MONTANA STATE UNIVERSITY

Epaxial muscles and ossified tendons in dinosaurs : anatomy, development, histology, and biomechanics
by Christopher Lee Organ

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University
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Abstract:
Intratendinous ossification in dinosaurs (including birds) is a wide spread phenomenon that has implications for physiology, posture, biomechanics, behavior, and systematics. Four separate studies were undertaken to elucidate ossified tendon biology in extinct dinosaurs and birds. The first investigation reconstructs dorsal epaxial musculature in extinct dinosaurs. Crocodilian and avian dorsal epaxial muscles are homologized. Using the extant phylogenetic bracketing approach, the three-layered trellis of Hadrosauriformes is homologized to the M. transversospinalis slips in crocodilians and the M. longus colli dorsalis thoracica in birds. These tendons are ossified in Hadrosauriformes and some birds. The parallel ossified tendons in other ornithischians are homologized to the M. longissimus dorsi in Alligator. The second investigation determines how ossified tendons in non-avian dinosaurs developed. Atrophied muscle was previously thought to be the origin of ossified tendons in non-avian dinosaurs. Using different age classes of hadrosaurs (Brachylophosaurus and Maiasaura) and turkeys (Meleagris), the developmental process of ossified tendons in hadrosaurs is shown to be homologous with intratendinous ossification in birds. But, the degree of ossification is greater in hadrosaurs, whose tendons also possess primary osteons, an external fundamental system and lines of arrested growth. The third investigation determines the histological diversity of ossified tendons in Dinosauria. Despite various anatomical locations and large differences in size, ossified tendons have uniform microstructure even in specimens that do not normally experience intratendinous ossification (such as Ceratosaurus and Camarosaurus). The greater degree of ossification noted above occurs in all non-avian dinosaurs. Also, variation in periosteal bone development occurs along the length of individual tendons. Ossified tendons from marginocephalians are unique in that they have larger portions of fibrolamellar bone and radial vascularity. In the fourth investigation, computer finite element models are constructed for two ornithopods to assess ossified tendon biomechanics. An Alligator is used to empirically determine joint properties. Ossified tendons probably reduced tail deflection and played a role in locomotion in all ornithopods. The ossified tendon trellis of Hadrosauriformes may have increased the skeleton's ability to bear large body mass. Neural spine height and bone material properties have the greatest impact on spinal rigidity.

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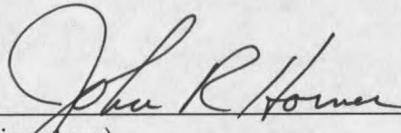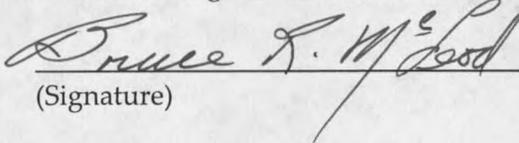
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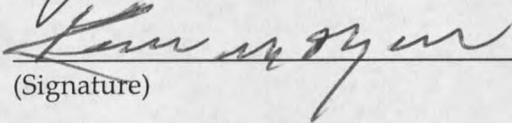
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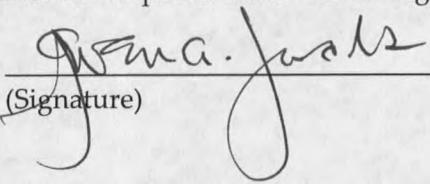
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ABSTRACT

