THE LIGAMENT SYSTEM IN THE NECK OF *RHEA AMERICANA* AND ITS IMPLICATION FOR THE BIFURCATED NEURAL SPINES OF SAUROPOD DINOSAURS

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ABSTRACT—The Extant Phylogenetic Bracket approach is applied to infer the kind of soft tissue that would have been associated with the bifurcated neural spines of the cervical vertebrae of sauropods. A median ligament ("ligamentum nuchae" or lig. supraspinale) extends along the tips of the neural spines and attaches to them in the cervical region of extant avian and non-avian diapsids, thus enabling a parsimonious inference that a homologous ligament would also have attached to the same sites in extinct diapsids, including sauropods. In the extant ratite bird, *Rhea americana*, "lig. nuchae" splits ventrally into two halves as the neural spines become bifurcated in the posterior cervical region, thereby maintaining its connection to both tips of each bifurcated neural spine. This shows the conservative nature of the connection between "lig. nuchae" and its osteological correlate. Furthermore, this ligament and the notches of the bifurcated neural spines enclose another ligament, lig. elasticum interspinale, that arises from the non-bifid neural spine of the most posterior "cervico-dorsal" and gives off branches inserting on the posterior surfaces of the neural spines of the middle to posterior cervicals in *Rhea*. This ligament in *Rhea* is suggested to be a good modern analog to the structure occupying the notches of the bifurcated neural spines of sauropods. A hypothetical reconstruction of the proposed ligament system is given using *Camarasaurus* and *Apatosaurus* as examples.

INTRODUCTION

Bifurcation of the cervical and dorsal neural spines characterizes several clades of sauropod dinosaurs including diplodocids, dicraeosaurids, *Camarasaurus*, and *Euhelopus* (McIntosh, 1990; Upchurch, 1998; Wilson and Sereno, 1998). For example, the notches on the neural spines are recognized in more than a half of the presacral vertebrae in *Camarasaurus grandis*, namely, from the third to the 19th presacrals (McIntosh et al., 1996a). In many of the neural spines, the notch is so deep that it completely divides the neural spine into two rami called the metapophyses (Osborn and Mook, 1921). Since this feature evolved several times independently in Sauropoda (Wilson and Sereno, 1998), one may ask: what kind of soft tissue occupied the notches between the metapophyses in the neck of sauropods? Answers to this question include two major hypotheses: (1) the notches housed a median epaxial muscle; or (2) they housed the nuchal ligament inserting on the skull. Riggs (1903) was the first to suggest the presence of axial muscles in the notches in sauropods, assuming that these muscles would have attached to the roughened "median plate" in the cervical neural arches of *Apatosaurus*. Osborn and Mook (1921) stated this hypothesis more explicitly, inferring that the notches of the cervical neural spines in *Camarasaurus* would have lodged large, axial muscles inserting on the neural spine of the axis. Alexander (1985) suggested that either an axial muscle or an elastin ligament would have occupied the notches in order to brace the long neck of these animals. Later, Alexander (1989) favored the latter interpretation, suggesting that a ligament similar to ligamentum nuchae of artiodactyls would have occupied the notches, reaching from the dorsal vertebrae to the skull. A similar, but particularly interesting hypothesis was suggested by Janensch (1929) for the neck of *Dicraeosaurus*. He also inferred the presence of a strong ligament with its branches inserting on the posterior sides of the neural arches in the middle and posterior cervical vertebrae. However, the morphology of this ligament is different from that of the mammalian lig. nuchae since it did not insert on the occipital region of the skull. Instead, the terminal insertion of the ligament as inferred by Janensch was the posterior area of the fourth cervical neural arch.

Among recent studies, Wilson and Sereno (1998) supported the ligament hypothesis of Alexander (1989) and further suggested that lig. nuchae in sauropods might have had branches inserting on each cervical vertebra, just as Janensch (1929) had proposed. A similar ligament system was also inferred for *Dicraeosaurus* and *Apatosaurus* by Frey and Martin (1997) and Martin et al. (1998). Stevens and Parrish (1999) inferred the presence of lig. nuchae in diplodocids based on the fact that it is commonly seen in modern Aves and Crocodylia. In contrast, Wedel et al. (2000) pointed out that the extant ratite bird, *Rhea americana*, also has bifurcated neural spines in its posterior cervical vertebrae, a condition that was first described by Mivart (1877). Wedel et al. (2000) further argued that in this bird the notches are occupied by musculus biventer cervicis, which is the most median epaxial muscle inserting on the occipital region of the skull in Aves. Using this as a modern analog, they suggested that m. biventer cervicis would also have occupied the notches in sauropod neural spines. Similarly, Dodson and Harris (2001) questioned the presence of lig. nuchae in sauropods for biomechanical reasons and argued that muscles, and not a ligament, lay in the notches.

The current study seeks to take a close look at this problem with special reference to the suggestion of Wedel et al. (2000). Based on the anatomy of ligaments associated with the neural spines and arches in extant diapsid reptiles, I have parsimoniously inferred that such ligaments would have filled at least a part of the notches in the sauropod neck. A literature survey and my own dissections of the neck of *Rhea* have also demonstrated that in this bird, contrary to Wedel et al. (2000), m. biventer cervicis does not occupy the notches of the neural spines. Instead, the bifurcated neural spines are associated with a ligament system that is unique to *Rhea* among modern Aves and that closely resembles the ligament inferred by Janensch (1929) for *Dicraeosaurus*. Therefore, in this paper I shall describe the significant aspects of the anatomy of this ligament in *Rhea*, and argue that this ligament system may be a good modern analog to ligaments of sauropods.

