

Thoracic Epaxial Muscles in Living Archosaurs and Ornithopod Dinosaurs

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ABSTRACT

Crocodylians possess the same thoracic epaxial muscles as most other saurians, but *M. transversospinalis* is modified by overlying osteoderms. Compared with crocodylians, the thoracic epaxial muscles of birds are reduced in size, disrupted by the synsacrum, and often modified by intratendinous ossification and the notarium. A phylogenetic perspective is used to determine muscle homologies in living archosaurs (birds and crocodylians), evaluate how the apparent disparity evolved, and reconstruct the thoracic epaxial muscles in ornithopod dinosaurs. The avian modifications of the epaxial musculoskeletal system appear to have coevolved with the synsacrum and notarium. The lattice of ossified tendons in iguanodontoidean dinosaurs (Hadrosauridae and Iguanodontidae) is homologized to *M. transversospinalis* in crocodylians and *M. longus colli dorsalis, pars thoracica* in birds. Birds have an arrangement of tendons within *M. longus colli dorsalis, pars thoracica* identical to that observed in the epaxial ossified tendons of iguanodontoid dinosaurs. Moreover, many birds (such as grebes and turkeys) ossify these tendons, resulting in a two- or three-layered lattice of ossified tendons, a morphology also seen in iguanodontoid dinosaurs. Although the structure of *M. transversospinalis* appears indistinguishable between birds and iguanodontoid dinosaurs, intratendinous ossification within this epaxial muscle evolved convergently. *Anat Rec Part A*, 288A:782–793, 2006. © 2006 Wiley-Liss, Inc.

Key words: archosaur; dinosaur; ossified tendon; ornithischian; ornithopod; axial; epaxial

Interest in muscular reconstruction in extinct dinosaurs has focused primarily on the shoulder girdle, pelvis, or limbs (Romer, 1923b, 1923a, 1927; Galton, 1969; Walker, 1977; Gatesy, 1994; Dilkes, 2000; Hutchinson, 2001a, 2001b; Carrano and Hutchinson, 2002), though exceptions do exist (Tsuihiji, 2004). Some of these studies examine epaxial muscles peripherally by grouping them into *M. dorsalis trunci*. But the thoracic vertebral column has diverged significantly in living archosaurs. For example, birds possess a synsacrum and many develop a notarium and “vertebral struts” (Storer, 1982). The epaxial musculature associated with avian vertebral fusion is reduced in size and divisions compared with crocodylians. In many birds, these muscles are disrupted by the anteromedial union of the iliac blades. In contrast, crocodylians have epaxial muscles similar to lepidosaurs, except for the synapomorphic *M. tendinoarticularis* that contains cranially directed cones of myosepta (Gasc, 1981) and tendinous modifications that insert onto osteoderms.

Mineralized tendons are another unique feature of spinal anatomy in some archosaurs, namely, ornithischian

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and avian dinosaurs (Vanden Berge and Storer, 1995; Norman et al., 2004a; Organ and Adams, 2005). In ornithischians, these tendons ossify, developing Haversian and periosteal bone (Moodie, 1927, 1928, 1929; Rothschild, 1987; Rothschild and Martin, 1993; Reid, 1996). The ossified tendons of birds occur throughout the body and may only mineralize or may develop Haversian bone, though never as well developed as the ossified tendons of ornithischians (Lieberkuhn, 1860; Retterer and Lelievre, 1911; Mathews, 1936; Johnson, 1960; Hudson et al., 1965; Abdalla, 1979; Landis et al., 1995; Landis and Silver, 2002; Adams and Organ, 2005).

Ossified epaxial tendons have long provided the impetus for interpreting spinal function in extinct dinosaurs such as hadrosaurids and ankylosaurids (Dollo, 1886; Ostrom, 1965; Coombs, 1995). However, the use of disparate model taxa has muddled clear interpretations of homology and function. For example, Molnar and Frey (1987) used crocodylian, whereas Dollo (1886) used avian analogues for muscle reconstruction. But recent studies (Hutchinson, 2001a, 2001b; Carrano and Hutchinson, 2002) have shown the resolution and robustness that an explicit phylogenetic context can provide for inferring the presence or absence and evolution of soft tissues. Muscle reconstruction that uses a phylogenetic context relies on osteological correlates (hard tissue indicators of soft tissue, such as bumps or scars) for inferring the condition of soft tissues (Bryant and Russell, 1992; Witmer, 1995). But ossified tendons are part of a soft tissue complex and therefore provide a more robust way to infer the presence of soft tissues from fossils. Unfortunately, ossified tendons only regularly occur in ornithischian dinosaurs (Serenó, 1986, 1999).

The iguanodontoid lattice of epaxial tendons (Fig. 5C and D) is usually described as an adaptation that stiffened the spine and influenced bipedal posture (Ostrom, 1964) or locomotion (Dollo, 1886). The function of the lattice was also instrumental in settling the debate over the ecology of these large herbivorous dinosaurs (they are now thought to be terrestrial as opposed to semiaquatic). Such arguments presume that the ossified lattice is an anatomical structure unique to Iguanodontidae. In addition, because ossified tendons are used in systematics, a better understanding of their muscular reconstruction is important for assessing characters commonly used to support multiple dinosaurian clades (e.g., Ornithischia and Iguanodontidae) (Serenó, 1999). This study's purpose is to determine thoracic epaxial muscle homologies between birds and crocodylians and to reconstruct this musculature in ornithopod dinosaurs using a phylogenetic approach. This reconstruction provides a foundation for interpreting the biology of thoracic epaxial muscles and ossified tendons in all dinosaurs.

MATERIALS AND METHODS

Osteological data were collected from extinct dinosaurs at the Museum of the Rockies (MOR), Royal Tyrrell Museum of Paleontology (RTMP), Field Museum of Natural History (FMNH), and the University of Chicago Department of Organismal Biology and Anatomy. Most of the structural data from ossified tendons were based on an articulated *Brachylophosaurus canadensis* (MOR-794) that possesses a three-layered lattice of ossified tendons in situ.

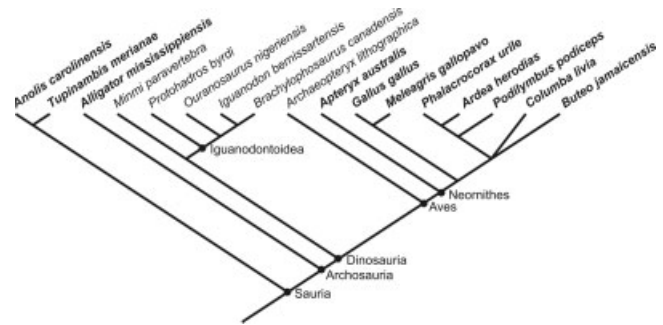


Fig. 1. Phylogenetic relationships of taxa used in this study. Bold taxa are extant. Modified from Gauthier (1986), Cracraft et al. (2004), and Sereno (1999).