Intratendinous ossification in dinosaurs (including birds) is a wide spread phenomenon that has implications for physiology, posture, biomechanics, behavior, and systematics. Four separate studies were undertaken to elucidate ossified tendon biology in extinct dinosaurs and birds. The first investigation reconstructs dorsal epaxial musculature in extinct dinosaurs. Crocodilian and avian dorsal epaxial muscles are homologized. Using the extant phylogenetic bracketing approach, the three-layered trellis of Hadrosauriformes is homologized to the M. transversospinalis slips in crocodilians and the M. longus colli dorsalis thoracica in birds. These tendons are ossified in Hadrosauriformes and some birds. The parallel ossified tendons in other ornithischians are homologized to the M. longissimus dorsi in *Alligator*. The second investigation determines how ossified tendons in non-avian dinosaurs developed. Atrophied muscle was previously thought to be the origin of ossified tendons in non-avian dinosaurs. Using different age classes of hadrosaurs (*Brachylophosaurus* and *Maiasaura*) and turkeys (*Meleagris*), the developmental process of ossified tendons in hadrosaurs is shown to be homologous with intratendinous ossification in birds. But, the degree of ossification is greater in hadrosaurs, whose tendons also possess primary osteons, an external fundamental system and lines of arrested growth. The third investigation determines the histological diversity of ossified tendons in Dinosauria. Despite various anatomical locations and large differences in size, ossified tendons have uniform microstructure even in specimens that do not normally experience intratendinous ossification (such as *Ceratosaurus* and *Camarosaurus*). The greater degree of ossification noted above occurs in all non-avian dinosaurs. Also, variation in periosteal bone development occurs along the length of individual tendons. Ossified tendons from marginocephalians are unique in that they have larger portions of fibrolamellar bone and radial vascularity. In the fourth investigation, computer finite element models are constructed for two ornithopods to assess ossified tendon biomechanics. An *Alligator* is used to empirically determine joint properties. Ossified tendons probably reduced tail deflection and played a role in locomotion in all ornithopods. The ossified tendon trellis of Hadrosauriformes may have increased the skeleton's ability to bear large body mass. Neural spine height and bone material properties have the greatest impact on spinal rigidity.

CHAPTER 1

DORSAL EPAXIAL MUSCULATURE IN DINOSAURS

Introduction

Archosaur epaxial musculature is generally considered conserved compared with the diversity of muscles in the appendicular skeleton. Consequently, interest in muscular reconstruction in extinct archosaurs has focused on the shoulder girdle, pelvis, or limbs (Romer 1923a; Romer 1923b; Romer 1927; Galton 1969; Walker 1977; Gatesy 1994; Dilkes 2000; Hutchinson 2001a; Hutchinson 2001b; Carrano and Hutchinson 2002). Some of these studies deal with epaxial muscles in a peripheral manner by grouping them into the "dorsalis trunci". But, the dorsal 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 dorsal epaxial musculature associated with avian vertebral fusion is reduced in size and divisions compared with crocodilians. In many birds the epaxial muscles are pinched off by the anteromedial union of the iliac blades. In contrast, crocodilians retain plesiomorphic epaxial muscles, except for the synapomorphic M. tendino-articularis that contains anteriorly directed cones of myosepta (Gasc 1981).

The only attempts at detailed reconstruction of dorsal epaxial musculature in extinct dinosaurs are concerned with ossified epaxial tendons in Minmi (Molnar and Frey 1987) and Iguanodon (Dollo 1886). Molnar and Frey (*idem*) used crocodilian while Dollo (*idem*) used avian anatomy comparisons for muscle reconstruction. But recent studies (Hutchinson 2001a; Hutchinson 2001b) have

shown the resolution power and robustness that an explicit phylogenetic context using many specimens can provide for muscle reconstruction and the 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 (Witmer 1995). But ossified tendons are more than just an osteological correlate consisting of bone surface rugosity or projections caused by muscle or tendon attachment. They are literally part of a soft tissue that became ossified and then fossilized. Therefore, ossified tendons are ideal for inferring soft tissues. Unfortunately, they only regularly occur in ornithischian dinosaurs, where they are used as a diagnostic character (synapomorphy).

Dorsal epaxial muscles are associated with breathing in birds (Baumel et al. 1990) and terrestrial locomotion in crocodilians (Frey 1985). The epaxial tendon trellis thought to be unique to hadrosaurs, lambeosaurs, and iguanodons (Hadrosauriformes) are always interpreted as rigidifying structures that affect bipedal posture (Ostrom 1964) and locomotion (Dollo 1886). Also, the existence of the trellis is used to argue for claims of semi-aquatic (Brown 1916; Colbert 1951) or terrestrial (Ostrom 1964) behavior. These arguments assume that the ossified trellis is an anatomical structure unique to Hadrosauriformes. In addition, because ossified tendons are also 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 Hadrosauriformes). This study's purpose is to reconstruct the dorsal epaxial musculature in extinct dinosaurs using a phylogenetic approach. The morphology and function of dorsal epaxial muscles are discussed in this context. This reconstruction will provide a basis for interpreting the biology of

epaxial muscles and ossified tendons in all dinosaurs. Furthermore, because the epaxial musculature in birds is poorly resolved (Baumel et al. 1993), this study will help elucidate the structure and function of the dorsal region in birds.

