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Homologies of the *Longissimus*, *Iliocostalis*, and Hypaxial Muscles in the Anterior Presacral Region of Extant Diapsida

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ABSTRACT Homologies of muscles of the *m. longissimus* and *m. iliocostalis* groups in the dorsal and cervical regions, as well as those of the subvertebral muscles and *mm. intercostales externi* that continue from the dorsal into the cervical regions, in extant Diapsida are proposed based on detailed dissections and published accounts of lepidosaurs, crocodylians, and birds. The morphology of tendons and innervation patterns suggest that the avian "*m. iliocostalis*" in the dorsal region include the homologs of both *m. longissimus* and *m. iliocostalis* in non-avian diapsids. The conserved nature of the morphology of tendons in palaeognath birds also revealed that the avian *mm. intertransversarii* in the cervical region consist of muscles of the both *m. longissimus* and *m. iliocostalis* groups despite having been treated as a single series of muscles, and thus are not homologous with muscles of the same name in Lepidosauria or Crocodylia. The avian *mm. inclusi* that lie medial to *mm. intertransversarii* are homologous with *mm. intercostales externi* in Lepidosauria and *mm. intercostales externi* and *m. scalenus* combined in Crocodylia. Innervation patterns suggest that a muscle ("*m. iliocostalis capitis*") connecting the atlas rib and occiput in Crocodylia includes contributions from the subvertebral layer and *m. cucullaris* complex, and possibly *m. iliocostalis* as well. The present findings may serve as a basis for revising the currently used avian nomenclature so that it will reflect homologies of muscles with their non-avian counterparts. J. Morphol. 268:986–1020, 2007.

KEY WORDS: Diapsida; Archosauria; Aves; axial musculature; homology; *m. longissimus*; *m. iliocostalis*

The muscle system of the avian neck has been regarded as highly derived among amniotes. Even for avian anatomists, it has been considered as "arduous and time consuming" to dissect (Burton, 1984) because it is "more complicated" than in any other anatomical regions of birds (Kuroda, 1962). Due in part to this complexity, the avian cervical axial muscles have rarely been studied in the context of comparative anatomy since studies by Vallois (1922) and Nishi (1938). This has been also the case with the dorsal (trunk) muscles, although recent work by Organ (2006) started rectifying this trend by assessing homologies of epaxial muscles in this region across extant diapsid clades. The lack of comparative anatomical work has probably led to a historical tendency of using terms specific to Aves, or otherwise adopting mammalian terms, for these muscles in the avian anatomical literature, exemplified by the standardized avian anatomical nomenclature (Vanden Berge, 1979; Vanden Berge and Zweers, 1993). In order to understand the morphology and evolution of the avian cervical and dorsal muscles, however, it is necessary for us to compare them with those of its extant outgroups, most importantly non-avian diapsids (Crocodylia and Lepidosauria: Fig. 1). Homology assessments of these muscles among extant diapsids, therefore, serve as the essential basis for such comparative study. I have previously discussed homologies of muscles belonging to *m. transversospinalis* group (most medial group of the epaxial musculature) among extant diapsids (Tsuihiji, 2005; see also Organ, 2006). In the present paper, homologies of the rest of the epaxial muscles, as well as those of the cervical hypaxial muscles among extant diapsids are discussed, based mainly on detailed dissections of specimens.

MATERIALS AND METHODS

The following specimens were dissected in order to confirm previous published accounts and to obtain new data on muscular anatomy. Most of the examined specimens are in the collections of the Division of Vertebrate Zoology, Peabody Museum of Natural History, Yale University (YPM): *Iguana iguana* (catalog numbers YPM 13325-13329, 13331, 13333, and 13334: 8 captive-bred specimens, snout-vent lengths ranging from 310 to 420 mm); *Varanus exanthematicus* (YPM 13317 and 13318: two captive-bred specimens, snout-vent lengths of 250 and 490 mm,

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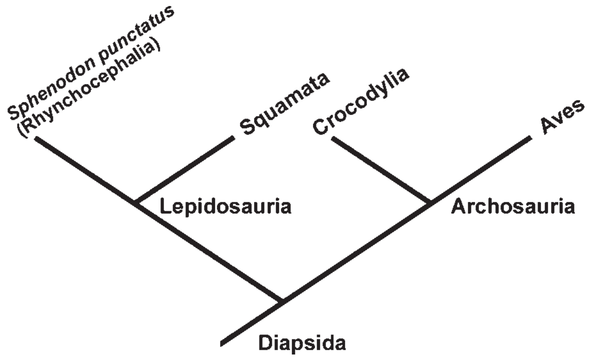

Fig. 1. Clade names employed in the present study with a cladogram depicting phylogenetic relationships among these clades (after Gauthier et al., 1988).

respectively); *Alligator mississippiensis* (YPM 13319-13324: 6 specimens, snout-vent lengths ranging from 260 to 570 mm, obtained from Rockefeller Wildlife Refuge, Louisiana Department of Wildlife and Fisheries); *Struthio camelus* (YPM 101216, 101219, and 101229: three captive-bred specimens, one adult neck with a skull length of 200 mm, and the cervical and dorsal regions of two nearly hatched embryos with skull lengths of 65 and 70 mm, respectively); *Rhea americana* (YPM 101221-101223: three captive-bred specimens, two adult necks with skull lengths of 160 and 170 mm, respectively, and the cervical and dorsal regions of one nearly hatched embryo with a skull length of 70 mm); *Gallus gallus* (YPM 101226 and 101227: two captive-bred adults with skull lengths of 70 and 75 mm, respectively); and *Meleagris gallopavo* (YPM 101229: captive-bred adult, size not measured). In addition, the cervical and dorsal regions of one adult *S. camelus* (Field Museum of Natural History, FMNH uncataloged: captive-bred specimen with a skull length of 220 mm) was examined. *Varanus salvadorii* (YPM 12095; captive specimen, size not measured), *Caiman crocodilus* (YPM 14680; captive specimen with a snout-vent length 400 mm), *Osteolaemus tetraspis* (YPM 14682; specimen wild-caught in Cameroon with a snout-vent length 440 mm), and *Sphenodon punctatus* (California Academy of Sciences, CAS 20888: with a snout-vent length of 250 mm) were also partially dissected. The sex of these specimens was not determined.

The above specimens were dissected with the aid of a binocular dissecting microscope. When necessary, specimens were stained with an iodine and potassium iodide solution as suggested by Bock and Shear (1972), in order to determine the detailed fiber arrangement of muscles. Some of the specimens were also stained with a methylene blue solution to provide better contrast between nerves and other tissues in order to confirm the innervation patterns of some of the axial muscles.

The term “homology” used in the present study corresponds to “primary homology” of de Pinna (1991), i.e., homologies of muscles proposed here are hypotheses based on the criterion of topological correspondence. More specifically, attachment sites on the skeleton and topological relationships to other muscles were used as primary criteria for inferring such homologies. For some of the muscles, innervation patterns by the spinal nerves were also used as another basis for proposing their homologies. In other words, if muscles retain similar origins and/or insertions, as well as similar innervation patterns in some cases, across the examined clades, then I hypothesize that they are homologous muscles. Due to a relatively small number of specimens dissected, I could not examine intraspecific variation of the muscle morphology in each taxon. While such variation does exist in diapsids (e.g., Raikow et al., 1990), it is unlikely to significantly compromise or alter results of the present homology assessments across widely separated clades.