Myological data were collected from donated specimens dissected on the campuses of Montana State University, Bozeman, Montana, and Harvard University, Cambridge, Massachusetts. Avian specimens included six orders: *Ardea herodias* (Ciconiiformes), *Columba livia* (Columbiformes), *Buteo jamaicensis* (Falconiformes), *Meleagris gallopavo* ($n = 7$) and *Gallus gallus* (Galliformes), *Phalacrocorax urile* (Pelecaniformes), and *Podilymbus podiceps* (Podicipediformes). Crocodylian specimens included *Alligator mississippiensis* ($n = 2$). Squamate specimens included a *Tupinambis merrianae* and *Anolis carolinensis* ($n = 3$).

Osteological data from an *Alligator mississippiensis* (MOR OST 130) were collected at the MOR. Osteological data from neornithine taxa were collected at the MOR and Montana State University (MSU), but mostly at the University of Michigan Museum of Zoology (UMMZ) and the Museum of Comparative Zoology (MCZ) at Harvard University. Specimens spanned seven orders: *Chuana torquata* (Anseriformes); *Limnodromus scolopaceus*, *Ptychorampus aleuticus*, *Larus glaucescens*, and *Alca torda* (Charadriiformes); *Accipiter cooperi* (Falconiformes); *Porphyrio mantelli* (Gruiformes); *Podilymbus gigas* ($n = 5$), *Podiceps auritus*, *Podilymbus podiceps* ($n = 8$), *Aechmophorus occidentalis*, and *Podilymbus major* (Podicipediformes); *Amazona amazonica* (Psittaciformes); and *Apterix australis* (Struthioniformes).

The nomenclature used for crocodylian anatomy follows Gasc (1981) and Frey et al. (1989), though some homologies and synonyms from Gasc (1981) are preferred. Within Sauria, epaxial muscles can be divided into three primary groups: *M. transversospinalis*, *M. longissimus*, and *M. iliocostalis* (Figs. 2A and 3A). The terminology from sauropsids and mammals is used here for divisions of *M. transversospinalis* because they are in wider use, though references to alternate names are provided in Table 1. Avian anatomical nomenclature follows the *Nomina Anatomica Avium* (Baumel and Witmer, 1993; Vanden Berge and Zweers, 1993).

Hypotheses of homology were generated by similarity of form (de Pinna, 1991), which consists of identifying homologies based on similarity of appearance. The vertebrae and their processes form the frame of reference on which musculoskeletal similarity criteria are based. Specifically, hypotheses of homology were based on musculoskeletal or aponeurotic patterns (i.e., common origins and insertions) as criteria of similarity. Presumed causally associated os-

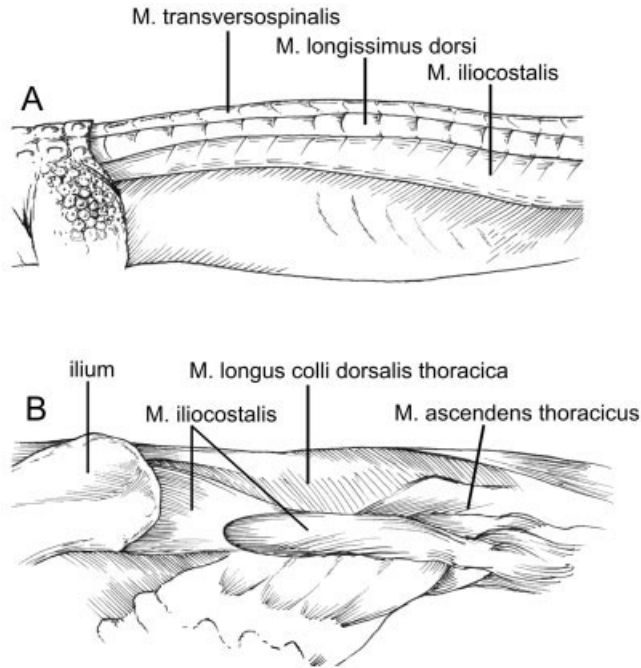


Fig. 2. Diagram of thoracic (dorsal) epaxial muscles in archosaurs. **A:** Right lateral view of major epaxial muscles in *Alligator*. **B:** Right lateral view of major thoracic epaxial muscles in *Meleagris*.

teological correlates of these soft tissues (e.g., muscles, tendons,) were then tracked in osteological specimens of extant taxa and tested in the fossil record for congruence.

An explicit phylogenetic framework (Bryant and Russell, 1992; Witmer, 1995) was used to infer unpreserved soft tissues. This method uses at least two living sister (bracket) taxa to provide phylogenetic support for hypothesizing the presence of unpreserved features in extinct organisms. Using Witmer's (1995) terminology, inferences are ranked according to the degree of phylogenetic support they provide. A level I inference is made when both extant bracketing taxa possess a soft tissue and associated osteological correlates. A level II inference is made when only one of the bracketing taxa possesses a soft tissue and associated osteological correlates. A level III inference is made when neither of the bracketing taxa possesses a soft tissue. I', II', and III' inferences are made the same as above but are used when soft tissues lack osteological correlates in the respective bracket taxa.

The phylogenetic framework used in this study (Fig. 1) is a composite from several sources. Gauthier (1986) is used for Sauria, Sereno (1999) for Dinosauria, and Craft et al. (2004) for Neornithes. Iguanodontoidea (Hadrosauridae and Iguanodontidae plus Protohadros and Ouranosaurus) is synonymous with Hadrosauriformes, but the former is preferred (Norman, 2004) and used here.

RESULTS

Crocodylia Dorsal Epaxial Muscles

Epaxial musculature among crocodylians is similar to the typical lepidosaur condition (Figs. 2 and 3), with only a few minor variations associated with dorsal osteoderms (Frey, 1982). Epaxial muscles within Crocodylia are also