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 University of Chicago Department of Organismal Biology and Anatomy. Most of the structural data from ossified tendons was based on an articulated *Brachylophosaurus canadensis* (MOR-794) that possesses a three-layered trellis of ossified tendons *in situ*.

Osteological data from birds were collected at the MOR and Montana State University (MSU), but mostly at the University of Michigan Museum of Zoology (UMMZ). Specimens were chosen based on availability and spanned seven orders: Anseriformes (*Chuana torquata*), Charadriiformes (*Limnodromus scolopaceus,* and *Ptychoramphus aleuticus*), Falconiformes (*Accipiter cooperi*), Gruiformes (*Porphyrio mantelli*), Podicipediformes (5 specimens of *Podilymbus gigas*, 8 specimens of *Podilymbus podiceps, and Aechmorphus occidentalis;* and 4 specimens of *Podilymbus major*), Psittaciformes (*Amazona amazonica*), and Struthioniformes (*Apteryx australis*).

Myological data were collected from donated specimens dissected on the campus of Montana State University, Bozeman. Avian specimens spanned five orders: Ciconiiformes (*Ardea herodias*), Columbiformes (*Columba livia*), Falconiformes (*Buteo jamaicensis*), Galliformes (7 specimens of *Meleagris gallopavo* and *Gallus domesticus*), and Podicipediformes (*Podilymbus podiceps*). Three

crocodilians (*Alligator mississippiensis*) and two lizards (*Tupinambis* and *Anolis carolinensis*) were also dissected.

The nomenclature used for crocodilian anatomy follows Gasc (1981) and Frey et al. (1989), though some homologies and synonyms from Gasc (*idem*) are preferred. Avian anatomy nomenclature follows Baumel et al. (1993).

Homology

The term "Homology", as used in this study, refers specifically to supraspecific homology (Roth 1994), which is a correspondence among characters in different taxa that share a recent common ancestor. That is, homologies are synapomorphies (Patterson 1982; de Pinna 1991; Roth 1994; Hawkins et al. 1997), which define monophyletic groups (clades). Homologies identified in this study are also taxic (characters). Transformational (change in character state) homology is considered by the inclusion of extinct forms.

Using these definitions, there are three ways to test hypotheses of homology: similarity, conjunction, and congruence. The first test is similarity, which is the simplest but weakest tool (de Pinna 1991). It consists of identifying homologies based on appearance. As Patterson (1982) notes, similarity is not a test, but provides supporting data for proposing a hypothesis of homology. Despite these caveats, it is powerful because any kind of similarity may be used, such as composition, ontogeny, position, and so on.

The second test for homology hypotheses is conjunction, whereby the proposed homologous structures are searched for in the same organism. If such structures are discovered, hypothesis falsification follows (Patterson 1982). For example, wings in a bird cannot be homologous with the hind limbs of mammals, because birds possess hind limbs as well. Despite the conclusiveness

of this test, it is of limited utility for transformation (character state) hypotheses of homology.

The third test, which is considered the strongest, is congruence. A homologous character should only arise once for a group (it should be a synapomorphy). This uses comparisons of other homologies in a phylogenetic framework to strengthen the proposed hypothesis of homology. The greater the number of structures found to be homologous between two taxa, the more support the proposed hypothesis has. Like many other historical sciences, this test uses a "convergence of independent evidence" approach where the hypothesis becomes more robust according to the degree of support (number of characters found to be congruent).