The nomenclature of the avian muscles follows Vanden Berge and Zweers (1993) in the second edition of Nomina Anatomica Avium unless otherwise noted. The nomenclature of the lepidosaurian musculature follows Nishi (1916) for the epaxial musculature and Maurer (1896) for the hypaxial musculature, both of which have been used widely. As Maurer (1896) did not deal with the subvertebral layer of the hypaxial musculature, I follow Evans (1939) for these muscles. Seidel (1978) gave the most detailed and precise description on the epaxial musculature in the presacral region of Crocodylia by using the nomenclature established by Vallois (1922). Therefore, I follow their nomenclature in describing the crocodylian epaxial musculature. The names of the crocodylian hypaxial muscles generally follow Maurer (1896), but those proposed in more recent, detailed anatomical work by Murakami (1988), Murakami et al. (1991), and Cong et al. (1998) are also cited.

Clade names used in the present study are shown in Figure 1. Among these names, how the name “Crocodylia” should be spelled, either as “Crocodylia” with a “y” or “Crocodilia” with an “i,” is a matter of some debate (e.g., Salisbury and Frey, 2001). In the present study, “Crocodylia” or “crocodylian” with a “y” is used in order to emphasize its status as a crown clade or its member, as was done in Brochu (2001).

In this paper, the position of a vertebra throughout the presacral region is counted anteroposteriorly, and is indicated by “V” plus a numeral. In other words, V1 represents the atlas, V2 is the axis, V15 refers to the 15th presacral, and so on.

RESULTS

M. Longissimus Group of Non-Avian Diapsids

Lepidosauria. The *longissimus* muscles in Lepidosauria consist of segmentally arranged tendons and the associated muscle fibers (Figs. 2A and 3A). Nishi (1916) divided *m. longissimus* group in the presacral region in Lepidosauria into *m. longissimus dorsi* and *m. longissimus cervicocapitis*. The former continues to the latter anteriorly without a sharp boundary separating them. The latter muscle inserts on the occipital region of the skull and V1, and consists of muscle fibers arising from the cervical and anterior dorsal vertebrae. In *Varanus varius* and *V. niloticus*, for example, slips of *m. longissimus cervicocapitis* arise from V3 through V12 according to Nishi (1916). Nishi (1916) further divided *m. longissimus cervicocapitis* in Squamata into three parts: *pars articuloparietalis* (which was further divided into two parts, *m. biventer cervicis* and *m. complexus major*), *pars transversalis capitis*, and *pars transversalis cervicis*. The most dorsally lying *pars articuloparietalis* inserts on the parietal while the middle part, *pars transversalis capitis*, inserts on the lateral and ventral edges of the paroccipital process. The ventrally lying *pars transversalis cervicis* inserts on the basal tubera (Nishi, 1916; Tschanz, 1986). In *Sphenodon punctatus*, on the other hand, *pars transversalis capitis* and *pars articuloparietalis* are interwoven and appear to be undifferentiated (Nishi, 1916). In addition to these three parts, Olson (1936) further distinguished *m. longissimus cervicis*, which inserts on the lateral process of the neural arch of V1, as another, separate muscle in the *m. longissimus cervicocapitis* complex. He also renamed

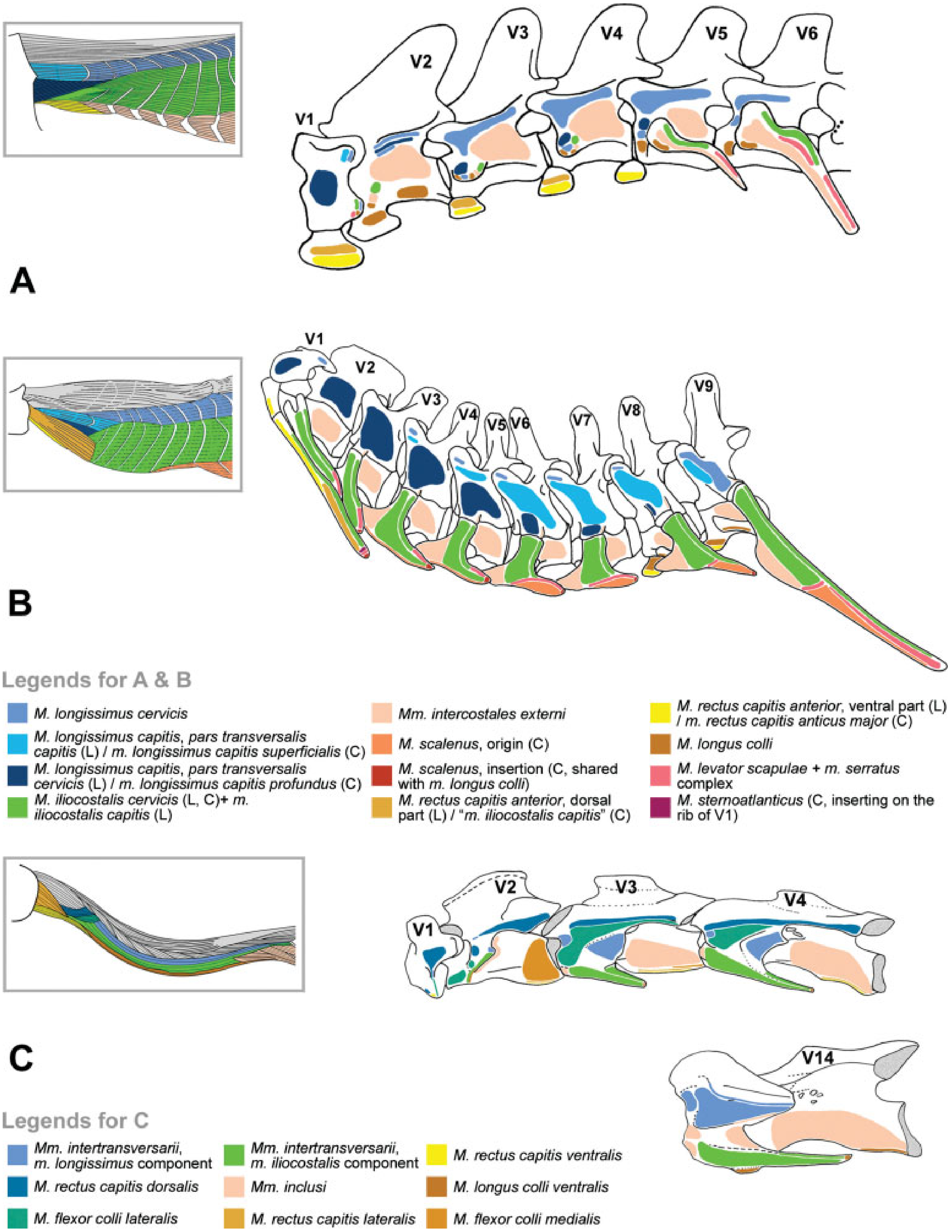

Fig. 2. The *longissimus*, *iliocostalis*, and hypaxial muscles in the anterior presacral region in Lepidosauria (**A**), Crocodylia (**B**), and Aves (**C**) in left lateral view. Left (in gray squares), semi-schematic illustrations of the axial musculature in superficial view, with the *m. transversospinalis* group colored in gray. Modified and redrawn from Nishi (1938, A and B) and Boas (1929, C). Right, detailed sites of attachment of these muscles on the cervical vertebrae in *Iguana iguana* (A), *Alligator mississippiensis* (B, data on the *longissimus* muscles mainly based on Seidel, 1978), and *Struthio camelus* (C), with those of the *serratus* muscles that arise from ribs also shown. Note that "*m. iliocostalis capitis*" (*sensu* Seidel, 1978) in Crocodylia includes contributions from several different muscle groups (see the text for details). C, Crocodylia; L, Lepidosauria.