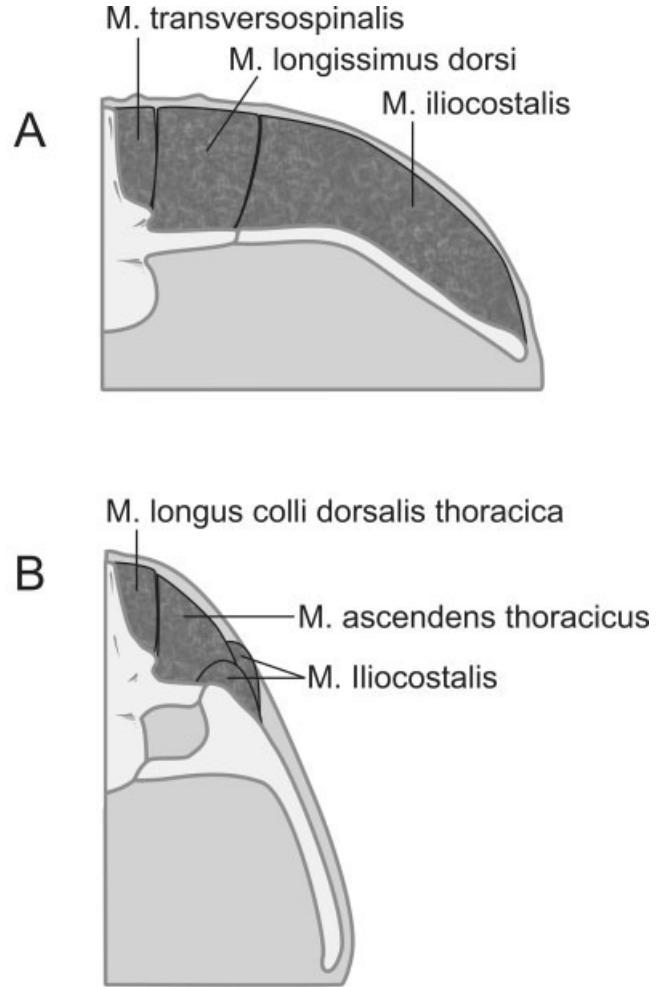


Fig. 3. Diagram of thoracic (dorsal) epaxial muscles in archosaurs. **A:** Anterior view of major epaxial muscles in *Alligator*. **B:** Anterior view of major thoracic epaxial muscles in *Meleagris*.

less diverse than those in other reptile groups, presumably because of constraints created by the osteoderms and the propulsive function of the tail (Gasc, 1981) as well as thoracic bracing (Frey, 1988b; Salisbury and Frey, 2001). The following anatomical descriptions are based on the dissections of *Alligator* as well as *Crocodylus*, *Caiman*, and *Alligator* from the literature (Vallois, 1922; Gasc, 1981; Frey, 1982; Molnar and Frey, 1987; Frey, 1988a; Frey et al., 1989; Murakami et al., 1991; Cong, 1998).

Musculus transversospinalis. Mm. interspinales [Mm. interneurales of Gasc (1981)] and Mm. interarcuales are the medial-most subunits of *M. transversospinalis* and connect spinous processes at their cranial and caudal edges. Their fascicles run cranial-caudal and are largely indistinguishable from one another. Therefore, they will be collectively named Mm. interspinales. Medial to these muscles lie the interspinal ligaments. Mm. interarticularis superiores connect successive pre- and postzygapophyses. The cranial border of Mm. interarticularis superiores inserts on the caudal aspect of the zygapophyseal joints by short fan-shaped tendons. Because the epaxial

TABLE 1. Summary of origins and insertions of thoracic (dorsal) epaxial muscles in Crocodylians

Muscle	Origin (osteological correlate)	Insertion (osteological correlate)
M. transversospinalis		
Mm. interspinales	Cranial edge of spinous process	Caudal edge of spinous process
Mm. interarticularis superiores	Lateral aspect of zygapophyseal joint and neural arch	Caudal surface of postzygapophysis
M. multifidus (M. neurospinalis) ^a	Lateral surface of spinous process	Caudal edge of the dorsal surface of spinous process
M. spinalis (M. spinoarticularis) ^a	Prezygapophysis and surrounding neural arch	Cranial edge of the dorsal surface of spinous process
M. semispinalis: M. articularis	Ventral portion of spinous process and fascia shared with M. tendinoarticularis	Caudal edge of the dorsal surface of spinous process; cranial edge and medioventral edge of scute rows. Caudodorsal surface of postzygapophysis, fascia shared with M. articularis, and medial fascia of M. longissimus dorsi
M. semispinalis: M. tendinoarticularis	Lateral aspect of zygapophyseal joint	Dorsal surface of transverse process, fascia of M. iliocostalis, fascia of M. tendinoarticularis
M. longissimus dorsi	Craniomedial aspect of the ilium	Caudal edge of transverse process
Mm. intertransversarii	Cranial edge of transverse process	Medial aspect of ribs near their articulation and medially by the fascia of M. longissimus dorsi
M. iliocostalis	Cranial aspect of the ilium	

^a Names used by Vallios (1922) and Tsuihiji (2005).

muscles are fibrous, the preceding muscle divisions were not easily distinguishable.

Lateral to the intrinsic vertebral muscles is the bulk of M. transversospinalis (Fig. 4A and B). M. multifidus is the medial-most subunit and lies next to the lateral surface of the spinous processes. The tendon from M. multifidus originates as a small mediolaterally flattened sheet cranial to the spinous process. This passes craniodorsal over two vertebrae and inserts on the caudodorsal surface of the third spinous process just under the attachment of the medial tendinous head of M. semispinalis (M. articularis).

Immediately lateral to the tendon of M. multifidus, separated by only a thin layer of fascicles, is M. spinalis. This muscle originates near the prezygapophysis as a mediolaterally flattened sheet and runs caudodorsally to insert on the craniodorsal surface of the spinous process five to seven vertebrae caudal (Fig. 4A and B). In the lumbar region, this tendon bifurcates twice, cranially receiving another tendon from the muscle belly and caudally a tendon from the cranial aspect of the spinous process. In crocodylians, the caudal extent of the tendon attaches to the overlying osteoderms.

M. semispinalis lies lateral to M. spinalis and is separated from it by a thin sheet of muscle fascicles that connect the tendon systems and could be categorized as belonging to either muscle. M. semispinalis is divisible into two subunits: M. articularis and M. tendinoarticularis. M. articularis is the medial division, which originates at the base of the spinous process and passes anterodorsally past four vertebrae. Here it flattens and splits into three tendinous heads. The median head flattens and attaches to the cranial margin of the transverse scute row. The medial head inserts on the caudodorsal surface of the next spinous process. The lateral head connects to the fascia of M. tendinoarticularis. The lateral division of the semispinalis is M. tendinoarticularis. Cra-

nially pointed cones of myosepta form successive subunits within this muscle. It is interconnected with M. articularis by a lateral tendon branch.

Musculus longissimus dorsi. Lateral to M. transversospinalis and separated from it by fascia lies the larger M. longissimus dorsi (Figs. 2A and 3A). Caudally pointed cones of myosepta form repeated subunits within this muscle. The medial myosepta connect to the lateral aspect of M. tendinoarticularis while the external margin connects to M. iliocostalis. Each conical subunit extends over three vertebrae and inserts on the distal part of the transverse processes. M. longissimus dorsi originates on the craniomedial aspect of the ilium and inserts on the dorsal aspect of the transverse processes. Ventral to the bulk of M. longissimus dorsi and lateral to Mm. interarticularis superiores are Mm. intertransversarii, which connect successive transverse processes. Fascicles from Mm. intertransversarii interweave with the ventral fascicles of M. longissimus dorsi.