Phylogenetic Framework for Soft Tissue Inferences

Reconstruction of unpreserved soft tissues in extinct taxa is problematic because of variables such as muscle attachment type, ontogeny, shifts in function, and so forth (Bryant and Seymour 1990; Bryant and Russell 1992). The best way to address these problems is by using an explicit phylogenetic framework (Witmer 1995) to infer unpreserved soft tissues. This method uses living sister (bracket) taxa to provide phylogenetic support for hypothesizing unpreserved features in extinct organisms. 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. This is unequivocal support for inferring an unpreserved soft tissue. A level I′ inference is made when both bracketing taxa possess a soft tissue that lacks osteological correlates. Level I′ inferences are less robust than a level I inference, but more supportive than a level II inference. A level II inference is made when one of

Figure 1. Phylogenetic framework used in this study. Stem-based groups are labeled at the branches and node-based groups are labeled at nodes. 1, Archosauria; 2, Dinosauria; 3, Ornithischia; 4, Saurischia; 5, Neornithes; 6, Galliformes. Bold taxa are extant. Modified from Gauthier (1986), Cracraft (1988), and Sereno (1999).

the bracketing taxa possesses a soft tissue and associated osteological correlates of the soft tissue in question. This provides limited support for inferring an unpreserved soft tissue. A level II' inference is made when one of the bracketing taxa possess a soft tissue that lacks osteological correlates. Level II' inferences are less robust than a level II inference, but more supportive than a level III inference. A level III inference is made when neither of the bracketi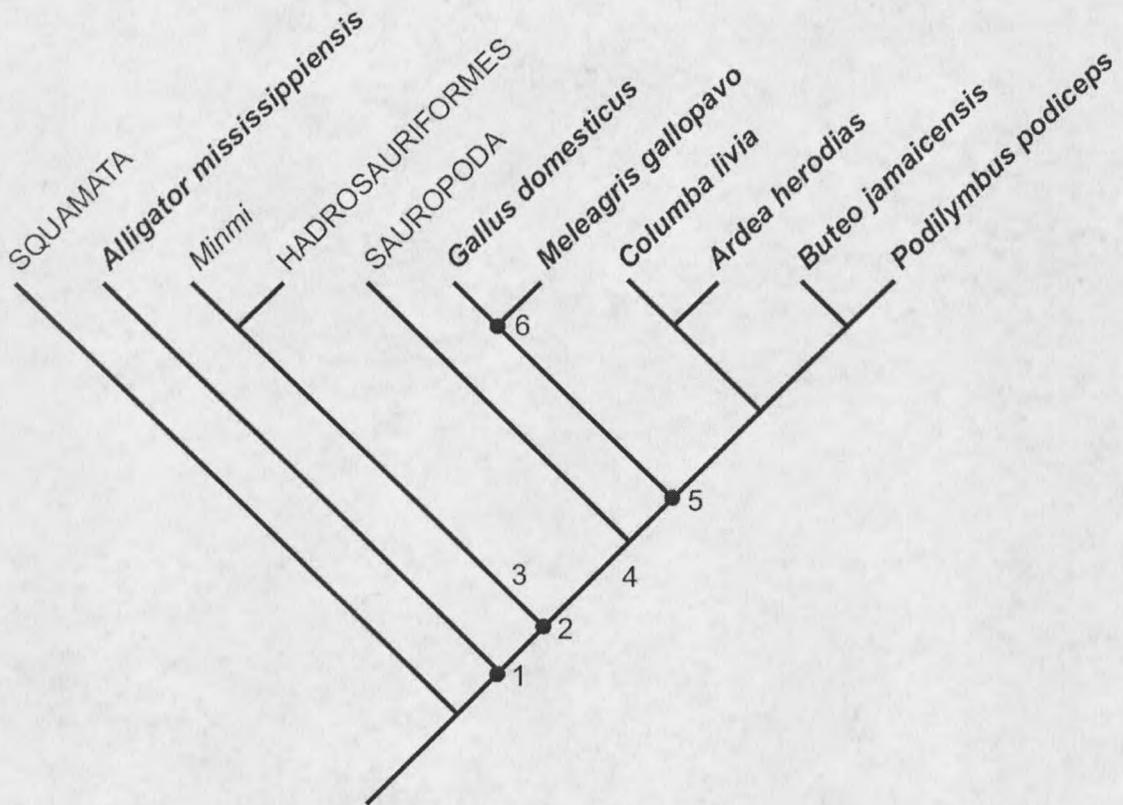ng taxa possesses a soft tissue. This provides no phylogenetic support for inferring an unpreserved soft tissue. Only level I , I', II, and II' inferences are used in this study. Limitations on level I' and II' are discussed on an individual basis.

The phylogenetic framework used in this study (Fig. 1) is constructed from several sources. Gauthier (1986) is used for the base of the tree, Sereno (1999) is used to expand Dinosauria, and Cracraft (1988) is used to expand Neornithes.