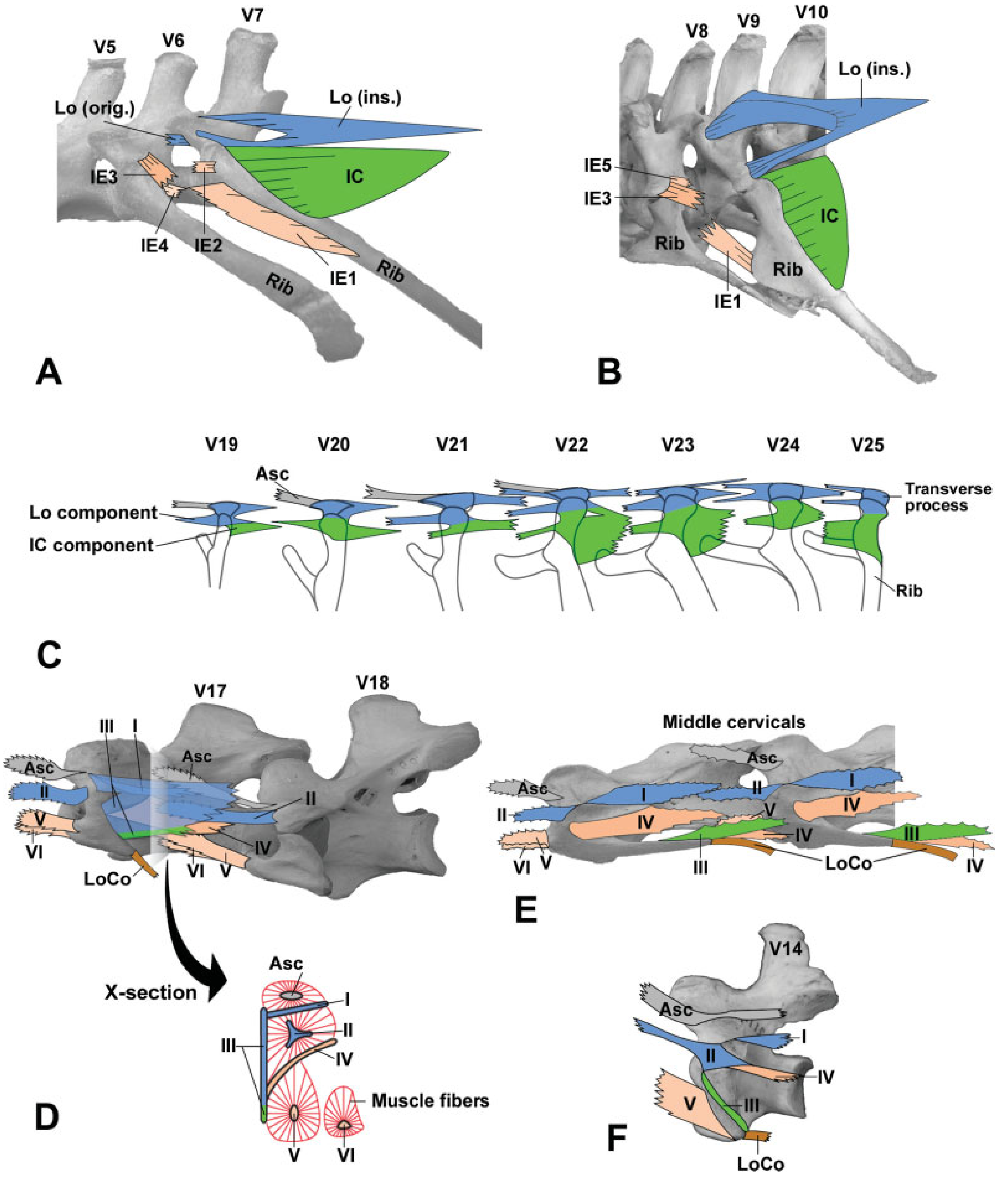

Fig. 3. Semi-schematic illustrations of tendinous systems of the *longissimus*, *iliocostalis*, and hypaxial muscles in diapsids in left lateral view (except for the cross-section in D). **A**, **B**: Tendons of *m. longissimus cervicis*, *m. iliocostalis cervicis*, and *mm. intercostales externi* in the posterior cervical region of *Iguana iguana* (A) and *Alligator mississippiensis* (B). **C**: Tendons of "*m. iliocostalis*" arising from the distal ends of the transverse processes and proximal parts of the ribs of V24 through V19 in *Struthio camelus*. **D**, **E**: Tendons of *mm. intertransversarii* and *mm. inclusi* in *S. camelus*. The segment between V18 and V17 with a cross-section showing how muscle fibers connect these tendons (D), and another segment in the middle cervical region (E). In D, the tendon III is shown translucent so that more medially lying tendons are visible. **F**: Tendons of *mm. intertransversarii* and *mm. inclusi* arising from V14 of *Meleagris gallopavo*. Asc, *m. ascendens cervicalis*; IC, *m. iliocostalis*; IE, *mm. intercostales externi*; ins., insertion; Lo, *m. longissimus*; LoCo, *m. longus colli ventralis*; orig., origin; I-VI, tendons I-VI of *mm. intertransversarii* and *mm. inclusi* as described in the text.

the three parts recognized in Nishi (1916) as *m. articuloparietalis*, *m. transversalis capitis*, and *m. transversalis cervicis*. However, it is important to recognize that Olson (1936) apparently confused the original terminology of Nishi (1916), naming the latter's *pars transversalis cervicis* as "*m. transversalis capitis*," and *pars transversalis capitis* as "*m. transversalis cervicis*," respectively, as has been pointed out by Tschanz (1986). Therefore, I here retain Nishi's (1916) original usage and call these parts inserting on the paroccipital process and basal tubera *m. longissimus capitis*, *pars transversalis capitis* and *pars transversalis cervicis*, respectively. Vallois (1922), on the other hand, divides *m. longissimus* group in the presacral region into *m. longissimus dorsi*, *m. longissimus capitis superficialis*, and *m. longissimus capitis profundus*. His description indicates that *m. longissimus capitis superficialis* and *m. longissimus capitis profundus* correspond to *pars articuloparietalis* and *pars transversalis capitis* of *m. longissimus cervicocapitis* of Nishi (1916), respectively. However, Vallois (1922) apparently failed to recognize *pars transversalis cervicis* inserting on the basal tubera.

As an example of the lepidosaurian *m. longissimus* system, a description of the one in *Iguana iguana* is given here based on studies by Olson (1936) and Tschanz (1986) as well as my dissections. In *I. iguana*, muscle fibers of *m. longissimus* in the dorsal and cervical regions arise in part by tendons from the lateral surfaces of the prezygapophyses (Fig. 3A) and extend anteriorly and slightly laterally. These fibers insert on a series of tendons arising from more anterior vertebrae. In lateral view, each tendon of insertion appears to be triangular with the apex directed posteriorly (Fig. 3A), and stacks with one another with more anterior ones lying more medially. The broader anterior end covers muscle fibers laterally while the posterior end tapers and passes into them posteriorly. The anterior end of the tendon bifurcates into the dorsomedial and ventrolateral branches. The dorsomedial branch wraps around the muscle fibers dorsally and merges with s*eptum intermusculare dorsi* that marks the boundary between the *m. longissimus* group and the medially lying *m. transversospinalis* group. Tendinous fibers of this tendon extend further medially within this septum and attach to the lateral surface of the prezygapophysis. These tendinous fibers also extend further anteriorly and become the tendon of origin of *m. semispinalis* (called D tendon in Tsuihiji, 2005). The ventrolateral branch of the *m. longissimus* tendon is further divided into two parts, lateral and medial. The lateral part is connected with the tendon of *m. iliocostalis* and attaches to the posterior aspect of the proximal part of the rib (Fig. 3A). The medial part extends medially ventral to muscle fibers of *m. longissimus*, and attaches to the lateral side of the neural arch at the base of the prezygapophysis dorsal to the ligament connecting the synapophysis and rib (*ligamentum tuberculi costae* of Nishi, 1916). This series of tendons of *m. longissimus* is present throughout the dorsal and cervical regions with the most anterior one attaching to the dorsal part of the lateral process of the neural arch of V1. This is the most anterior tendon of insertion of *m. longissimus cervicis*. Muscle fibers also arise from the anterolateral aspect of this anterior-most tendon, extend anteriorly, and insert on the distal part and ventral edge of the paroccipital process (Fig. 4A). These fibers comprise *pars transversalis capitis* of *m. longissimus capitis*. Some fibers arising from this tendon also contribute to the lateral part of *pars articuloparietalis*, suggesting that this part does include a *m. longissimus* component contrary to my previous study (Tsuihiji, 2005), in which I proposed that this part belonged exclusively to the *m. transversospinalis* group.