Musculus iliocostalis. M. iliocostalis is the most lateral of the epaxial muscles. Whereas M. transversospinalis and M. longissimus are relatively uniform in width along their length, M. iliocostalis is reduced in size cranially. Its primary origin is on the cranial aspect of the iliac blades and is composed of obliquely oriented fibers that run craniolateral to cover the ribs near their articulation with the dorsal vertebrae. Medially, M. iliocostalis inserts on the fascia of M. longissimus dorsi.

Neornithes Dorsal Epaxial Muscles

The dorsal epaxial muscles of extant birds are reduced in size compared with crocodylians and lepidosaurs (Figs. 2B and 3B). As a consequence, the epaxial musculature in birds is poorly understood and has been compared with mammalian spinal muscles by Baumel et al. (1993). How-

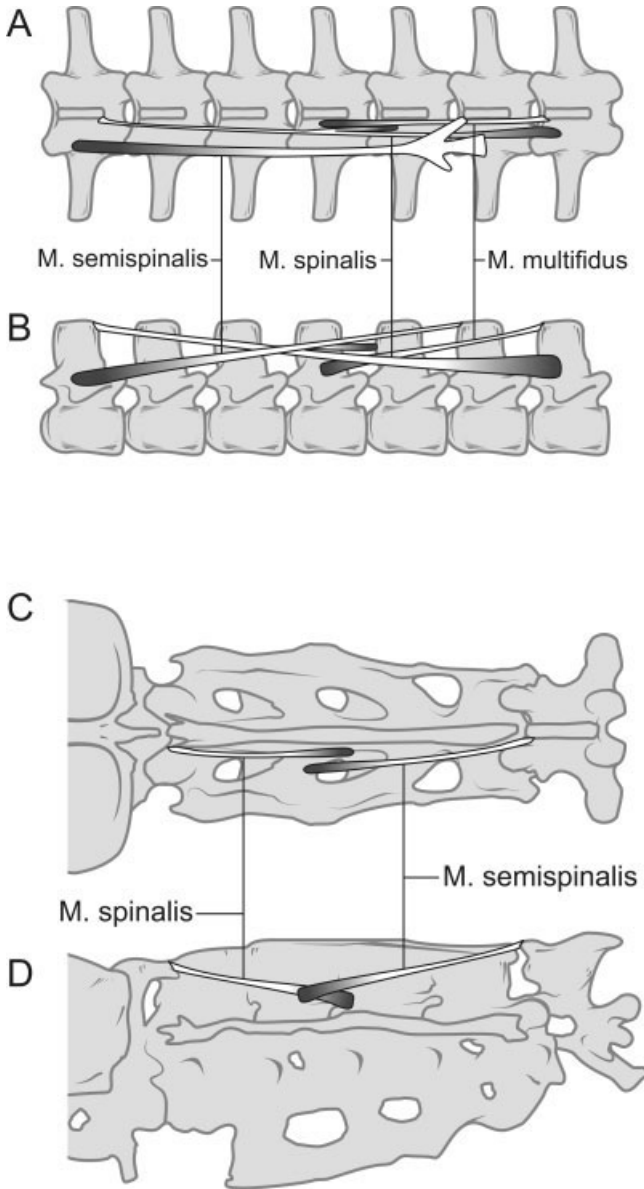


Fig. 4. Schematic diagram of the subunits of *M. transversospinalis* in archosaurs. **A** and **B**: Subunits of *M. transversospinalis* excluding the tendinoarticularis in *Alligator*. **C** and **D**: Subunits of *M. longus colli dorsalis*, pars thoracica in *Meleagris*. Right lateral view in both panels.

ever, Tsuihiji (2005) gave an excellent description and comparison of cervical and thoracic epaxial muscles in archosaurs. The homologies presented below agree with Tsuihiji (2005), which should be consulted for a more detailed analysis of homologies, including innervation patterns. In addition, several references described dorsal epaxial muscles as a whole (Harvey et al., 1968; Zusi and Bentz, 1984; Baumel et al., 1993) and were vital in the following descriptions. Avian muscle origins and insertions are summarized in Table 2.

Musculus longus colli dorsalis thoracica. In birds that possess fused dorsal vertebrae, called the no-

tarium (e.g., *Podilymbus*, *Gallus*, *Meleagris*, and *Columba*), *Mm. interspinales* are absent in the thoracic region because of vertebral fusion. Even at the notarial-synsacral articulation and unfused thoracic vertebrae, the interspinous ligament is more developed than *Mm. interspinales*, which is a mere sheet of fascicles overlying the ligament. In birds with free thoracic vertebrae (e.g., *Buteo*), *Mm. interspinales* are reduced to a thin sheet of fascicles overlying the interspinous ligament as well. In the cervical region, *Mm. intercrustales* are well developed (Tsuihiji, 2005), but these muscles are not distinguishable from *Mm. interspinales* in the thoracic region in birds. *Mm. intercrustales* are also disrupted by the notarium when present, which generally lacks laterally projecting zygapophyses associated with these muscles. However, on the caudal-most free vertebra of the notarium and on the free dorsal vertebra, a fan-shaped tendon attaches to the caudal aspect of the zygapophyseal joint in all birds examined. This tendon passes caudad to blend with the fascicles of *M. longus colli dorsalis*, pars thoracica. Tsuihiji (2005) homologized the avian *Mm. intercrustales* with the crocodylian *Mm. interarcualis superiores*. The relative positions and origins and insertions presented here concur with this homology assessment.

The bulk of *M. longus colli dorsalis*, pars thoracica continues uninterrupted into *M. longus colli dorsalis*, pars caudalis of the neck and lies immediately lateral to the spinous processes (Figs. 2B and 3B). It has obliquely running tendons that form a lattice on its medial surface. These insert on the craniodorsal and caudodorsal surfaces of the spinous processes, a complex morphology also seen in *M. transversospinalis* of crocodylians. Tsuihiji (2005) homologized the avian *M. longus colli dorsalis*, pars thoracica with the crocodylian *M. transversospinalis*, a conclusion with which the data presented here agree. Confusingly, this muscle is sometimes also called *M. longissimus dorsi* in birds (Harvey et al., 1968), but *M. longus colli dorsalis*, pars thoracica is preferred to avoid confusion with *M. longissimus* in crocodylians, with which it is apparently not homologous.

Like the homologous *M. transversospinalis* of other sau- rians (Gasc, 1981), *M. longus colli dorsalis*, pars thoracica is composed of various subunits defined by their long tendons (Fig. 4C and D). The tendons of *M. longus colli dorsalis*, pars thoracica pass caudad through the canal formed the medial fusion of the preacetabular iliac blades. *M. longus colli dorsalis*, pars thoracica ends at the caudal margin of the canal or outside it on the dorsal surface of the synsacrum medial to the cranial part of *M. levator caudae*. Unlike those in crocodylians, the fascicles of this avian muscle are sometimes blended and not easily divisible, as was also noted by Zusi and Bentz (1984) for hummingbirds.

