possessed in their necks. In osteohistological thin sections, the orientation of mineralized fibrocartilage or possibly Sharpey's fibres hypothetically can suggest a specific ligament type (Cerda et al. 2022).

Ligaments attach to bone via entheses. A ligament enthesis, like that of a tendon, comprises a four-part transitional structure that begins with the ligament itself and continues into the bone to which it attaches (Schwartz and Thomopoulos 2012: fig. 11.1; Tellado et al. 2015: fig. 2; Bayrak and Huri 2018: fig. 1). In the first stage, furthest from the bone, the ligament consists of collagen type I. The next stage, moving closer to the bone, contains collagen type II and type III and non-mineralized fibrocartilage. The third stage, closer still to the bone, contains collagen type II and type X with mineralized fibrocartilage. In the final stage, the mineralized fibrocartilage merges with the bone and collagen type I and numerous osteoblasts/osteocytes are present (Apostolakos et al. 2014; Tellado et al. 2015; Bayrak and Huri 2018). During this transition, the amount of collagen organization decreases dramatically because the mineralization increases the closer it is to bone. This gradual change is the diagnostic characteristic of ligament and tendon structures and is crucial to understand the presence of a ligament or tendon attachment in fossil vertebrates (Tellado et al. 2015).

Mineralized fibrocartilage commonly occurs in undulating or ribbon-like patterns near the exterior of the primary bone next to robustly developed secondary reconstructions (Cerda et al. 2015; Horner et al. 2016; Wilson et al. 2016). Although bone mechanics are complicated by several factors (Currey 1984), in general bone is stronger under tension and compression, and the 'grain' of the bone is parallel to the forces acting on the bone (McGowan 1999). The exact forces that different types of ligaments (epaxial, sagittal, and parasagittal) exert on cervical hemispinous processes has yet to be documented in extant animals, let alone extinct ones. Nevertheless, hypothetically, dorsoventrally orientated, suspensory laminae from a nuchal ligament should exert roughly uniform parallel forces, while a directly attached, craniocaudally orientated supraspinal ligament hypothetically should exert a more radial distribution of forces (Fig. 4). A complicating factor to this hypothesis is that if sauropods possessed interlaminar elastic ligaments, muscles might also attach to the spinous process or hemispinous process tips (as some do in in *Alligator* [Cong et al. 1998] and birds [Boas 1929]) and create directional structures within the bone that could be mistaken as structures with a ligamentous affiliation. Sauropod muscle reconstructions, such as those of Schwarz et al. (2007), typically show cervical muscle masses laying alongside the spinous processes rather than attaching directly to their tips, but how complete these reconstructions are remains unclear.

Currently, the osteohistological method of inferring directional dorsal forces is one of the most viable methods to constrain the ligament configuration for sauropods. Dinosaur spinous process tips have many secondary osteons near the regions of supposed mineralized fibrocartilage (Cerda et al. 2015; Horner et al. 2016; Wilson et al. 2016). The development of osteons, particularly secondary osteons, within bones is thought to better handle mechanical and compressive forces acting on the bone to prevent fractures (Enlow 1962; O'Brien et al. 2003; Chang and Liu 2022). The direction of the forces of stress is recorded by the orientations of the long axes of osteons that reflect increasing or reoccurring forces acting on the bone (Petrtýl et al. 1996; Chang and Liu 2022). However, it must be noted that secondary osteons also can develop to repair damaged bone (Bentolila et al. 1998; Chang and Liu 2022), so osteon orientation may additionally reflect the strengthening of bone that was subjected to micro-damage.

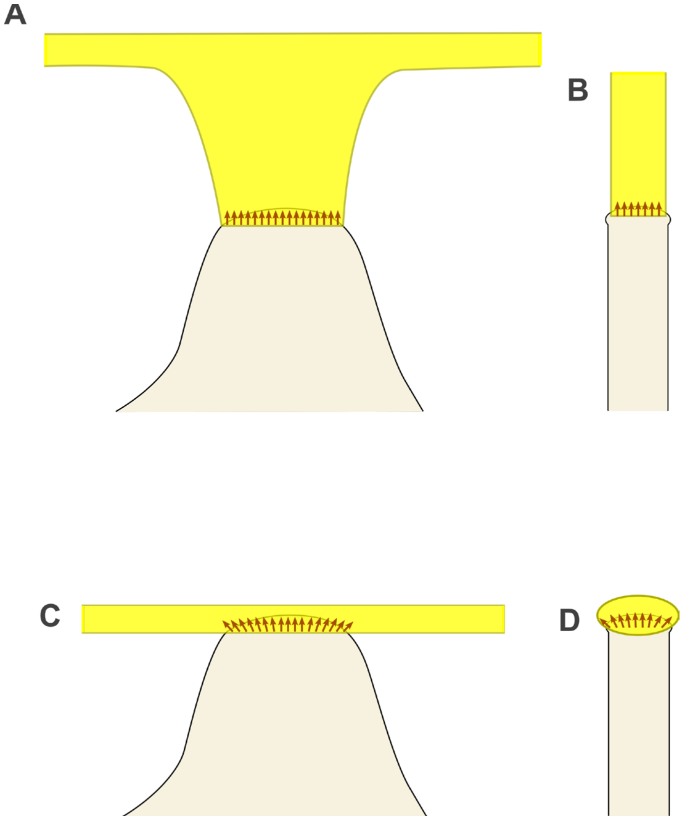


Figure 4. Schematic diagrams showing the distal end of the hemispinous process of cervical 9 of *Diplodocus* with hypothetical ligament types and attachments (yellow) and arrows (maroon) in the hypothesized orientations of mineralized fibrocartilage at the bone–ligament interface. A and B, Mammal-like nuchal ligament in right lateral view (A) and cranial (B) views. C and D, Reptile-like supraspinal ligament in right lateral (C) and cranial (D) views. Note the hypothesized parallel orientations with the suspensory nuchal ligament and radial orientations with the supraspinal ligament. Possible muscle attachments not shown here.