From the anterolateral aspects of the synapophyses of V6 through V3 and lateral surfaces of the neural arches of V2 and V1, another series of fiber bundles of *m. longissimus* arises and extends anteroventrally. The bundles arising from V6 through V2 insert on the lateral process of the neural arch of V1, medial to the insertions of *m. iliocostalis cervicis* and *m. levator scapulae* (Fig. 2A). Those arising from V5 or V4 through V1 insert on the basal tubera together with *m. iliocostalis capitis* (Fig. 4A,B), comprising *pars transversalis cervicis* of *m. longissimus capitis*.

Crocodylia. Vallois (1922) and Seidel (1978) recognized the following muscles in the *m. longissimus* group in the dorsal and cervical regions of *Alligator mississippiensis*: *m. longissimus dorsi*, *mm. intertransversarii dorsales*, *m. longissimus cervicis*, *m. longissimus capitis superficialis*, and *m. longissimus capitis profundus*. The morphology of these muscles in *A. mississippiensis* is described below based on studies by Seidel (1978) and my own dissections, supplemented by other published accounts.

As in Lepidosauria, the basic architecture of the *m. longissimus* group in Crocodylia is a segmental repetition of tendons connected by muscle fibers, as seen in *m longissimus dorsi* and the posterior part of *m longissimus cervicis*. In these muscles, each tendon is typically cone-shaped with the apex directed posteriorly (Seidel, 1978) and passing into muscle fibers (Fig. 3B). The lateral part of the anterior end of the tendon attaches to the posterior edge of the transverse process. The medial part of the anterior end attaches to *septum intermusculare dorsi*, and continues further anteromedially as the tendon of origin of *m. tendinoarticularis*, which is the most lateral part of the *m. transversospinalis* group. Furthermore, the lateral-most part of the anterior end of the tendon of *m. longissimus* also attaches to the thin septum separat-

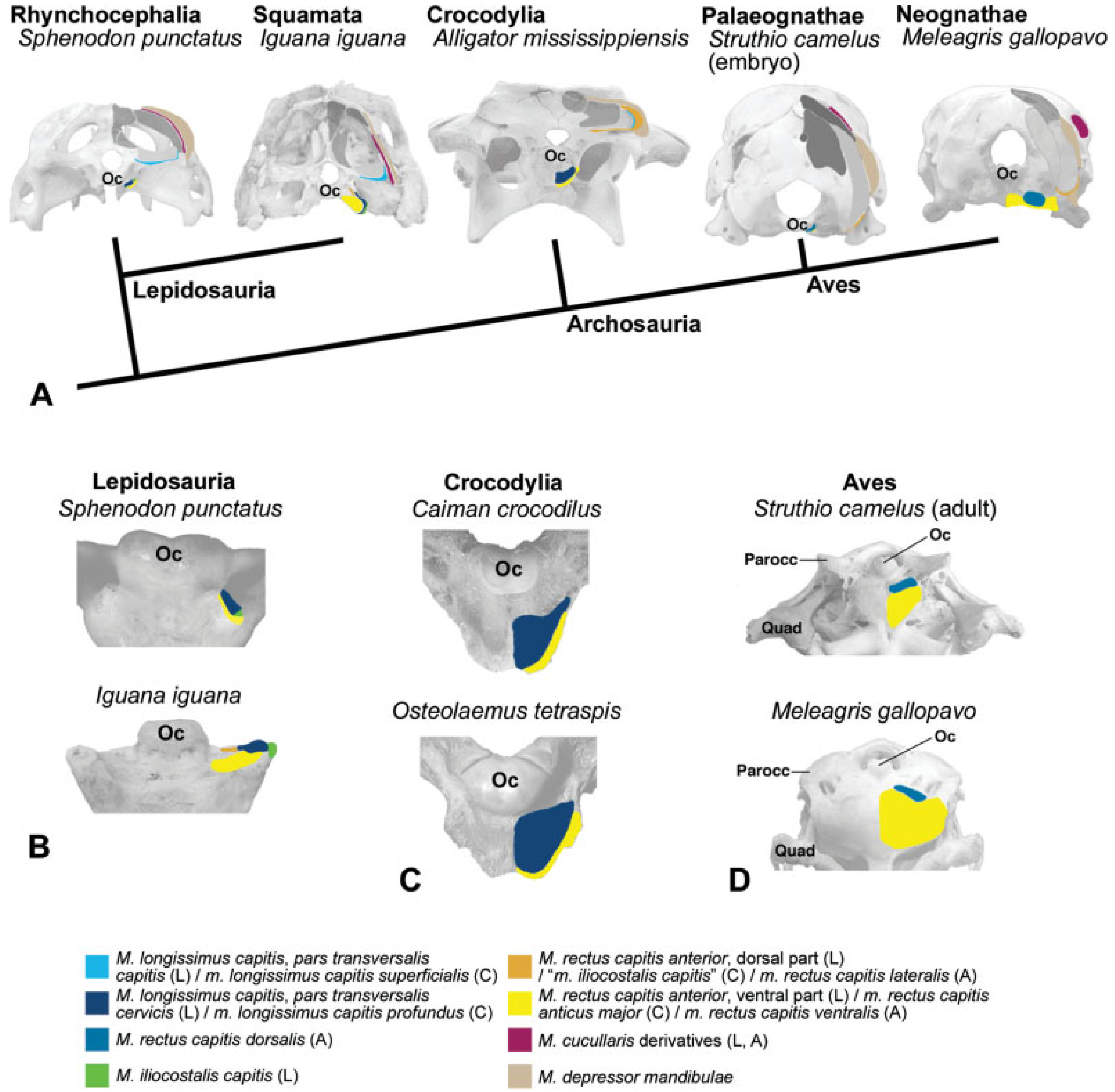

Fig. 4. Attachments of muscles on the occipital region of diapsids (**A**) with details of those on the basal tubera or basitemporal plate (**B**–**D**). Attachments of muscles of the *m. transversospinalis* group are colored in gray in A. A and C in posterior view, and B and D in ventral view. Note that "*m. iliocostalis capitis*" (*sensu* Seidel, 1978) in Crocodylia includes contributions from several different muscle groups including the *m. cucullaris* component (see the text for details). A, Aves; C, Crocodylia; L, Lepidosauria; Oc, occipital condyle; Parocc, paroccipital process; Quad, quadrate.

ing this muscle from *m. iliocostalis* (Seidel, 1978; Murakami et al., 1991). Muscle fibers connect two successive tendons of *m. longissimus*, arising from the deep surface of one tendon and inserting on the superficial surface of the next anterior one (Seidel, 1978). Seidel (1978) also described small bundles originating from *septum intermusculare dorsi* that penetrate one tendon and insert on the next anterior one. However, I could not recognize such fibers in my dissections. Muscle fibers also arise directly from the dorsal surface of the transverse process and insert on the tendon arising from the next anterior transverse process.