Institutional Abbreviations: **OMNH**, Sam Noble Oklahoma

Museum of Natural History, University of Oklahoma; **YPM**, Peabody Museum of Natural History, Yale University.

MATERIALS AND METHODS

Three specimens of *Rhea americana* were dissected, two adults (cervical region only) and one nearly hatched embryo, in order to identify the soft tissues associated with the bifurcated neural spines. Skeletons of *Rhea* (YPM 564 and 6503 in the Division of Vertebrate Zoology) were examined for osteological features associated with attachments of ligaments and muscles in the neck. Several specimens of *Alligator mississippiensis* and *Iguana iguana* were also dissected in order to identify the sites of attachment of lig. interspinale and lig. supraspinale in non-avian diapsids. Osteological correlates of these ligaments in the extant diapsids examined were then compared with putative muscular and ligamentary attachment sites in the cervical and anterior dorsal vertebrae of *Apatosaurus ajax* (YPM 1860 in the Division of Vertebrate Paleontology), *Camarasaurus grandis* (YPM 1905), *Apatosaurus* sp. (OMNH 1095, 1326, 1344, 1404, 1421, and 1423), and *Camarasaurus* sp. (OMNH 1383). I employed the phylogenetic method for reconstructing the soft tissue anatomy for fossil taxa as proposed by Bryant and Russell (1992) and, more specifically, the Extant Phylogenetic Bracket (EPB) approach of Witmer (1995), and attempted to make parsimonious reconstructions of these ligaments in the sauropod neck.

RESULTS

Ligament System in *Rhea*

In the vertebral column of *Rhea americana*, Mivart (1877) defined the first dorsal vertebra as the most anterior vertebra with its ribs articulating with the sternum. Anterior to this vertebra, he recognized 14 cervical and three "cervico-dorsal" vertebrae. This terminology will be used for the following description of the ligament system of this bird.

Barkow (1856), Boas (1929), and Van der Leeuw et al. (2001) have described the peculiar ligament system in the cervical region of *Rhea* in substantial detail. Most birds have elastic ligaments (lig. elasticum interlaminare) that connect the bases of the neural spines of adjacent vertebrae throughout the neck. *Rhea* has a second type of elastic ligament in the middle and posterior cervical regions, which was described by Barkow (1856) as lig. elasticum interspinale superficiale longum plus lig. elasticum interspinale superficiale breve (mistakenly cited as ligmenta elasticae interspinales profunda et superficiales by Baumel and Raikow, 1993). Baumel and Raikow (1993) renamed the combined ligament as lig. elasticum interspinale in Nomina Anatomica Avium, and thus this name will be used in the following description. Lig. elasticum interspinale is a long ligament that originates from the scar on the anterior surface of the non-bifid neural spine of the 17th presacral (i.e., the last "cervico-dorsal"). As it extends anteriorly, this ligament gives off a series of branches, each of which inserts successively on the posterior surfaces of the neural spines of the ninth to 14th (the last) cervical vertebrae, and eventually terminates on the posterior surface of the neural spine of the eighth cervical (Fig. 1). Thus, lig. elasticum interspinale of *Rhea* crosses multiple joints and is, in this respect, similar to lig. nuchae of artiodactyl mammals (e.g., Dimery et al., 1987). Concerning the evolutionary origin of lig. elasticum interspinale, Boas (1929) inferred that it would likely have become split and differentiated from lig. elasticum interlaminare. Consequently, lig. elasticum interspinale in *Rhea* is probably homologous with a part of lig. elasticum interlaminare in other birds.

Lig. elasticum interlaminare is absent in the middle cervical region of *Rhea* (Boas, 1929; Van der Leeuw et al., 2001), but is present in the anterior and posterior cervical regions, where it attaches to scars on the anterior and posterior areas of the neural arch. As Wedel et al. (2000:fig. 19) illustrate, this scar is situated in a concavity below the cleft of the neural spine (Fig. 2). Lig. elasticum interlaminare together with branches of lig. elasticum interspinale insert on the posterior surfaces of the neural spines of the 11th to 14th cervical vertebrae (Fig. 1B). The insertions of the latter branches are dorsal to those of lig. elasticum interlaminare, but the scars of these insertions are not separate and cannot be distinguished in osteological specimens (Fig. 2B).

My dissections reveal that lig. elasticum interspinale is robustly developed and lies mostly above the level of the neural spine in adult specimens (Fig. 2C, D), whereas it is rather flat and partially fits and lies on the shallow cleft of the neural spine in a nearly hatched embryo. This ligament is wrapped by a ligamentous or fascial sheath, which attaches to the tip of the bifurcated neural spine as well as on the lamina connecting the neural spine and the postzygapophysis on the neural arch (Fig. 2C, D). This sheath continues dorsally into a fascial sheet overlying the axial musculature, namely fascia dorsalis of Landolt and Zweers (1987). Inside of this sheath, lig. elasticum interspinale runs over the cleft of the neural spines. The attachment of the sheath to the tips of the bifurcated neural spines is marked by scars, and ligamentous fibers originating from these scars extend antero-dorsally, merging with the rest of the sheath. As the degree of bifurcation of the neural spine decreases and eventually disappears in the anterior region of the neck, the sheath transforms into a mere vertical ligamentous septum that attaches to the non-bifurcated neural spines and separates the right and left halves of the epaxial muscles. Thus, this ligamentous sheath surrounding lig. elasticum interspinale can be interpreted as a modification of the median, vertical ligament seen in other birds.