To better understand the possible ligament system that supported the necks of sauropods with bifurcate cervical hemispinous processes, we examined the cervical vertebrae of three sauropod genera: *Diplodocus*, *Apatosaurus*, and *Camarasaurus*. All three were examined macroscopically for gross morphological structures that would suggest the presence of a specific epaxial, cervical ligament. The distal ends of cervical hemispinous processes of *Diplodocus* and *Apatosaurus* were further examined microscopically (histologically) for structures that suggest the presence of one or another type of ligament using the following assumptive and as-yet untested reasoning: at the site of ligament enthesis, the mineralized fibrocartilage closest to the site of transition between bone and ligament should be orientated to the direction of the forces that were acting on the ligament. As suggested above, in a mammalian nuchal ligament (or a nuchal-ligament-like, avian-style interspinal elastic ligament), the laminae (or sheath) extends ventrally from the funiculus and attaches to either the spinous process or to a hemispinous process (Tsuihiji 2004; Harris 2024). The mineralized fibrocartilage at the site of such insertion hypothetically should be orientated approximately dorsoventrally, parallel to the force exerted by the suspending laminae (Fig. 4A, B; Harris 2024). In contrast, the position of mineralized fibrocartilage from a craniocaudally orientated supraspinal ligament hypothetically should pull in different directions at different points along the tip of the spine and therefore exhibit a more radial pattern of orientations (Fig. 4C, D). The forces acting on the spines hypothetically then should be reflected in the cortical bone and preserved mineralized fibrocartilage (see below).

Identifying which type(s) of epaxial, cervical ligament(s) sauropods possessed is necessary to facilitate biomechanical models that examine whether or not such ligaments were capable of providing entirely passive support for the neck and, if not capable, what postural strategies sauropods employed to minimize energy expenditure in holding up their necks. Such models then can apply to better understanding sauropod feeding mechanics.

MATERIALS AND METHODS

The sauropods specimens examined for this work all come from the Upper Jurassic Morrison Formation of the western United States (Fig. 5). Two specimens, WDC FS-615 and CM 84, both came from unspecified members of the Morrison Formation in Wyoming (see Ikejiri et al. [2006] for notes on the WDC specimen). Other specimens, including BYU 11894 and 12945 and CM 3018, all came from the Brushy Basin Member of the Morrison Formation in Colorado and Utah.

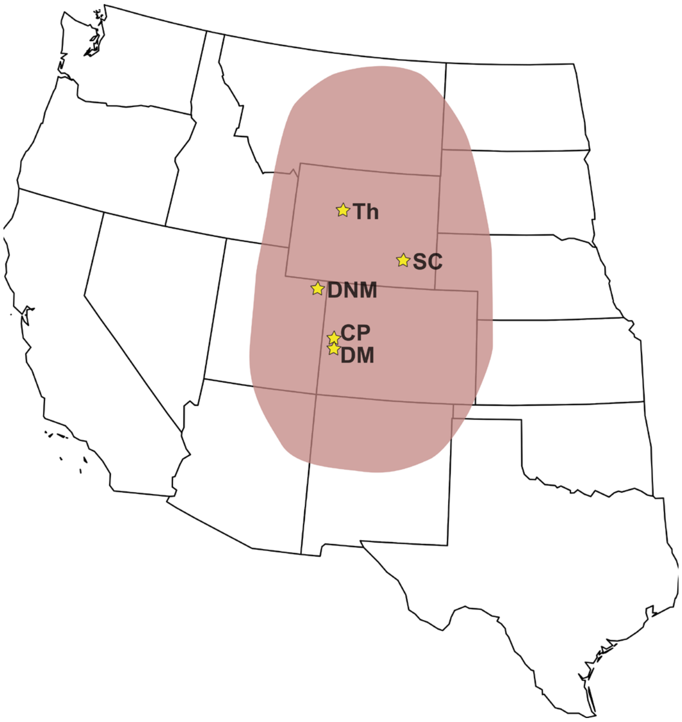


Figure 5. Approximate extent (red) of the Upper Jurassic Morrison Formation depositional basin across western United States and the locations from which the specimens analyzed herein were collected. Institutional abbreviations: CP, Cactus Park, Colorado; DM, Dry Mesa, Colorado; DNM, Dinosaur National Monument, Utah; SC, Sheep Creek, Wyoming; Th, Thermopolis, Wyoming.

Table 1. Sauropod dinosaur specimens for which cervical vertebrae were examined for gross morphological and/or microscopic features suggesting ligament attachment sites. See text for institutional abbreviations and additional specimen details.

Taxon	Specimen	Spinous Process	Pseudospinous Tuberculum
Apatosaurus/ Brontosaurus	BYU 11894	w†	w
	BYU 12584	w	w
	BYU 17020	w	a
	BYU 18531	p	w
	CM 555	w	w
	CM 3018	w	w
Diplodocus	BYU 12613	w	w
	BYU 21863	w	w
	BYU 22468	a	w
	CM 84	w	w
	WDC BB 561	p	a
	WDC BB 1239	p	a
	WDC BB 771	p	a
	WDC FS 615	p†	a
Camarasaurus	BYU 12945	a	a
	CM 584	p	a
	CM 11069	w	a
	CM 11338	w	a
	CM 36701	p	a

Abbreviations: a, absent; p, present and poorly preserved; w, present but well preserved; †, specimen examined histologically or via micro-CT scanning.

The tip of a *Diplodocus* cervical hemispinous process, from what appears to be cervical 12 (± 1) based on comparison with the cervicals figured by Hatcher (1901, pl. 3), was obtained from WDC FS-615 and thin sectioned following typical histological procedures (Cuccu et al. 2024). Sampling was completed by hand to minimize damage to the bone (Fig. 6). To avoid mislabeling interspinal ligament fibrocartilage, the thin sections were cut closer to the middle portion of the hemispinous process, rather than the cranial or caudal edges, to emphasize observation of orientations from epaxial cervical ligaments. The samples were embedded in Buehler EpoThin 2 resin, cut by a BUEHLER IsoMet Low-Speed Saw, mounted onto slides and stabilized as needed with PaleoBond cyanoacrylate glue, prior to polishing to appropriate thickness using a BUEHLER MetaServ 250 Grinder-Polisher. The slides were successively ground to 0.5 mm using a 320 grit disk, 0.25 mm using a 600 grit disk, and 0.15 mm using an 800 grit disk. The final thicknesses varied between each thin section, but all were ground down thinner than 115 µm to properly reveal the bony structure.