In addition to *m. longissimus dorsi*, studies by Vallois (1922) and Seidel (1978) recognized another series of muscle, *mm. intertransversarii dorsales*, as a part of the *m. longissimus* group in the dorsal region. In these studies, each slip of *mm. intertransversarii dorsales* was described as consisting of muscle fibers that connect two successive transverse processes, arising from the anterior edge of one transverse process and inserting on the posterior edge of the next anterior one. In my dissections, however, muscle fibers corresponding to *mm. intertransversarii dorsales* are continuous with those of *m. longissimus dorsi* that connect successive tendons. Murakami et al. (1991) also described that there is no fascia present separating these two muscles. Therefore, *mm. intertransversarii dorsales* are considered here simply as deep fibers of *m. longissimus dorsi*. In contrast, Murakami et al. (1991) argued that *mm. intertransversarii dorsales* represent a part of *m. iliocostalis dorsi* because the former series of muscles is innervated by a twig arising from the nerve that supplies the latter muscle, while Cong et al. (1998) described it as being innervated by the ventral ramus of the spinal nerve and accordingly considered it as a part of the hypaxial musculature.

The segmentally arranged *m. longissimus dorsi* continues into the posterior cervical region, where the muscle is now called *m. longissimus cervicis*. In the cervical region, however, the middle and ventral parts of this muscle system differentiate into two separate muscles, *m. longissimus capitis superficialis* and *m. longissimus capitis profundus* (Fig. 2B). Cone-shaped tendons seen in the dorsal region continue to be present throughout the cervical column, albeit being rather feebly developed anteriorly, contrary to the description by Seidel (1978) that at the level of V5 these tendons are reduced to a series of mere tendinous arches that corresponds to the dorsomedial parts of the cone-shaped tendons. The ventral part of each tendon attaches to the distal part of the posterior edge of the transverse process together with the tendon of *m. iliocostalis cervicis* while the dorsal part attaches to the posterolateral aspect of the prezygapophysis (Fig. 2B). The most anterior one of these tendons arises from V1, and its dorsal part that attaches to the lateral surface of the neural arch of V1 just below its postzygapophysis serves as the tendon of insertion of *m. longissimus cervicis* described below. These tendons cut through the muscular mass of these three *longissimus* muscles, making the segmental arrangement of this muscle group still recognizable.

Among these three muscles in the cervical region, *m. longissimus cervicis* lies most dorsally. Seidel (1978) described this muscle in *Alligator mississippiensis* as arising from the prezygapophyses of V5 through V7 as well as from the dorsomedial parts of the tendons attaching to the prezygapophyses of V4 through V7 and inserting on V1 by the tendon mentioned above. This description, however, was based on the notion that crocodylians have only seven cervical vertebrae based on the anterior extent of the coelom while it is usually considered that they have nine cervical vertebrae based on the position of the first rib articulating with the sternum (e.g., Hoffstetter and Gasc, 1969). Here I adopt the latter definition of the cervical vertebrae, and therefore regard V8 and V9 as the two most posterior cervical vertebrae. Muscle fibers and segmental tendons of *m. longissimus* arise from these vertebrae as in the more posterior region, and pass into *m. longissimus cervicis* as defined by Seidel (1978) without a break. Accordingly, I regard these muscle fibers and tendons arising from V8 and V9 as additional origins of *mm. longissimus cervicis* in the present study (Fig. 2B).

Muscle fibers of *m. longissimus capitis superficialis*, which is the middle part of the *m. longissimus* group in the cervical region, arise from the lateral aspects of the neural arches and extend anterolaterally. According to Seidel (1978), the origins of these fibers are V8 through V5 in *Alligator mississippiensis*. In my dissection, however, I found that the origins of this muscle include V4 and V9 as well (Fig. 2B). Although these fibers comprise a fusiform muscle as a whole, I found that the tendinous sheets cut it through segmentally as mentioned above. The muscle inserts mainly on the distal tip of the paroccipital process by a tendon (Fig. 4A).

The most ventral *longissimus* muscle in the cervical region, *m. longissimus capitis profundus*, arises mainly from the lateral surfaces of the neural arches ventral to *septum intermusculare dorsi* and/or transverse processes. Frey (1988a) described slips of this muscle as arising from V7 through V1, while Seidel (1978) recognized small contributions from the transverse processes of V8 and V9 as well. I confirmed that the origins of this muscle extend at least as far posteriorly as to the transverse process of V8 in specimens that I dissected (Fig. 2B). Muscle fibers extend anteroventrally and slightly laterally from their origins, and insert mainly on the smooth depression of the basal tubera (Fig. 4A,C). A strong tendon develops laterally, wraps around the fleshy insertion of the muscle, and inserts on the proximal edge of the rugose margin of the basal tubera. Some muscle fibers also insert on the medial surface of this tendon.

Homologies of the *longissimus* muscles between Lepidosauria and Crocodylia. Between Lepidosauria and Crocodylia, the morphology of muscles belonging to the *m. longissimus* group is fairly conserved, allowing a robust inference on their homologies. Although *m. longissimus dorsi* (including *mm. intertransversarii dorsales*) in Crocodylia is much more strongly developed than the muscle of the same name in Lepidosauria, their attachment sites are very similar between these clades if we take the great expansion of the diapophysis (transverse process) in the former into the consideration. The homology of this muscle between these clades, therefore, is readily recognized. The anterior continuation of *m. longissimus dorsi*, *m. longissimus cervicis*, terminates on V1 in both Lepidosauria and Crocodylia, and can similarly be considered homologous between these two clades.

The lepidosaurian *m. longissimus capitis*, *pars transversalis capitis* can be homologized with the crocodylian *m. longissimus capitis superficialis* based on the similar sites of insertion on the paroccipital process of the skull (Fig. 4A). Similarly, both the lepidosaurian *m. longissimus capitis*, *pars transversalis cervicis* and the crocodylian *m. longissimus capitis profundus* extend anteroventrally to insert on the basal tubera, and are accordingly considered homologous with each other.

As mentioned above, the lepidosaurian *m. longissimus capitis*, *pars articuloparietalis* does seem to include the *m. longissimus* component as argued by Nishi (1916) but contrary to Tsuihiji (2005). However, it is still likely that this part also includes the *m. transversospinalis* component. In addition to morphological evidence proposed by Tsuihiji (2005), the innervation patterns of this part described by Nishi (1916) also support this hypothesis. In *Varanus*, Nishi (1916) described that, while the lateral part of *pars articuloparietalis* (*m. complexus major*) is innervated by lateral branches of dorsal rami of spinal nerves as is the rest of *m. longissimus cervicocapitis*, the medial part of *pars articuloparietalis* (*m. biventer cervicis*) is innervated by a nerve branch arising from *plexus cervicalis dorsalis*. This nerve plexus is formed through fusion of medial branches of dorsal rami of the first and second spinal nerves as well as the dorsal branch of the hypoglossal nerve, and gives rise to nerve branches supplying *m. spinalis capitis* and a part of *m. rectus capitis posterior*, both of which belong to the *m. transversospinalis* group, in addition to the branch supplying the medial part of *pars articuloparietalis*. It is generally considered that in Lepidosauria the *m. transversospinalis* group is innervated by the medial branch of the dorsal ramus of the spinal nerve while *m. longissimus* group is innervated by the lateral branch of the dorsal ramus (e.g., Nishi, 1916; Gasc, 1981). Therefore, this observation by Nishi (1916) supports the hypothesis that the medial part of *pars articuloparietalis* belongs to the *m. transversospinalis* group. Tsuihiji (2005) homologized the lepidosaurian *pars articuloparietalis* with the avian *m. complexus* and the lateral part of the crocodylian *m. transversospinalis capitis*. If the above argument on the former lepidosaurian muscle holds true, it then follows that the latter crocodylian and avian muscles may also contain the *m. longissimus* component, in addition to the *m. transversospinalis* component as argued by Tsuihiji (2005).