This median ligament is sometimes called "lig. nuchae" in the avian literature (e.g., Barkow, 1856; Yasuda, 2002), although it is not formally named in the current edition of Nomina Anatomica Avium (Baumel and Raikow, 1993). According to Barkow (1856), this median ligament is weakly developed in birds in general and is absent in several taxa. When present, it extends from the dorsal midline in the posterior cervical region and attaches to the dorsal edge of the neural spines. Its anterior-most insertion may vary among taxa. For example, Barkow (1856) described that the ligament extends as far anteriorly as the fourth cervical in *Sarcoramphus papa* (King Vulture), but it is restricted to the posterior cervical region in *Piculus aurulentus* (Yellow-browed Woodpecker). In *Gallus gallus* (Domestic Chicken), Barkow (1856) noted that "lig. nuchae" is completely absent. However, Yasuda (2002) showed that it is present in *Gallus* and that it extends far anteriorly, inserting on the neural spine of the axis. In the specimens of *Rhea* that I dissected, this ligament also terminates on the neural spine of the axis.

The gross morphology and sites of attachment of the avian "lig. nuchae" resemble those of lig. supraspinale, which is sometimes also called lig. nuchae, in non-avian diapsids. This ligament attaches to the dorsal edges of the neural spines throughout the cervical region in *Alligator mississippiensis* and *Iguana iguana*. Although Frey (1988) claimed that its terminal insertion in *A. mississippiensis* is on the axial neural spine, my own dissections reveal that this ligament actually inserts on the occiput in both *A. mississippiensis* and *I. iguana*. The similarities in the topology and sites of attachment between the avian "lig. nuchae" and lig. supraspinale in non-avian diapsids suggest that these ligaments are homologous. This allows the application of the EPB approach in reconstructing this ligament in extinct diapsids, including non-avian dinosaurs. As the anterior-most insertion of this ligament differs between the two
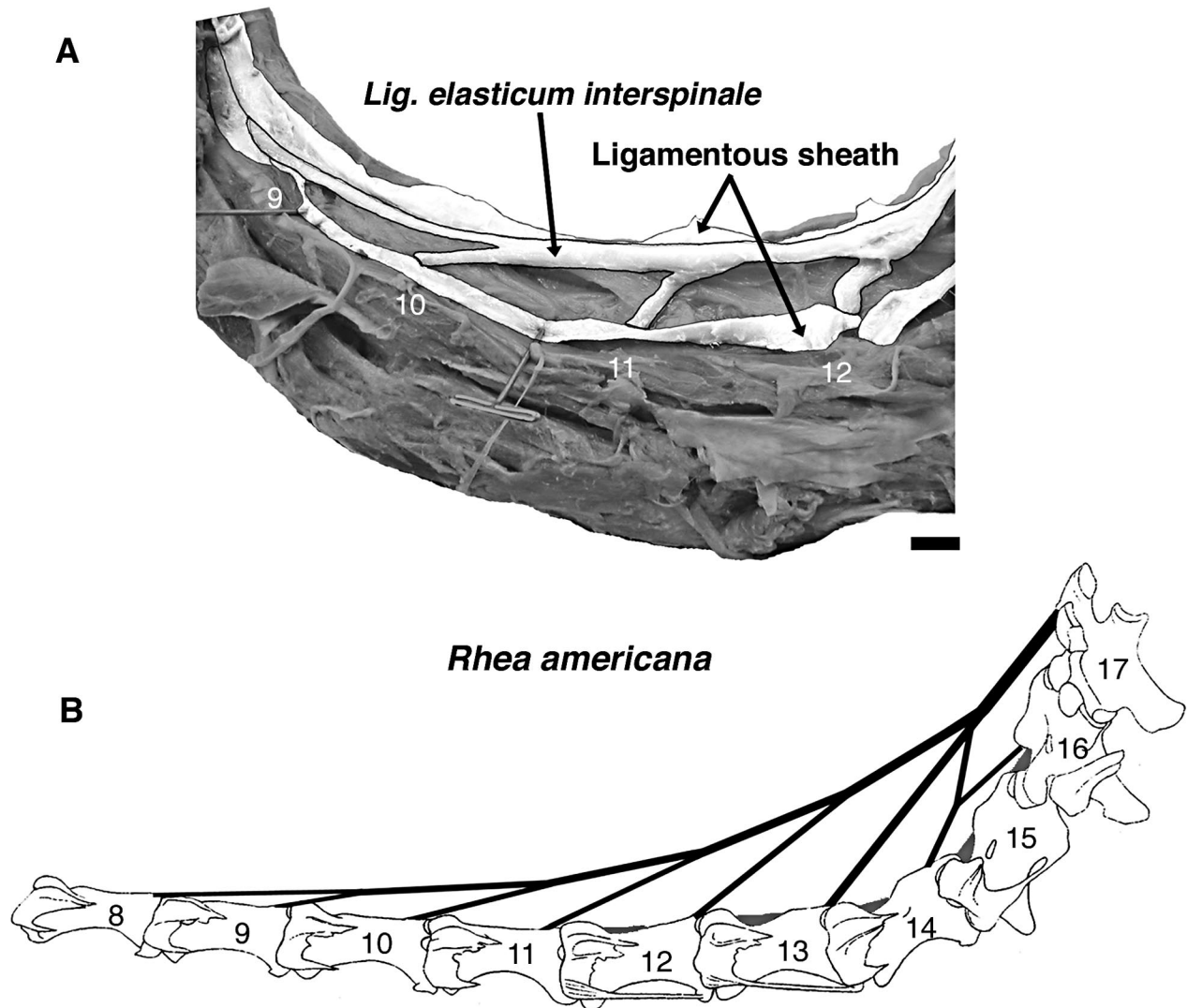
FIGURE 1. Elastic ligaments in the neck of *Rhea americana*. A, partially dissected posterior part of the neck showing branches of ligamentum elasticum interspinale (left dorso-lateral view). The ligamentous sheath wrapping around the ligament has been cut and opened, thereby exposing the ligament. Scale bar equals 1 cm; B, schematic diagram showing the configuration of lig. elasticum interspinale (black line) and lig. elasticum interlaminare between adjacent vertebrae (gray line) in the middle to posterior cervical regions, left lateral view (modified from Boas, 1929). The position of each vertebra is indicated by a number (e.g., 8 = the eighth presacral vertebra).