Additionally, the distal portion of a cervical hemispinous process from *Apatosaurus* sp., BYU 11894, was collected for nondestructive micro-CT scanning (Fig. 7). The degree of spinal bifurcation in this specimen implies it is at least cervical 8, if not from a position farther caudally, based on comparison with the cervicals of *Apatosaurus louisae* figured by Gilmore (1936, pl. 24); its small size suggests it is from a juvenile individual. The scanning took place at Micro Photonics Inc., Allentown, PA, USA, using a SkyScan 1273 instrument equipped with a 6 Mp X-ray camera. The *Apatosaurus* sample was imaged at an isotropic voxel size of 26 µm at 130kV and 300 uA of X-ray energy coupled with a 1 mm copper filter to minimize beam hardening. The sample was rotated 360° using 0.2° steps to collect 1801 projection images that were then reconstructed into an 8-bit BMP stack using Bruker NRecon 2 (du Plessis et al. 2017). The micro-CT images were processed using Dragonfly to enhance the visibility of cortical and trabecular bone structures.

Additional *Diplodocus*, *Apatosaurus*, and *Camarasaurus* cervical vertebrae at BYU and CM were examined for gross morphological evidence of sites of possible epaxial cervical ligament attachment similar to those that have been hypothesized for extant animals (Tab. 1).

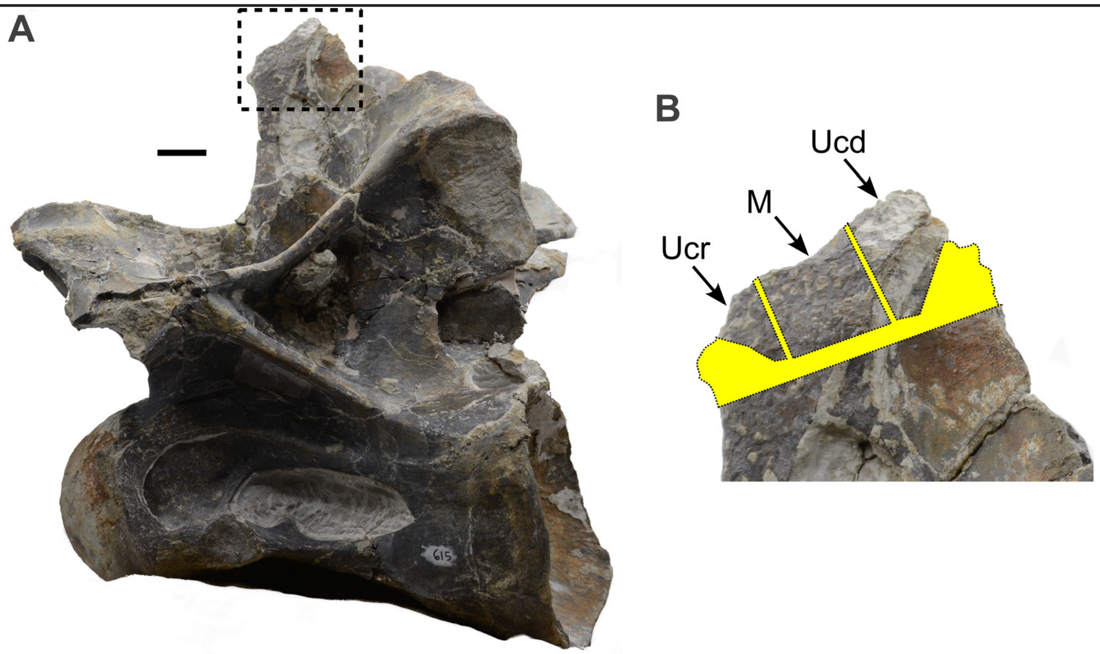
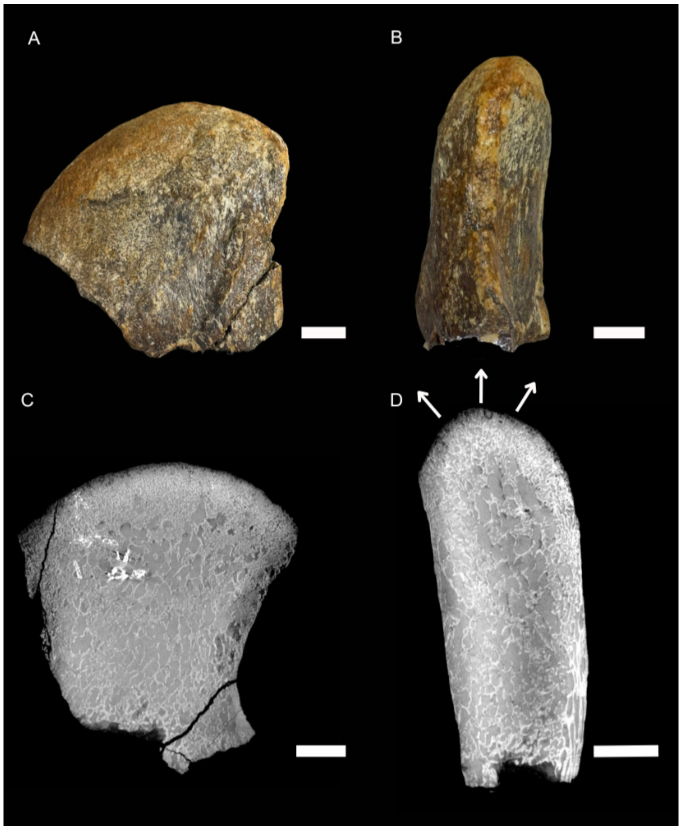


Figure 6. Left lateral view of *Diplodocus* cervical vertebra (possibly cervical 12) WDC FS-615 and locations of samples taken for histological analysis. A, Whole vertebra (scale bar = 10 cm); dashed box shows area of close-up in B. B, Close-up of distal hemispinous process showing locations of samples taken for histological thin sectioning (cuts along yellow outlines). Abbreviations: M, middle; Ucd, upper caudal; Ucr, upper cranial. Scale = 10 cm.

Institutional abbreviations: BYU, Brigham Young University, Provo, Utah, USA; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; MOR, Museum of the Rockies, Bozeman, Montana, USA; WDC, Wyoming Dinosaur Center, Thermopolis, Wyoming, USA.