M. Iliocostalis Group in Non-Avian Diapsids

Lepidosauria. In the presacral region of Lepidosauria, the following three muscles are recognized in the *m. iliocostalis* group: *m. iliocostalis dorsi*, *m. iliocostalis cervicis*, and *m. iliocostalis capitis* (Nishi, 1916; Olson, 1936; Tschanz, 1986). This distinction is based on their sites of insertion, whether they are on the dorsal ribs, cervical ribs, or occiput (Tschanz, 1986), and these muscles continue into one another without a sharp boundary.

In *Iguana iguana* (e.g., YPM 13334), each tendon of *m. iliocostalis dorsi* in the dorsal region and *m. iliocostalis cervicis* in the posterior cervical region arises from the posterodorsal edge of the proximal part of each rib and extends posterolaterally (Fig. 3A). The dorsomedial edge of this tendon merges with the ventrolateral branch of the *m. longissimus* tendon. Muscle fibers of these *m. iliocostalis* connect two successive tendons, arising from the anterior/lateral surface of one tendon and inserting on the posterior/medial surface of the next anterior one. Some fibers also arise from the lateral surface of the ventrolateral branch of the tendon of *m. longissimus* (Tschanz, 1986). In the *Varanus salvadorii* (YPM 12095) and *V. exanthematicus* (YPM 13318) specimens that I dissected, on the other hand, muscle fibers of *m. iliocostalis dorsi* and *m. iliocostalis cervicis* arise from the lateral surface of the tendon of *m. longissimus* that attaches to the lateral surface of the prezygapophysis as well as to the posterodorsal edge of the proximal part of the rib. These fibers are much longer than those in *I. iguana*, extend anteroventrally, and insert medially on an anteroposteriorly long tendon of *m. iliocostalis* that arises from the proximal part of the rib. Gasc (1981) misidentified this *m. iliocostalis* as *m. longissimus* in varanids, and then mistakenly described a hypaxial muscle (probably a part of *mm. intercostales externi*) as *m. iliocostalis* (fig. 15 in Gasc, 1981). This misidentification led him to describe that *m. iliocostalis* of varanids as unique among lepidosaurs “in that differentiation is transverse rather than longitudinal,” and “each bundle covers the ribs” (Gasc, 1981, p. 383). My observation indicates that the arrangement of this muscle in *Varanus* is longitudinal, as in other lepidosaurs, with each slip greatly elongated anteroposteriorly, as Nishi (1916) described previously.

In the middle to anterior cervical regions, ribs become shorter and eventually disappear. Following this change, the origin of the tendon of *m. iliocostalis cervicis* shifts from the rib to the synapophysis (Fig. 2A). In the *Iguana iguana* specimens that I dissected, the segmental arrangement of the tendons is maintained as far anteriorly as V5. That is, each tendon of *m. iliocostalis cervicis* attaches to each rib up to this point. The next anterior tendon, however, attaches to the synapophyses of both V4 and V3. Similarly, the next anterior one, which is the most anterior tendon of this muscle, attaches to the synapophysis of V2 as well as to the lateral process on the neural arch of V1. This tendon shares these attachments with *m. levator scapulae*.

The last *iliocostalis* muscle, *m. iliocostalis capitis*, consists of muscle fibers that insert on the lateral edge of the basal tubera by a strong tendon (Fig. 4A,B). In *Iguana iguana*, fibers of this muscle arise from the lateral surface of the fascia separating *m. iliocostalis* and *m. longissimus*, anteromedial to the most anterior tendon of *m. iliocostalis cervicis*.

Crocodylia. The same three muscles as recognized in Lepidosauria were described in the crocodylian *m. iliocostalis* group in the presacral region by Seidel (1978) while Vallois (1922) and Frey (1988a) did not recognize a muscle corresponding to the lepidosaurian *m. iliocostalis capitis*.

As in Lepidosauria, *m. iliocostalis dorsi* and *m. iliocostalis cervicis* in Crocodylia consist of segmental tendons arising from ribs and muscle fibers connecting them (Figs. 2B and 3B), with the most anterior tendon of *m. iliocostalis cervicis* arising from the dorsal edge of the rib of V1. In *Alligator mississippiensis*, each tendon arises from the posterior edge of the rib (vertebral segment in the dorsal region) and extends posterolaterally (Fig. 3B). The dorsomedial end of each tendon attaches to the costovertebral articulation or distal end of the transverse process together with the most ventrolateral part of the tendon of *m. longissimus*. Muscle fibers arise from the anterior surface of the tendon and the lateral surface of the shaft of the rib, and insert on the posterior surface of the next anterior tendon. In the dorsal region, some fibers of *m. iliocostalis dorsi* extend into the space between the adjacent transverse processes, arising from the anterior edge of one transverse process and inserting on the posterior edge of the next anterior one. In specimens of *A. mississippiensis* that I dissected (e.g., YPM 13323), a thin fascia separates these fibers from the dorsally lying intertransversal part of *m. longissimus dorsi*. This fascia disappears in the cervical region, where muscle fibers of the *m. longissimus* and *m. iliocostalis* groups are not clearly separated from each other.

The morphology of *m. iliocostalis dorsi* in *Caiman crocodilus* described by Murakami (1988) and Murakami et al. (1991) is generally the same as that in *Alligator mississippiensis*. These studies, however, found that the ventromedial portion of this muscle in *C. crocodilus* is innervated by branches of the intercostal nerve, instead of the iliocostalis nerve that innervates the rest of this muscle, and separated the former as the ventral part of *m. iliocostalis*. The distinction of these two parts was based solely on these innervation patterns, and these studies otherwise described no clear boundary separating them in terms of the muscular morphology. I confirmed the absence of such a morphological boundary within *m. iliocostalis dorsi* of *A. mississippiensis* as well. I did not examine the detailed innervation patterns in my dissections, and thus it is yet to be determined if *A. mississippiensis* has the separately innervated ventral part of *m. iliocostalis* as in *C. crocodilus.*

In front of the most anterior slip of *m. iliocostalis cervicis*, Seidel (1978) recognized "*m. iliocostalis capitis*" as an *iliocostalis* muscle that connects the rib of V1 with the occiput. In *Alligator mississippiensis*, muscle fibers of this muscle arise from the lateral surface of the posterior half of the rib of V1 and the tendon arising from its dorsal edge (Seidel, 1978; Fig. 2B). This muscle wraps around the distal and ventral edges of the paroccipital process and inserts on them by fleshy fibers and a tendon (Fig. 4A).

Homologies of the *iliocostalis* muscles between Lepidosauria and Crocodylia. The morphology of *m. iliocostalis dorsi* and *m. iliocostalis cervicis* is basically the same between Lepidosauria and Crocodylia, and accordingly their homologies between these two clades are well-established. The homology of *m. iliocostalis capitis* is more problematic. While this muscle in Lepidosauria inserts on the basal tubera, there is no *iliocostalis* muscle inserting on the latter structure in Crocodylia (Fig. 4A–C). Instead, Seidel's (1978) "*m. iliocostalis capitis*" inserts on the paroccipital process. Fürbringer (1876), however, described this crocodylian muscle as *m. atlantimastoideus* and regarded it as a part of the *m. cucullaris* complex. Cong et al. (1998), on the other hand, considered this muscle as a merged slip of *m. episternomastoideus* (= *m. sternomastoideus*, a part of the *m. cucullaris* complex) and *m. rectus capitis lateralis* (a part of *m. longus capitis*). The homology of this muscle will be discussed below in detail with an emphasis on its innervation patterns, which suggest that this is actually a composite of muscles from several different muscle groups.