extant archosaurian clades, it cannot be conclusively inferred in non-avian dinosaurs whether the ligament inserted on the occiput or on the axis based solely on this approach. However, using the EPB approach, it is rather safe to infer the presence of this ligament attaching to the dorsal edges of the neural spines at least in the middle to posterior cervical regions in non-avian dinosaurs (a Level I inference; Witmer, 1995). Thus, it would be most parsimonious to infer that lig. supraspinale would have attached to the neural spines of the sauropod cervical vertebrae regardless of the shape of their neural spines. The ligamentous sheath and ''lig. nuchae'' in *Rhea* provides an indirect line of support for this parsimonious inference. Namely, in the anterior to middle cervical regions of *Rhea*, ''lig. nuchae'' is a median, vertical ligament like those seen in other birds and attaches to the non-bifurcated neural spines. As the neural spines become bifurcated in the posterior cervical region, this ligament also splits ventrally into two halves such that it maintains its connection to the tips of each neural spine. These two halves of ''lig. nuchae'' and the bifurcated neural spines

enclose lig. elasticum interspinale. This indicates that the connection between ''lig. nuchae'' and the tips of the neural spines is very conservative even when the morphologies of this ligament and the neural spines are altered.

In extant diapsids, epaxial muscles are present lateral to ''lig. nuchae.'' They tend to bulge up, thereby burying ''lig. nuchae'' between the muscles on either side. On the other hand, no epaxial muscles are present directly beneath this ligament. In *Rhea*, for example, m. biventer cervicis and m. longus colli dorsalis lie lateral or dorso-lateral to the ligamentous sheath (Fig. 2C, D) and are, therefore, above the tips of the neural spines. Thus, the cleft in the bifurcated neural spine is not occupied by m. biventer cerivicis as claimed by Wedel et al. (2000).

Morphology of the Neural Spines in *Apatosaurus* and *Camarasaurus*

In *Apatosaurus* and *Camarasaurus*, most of the cervical and anterior dorsal vertebrae bear bifurcated neural spines. For ex-
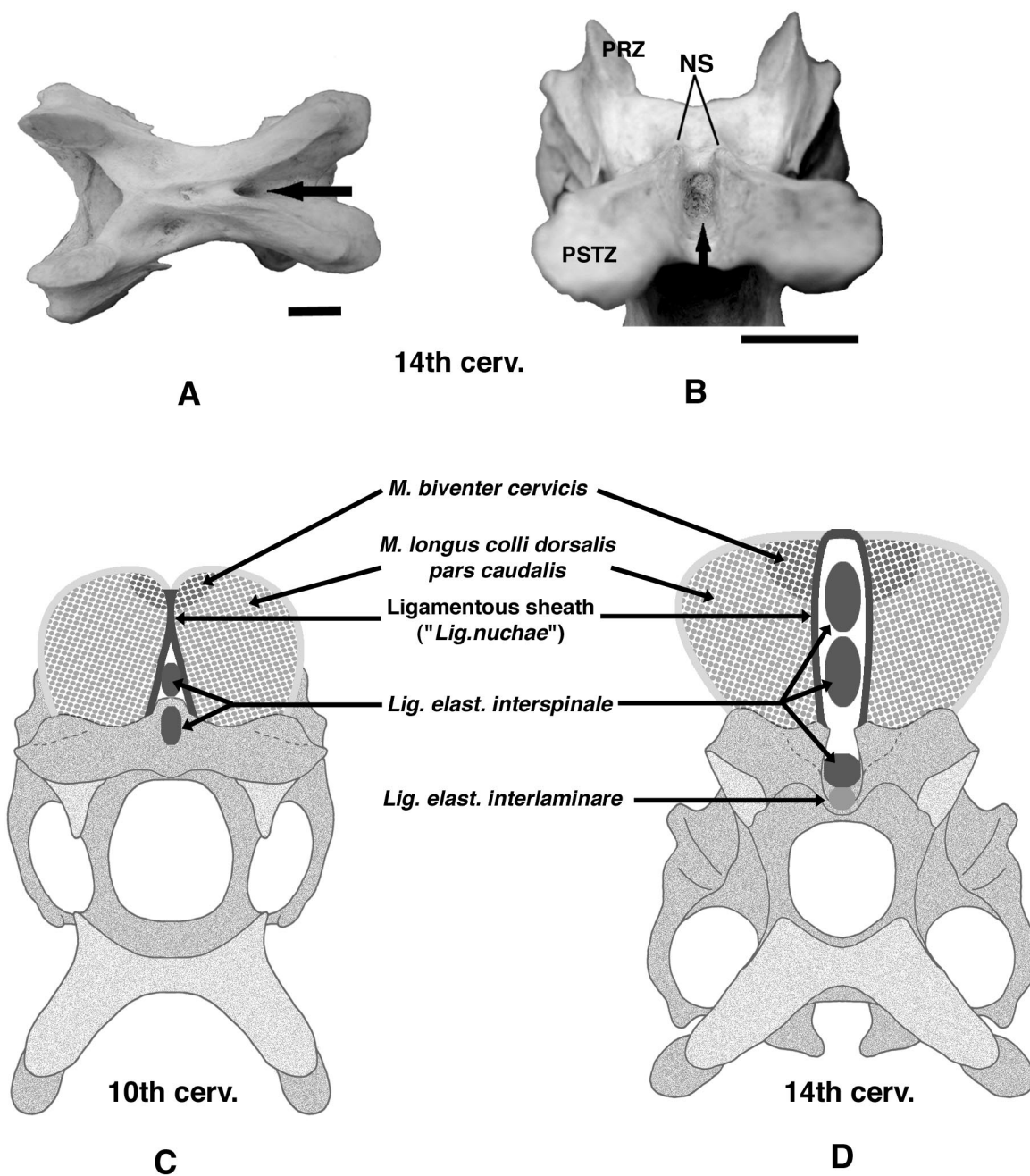
Rhea americana