RESULTS

Microscopic Structures

WDC FS-615 produced 11 thin sections that revealed 'thread-like' structures that appear to be mineralized fibrocartilage or possibly Sharpey's fibres based on their location at the apex of the hemispinous process (Aaron 2012; Horner et al. 2016; Cerda et al. 2022). The distal middle section (M) of the hemispinous process of this specimen appears to have undergone extensive weathering that removed much of the cortical bone needed for examination. Orientated fibres were observed in the M sampling section of the hemispinous process (Fig. 6). However, they were located at a more proximal level rather than the dorsal-most location of the hemispinous process where an exterior ligament attachment would be expected. WDC FS-615 overall exhibited presumed mineralized fibrocartilage arranged in

<**Figure 7.** Gross morphological (A, B) and micro-CT (C, D) images of the distal end of the hemispinous process of *Apatosaurus* BYU 11894 showing dense cortical bone near the exterior and trabecular bone toward the interior. A, Lateral view of hemispinous process tip. B, Anterior view of hemispinous process tip. C, Micro-CT image in sagittal section of hemispinous process tip; the directions of osteons were not observed. The white spots are higher density regions in the hemispinous process. D, Micro-CT image in coronal section showing radially orientated bone fabric in the dorsal-most region of the hemispinous process. White arrows point in the general directions of the bone fabric. Scale bars = 10 mm.

a non-uniform pattern, but due to the weathering-induced quality of preservation, the entire pattern is preserved only in a few positions rather than equally around the entire spine tip (Fig. 8). In cranial view, the mineralized fibrocartilage was orientated both dorsolaterally and dorsally. The sections from WDC FS-615 upper cranial (Ucr) and M exhibited weathering on the dorsal-most region of interest in the hemispinous process, and the observed orientated fibres were located slightly deep to the exterior surface of the hemispinous process (Figs. 6, 8) and therefore should be interpreted with caution. The caudal sections, with particular interest in upper caudal (Ucd) #1, are the best preserved and provide greater reliability of the direction of exterior forces acting on the hemispinous process (Fig. 9). The mineralized fibrocartilage reflects a non-uniform orientation to a degree, but is orientated in a strong left lateral direction (Fig. 9A) that was not expected for a supposed dorsally located ligament.

The density of the well-preserved *Apatosaurus* hemispinous process tip BYU 11894 inhibited interpretation of the micro-CT images (sensu Hipsley et al. 2020). Lateral and coronal slices of the hemispinous process show that the pattern of bone orientation, at least in the distalmost part, is in specific vertical directions in a radial pattern (Fig. 7D).

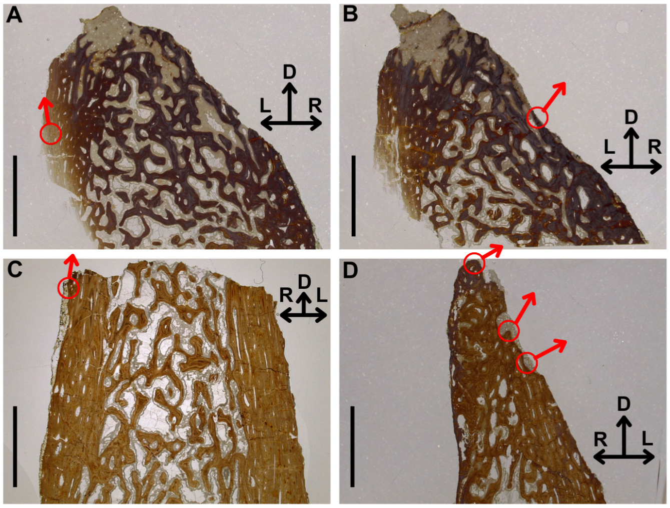


Figure 8. Entire thin sections (differing thicknesses) from the distal tip of the hemispinous process of *Diplodocus* cervical vertebra WDC FS-615 showing general orientation of presumed mineralized fibrocartilage. The left side of every thin section had a greater abundance of orientated mineralized fibrocartilage and thickened osteons. The distal tip of the spine underwent weathering that removed the dorsal-most region of interest, so orientated mineralized fibrocartilage could not be used confidently as evidence of a ligament attachment. See Fig. 6 for locations of samples. A, Ucr #2. B, Ucr #3. C, M #5. D, Ucd #1. Red arrows point in the general orientation of presumed mineralized fibrocartilage. Red circle = location of mineralized fibrocartilage; trifid arrows indicate directions. Abbreviations: D, dorsal; L, left lateral; R, right lateral. Scale bar = 0.5 cm.

Gross Osteological Features

In addition to the microscopic analysis, multiple cervical vertebrae from *Diplodocus*, *Camarasaurus*, and *Apatosaurus*—taxa that have bifurcate hemispinous processes on at least some of their cervical vertebrae—at BYU and CM were examined for gross-scale structures that might suggest one or another type of cervical ligament. Among the vertebrae examined, none possessed marked rugosities at expected ligament attachment sites on the distal hemispinous processes such as those seen in many theropod dinosaurs (Wilson et al. 2016). However, most of the examined *Apatosaurus* and *Diplodocus* cervical vertebrae possess robustly developed pseudospinous tubercula (sensu Harris 2006) positioned sagittally on the floor of the sulcus between the hemispinous