Results

Crocodilia

Epaxial musculature in crocodilians is straightforward and does not differ dramatically from the condition encountered in squamates. However, epaxial muscles are less diverse in crocodilians than those in squamates because of osteoderms and the propulsive function of the tail (Gasc 1981). The following anatomy is based on the dissections of *Alligator* and the literature (Vallois 1922; Gasc 1981; Frey 1982; Molnar and Frey 1987; Frey et al. 1989).

Intrinsic Vertebral Muscles Mm. interneuralis (also called M. interspinales) and Mm. interarcuales connect neural spines together at their anterior and posterior edges. Their fibers run anteroposterior and are indistinguishable from one another. Therefore, they will together be referred to together as the Mm. interneuralis. Medial to this muscle lies the interspinal ligament. Mm. interarticularis superiores connects successive pre and postzygapophyses. The anterior border of the Mm. interarticularis superiores inserts on the posterior aspect of the zygapophyseal joint by a short fan shaped tendon. Because the epaxial muscles are fibrous, the preceding muscle divisions were not easily distinguishable. Lateral to this muscle is the Mm. intertransversarii, which connects successive transverse processes.
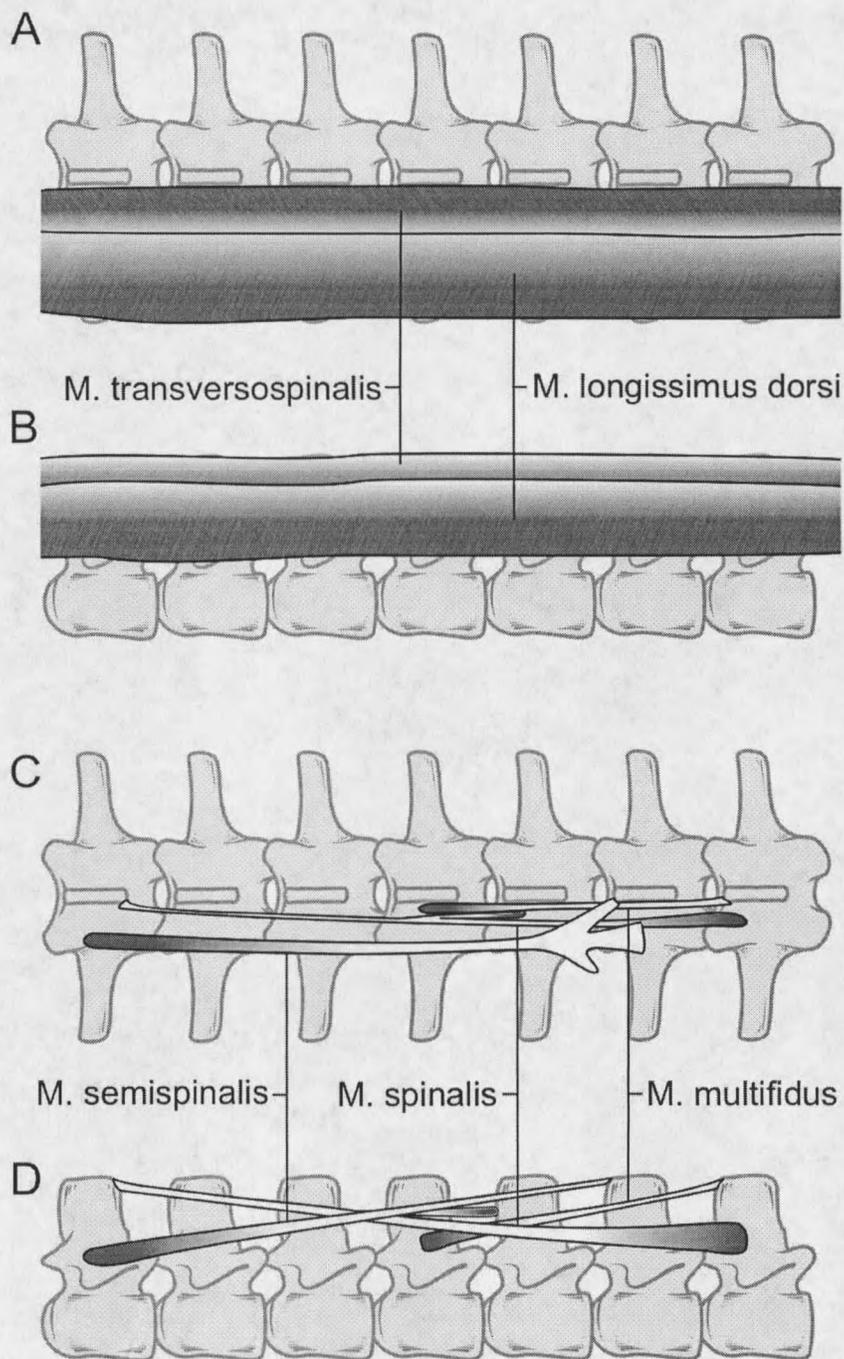
Figure 2. Diagram of dorsal epaxial muscles in *Alligator*. A and B, dorsal and lateral views of major muscles. C and D, slips of the M. transversospinalis excluding the tendino-articularis. Anterior is to the right.