M. Longissimus and *M. Iliocostalis* in Aves

It has not been clearly determined which parts of the epaxial musculature in the dorsal and cervical regions in Aves belong to the *m. longissimus* and *m. iliocostalis* groups. Vallois (1922) proposed that *m. ascendens thoracicus*, superficial part of *m. longus colli dorsalis, pars thoracica*, and muscles connecting two successive transverse processes (his *mm. intertransversarii dorsi*) in the dorsal region, as well as *mm. intertransversarii* and *m. ascendens cervicalis* in the cervical region, comprise the *m. longissimus* group. In addition, *m. complexus*, *m. flexor colli lateralis*, and *m. rectus capitis dorsalis* (his *m. longissimus capitis*, part of *mm. intertransversarii cervicis*, and *m. transversarius capitis*, respectively) were regarded as muscles of the *m. longissimus* group differentiated in the anterior cervical region. The *m. iliocostalis* group, on the other hand, was proposed as consisting of a muscle arising from the anterior edge of the ilium and inserting on vertebral segments of the middle and posterior ribs in the dorsal region, but was considered as absent in the cervical region by Vallois (1922).

Nishi (1938), while considering the *m. iliocostalis* group in the dorsal region (his *m. iliocostalis dorsi*) as consisting of the same muscle as hypothesized by Vallois (1922), identified a muscle that arises from the ilium and the transverse processes and inserts on the transverse processes of more anterior vertebrae in the dorsal region as belonging to the *m. longissimus* group (his *m. longissimus dorsi*). In the cervical region, he considered *mm. intertransversarii* as consisting of both *m. iliocostalis* and *m. longissimus*. This hypothesis was based mainly on the innervation patterns of these muscles by the spinal nerves. According to Nishi (1938), the lateral branch of the dorsal ramus of the spinal nerve supplies *mm. intertransversarii* while the cutaneous branch arising from this lateral branch penetrates this series of muscles, suggesting that the parts of *mm. intertransversarii* lying dorsal and ventral to this cutaneous branch represent the *m. longissimus* and *m. iliocostalis* groups, respectively. As Vallois (1922), Nishi (1938) regarded *m. complexus*, *m. flexor colli lateralis*, and *m. rectus capitis dorsalis* (his *m. longissimus capitis superficialis*, *m. transversalis cervicis*, and *m. transversalis capitis*, respectively) as muscles of the *m. longissimus* group differentiated in the anterior cervical region.

More recently, Zusi and Bentz (1984) and Zusi (1985) included both *m. iliocostalis dorsi* and *m. longissimus dorsi sensu* Nishi (1938) in their "*m. iliocostalis*." Zusi and Bentz (1984) and Zusi (1985) also suggested that *mm. intertransversarii* continue directly from "*m. iliocostalis*" in the dorsal region, implying that the latter series of muscles is serially homologous with the former.

In this section, the morphology of the avian "*m. iliocostalis*" and *mm. intertransversarii* are examined in detail. A particular emphasis is on the morphology of their tendinous systems, which serve as a basis for homology assessments of these muscles.

"*M. iliocostalis*" in the dorsal region. Zusi and Bentz (1984) and Zusi (1985) described "*m. iliocostalis*" as arising from the anterior margin of the ilium and the lateral parts of the transverse processes of the dorsal vertebrae, and inserting on the lateral parts of the transverse processes and adjacent posterodorsal edges of the vertebral segments of the ribs of the more anterior dorsal vertebrae. Zusi (1985) described a complex system of tendons and its associated muscle fibers comprising this muscle in *Atrichornis clamosus* as follows. A series of flattened tendons of origin arises from the anterolateral tips of the transverse processes and anterior edge of the ilium. Additionally, a long tendon of origin shared by *m. ascendens thoracicus* also arises from the ilium. Fibers arising from these tendons insert on a series of tendons of insertion that arises from the posterolateral edges of the transverse processes. Muscle fibers also insert on the dorsolateral surfaces of the ribs directly.

Based on innervation patterns by the spinal nerve in *Struthio camelus*, Tsuihiji (2005) supports the hypothesis of Nishi (1938) that "*m. iliocostalis*" (*sensu* Zusi and Bentz, 1984; Zusi, 1985) includes the homologs of both *m. iliocostalis* and *m. longissimus*. This hypothesis is further examined here based on the morphology of "*m. iliocostalis*" in an adult *S. camelus* (FMNH uncataloged). In this bird, "*m. iliocostalis*" arises most posteriorly from the anterior margin of the ilium as a dorsoventrally broad muscle sheet. Additionally, fibers arise from three series of tendons of origin that arise from the lateral edges of the transverse processes as well as the adjacent, lateral surfaces of the proximal parts of the ribs and extend anteriorly (Fig. 3C). The first series arises from the anterior aspects of the lateral edges of the transverse processes of V25 through V22. The one arising from V22 is dorsally continuous with the tendon of origin of *m. ascendens thoracicus*. The second series of tendons arises from the proximal parts of the vertebral segments of ribs. Anteriorly, this second series of tendons continues to be present into the cervical region. This is the tendon II of *mm. intertransversarii* described below (Fig. 3D,E). The third, ventral series of tendons of origin similarly arises from the proximal parts of the vertebral segments of ribs, but are apparently absent on V20 and more anteriorly.

The insertions of "*m. iliocostalis*" are on the posterior aspects and lateral edges of the transverse processes and proximal parts of the vertebral segments of the ribs by fleshy fibers as well as by two series of tendons of insertion (Fig. 3C). The first series of tendons arises from the posterior edges of the transverse processes, and continues anteriorly as the tendon I of *mm. intertransversarii* described below (Fig. 3D,E). The second series of tendons of insertion arises from the posterior edges of the proximal parts of the vertebral segments of the ribs, and medially merges with the tendon of insertion of *mm. levatores costarum*. Each tendon of this second series arising from V22 through V17 has a shallow, anterolaterally facing pocket to which muscle fibers arising from the next anterior tendon of the same series attach. This series of tendons continues anteriorly as the tendon III of *mm. intertransversarii* (Fig. 3D,E). Muscle fibers arising from the most dorsal series of tendons of origin mainly occupy the space between the successive transverse processes, inserting mainly on the medial surface of the dorsal tendon of insertion arising from the next transverse process as well as on the posterior edge of this transverse process itself. Muscle fibers arising from the third, ventral series of tendons of origin attach mainly to the distal and medical aspects of the ventral series of tendons of insertion while those arising from the second, middle series of tendons of origin insert on the both dorsal and ventral series of tendons of insertion and on the lateral aspects of the ribs directly.