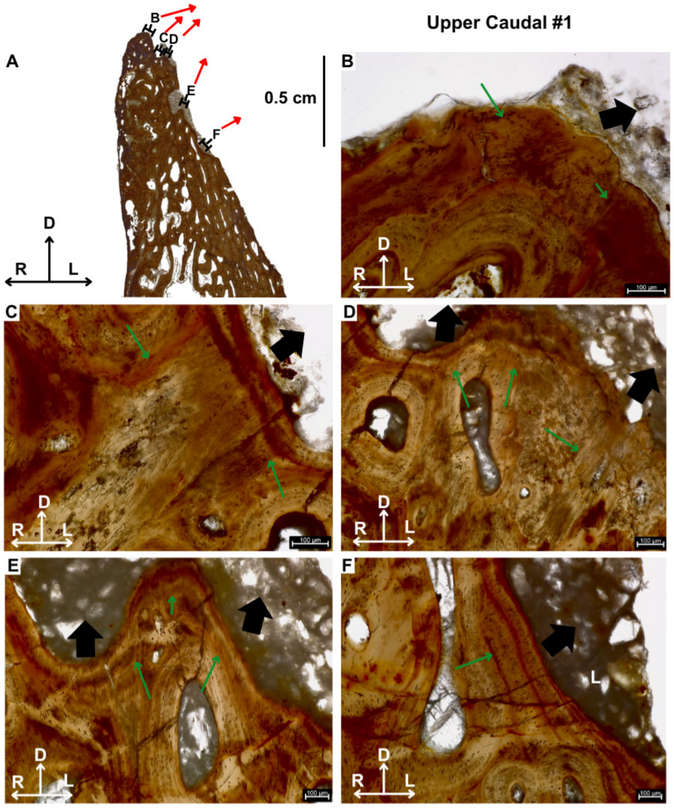


Figure 9. Ucd #1 thin section from the distal tip of the hemispinous process of *Diplodocus* cervical vertebra WDC FS-615 in cranial view. A, Thin section of specimen showing the general directions of orientation (red arrows) of presumed mineralized fibrocartilage along the exterior in cranial view. Letters refer to subsequent, close-up parts of the figure. B–F, Close-up views of mineralized fibrocartilage and their orientations in the regions indicated in A. Green arrows = mineralized fibrocartilage, black arrows point in the direction of orientation of mineralized fibrocartilage, trifid arrows indicate directions. Abbreviations: D, dorsal; L, left lateral; R, right lateral. Scale bar = 100 µm.

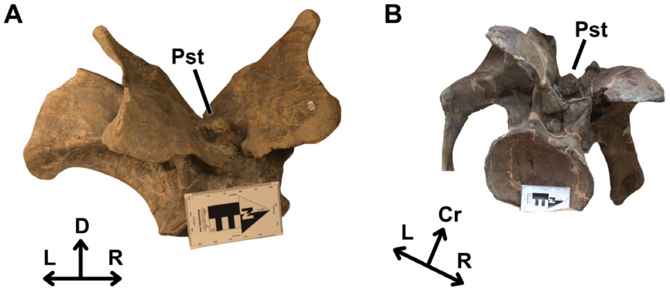


Figure 10. Pseudospinous tubercula (Pst) on *Apatosaurus* cervical vertebrae. A, BYU 12584 in oblique left dorsolateral view; the pseudospinous tuberculum is robustly developed on the caudal region of the vertebral arch. B, BYU 18531 (C7); the pseudospinous tuberculum is located on the caudal region of the vertebral arch. Trifid arrows indicate directions. Abbreviations: Cr, cranial; D, dorsal; L, left lateral; R, right lateral.

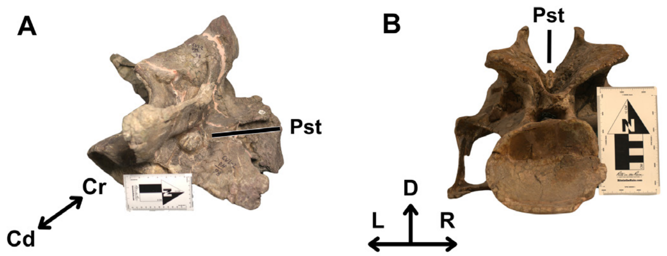


Figure 11. Pseudospinous tubercula on *Diplodocus* cervical vertebra. A, BYU 22468 in dorsal view; the pseudospinous tuberculum is robustly developed on the caudal region of the neural arch. B, BYU 12613 in caudal view; the pseudospinous tuberculum is located farther cranially and is smaller in size. Two-way and trifid arrows indicate directions. Abbreviations: Cd, caudal; Cr, cranial; D, dorsal; L, left lateral; R, right lateral.

Figure 12. *Apatosaurus* CM 3018 showing pseudospinous tubercula (Pst) on the 8th and 9th cervicals.

processes over the caudal half of the vertebral canal (Figs. 10–12). In *Diplodocus* CM 84, pseudospinous tubercula are present from cervical 7 through 15, and in *Apatosaurus* CM 3018, from cervical 6 through 12, then they are absent on the 13th and 14th cervical vertebrae but appears again on the 15th cervical. CM 11338, a juvenile *Camarasaurus*, appears to lack pseudospinous tubercula, but one *Camarasaurus* cervical, BYU 12945, has a large, triangular, cranially pointed bony process between the cranial zygapophyses (Fig. 13).

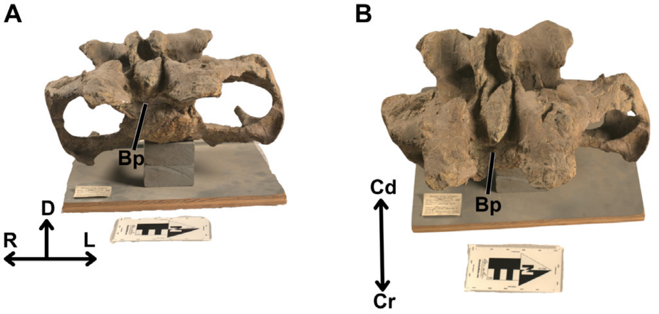


Figure 13. Possibly juvenile *Camarasaurus* cervical vertebra (approximately cervical 8) BYU 12945 showing a triangular bony process (Bp) projecting cranially between the cranial zygapophyses. A, Oblique anterodorsal view. B, Dorsal view. Two-way and trifid arrows indicate directions. Abbreviations: Bp, bony process; Cr, cranial; D= dorsal; L, left lateral; Cd, caudal; R, right lateral.

DISCUSSION

Microscopic Structures

The WDC FS-615 thin sections show a non-uniform pattern of possible mineralized fibrocartilage (Figs. 8, 9) that, based on our initial assumption of a correlation between directionality and attaching ligament type, support the hypothesis that *Diplodocus*, and perhaps other flagellicaudatan sauropods, possessed paired supraspinal ligaments, rather than paired, mammal-style nuchal ligaments in their necks. The presence of supraspinal ligaments in sauropod necks was previously hypothesized by Schwarz et al. (2007) and Woodruff (2016); the work presented herein is the first actual support for this hypothesis.