<u>M. Transversospinalis</u> Lateral to the intrinsic vertebral muscles are a series of slips that form the bulk of the M. transversospinalis (Fig. 2). The M. multifidus, M. neurospinalis of Frey (1982) and Vallios (1922), is the most medial slip and lies next to the lateral surface of the neural spines. The tendon from the M. multifidus originates as a small mediolaterally fattened sheet in front of the neural spine. This passes anterodorsal over two vertebrae and inserts on the posterior summit of the third neural spine just under the attachment of the medial tendinous head of the M. semispinalis (M. articulo-spinalis).

Immediately lateral to this tendon, separated by only a thin layer of muscle fibers, is the M. spinalis, M. spino-articularis of Frey (1982) and Vallios (1922). This muscle slip originates near the prezygapophysis as a mediolaterally flattened sheet and runs posterodorsally to insert on the anterior summit of the neural spine five to seven vertebrae posterior (Fig. 2C and D). In the lumbar region, this tendon bifurcates twice, anteriorly receiving another tendon from the muscle belly and posteriorly a tendon from the anterior aspect of the neural spine.

The M. semispinalis lies lateral to the M. spinalis and is separated from it by muscle tissue (Fig. 2C and D). It is divisible into different sections, the M. articulo-spinalis and M. tendino-articularis. The M. articulo-spinalis is the medial division, which originates at the base of the neural spine and passes anterodorsally past four vertebrae. Here it flattens out and splits into three tendinous heads. The medial head inserts on the posterior aspect of the summit of the next neural spine. The lateral head connects to the fascia of the M. tendino-articularis.

The lateral division of the semispinalis is the M. tendino-articularis. Anteriorly pointed cones of myosepta form successive slips in this muscle. It is

interconnected to the M. articulo-spinalis by a lateral tendon branch.

M. Longissimus Dorsi Lateral to the M. transversospinalis and separated from it by myosepta lies the larger M. longissimus dorsi (Fig. 2A and B). Posteriorly pointed cones of myosepta form the slips of this muscle. The internal margin connects to the lateral aspect of the M. tendino-articularis while the external margin connects with the M. iliocostalis. Each conical slip extends over three vertebrae and inserts on the distal part of the transverse processes. Fibers from the M. intertransversarii interweave with the fibers of the M. longissimus dorsi. The muscle originates on the anteromedial aspect of the ilium and inserts on the dorsal aspect of the transverse processes.

Neornithes

The dorsal epaxial musculature in birds is poorly understood with the M. longissimus dorsi compared with mammalian spinal muscles by Baumel, et al. (1993). Therefore, aside from several references that describe the dorsal epaxial muscles as a whole (Harvey et al. 1968; Zusi and Bentz 1984; Baumel et al. 1993), epaxial muscle divisions are based on the dissections of this study.

Intrinsic Vertebral Muscles The intrinsic vertebral muscles of the dorsal region are reduced because of dorsal vertebral fusion into the notarium. The Mm. interneuralis (also called Mm. interspinales) are absent. Even at the notarial-synsacral articulation and free dorsal vertebrae, the interspinus ligament is more developed than the Mm. interneuralis. The Mm. intercristales in birds might be homologous to Mm. interarcuales based on its lateral position to the Mm. interneuralis.