The medial-most division of *M. longus colli dorsalis*, pars thoracica is homologized to *M. spinalis* in crocodylians based on its origin at the base of the spinous process and tendons that run caudodorsally attaching to the cranial aspect of the spinous processes or corresponding locations on the crest of the notarium or synsacrum. Tsuihiji (2005) offers the same homology, but also incorporates evidence from innervation patterns. The number of tendons is variable and appears to be dependent on the degree of synsacral and notarial development. For example, in Galliformes only three tendons are present. The first tendon attaches onto the dorsal surface of the spinous

TABLE 2. Summary of origins and insertions of thoracic (dorsal) epaxial muscles in Neornithes

Muscle	Origin (osteological correlate)	Insertion (osteological correlate)
M. longus colli dorsalis, pars thoracica ^a		
Mm. interspinales ^b	Cranial edge of spinous process	Caudal edge of spinous process
Mm. intercostales ^b	Lateral aspect neural arch	Lateral aspect neural arch and postzygapophysis
M. spinalis	Dorsal aspect of neural arch and Zygapophyseal joint	Cranial edge of the dorsal surface of spinous process or similar position on the spinous ridge of notarium
M. semispinalis	Neural arch and medial portion of transverse process	Caudal edge of the dorsal surface of spinous process or similar position on the spinous ridge of notarium
M. ascendens thoracicus	Dorsal surface of transverse processes	Dorsal aspect of postzygapophysis
Mm. intertransversarii ^b	Cranial edge of transverse process	Caudal edge of transverse process
M. iliocostalis, ventral part	Craniolateral margin of ilium and the distal edges of transverse processes	Distal edge of transverse process and exterior surface of the associated rib
M. iliocostalis, dorsal part	Aponeurosis, which arises from the craniolateral margin of ilium	Distal edge of transverse process

^a The tendons of M. longus colli dorsalis, pars thoracica are ossified in Charadriiformes, Podicipediformes, *Phalacrocorax*, and in *Meleagris*.

^b Muscle is absent or highly reduced in birds with a notarium.

process of the free vertebra at the notarial-synsacral articulation. The other two tendons attach to the roof of the canal formed by the medial connection of the cranial iliac blades. In other birds, such as *Buteo*, *Podilymbus*, and *Ardea*, these tendons run along the entire thoracic region. In *Ardea* in particular, these tendons are sheet-like and form an almost continuous aponeurosis through M. longus colli dorsalis, pars thoracica. The tendons of M. longus colli dorsalis, pars thoracica are ossified in Charadriiformes, Podicipediformes, *Phalacrocorax*, and in some *Meleagris* specimens. In all birds that possess them, ossified epaxial tendons are fused to the spinous processes. These are the “vertebral struts” of Storer (1982) and their length varies from short vertebral projections (e.g., *Chuana*) to long rods formed by the entire tendon (e.g., *Ptychoramphus*), including the myotendinous junction.

The lateral division of M. longus colli dorsalis, pars thoracica is homologized to M. semispinalis (M. articulo-spinalis) in crocodylians, a hypothesis of homology concordant with Tsuihiji (2005). This assessment is based on the muscle’s origin on the ventral portion of the spinous process and its insertion on the caudodorsal margin of the spinous processes or corresponding locations on the notarial or synsacral crests. This division of M. longus colli dorsalis, pars thoracica is lateral to M. spinalis, from which it is separated by a thin sheet of muscle fascicles. Although it often passes along the thoracic region uninterrupted, in Galliformes M. semispinalis inserts on the dorsal surface of the spinous process of the first free dorsal vertebra by one long tendon and on the caudal region of the notarium by two long tendons. Thus, as in M. spinalis, some tendinous insertions over the notarium may be absent for this muscle as well.

M. longus colli dorsalis, pars thoracica also possesses a lateral series of tendons that often blend into an aponeurosis. The superficial tendons of this muscle are weakly developed or absent in some birds, such as in Ciconiiformes, Galliformes, Pelecaniformes, and Falconiformes, though they may be more developed cranially, as in *Buteo*. In contrast, the superficial tendons of M. longus colli dorsalis, pars thoracica are more developed in Charadri-

iformes, Podicipediformes, and Struthioniformes (Fig. 5A). Apparently, these tendons represent the origin of the M. spinalis capitis homologue that is present in the neck in other saurians but extends into the dorsal region in Aves (Tsuihiji, 2005).

In birds that regularly develop ossified epaxial tendons, it is rare for all the tendons belonging to M. longus colli dorsalis, pars thoracica to ossify. However, one species (*Alca torda*; Fig. 5B) undergoes intratendinous ossification in all three sets of tendons, a situation identical with that seen in iguanodontoid dinosaurs.

Musculus ascendens thoracicus. M. ascendens thoracicus is lateral and superficial to M. longus colli dorsalis, pars thoracica (Figs. 2B and 3B). It originates from the dorsal surface of the transverse processes. After inserting on the dorsal aspect of the postzygapophyses of the dorsal vertebrae, or notarium if present, it passes forward to insert on cervical vertebrae, where it is called M. ascendens cervicalis. The insertions on the transverse processes are tendinous in taxa without a notarium and are fleshier in taxa with a notarium. This muscle’s lateral position to M. longus colli dorsalis, pars thoracica and its attachment onto the postzygapophyses suggest it is homologous with M. tendinoarticularis in crocodylians. Tsuihiji (2005) proposes the same homology, but also incorporates evidence from innervation patterns.

Musculi intertransversarii. Mm. intertransversarii are present in the cervical region, but are absent over the notarium owing to ossification between transverse processes, though M. longus colli dorsalis, pars thoracica sends fascicles ventrad through the transverse foramina. The cranial free dorsal vertebrae contain Mm. intertransversarii connecting them to the transverse processes of the neck and the notarium. The notarium of Podicipediformes does not extend to the transverse processes, which are not co-ossified, but the Mm. intertransversarii are still reduced to a sheet of fascicles over the ligament between transverse processes. Mm. intertransversarii are most developed in *Buteo*. A thick tendon of M. iliocostalis laterally