The strong, left lateral orientation of the mineralized fibrocartilage from the dorsal-most region of the hemispinous process WDC FS-615 Ucd #1 (Fig. 9A) was unexpected. It suggests a supraspinal ligament that did not attach exactly, entirely, or exclusively at the distal tip of the spine. It resembles the pattern documented in Ankole-Watusi cattle, in which the supraspinal ligament (considered a nuchal ligament by Woodruff [2014]) attaches to the lateral sides, rather than the apices, of the cervicothoracic hemispinous processes. This position appears to be a function of the fact that Ankole-Watusi cattle lack the robustly developed ‘withers’ commonly seen in other euungulates. While Ankole-Watusi cattle are an outlier in the extant animal kingdom, perhaps flagellicaudatan sauropods used a similar ligament configuration to support their massive necks, as predicted by Woodruff (2014). The evidence presented by the WDC FS-615 Ucd #1 thin section is intriguing, but examination of additional, better preserved and more intact sauropod cervical hemispinous processes is needed to see if the extreme lateral orientation is present in other vertebrae as well or if this is simply an individual specimen feature.

The micro-CT images from the *Apatosaurus* hemispinous process, BYU 11894, reveal the complex structure of the cortical bone. In particular, the medial portion of the hemispinous process has cortical bone orientated in an almost vertical and radial direction (Fig. 7), reflecting the likely presence of a suspensory, epaxial structure acting on the bone in this location. As previously mentioned, osteon long axes will be organized to the direction of the greatest force acting on the bone because bone is strongest under tension and compression (McGowan 1999). It can, therefore, be inferred that the observed direction of the cortical bone found in the distal-most region reflects the direction of the highest amount of force and suggests that flagellicaudatan sauropods possessed an epaxial, supraspinal ligament. However, the micro-CT images are somewhat ambiguous as to the specific mode of the ligamentous attachment. The orientation of cortical bone could reflect tendon attachment rather than (or in addition to) ligament attachment because both could exert identical forces on the bone. If flagellicaudatan sauropods used a ligament system similar to Ankole-Watusi cattle, then the direction of the cortical bone would be expected to be dramatically orientated to the lateral side of the hemispinous process. Instead, the micro-CT images reveal a nearly perfect radial pattern consistent with the hypothesized distribution for a dorsally situated supraspinal ligament system.

Future research could examine the pairing of both mineralized fibrocartilage and osteon orientation by first micro-CT scanning a hemispinous process tip, then producing thin sections of the same hemispinous process tip. Identifying the mineralized fibrocartilage from the thin sections and pinpointing the same location within the micro-CT may allow the orientation of the mineralized fibrocartilage to be identified in other micro-CT images with greater confidence, thus avoiding destructive testing.

Gross Osteological Features

As noted above, none of the distal tips of the cervical hemispinous processes that were examined possessed marked textures or rugosities that would suggest strong muscle or ligament attachment. In regions of spinous processes where ligament formation is present, rugose structures or projections may be due to metaplasia (Horner et al. 2016; Wilson et al. 2016). Metaplasia is caused by pathological or stress induced forces in mammals and birds (Wilson et al. 2016). The development of rugosities is non-uniform, however. Rugosities in mammals become more prevalent in older and larger individuals, and are less developed or absent in both smaller taxa and younger individuals. This non-uniform development is seen in other dinosaur clades as well (Wilson et al. 2016), ranging in theropods from well-developed rugosities in large taxa and individuals to poorly developed to nonexistent rugosities in smaller taxa and individuals. Theropod dinosaurs may have metaplastically mineralized portions of their supraspinal and interspinal ligaments to stiffen the skeleton due to increasing stress acting on the body (Wilson et al. 2016). As the theropod grows, stiffening of the skeleton increases passive support of the spinal column, which is ergonomically advantageous. At least some titanosaurs also exhibit development of a mineralized supraspinal ligament (Cerda et al. 2015), which similarly could have stiffened the sacral region and increased passive support of the spine to facilitate movement of these dinosaurs. Interestingly, Cerda et al. (2015) noted that other large sauropods with well-preserved sacra, such as *Diplodocus longus*, lack a supraspinal rod, implying that their sacra were not subjected to similar stresses as in titanosaurs.

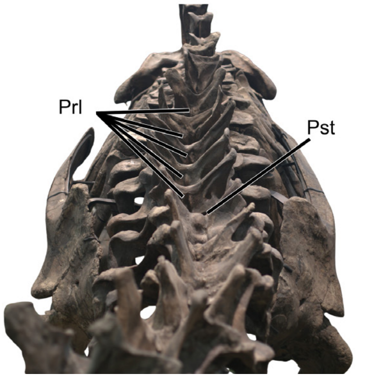


Figure 14. Midline prespinal laminae (Prl) in bifurcate thoracic vertebrae of *Apatosaurus louisae* CM 3018 located ventral to the bottom of the sulcus between the hemispinous processes. Note the absence of pseudospinous tubercula (Pst) on these vertebrae until the 15th cervical.

As previously noted, interlaminar elastic ligaments connect the bases of the spinous processes of individual cervical vertebrae in birds and crocodylians (Frey 1988; Tsuihiji 2004; Schwarz et al. 2007). Many of the sauropod cervical vertebrae examined from BYU and CM possess rugose, 'knob-like' pseudospinous tubercula (Figs. 10–12) that we hypothesize are interlaminar elastic ligament insertion points. In the limited sample that was examined, and were not affected by mechanical preparation marks, the gross bony texture of these tubercula tended to have an craniocaudal orientation, perpendicular to what would be expected if the tubercula were subject to suspensory forces from above by nuchal laminae, but as would be expected for structures subject to tensional and compressional ligaments forces in craniocaudal directions. The anatomical implications of the disappearance of pseudospinous tubercula near or within the thoracic region is unclear: either an interlaminar elastic ligament did not persist into the thoracic series, or possibly its position shifted ventrally, perhaps onto the short, vertical prespinal laminae (sensu Wilson 1999) that lie along the midline ventral to the bottom of the sulcus between the hemispinous processes (Fig. 14). These observations need to be bolstered by further sampling of taxa and individuals within Flagellicaudata. Additional testing and support of this interpretation, including via histology to see if the microstructure matches the observed gross-scale orientations of the tubercula, also is needed. The peculiar, cranial bony projection in an observed cervical vertebra of *Camarasaurus*, BYU 12945 (Fig. 13), may constitute ossification or metaplasia of an interlaminar elastic ligament and thus support the presence of such a ligament system outside Flagellicaudata, but this, too, requires further testing.