FIGURE 2.   Topological relationships among the vertebra, ligaments and median epaxial muscles in *Rhea americana*. A and B, the 14th (the last) cervical vertebra (YPM 564), with arrows indicating the site of attachment of ligamentum elasticum interspinale and lig. elasticum interlaminare. A, dorsal view; B, postero-dorsal view. Scale bars equal 1 cm; C and D, schematic diagrams of ligaments and muscles associated with the neural spines, posterior view of a cross section at the levels of the 10th (C) and 14th (D) cervical vertebrae (illustration of the vertebrae based on YPM 564). Multiple branches of lig. elasticum interspinale are shown. The most ventral one inserts on the illustrated vertebra and more dorsal ones represent those that extend further anteriorly. **Abbreviations**: **NS**, neural spine; **PRZ**, prezygapophysis; **PSTZ**, postzygapophysis.

ample, Gilmore (1936) inferred that in *Apatosaurus* the sixth cervical is the anterior-most and the sixth dorsal (21st presacral) is the posterior-most vertebra to have a notch on the neural spine. In *Camrasaurus grandis*, the fifth or sixth cervical is the most anterior vertebra with the distinct cleft in the neural spine although an incipient notch already appears on the third cervical (McIntosh et al., 1996a, b). McIntosh et al. (1996a) observed

that the bifurcation ends on the seventh dorsal (19th presacral) vertebra in this species. Gilmore (1925) recognized the notch on the neural spines from the seventh cervical to the sixth dorsal (19th presacral) vertebrae in *Camarasaurus lentus*.

A prominent feature on the posterior cervicals and anterior dorsals of *Apatosaurus* and *Camarasaurus* is a rugose, knob-like, posterior projection at the base of the cleft of the neural
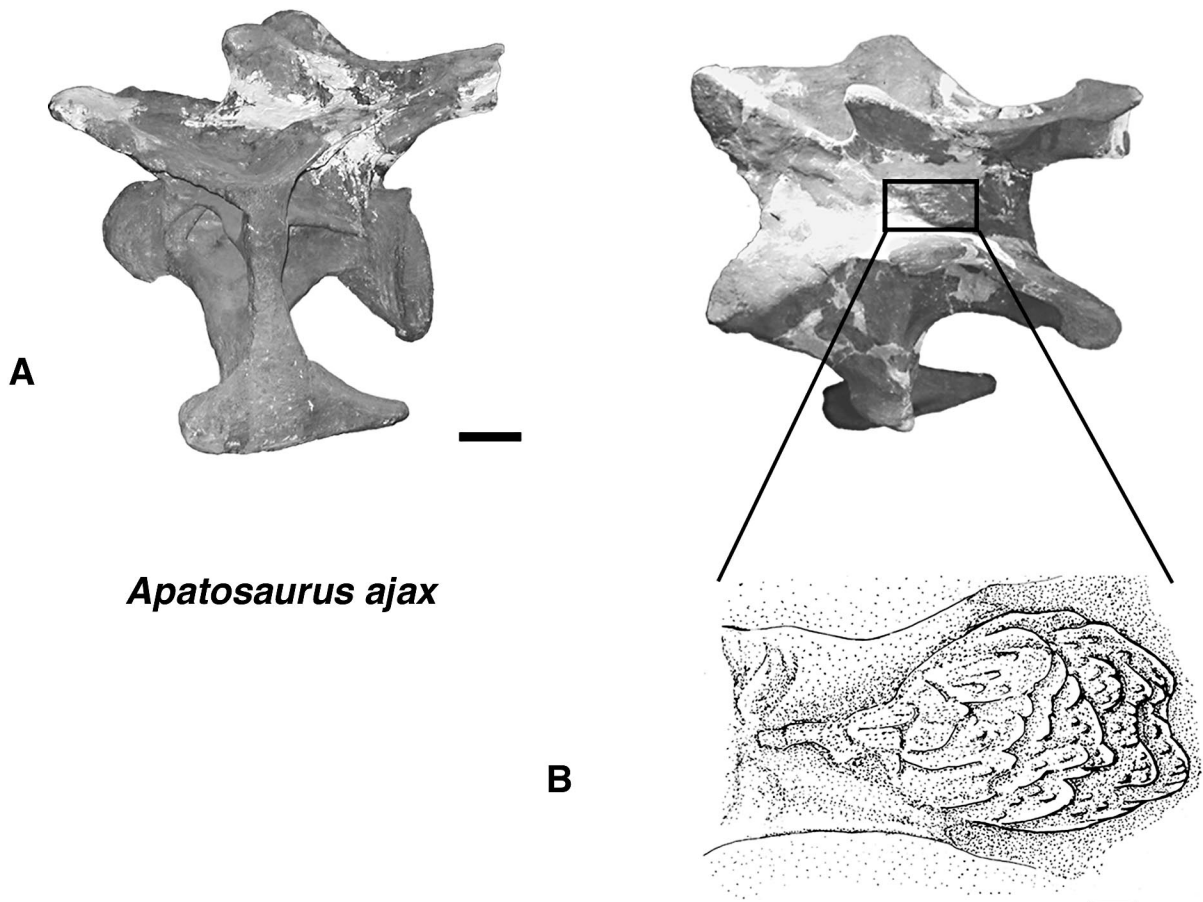
FIGURE 3. Posterior cervical vertebra of *Apatosaurus ajax* (YPM 1860). Anterior is toward the left. **A**, left lateral (left) and dorsal (right) views of the specimen. **B**, drawing of the site of the ligament attachment on the neural arch (dorsal view). Note the strong development of the scar posteriorly. Scale bars equal 5 cm for A and 1 cm for B.