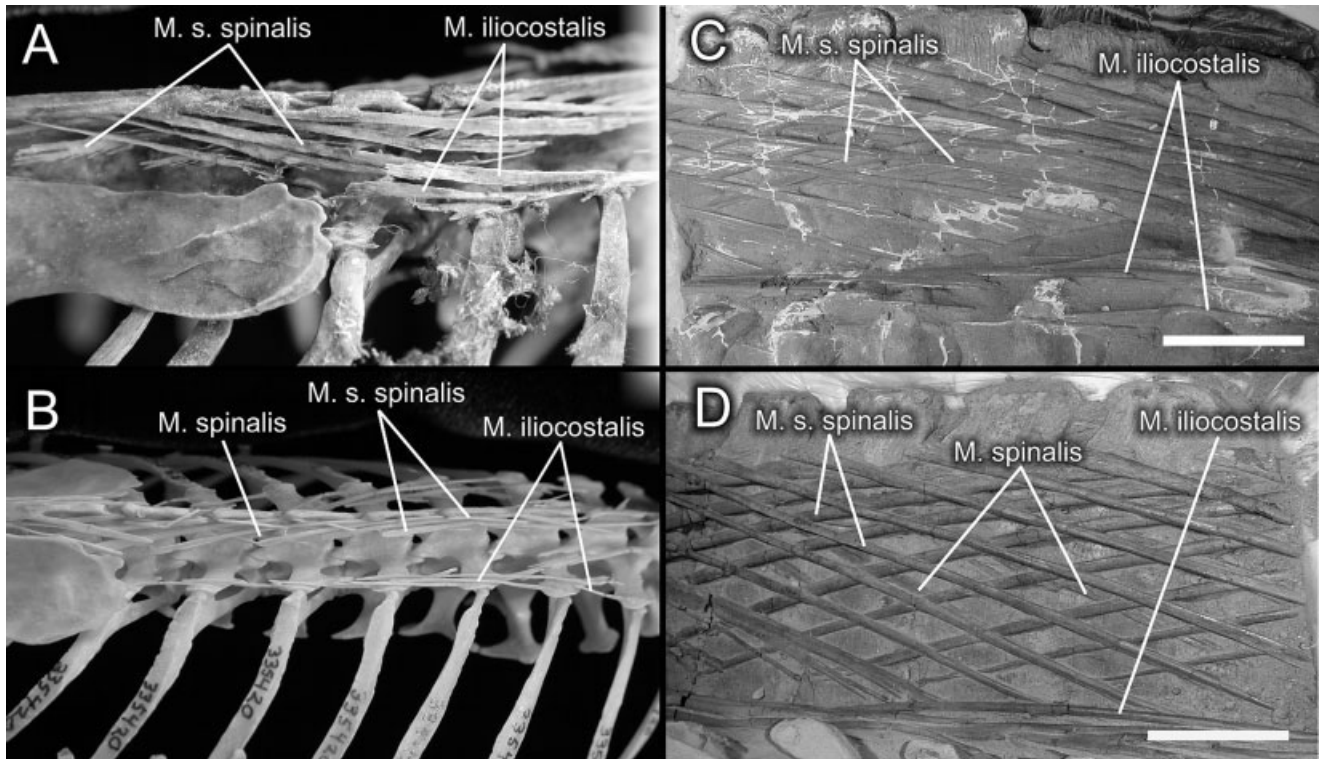


Fig. 5. Ossified epaxial tendons in dinosaurs. The tendon-lattice of *M. longus colli dorsalis, pars thoracica* in (A) *Podiceps auritus* (Podicipediformes) and (B) *Alca torda* (Charadriiformes). C: The three-layered lattice of the thoracic region in the hadrosaur *Brachylophosaurus canadensis* (Iguanodontidae). D: Lattice in the sacral region of *Brachylophosaurus*. Right lateral view in all panels. Scale bars = 10 cm.

bounds this muscle. In some taxa, this tendon is heavily ossified (see *M. iliocostalis* below).

Musculus iliocostalis. *M. iliocostalis* is lateral and caudal to *M. ascendens thoracicus* and has two divisions, one caudoventral and one craniodorsal. The caudoventral portion originates on the cranio-lateral margin of the iliac blades and inserts on the distal margins of the transverse processes and proximal region of the associated rib. It bears an aponeurosis cranially, from which the craniodorsal portion of *M. iliocostalis* originates. Cranial fascicles of both divisions blend along the aponeurosis they share. In *Ardea*, both divisions merge onto a large and tough superficial aponeurosis (*fascia dorsalis*) that ensheathes the entire lateral portion of the trunk. In *Podilymbus*, the fascia dorsalis is reduced and the main muscle belly is restricted caudally. Longitudinally oriented tendons are often present deep within *M. iliocostalis* and insert on the distal posterior margins of the transverse processes of the dorsal vertebra, or on the lateral margin of the notarium if it is present. These tendons ossify in *Ptychoramphus*, *Amazona*, *Buteo*, and *Chuana*. Homologizing this muscle with crocodylian epaxial muscles proved difficult based on attachment sites alone, but innervation data by Tsuihiji (2005) convincingly supported homologizing the caudoventral portion of the avian *M. iliocostalis* with the crocodylian *M. iliocostalis* and the craniodorsal portion with the crocodylian *M. longissimus dorsi*.

DISCUSSION

Within Archosauria, the muscle homologies hypothesized here do not significantly differ from those presented elsewhere (Tsuihiji, 2005). Several interesting changes appear to have occurred during the evolution of Aves, notably, the loss of *M. multifidus*. The division of *M. semispinalis* into *M. articulospinalis* and *M. tendinoarticularis* within crocodylians is also seen in Aves, suggesting that this feature is synapomorphic for Archosauria. However, in crocodylians, this division is tightly coupled to the thoracic bracing system involved with osteoderms to which these muscles attach (Frey, 1985). Its role in Aves (if any) is unclear.

The transition in *M. transversospinalis* between the cervical and dorsal regions in crocodylians is gradual (Seidel, 1978). Vertebral morphology also lacks a dramatic shift between these regions. In contrast, the muscular transition in birds from the cervical to the dorsal regions is gradual (Boas, 1929), but there is often a dramatic transition in vertebral structure because of the co-ossification of vertebral elements and tendons in the thoracic region. As a consequence, the avian thorax is compact and rigid compared with their long and flexible necks. In addition, the epaxial musculature is disrupted along the notarium and the synsacrum. *M. longus colli dorsalis, pars thoracica* in most extant birds is separated from *M. levator caudae*, with which it was almost certainly continuous ancestrally. There is also good evidence that the tail

and associated caudal epaxial muscles were progressively decoupled from the body on the evolutionary line to birds (Gatesy and Dial, 1996a). Furthermore, complete fusion of thoracic vertebrae into a notarium occurs in Tinamiformes, Podicipediformes, Phoenicopteriformes, Galliformes, and Columbiformes, and partial fusion of vertebral vertebrae occurs in Pelecaniformes, Ciconiiformes, Falconiformes, Gruiformes, and Caprimulgiformes (Storer, 1982). Intrinsic vertebral muscles (e.g., *Mm. interspinales*) are reduced or absent in extant birds. When compared with the flexible and long necks of most birds, these data suggest that the thoracic region has also been compartmentalized and functionally decoupled from the neck during the evolution of birds from nonavian dinosaurs. Such compartmentalization, which is also found in the shoulder girdle and hindlimb in birds, is linked to the evolution of “locomotor modules” (Gatesy and Dial, 1996b) and the development of the complex avian flight apparatus.