Dicraeosaurids with their dramatically elongate and bifurcate cervical spinous processes, stand out among sauropods. This feature is most notable in *Amargasaurus* and *Bajadasaurus*, but also occurs in *Dicraeosaurus* (Janensch 1929; Gallina et al. 2019; Cerda et al. 2022). A supraspinal ligament may have been present in sauropods with shorter spinous processes, but likely were not possible in the necks of *Amargasaurus* and *Bajadasaurus* in which the extreme narrowness of the tips of the spinous processes probably would not have permited effective attachment of a supraspinal ligament. Furthermore, the extreme spine elongation would have made it difficult for a dorsal supportive structure to efficiently assist in passively supporting the neck and head. Cerda et al. (2022) noted the presence of Sharpey's fibres throughout the entirety of the spinous processes in *Amargasaurus*. The general craniocaudal orientation of the fibres across the entire heights of the spinous processes indicate a complex system of interspinal ligaments. Perhaps during the process of spinous process elongation in these taxa, the supraspinal ligament was lost and a robust, complex system of interspinal or interlaminar ligaments was developed to take the place as a suspensory structure. However, Cerda et al. (2022) did not examine the cervical vertebrae of *Amargasaurus* for evidence of interlaminar elastic ligaments in addition to interspinal ligaments. At least some cervicals of *Dicraeosaurus* and *Pilmatueia* have pseudospinous tubercula (Janensch 1929; Coria et al. 2019), suggesting the presence of interlaminar elastic ligaments, but none have been reported in *Amargasaurus* (Salgado and Bonaparte 1991) and *Bajadasaurus* (Gallina et al. 2019), although the limited sample of cervical vertebrae (only cervical ?5 among elements with bifurcate spines) in the latter does not reveal if one may have been present farther caudally in the cervical series. The implications of these absences are unclear, but the cervicals of *Amargasaurus* and *Bajadasaurus* should be examined for alternative points of possible interlaminar elastic ligament attachment. This variability again emphasizes that even within a clade (such as Dicraeosauridae), cervical ligament configurations may vary markedly.

BROADER IMPLICATIONS AND DIRECTIONS FOR FUTURE RESEARCH

The research documented herein supports the presence of both supraspinous and interlaminar elastic ligaments in sauropod dinosaurs with bifurcate spinous processes, particularly flagellicaudatan sauropods. However, our results do not contribute to our understanding of vertebral ligament morphology in sauropods possessing single, non-bifurcate processes. Homologous attachment sites for both supraspinal and interlaminar elastic ligaments in such taxa remain to be identified and examined (including histologically) for bone orientation to see if they, too, support possession of such ligaments more broadly within Sauropoda. Nevertheless, extant phylogenetic bracketing (Witmer 1995) of sauropods between Crocodylia and Aves dictates that at least interlaminar elastic ligaments would be expected and should be the baseline hypothesis across Sauropoda, and perhaps Sauropodomorpha more broadly.

Based on this research, sauropods most parsimoniously possessed a crocodylian-like tandem system of supraspinal and interlaminar elastic ligaments in their necks (but see above for an important caveat concerning the supraspinal ligament in *Alligator*), but not a mammal-like nuchal ligament system as proposed by Janensch (1929), or a *Rhea*-like interspinal elastic ligament, as proposed by Tsuihiji (2004). However, alternate or additional ligamentous systems are conceivable, but this would require further testing. For example, some sauropods may have had equine-like nuchal ligaments, or *Rhea*-like interspinal elastic ligaments, with laminae that attached only to the caudal-most cervical vertebrae, to support only the base of the neck, and thus would not leave histological signatures on more cranial cervical vertebrae. Also, as in some birds, interlaminar elastic ligaments may only occur in some regions of the neck (e.g., the caudal region), or be stronger in some regions than others (Boas 1929). Furthermore, there may have been different configurations of ligaments among taxa, so a single, blanket hypothesis across Sauropoda may not be viable.

The presence in sauropods of cervical supraspinal and interlaminar elastic ligaments rather than mammal-style nuchal ligaments may have palaeoecological ramifications, specifically for their abilities to passively (non- or minimally muscle aided) maintain elevated necks for extended periods of time without substantial energy expenditure. Sauropod necks were famously pneumatized as a weight-reducing adaptation (Apostolaki et al. 2015), but they still would have been relatively heavy by virtue of the addition of soft tissues as well as their large (adult) sizes and thus might be expected to have benefited from passive support. However, whether or not a tandem system of supraspinal and interlaminar elastic ligaments was capable of providing such passive support is unknown. Long-necked mammals, such as giraffes, benefit from the passive, suspensory effects of a nuchal ligament, but this does not seem to be a suitable model for sauropods and thus giraffes make poor analogues. Long-necked birds, such as 'ratites', can maintain elevated necks for extended periods using only interlaminar elastic ligaments (or, in *Rhea*, interlaminar plus interspinal elastic ligaments), but how analogous their necks are to those of sauropods in this regard remains to be determined. The postural range attainable by 'ratite' necks seems to exceed that of sauropods (Dzemski and Christian 2007), and some avian neck postures, such as vertical or S-shaped, may resolve the need for passive ligamentous support in those birds at least some of the time. Stacking sauropod cervicals vertically would greatly reduce the need for counter-gravitational support mechanisms in their necks (Paul 2017), but whether some or all sauropods were capable of such postures is unclear. Superimposing different ligament configurations onto existing models constructed in an attempt to understand sauropod neck postures and mobility (e.g., Vidal et al. 2020a; Boisvert 2024) is a potentially fruitful approach to better evaluate any capacity for passive neck support in these animals.

In addition to a system of supportive ligaments, sauropod vertebrae are heavily pneumatized. Pneumatic diverticula usually have been postulated as weight-reducing adaptations in sauropods (Wedel 2003; Schwarz et al. 2007), but also have been hypothesized to have possibly provided some counter-gravitational support in their necks as well (Schwarz-Wings and Frey 2008). Conti (2024) followed Schwarz et al. (2007) and Schwarz-Wings and Frey (2008) in hypothesizing that a system of pneumatic diverticula in sauropod necks would have been by itself insufficient to passively support the weight of the neck; ligamentous systems would be required as well. Conti (2024) also estimated the approximate thickness of a supraspinal ligament in *Apatosaurus* to have been 0.9–2.3 cm, depending on the specific model used, to maintain the neck in a state of equilibrium at an assumed horizontal osteological neutral pose (ONP), but it is unclear whether or not this 'state of equilibrium' is the same as passive support. The further contribution of interlaminar elastic ligaments to a supraspinal-ligament-plus-pneumatic-diverticula system remains unknown and is a potential avenue for future modelling and research. Interlaminar elastic ligaments alone do not seem capable of passively supporting horizontal neck posture in at least *Meleagris* (Bennett and Alexander 1987), but conceivably, supraspinal and interlaminar elastic ligaments together may have been capable of passive support without the pneumatic system, although this would not necessarily exclude the participation of the latter. Of course, all of this presumes that sauropod necks enjoyed passive support at all; it is possible that cervical muscles alone supported the neck (Graff et al. 2012), despite the additional metabolic investment required.