spine (e.g., Gilmore, 1936) while there is only a faint scar on the anterior surface of the neural arch on these vertebrae. Among the specimens examined, such a knob-like, posterior projection was recognized in YPM 1860 (Fig. 3; posterior cervical of *Apatosaurus ajax*), OMHH 1095, 1404, and 1344 (posterior cervicals of *Apatosaurus* sp.), YPM 1905 (posterior cervical of *Camarasaurus grandis*), and OMNH 1383 (posterior cervical of *Camarasaurus* sp.). In extant diapsid reptiles, including birds, the anterior and posterior areas of the neural spine and the dorsal lamina of the neural arch serve as areas of attachment of ligaments that connect two successive vertebrae. These ligaments are lig. elasticum interlaminare in Aves as described above, and are called lig. interspinale (not to be confused with lig. elasticum interspinale of *Rhea*) in non-avian diapsids. These attachment areas are commonly marked by roughened tuberosities and/or concavities in extant diapsids (e.g., Baumel and Witmer, 1993). The presence of rugose scars in the cervicals of sauropods allows a parsimonious (Level 1) inference that lig. elasticum interlaminare/lig. interspinale would have attached to these rugosities. Therefore, Gilmore's (1936) hypothesis suggesting that these scars "doubtless served as the attachment of one of the powerful intervertebral muscles" is not supported by the EPB approach.

The weak scar on the anterior side of the neural arch in the posterior cervicals suggests that lig. elasticum interlaminare/lig. interspinale attaching to it was weakly developed. Therefore, the prominent, knob-like tuberosity that is present only on the posterior aspect probably served as an area of insertion for an additional, stronger ligament inserting posteriorly besides the weak lig. elasticum interlaminare/lig. interspinale. As described above, two ligaments, lig. elasticum interlaminare and a branch of lig. elasticum interspinale, insert on the posterior aspects of the neural arches of the posterior cervicals in *Rhea*. Lig. elasticum interspinale originates from the last "cervico-dorsal" and its tensional force apparently helps to support the weight of the neck of this bird especially when the posterior part of the neck slopes downward and thus lies below the level of the origin of the ligament (see, for example, fig. 1 in Van der Leeuw et al., 2001). This type of ligament would explain the presence of the prominent, rugose projection present only on the posterior side of the sauropod cervicals and would meet the functional demands of bracing the long neck. Therefore, I propose lig. elasticum interspinale in *Rhea* as a good modern analog for the ligament system in the necks of sauropods. Based on this, I suggest that in sauropods such a strong ligament would probably have arisen from one or more neural spines of the dorsal vertebrae and would have given off branches as it extended anteriorly. These branches would have inserted on the posterior sides of the posterior cervicals and perhaps on the anterior dorsals as well (Fig. 4). The trough between the metapophyses would have served as a passage for this ligament. The possible origin of this ligament is the first non-bifurcated neural spine, which is on the eighth dorsal (20th presacral) in *Camarasaurus grandis* and on the seventh dorsal (22nd presacral) in *Apatosaurus* (Gilmore, 1936; McIntosh et al., 1996a). The anterior extent of this ligament may also be inferred based on osteolog-
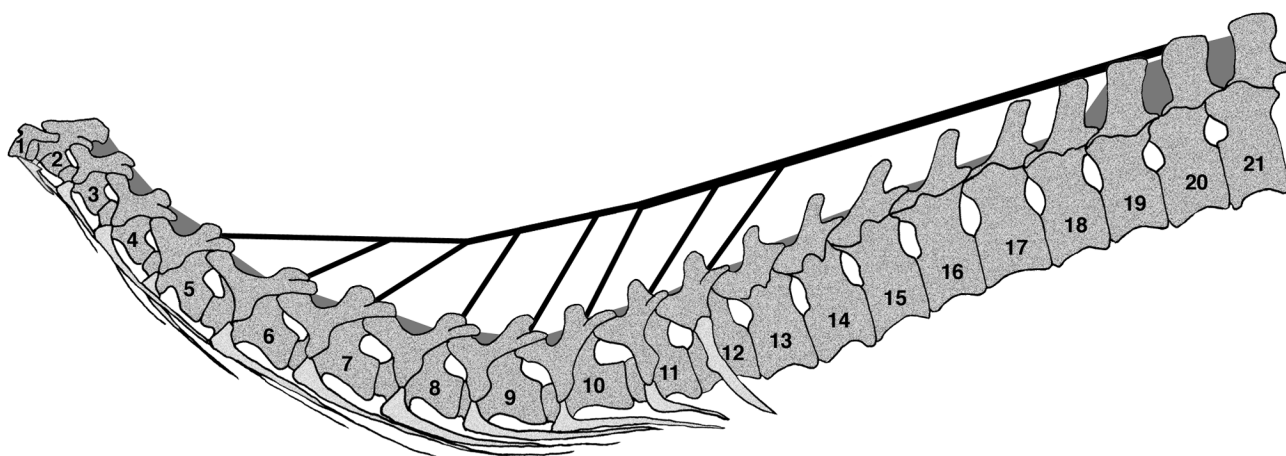
Camarasaurus grandis