Changes in epaxial musculature of the thoracic region are hypothesized to coincide with the evolution of the notarium and synsacrum, which in turn are hypothesized to correspond with the evolution of locomotor modules and modifications of the forelimb and shoulder into a wing during the evolution of birds from nonavian theropod dinosaurs. Evolution of the thoracic epaxial musculature probably followed a progressive increase in sacral vertebrae within Dinosauria. Cranial expansion and medial migration of the preacetabular ilium correlate with vertebral fusion (Hutchinson, 2001b) and notarial development, which began in *Archaeopteryx* (Baumel et al., 1993). Therefore, specialized epaxial musculature, such as the loss of *M. multifidus*, reduced muscle mass, and the overlap of *M. iliocostalis* and *M. longissimus*, likely occurred in step with these osteological changes preceding the evolution of Neornithes.

The respiratory function of avian epaxial muscles likely originates with these musculoskeletal changes. Thoracic epaxial muscles have been suggested to have played a role in ventilation during nonavian theropod locomotion, where they aided in inhalation by flexing during the second half of the limb support phase (Carrier and Farmer, 2000). Although lung morphology in nonavian dinosaurs remains contentious (Ruben et al., 2003), it is clear the musculoskeletal changes that characterize breathing in modern birds began in nonavian theropods (O'Connor and Claessens, 2005) and that changes in thoracic epaxial muscle structure and function were vital for the transition.

Muscle Reconstruction in Extinct Dinosaurs With Ossified Tendons

The extant phylogenetic bracket has been applied to separate attachments of the same soft tissue to increase the preciseness of inference (Carrano and Hutchinson, 2002). Similarly, soft tissue attachments to ossified tendons themselves will be discussed, followed by the role ossified tendons play in inferring the different subunits of the epaxial musculature.

A bony core with unmineralized flexible termini is common in nonvertebral ossified tendons in birds (Vanden Berge and Storer, 1995; Landis and Silver, 2002). As a result, they have a tapered terminus that continues as unmineralized tendon and a terminus that mineralizes into either a myotendinous junction or aponeurosis, re-

sulting in a fimbriated appearance. Ornithischian ossified tendons have identical morphologies indicating that they had similar attachments to soft tissues.

The fibers of *M. longus colli dorsalis, pars thoracica* attach along the entire length of its tendons through a paratenon sheath that surrounds a bony core. However, in grebes, thoracic epaxial tendons are completely mineralized and the fibers of *M. longus colli dorsalis, pars thoracica* insert directly along their surface. The direct muscle attachment along ossified epaxial tendons in grebes leaves longitudinal striations that mark the direction of the inserting muscle fibers. The same longitudinal striations can be seen on ornithischian ossified tendons, indicating a similar muscular interface, one that lacks a paratenon intermediate.

As noted above, crocodylians and birds both possess a rhomboidal lattice of tendons associated with the subunits of *M. transversospinalis* (avian *M. longus colli dorsalis, pars thoracica*), which lies vertically along the lateral aspects of the spinous processes. Ossified tendons in iguanodontoid dinosaurs also form a rhomboidal lattice structure along the spinous processes of the thoracic, sacral, and caudal vertebrae (Fig. 5C and D). The lattice begins in the caudal-most cervicals, as is in *Iguanodon* (Norman, 1980), or the cranial-most thoracic vertebrae, as in *Brachylophosaurus* (Prieto-Márquez, 2001), and extends into the distal third of the tail. The lattice consists of three layers, though all three might not be preserved and the medial-most layer is usually weakly developed (Dollo, 1886; Norman, 1986; Prieto-Márquez, 2001).

Using crocodylians alone to understand iguanodontoid tendons has been perplexing because *M. transversospinalis* has two sets of tendons that run caudoventral, surrounding one set that runs caudodorsal. But iguanodontoid epaxial ossified tendons run opposite: two sets of tendons that run caudodorsal, surrounding one set that runs caudoventral. Bringing avian anatomy into the analysis significantly clarifies the issue, because they have an arrangement of tendons identical to that seen in iguanodontoid dinosaurs. Moreover, in birds that ossify epaxial tendons, the medial-most layer is often weakly developed, a morphology also seen in iguanodontoid dinosaurs. In both groups, the outer two layers of tendons are strongly ossified. Using the homologies and osteological correlates discussed above (and summarized in Tables 1–3), it is a level I inference to reconstruct *M. transversospinalis* as partitioned into *M. spinalis* medially and *M. semispinalis* laterally. *M. semispinalis* is further subdivided into *M. articularis* medially and *M. tendinoarticularis* laterally. Moreover, the ossified tendons themselves provide direct support for this reconstruction because they are fossilized portions of the muscle-tendon systems. Like *M. transversospinalis*, the intrinsic (*Mm. interspinales* and *Mm. interarticularis superiores*) and lateral (*M. longissimus* and *M. iliocostalis*) epaxial muscles enjoy a level I phylogenetic reconstruction. And like *M. spinalis* and *M. articularis*, ossified tendons provide direct evidence for the existence of *M. iliocostalis*. Reconstruction of *M. multifidus* is more equivocal (level II inference), because this muscle is absent in birds and no ossified tendons corresponding to *M. multifidus* are present in iguanodontoid dinosaurs.

Given the data and analysis presented above, iguanodontoid dinosaurs possessed typical archosaurian epaxial muscles, but also strongly developed a lateral tendon

TABLE 3. Hypothesized muscle homologies between crocodylians and birds, and hypothesized reconstruction of thoracic epaxial muscles in Iguanodontoidea

Lepidosauria	Crocodylia	Neornithes	Iguanodontoidea ^b
<i>M. transversospinalis</i>	<i>M. transversospinalis</i>	<i>M. longus colli dorsalis, pars thoracica</i>	<i>M. transversospinalis</i> (I)
<i>Mm. interspinales</i>	<i>Mm. interspinales</i>	<i>Mm. interspinales</i>	<i>Mm. interspinales</i> (I)
<i>Mm. interarticularis superiores</i>	<i>Mm. interarticularis superiores</i>	<i>Mm. intercostales</i>	<i>Mm. interarticularis superiores</i> (I)
<i>M. multifidus</i>	<i>M. multifidus</i> (<i>M. neurospinalis</i>) ^a		<i>M. multifidus</i> (II)
<i>M. spinalis</i>	<i>M. spinalis</i> (<i>M. spinoarticularis</i>) ^a	<i>M. spinalis</i> (<i>M. longus colli dorsalis, pars thoracica, medial part</i>) ^a	<i>M. spinalis</i> (I ^c)
<i>M. semispinalis</i>	<i>M. articulospinalis</i>	<i>M. semispinalis</i> (<i>M. longus colli dorsalis, pars thoracica, lateral part</i>) ^a	<i>M. articulospinalis</i> (I ^d)
	<i>M. tendinoarticularis</i>	<i>M. ascendens thoracicus</i>	<i>M. tendinoarticularis</i> (I)
<i>M. longissimus dorsi</i>	<i>M. longissimus dorsi</i>	<i>M. iliocostalis, dorsal part</i>	<i>M. longissimus dorsi</i> (I)
<i>Mm. intertransversarii</i>	<i>Mm. intertransversarii</i>	<i>Mm. intertransversarii</i>	<i>Mm. intertransversarii</i> (I)
<i>M. iliocostalis</i>	<i>M. iliocostalis</i>	<i>M. iliocostalis, ventral part</i>	<i>M. iliocostalis</i> (I ^c)

^a Names used by Vallios (1922) and Tsuihiji (2005).