The effects of different configurations of epaxial, sagittal or parasagittal cervical ligament systems of sauropods on interpretations of their feeding styles are another avenue for future research. The question of whether any particular sauropod was a high browser or a low browser/grazer depends on the biomechanics of whether or not its neck could be passively maintained in any feeding posture for a sufficient length of time to permit obtaining enough food to power the physiology of such a large animal, particularly to balance the energy expended in holding the neck up while obtaining food. Flagellicaudatans have been hypothesized to have been low browsers/grazers with more horizontal neck postures (Stevens and Parrish 1999; Woodruff 2016; Boisvert 2024), but the degree to which their cervical vertebrae were posturally restricted is unclear and dependent on assumptions of bone articulation and soft-tissue reconstruction (Taylor et al. 2009; Taylor and Wedel 2013; Taylor 2014). The apparent presence of a tandem system of supraspinal and interlaminar elastic ligaments cannot resolve this question until biomechanical models elucidate whether or not such systems could provide passive neck support at all, as well as determine whether or not such support is posture dependent. The data presented herein only point to the ligament systems that at least flagellicaudatan sauropods possessed that can form the basis for such modelling.

Conti (2024) also discussed the general morphology of cervical spinous processes as an identifier for neck orientation. Taxa with dorsoventrally tall and craniocaudally short hemispinous processes relative to the heights of their respective centra, such as flagellicaudatan sauropods and bovines, were suggested to have had a more horizontal neck ONP. Taxa with elongated spinous processes relative to the heights of their respective centra, such as brachiosaurid sauropods and giraffes, were suggested to have had more vertical ONP. How these apparent relationships relate to epaxial ligament systems is presently unclear, but the gradual increase in hemispinous process height in crocodylian necks is more similar to the pattern exhibited by flagellicaudatan sauropods than to that of many mammalian necks (Schwarz et al. 2007). Further research is needed, however, to confirm whether or not such height measurements accurately reflect ONP and thus affect, or are affected by, different ligament restorations and configurations, as well as if the ONP reflects adult or juvenile stages of ontogenetic development that can alter the range of motion in digital models (Vidal et al. 2020b).

Lastly, we note that sites of ligament attachment on flagellicaudatan cervical spinous processes may be thin and therefore are likely among the first regions to be affected by pre- and peri-burial taphonomic processes and post-exhumation weathering. Thus, specimens selected for future histological and/or micro-CT work need to be assessed for quality of preservation because specimens exhibiting signs of weathering may not be informative.

CONCLUSIONS

Previous hypotheses and reconstructions of sauropod epaxial cervical ligament systems have differed, making pinpointing the exact system(s) present difficult. While the research presented here is from a small sample and therefore not comprehensive, prepared thin sections, micro-CT images, and examination of gross morphological features of cervical vertebrae of *Apatosaurus* and *Diplodocus* support the presence of both a supraspinal ligament system and an interlaminar elastic ligament system within at least a portion of the cervical region. The histological thin sections of *Diplodocus* (WDC FS-615) exhibited presumed mineralized fibrocartilage in an orientation that aligns with the expected direction for a supraspinal ligament that are arranged in a non-uniform pattern. Weathering altered much of the dorsal area of the hemispinous process, making it difficult to directly infer the extent or morphology of a supraspinous ligament. To seek additional evidence of orientated structures such as mineralized fibrocartilage or Sharpey's fibres, an *Apatosaurus* hemispinous process (BYU 11894) underwent micro-CT scanning and revealed orientated, gross-scale bone in a radial pattern, the expected direction from a supraspinal ligament. This is comparable to the WDC FS-615 thin sections as suggesting support for a directly attaching supraspinous ligament.

Micro-CT (or possibly nano-CT) scanning has the potential in similar, future research to avoid destructive testing on fossil samples. However, due to the density of BYU 11894, only the orientated cortical bone could be observed; the images did not reveal details of the fine fibres that were found in the thin sections. Furthermore, the discovery of radially orientated cortical bone does not eliminate the possibility that the dorsal force acting on the hemispinous process could have come from another structure, such as a tendon or series of tendons.

Lastly, pseudospinous tubercula were identified in many *Diplodocus* and *Apatosaurus* specimens. Additionally, a *Camarasaurus* cervical vertebra (BYU 12945) had an unusual, cranially orientated, bony projection. Preliminarily, these features suggest that at least these sauropod taxa had, in addition to an inferred supraspinal ligament system, a system of interlaminar elastic ligaments similar to those present in birds and crocodylians, as would be expected from extant phylogenetic bracketing, obviating the need to hypothesize convergent evolution with nuchal-ligament-bearing mammals.

As noted earlier, the orientations of mineralized fibrocartilage at a proposed ligament insertion site were themselves hypothetical. Further research along these lines can be better advanced through dissection of the three main types of ligaments seen in extant animals to determine the details of how each ligament type attaches to the cervical vertebrae, and through osteohistology to determine if the attachment sites indeed exhibit orientation of mineralized fibrocartilage diagnostic for each ligament type. This would establish whether or not histology can truly be used to identify ligament type in fossil taxa.

Even if flagellicaudatan sauropods did possess both a paired supraspinal and interlaminar elastic ligaments, the extent of either system, as well as attachment site morphology, could vary across the cervical vertebral series, as is seen in extant animals. Cervical vertebrae from the cranial, middle, and caudal sections of the cervical series would need to be individually tested to observe if the mineralized fibrocartilage are present in all of the vertebrae or only present in specific regions. Further research is thus needed to provide additional support for the presence of a dorsal or dorsolaterally situated supraspinal ligaments and midline interlaminar elastic ligaments in the necks of flagellicaudatan and other sauropods, but the approach detailed herein has the potential to be used for any extinct animals to properly identify the type of epaxial ligaments used in their vertebral columns.

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