FIGURE 4. Hypothetical reconstruction of the ligament system in the neck of *Camarasaurus grandis* by using that of *Rhea* as a modern analog (profile of the vertebrae modified from Gilmore, 1925: pl. 17). Black lines represent the ligament analogous to ligamentum elasticum interspinale shown as if dorsally stretched out, and gray areas represent lig. elasticum interlaminare/lig. interspinale. The position of each vertebra is indicated by a number, and the cervical vertebrae are shown with their ribs attached (i.e., the 12th presacral is the last cervical). The origin of the former ligament is here inferred to be the most anterior non-bifid dorsal neural spine (i.e., the eighth dorsal). In *Camarasaurus grandis* (YPM 1905), the most anterior vertebra with the distinctly bifurcated neural spine is the sixth cervical (McIntosh et al., 1996b). Thus, the next anterior vertebra (fifth cervical) is here inferred to be the terminal insertion of this ligament. The most posterior cervical is depicted as the most posterior insertion of this ligament, but this is admittedly conjectural.

ical information. For example, Gilmore (1936) recognized the prominent, posterior projection starting on the 10th cervical in *Apatosaurus*. However, considering the fact that in *Apatosaurus* a well-bifurcated neural spine is present as far anterior as the seventh cervical (Gilmore, 1936), the terminal insertion of this ligament may be the sixth or seventh cervical. Regardless of exactly where it terminated, this ligament would have extended only to the middle cervical region in *Apatosaurus*.

Osborn and Mook (1921) found that in *Camarasaurus* vertical rugose areas are present in the anterior surfaces of the third to fifth cervical neural spines but absent in more posterior cervicals. Well-developed rugosities are also present in the posterior concavities of the neural spines in the anterior cervicals in *Camarasaurus* (e.g., YPM 1905, *Camarasaurus grandis*). Furthermore, a ridge-like rugosity is present in the anterior surface of OMNH 1421, an anterior (? fifth) cervical of *Apatosaurus* sp. Together, these observations suggest the presence of the strongly developed lig. elasticum interlaminare/lig. interspinale connecting adjacent vertebrae in the anterior cervical region. As inferred above, the anterior cervical region would not have been supported by a lig. elasticum interspinale-like ligament in those sauropods and thus the strong development of lig. elasticum interlaminare/lig. interspinale would have been critical in supporting the extended neck in this region.

DISCUSSION

The bifurcated neural spines in the necks of sauropods represent an apomorphic condition that evolved several times independently within Sauropoda and present a challenging case for reconstructing the associated soft tissues. Bryant and Russell (1992) and Witmer (1995) proposed a rigorous method for inferring unpreserved attributes (i.e., soft tissues) in fossil taxa based on the phylogenetic distributions of such attributes in their extant sister (bracketing) taxa. If a soft tissue and its osteological correlate are present in the first two extant outgroups of a fossil taxon, and if the osteological correlate is also found

in the fossil taxon, the presence of this tissue in the fossil taxon can parsimoniously be inferred with little speculation. In the present study, this approach has been applied to the ligament system of the sauropod neck.