^b Inferred epaxial muscles with extant phylogenetic bracket level of inference in parentheses.

^c Indicates inference level plus evidence of soft tissue from ossified tendons.

^d Indicates that two layers of ossified tendons are present.

layer in *M. articulospinalis* similar to those seen in many birds. In fact, *Alca* (Fig. 5B) displays a three-layered lattice of tendons in *M. longus colli dorsalis, pars thoracica* identical to that seen in the *M. transversospinalis* in iguanodontoid dinosaurs. The three-layered lattice within *M. transversospinalis* is parsimoniously interpreted as homologous between birds and iguanodontoid dinosaurs. This suggests that the avian morphology of *M. longus colli dorsalis, pars thoracica* (*M. transversospinalis*) evolved within the base of the dinosaurian evolutionary tree. Ossification of the tendon lattice within *M. transversospinalis*, whether two layers ossify or three layers ossify, is evidently convergent given the lack of mineralization in these tissues within the rest of Dinosauria.

Parallel bundles of ossified tendons situated along the dorsal and lateral surfaces of transverse processes are also commonly found in iguanodontoid and other ornithopod dinosaurs. These tendons likely belong to *M. iliocostalis*, because in birds, *M. iliocostalis* sometimes has longitudinally arrayed tendons that also ossify, though these are usually at the tips of the transverse processes. Given the size of these bundles, this muscle was better developed in Iguanodontoidea and other ornithopods than in Aves. It is also possible, given the medial location of many tendon bundles adjacent to the neural arch, that at least some of them belonged to *M. longissimus dorsi*. If true, this suggests that the merging of the dorsal portion of *M. iliocostalis* (*M. longissimus dorsi*) onto the ventral portion of *M. iliocostalis* in Aves evolved sometime after Ornithischia and Saurischia split, because the bundles of ossified tendons extend over the entire dorsal region in ornithopod dinosaurs.

There are rare fossil specimens that possess ossified epaxial tendons not normally found in conspecifics or sister taxa. For example, Molnar and Frey (1987) reconstructed *M. transversospinalis* in *Minmi* from ossified tendons that form a lattice typical of *M. transversospinalis* in crocodylians. The ossified tendons in *Dryosaurus* (Galton, 1981) and *Camptosaurus* (Gilmore, 1925) are probably

part of *M. transversospinalis* as well. These specimens suggest a widespread occurrence of intratendinous ossification within *M. transversospinalis* in Ornithopoda.

Other ornithopods, such as *Heterodontosaurus* (Santa Luca, 1980), *Tenontosaurus* (Forster, 1990; Winkler et al., 1997), and *Hypsilophodon* (Galton, 1974), and ornithischians such as *Lesothosaurus* (Thulborn, 1972), *Scelidosaurus* (Norman et al., 2004b), *Pachycephalosaurus* (Sues and Galton, 1987), *Styracosaurus* (Brown and Schlaikjer, 1937), and *Triceratops* (Hatcher et al., 1907), display parallel bundles of ossified tendons. It is probable, based on published descriptions, that these tendons are from *M. transversospinalis* when arrayed along the spinous processes, their bundled architecture due to short spinous processes. In fact, the presence of a well-formed three-layered lattice of ossified tendons in a chasmosaurid (Holmes and Organ, 2005) suggests that all members of Cerapoda possessed mineralized, if not ossified, tendons in *M. transversospinalis*. However, bundles of ossified tendons at the base of the neural arch that run axially are most likely part of *M. iliocostalis* (or perhaps also part of *M. longissimus dorsi* as well).

Dollo (1886) proposed that the iguanodontoid lattice formed by atrophy of muscle tissue into ligament, which then ossified. Given the results of this study and others (Adams and Organ, 2005), this scenario seems highly unlikely. Yet, Dollo (1886) set a precedent for interpreting ossified tendons in ornithischian dinosaurs in functional terms of rigidity without a thorough functional analysis (Brown, 1916; Broili, 1922; Colbert, 1951; Ostrom, 1964; Norman, 1980, 1986; Rothschild, 1987; Bultynck, 1992; Coombs, 1995). There are several ways that intratendinous ossification can function. The most general is that they stiffen the surrounding anatomy, as in woodcreepers, stiffening the entire skeleton (Bledsoe et al., 1993). When tendons are initially stretched, time and energy are spent bringing them to tension before they can transfer loads. This phenomenon is known as creep, and reducing it has been suggested as a potential function for ossified tendons

in birds (Bock and von Wahlert, 1965; Bennett and Stafford, 1988). Still others have proposed that ossified tendons prevent material fatigue due to repeated long-term loading (Buchanan and Marsh, 2001). But the most common functional interpretation is that ossified tendons store more elastic energy than unmineralized tendons (Landis et al., 1995; Sarin et al., 1999; Olson, 2000; Silver et al., 2000, 2001; Landis and Silver, 2002; Freeman and Silver, 2004). Clearly, avian ossified tendons develop in response to stress, similar to other osteological tissues, but the seemingly random phylogenetic and anatomical patterns of occurrence make such interpretations difficult to adopt generally. For example, turkeys possess ossified tendons in the shank, which are thought to store and return energy during the stride cycle, but most cursorial birds, like ratites, lack such innovations. As Sarin et al. (1999) noted, intratendinous ossification has a strong genetic component. The presence of intratendinous ossification is therefore not so easily explained by mechanical stress and biomechanics alone.

While function is perhaps the most exciting aspect of morphological studies concerning extinct dinosaurs, it should not be inferred before an attempt at detailed muscular reconstruction on which to base analyses. Furthermore, when evaluating function, adaptation should never be assumed a priori, as it has been for the ossified tendon lattice in *Iguanodontoidea*. An evolutionary null hypothesis should be considered until the burden of evidence demonstrates otherwise. For example, given the high degree of systematic mineralization of many birds (e.g., synsacrum, notarium, trachea), ossified tendons may be a correlated response for the selection of skeletal co-ossification or even for the selection of mineral use in egg formation or muscle physiology. Ossification of *M. transversospinalis* tendons may have been adaptive for increasing spinal rigidity, but biomechanical studies are needed to evaluate such questions in detail.

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