First, as both of the avian ''lig. nuchae'' and lig. supraspinale in non-avian diapsids lie between the two sides of the epaxial musculature and attach to the tips of the neural spines, it was inferred that that these ligaments are homologous with each other. Accordingly, the presence of this ligament attaching to the tips of the neural spines in the sauropod neck was inferred by using the dorsal edge of the neural spine as its osteological correlate. As the association between this ligament and its osteological correlate holds for the all living diapsids examined, this inference is parsimoniously most plausible (a Level I inference). Since the ligamentous sheath, which is putatively homologous with lig. supraspinale, attaches to the tips of the bifurcated neural spines in *Rhea*, this association appears to be a conservative feature that may also apply to sauropods. The same approach was then used for lig. elasticum interlaminare/lig. interspinale of sauropods and its association with the scars on the anterior and posterior sides of the neural arch, which is another safe (Level I) inference. Therefore, the presence of the ligament system occupying at least a part of the notches in the sauropod neural spines is likewise robustly supported. Unfortunately it is impossible with the methods I used in this study to infer the volume of this ligament system, i.e., how much of the notched area of the neural spines was occupied by ligaments. Thus, it is still possible that a part of the notches was occupied by a median epaxial muscle in sauropods (Fig. 5). In fact, in extant birds and crocodylians the most dorsal epaxial muscles (i.e., the avian m. biventer cervicis and m. longus colli dorsalis and the crocodylian m. transversospinalis capitis) are so well-developed that the tips of the neural spines are ''buried'' between the two sides of these muscles. Consequently, the notion that a median epaxial muscle was present in the notches of sauropod neural spines may still be correct, though this mus-
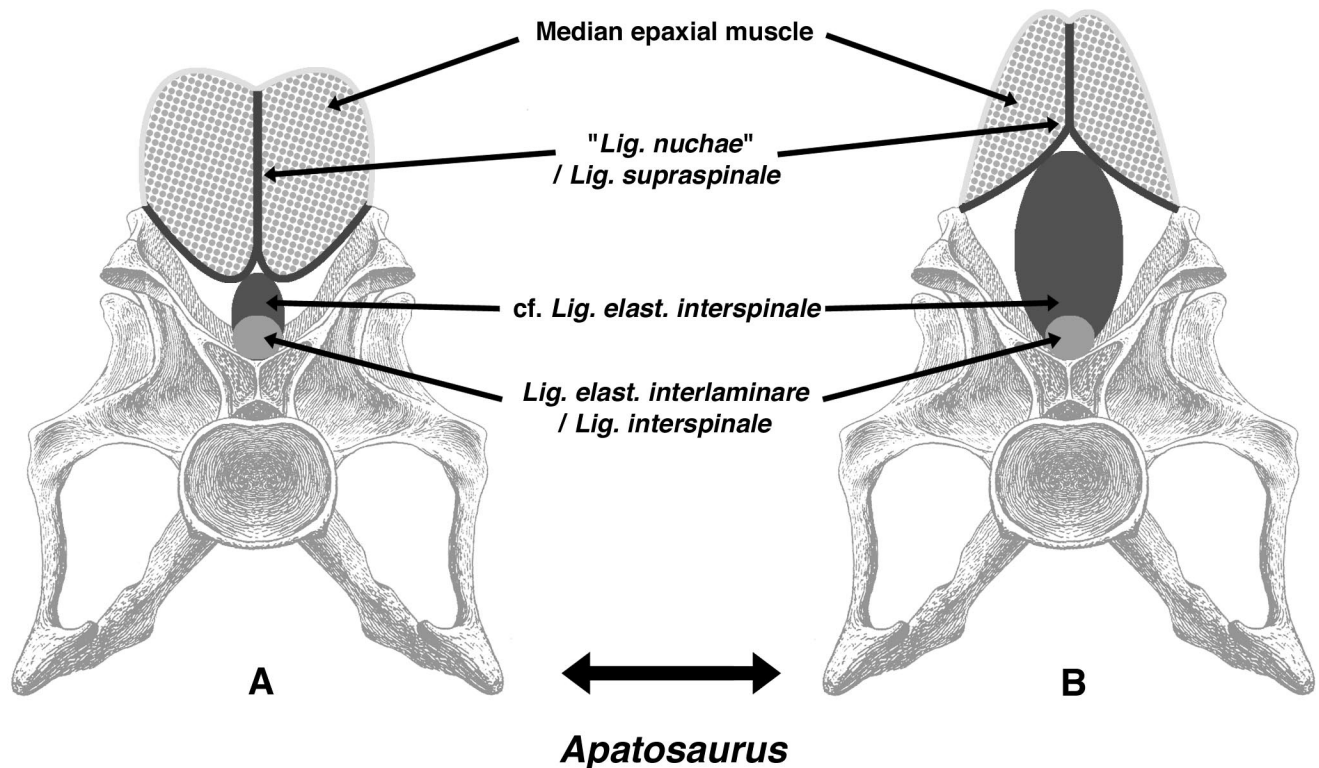
FIGURE 5. Alternative reconstructions of soft tissues associated with the bifurcated neural spine on a posterior cervical in *Apatosaurus*, posterior view of a cross section (illustration of the vertebrae modified from Gilmore, 1936: pl. 24). **A**, ligaments are small and the notch in the neural spines is filled mainly by a median epaxial muscle. **B**, ligaments completely fill the notch and a median epaxial muscle is on top. Depending on the volume of the ligaments, an epaxial muscle could have occupied some or none of the notch of the neural spine.

cle is unlikely to have filled the notches completely. Therefore, the question remains whether these notches were occupied only by ligaments, or by ligaments and muscles.

Finally, the morphology of the ligament attaching to the posterior projection on the neural arch was inferred (Fig. 4). In this case, the EPB approach could not be used, and the reconstruction in this study was based solely on the ligament system of the *Rhea* neck serving as a modern analog. Consequently, this inference is not predicted based on phylogenetic information (a Level III inference; Witmer, 1995). While the presence of the ligament associated with the notches of the neural spines in sauropods is robustly supported by phylogenetic and osteological information, the morphology of this ligament is proposed here only as a working hypothesis that will need to be tested in the future.

Interestingly, the postulated ligament (Fig. 4) is very similar to ''lig. nuchae'' that Janensch (1929) reconstructed for *Dicraeosaurus* without using a particular extant animal as a model. However, the most parsimonious hypothesis based on the EPB approach applied here is that the diapsid ''lig. nuchae'' (lig. supraspinale) would have attached to the tips of the neural spines in sauropods, rather than to the rugose projections on the neural arches as suggested by Janensch (1929). Therefore, I propose that the ligament inserting on these projections was not homologous with the diapsid ''lig. nuchae'' but rather it differentiated from lig. elasticum interlaminare/lig. interspinale, similar to the case of lig. elasticum interspinale in *Rhea* (Boas, 1929).

Functionally, the tensional force of this postulated ligament would work most effectively when the neck tilts downward and the insertions of the ligament are below the level of its origin. Stevens and Parrish (1999) reconstructed the neutral posture of the neck in both *Apatosaurus* and *Diplodocus* as extending almost straight forward with a downward slope. As they suggested, a ligament like the one I propose would have been taut in this posture and would have exerted a stronger tensional force than it would in a more erect neck posture. Furthermore, its insertion on scars at the bases of the cleft between the metapophyses, rather than on the top of the neural spine, would have increased the leverage of the tensional force of the ligament by lowering the positions of its insertion, thereby making this ligament a more effective bracing device.

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