The morphology of "*m. iliocostalis*" in Aves described above, especially that in the posterior dorsal region, is quite unique among diapsids and at first glance does not appear to be readily comparable to that of *m. longissimus, m. iliocostalis*, or both combined in Lepidosauria or Crocodylia. In the anterior dorsal region where there are fewer series of tendons present than in the posterior dorsal region, however, this avian muscle shows some similarities with *m. longissimus* and *m. iliocostalis* in non-avian diapsids. First, the ventral series of tendons of insertion of the avian "*m. iliocostalis*" arises from the proximal part of the rib (Fig. 3C), as do the *m. iliocostalis* tendons in non-avian diapsids (Fig. 3A,B). Furthermore, the medial and lateral surfaces of successive tendons of the former series in Aves are connected by muscle fibers, which is also a characteristic seen in the non-avian *m. iliocostalis*. The dorsal half of the avian "*m. iliocostalis*," on the other hand, arises by a series of tendons that extends anteriorly and inserts on the dorsal and ventral series of tendons that extend posteriorly (Fig. 3C). As described above, *m. longissimus* in non-avian diapsids consists of muscle fibers that extend anteriorly and insert on posteriorly extending tendons (Fig. 3A,B). Although the dorsal and ventral tendons of insertion of the avian "*m. iliocostalis*" are separate, the latter expands dorsoventrally in the posterior cervical region to fuse with the former, together forming a series of tendons (tendons I plus III of *mm. intertransversarii*: Fig. 3D) that is morphologically similar to the tendons of insertion of the lepidosaurian *m. longissimus*. Based on these comparisons, I propose here that the dorsal and ventral parts of the avian "*m. iliocostalis*" represent homologs of *m. longissimus* and *m. iliocostalis* in non-avian diapsids, respectively, as suggested by the innervation pattern in Tsuihiji (2005).

***Mm. intertransversarii* in the cervical region.** The avian *mm. intertransversarii* form the principal lateral musculature of the neck (Fig. 2C), and connect mainly the transverse processes and ribs of two successive vertebrae (e.g., Zusi and Storer, 1969). As mentioned above, this series of muscles is the cervical continuation, or serial homolog, of "*m. iliocostalis*" in the dorsal region (Zusi and Bentz, 1984; Zusi, 1985). Each segment of *mm. intertransversarii* is often described as multipennate, consisting of complexly interdigitating tendons and associated muscle fibers. For example, Landolt and Zweers (1985) described fibers of this series of muscles in *Anas platyrhynchos* as arising from the ventral surface of *aponeurosis transversa* and several other tendons that extend anteriorly from processes on the anterior aspect of the transverse process. These fibers insert on surfaces of posteriorly extending tendons that arise from the transverse process of the next anterior vertebra. Muscle fibers also insert directly on the dorsal surface of the rib as well as on the tendon of insertion of *m. longus colli ventralis*. Medial to these tendons and muscle fibers lies another series of muscle slips called *mm. inclusi*, although it is sometimes regarded merely as a part of *mm. intertransversarii* (e.g., Zusi and Storer, 1969). According to Landolt and Zweers (1985), there are three layers present in each segment of *mm. inclusi* connecting two adjacent vertebrae in *A. platyrhynchos*. There are three tendons of origin that arise from the anterior process of the rib and anterior aspect of the transverse process and extend anteriorly. Muscle fibers of the most lateral layer insert on the lateral aspect of the neural arch. Fibers of two more medial layers insert on the inner surface of the vertebrocostal canal and the ventral surface of the centrum.

I examined the morphology of *mm. intertransversarii* in the adult *Struthio camelus*, one specimen of the articulated trunk and neck (FMNH uncataloged) and two necks (YPM 101216 and 101217). Because *mm. inclusi* and *mm. intertransversarii* together comprise a multipennate muscle system, the former series of muscles is also described here. In describing these muscles, I emphasize the inter-relationships and morphology of their tendons as Zusi and Storer (1969) did for their description on *Podilymbus*. Unlike Zusi and Storer (1969), however, I designate individual tendon by number in the following description.

The transition from "*m. iliocostalis*" in the dorsal region to *mm. intertransversarii* in the cervical region is rather gradual, and the boundary between these two nominal muscles is somewhat arbitrarily determined. As described above, tendons of *mm. intertransversarii* continue from tendons of "*m. iliocostalis*." In other words, the former are serially homologous with the latter. These muscles lie ventrolateral to *m. ascendens thoracicus* in the dorsal region and *m. ascendens cervicalis* in the cervical region. In the posterior cervical region, the tendon of origin of *m. ascendens cervicalis* arises from the anterior edge of the transverse process (Fig. 3D). Muscle fibers that arise from the ventral surface of this tendon extend anteroventrally to insert on the dorsal surface of the transverse process of the next anterior vertebra, as well as on the dorsal surface of a rather broad, horizontal tendon (tendon I) of *mm. intertransversarii* extending posteriorly from its posterior edge (Fig. 3D). In turn, fibers arising ventrally and distally from the tendon I extend posteroventrally to connect this tendon with the dorsal aspect of the next ventral tendon (tendon II) arising from the next posterior vertebra, as well as to attach to the shallow depression on the anterior aspect of the transverse process between the attachments of tendon of *m. ascendens cervicalis* and tendon II on this vertebra.

The tendon II arises from the lateral edge of the transverse process and extends anteriorly below the tendon I. By muscle fibers, the tendon II is connected with three tendons, here designated as the tendons I (described above), III, and IV, that arise from the next anterior vertebra (Fig. 3D). The tendon III extends posteriorly from a moundlike prominence on the lateral edge of the transverse process as well as from the proximal part of the dorsal edge of the rib. The tendon IV, on the other hand, extends posteriorly from a crest on the transverse process (Fig. 3D). The tendon IV is serially homologous with the tendon of insertion of *mm. levatores costarum* in the dorsal region, and is laterally continuous with the ventral part of the tendon III. Muscle fibers arising from the tendon II attach to the ventral surface of the tendon I, medial surface of the tendon III, and dorsal/lateral surface of the tendon IV (Fig. 3D), as well as to a depression between ridges of the origins of the tendons I and IV on the transverse process.

In addition to those attaching to the tendon II, muscle fibers extend posteriorly from the tendon III and attach to an anterolaterally facing pocket on the next posterior tendon III in the most posterior cervical regions. More anteriorly, however, this pocket disappears while this tendon becomes wider dorsoventrally and is fused with the tendon I medially. Some fibers arising posteriorly from the tendon III also attach to the lateral and ventrolateral surfaces of the next posterior rib. Muscle fibers extending posteriorly from the tendon IV attach to the anterolateral aspect of the tubercular process of the same rib.

Ventral to the tendon II lies another tendon, here called the tendon V, that arises from the anterior aspect of the rib. This tendon extends anteriorly ventromedial to the tendon IV (Fig. 3D). In addition to attaching to the internal aspect of the latter tendon, muscle fibers arising from the tendon V insert on the dorsal edge and medial surface of the fused rib. The ventral ramus of the spinal nerve and the vertebral artery and vein (*arteria* and *vena vertebralis ascendens* of Baumel, 1993) extend ventrally medial to the tendon V and the associated fibers (Landolt and Zweers, 1985). Medial to these nerve and vessels extends anteriorly another tendon (tendon VI) that arises from the ventral aspect of the anterior end of the rib. Muscle fibers arising from this tendon insert on the ventral and lateral aspects of the centrum, lateral aspect of the carotid process, and ventral aspect of the capitular process of the rib of the next anterior vertebra. The tendons IV, V, and VI and their associated muscle fibers comprise muscle slips of *mm. inclusi*.

The general topological relationship among these tendons remains similar in the middle and anterior cervical regions although their morphology changes gradually anteriorly. Starting at around V16, the tendon III elongates longitudinally and its origin on the rib is shifted distally so that it become fused with the tendon of insertion of *m. longus colli ventralis* that attaches to the tip of the rib. At the same time, the dorsal half of the tendon III becomes very thin, and an opening appears between the dorsal and ventral halves of this tendon on its anterior part. A small amount of muscle fibers arising posteriorly from the tendon III still attach to the anteroventral part of the next posterior tendon III. At the same time, some muscle fibers arising from the tendon II start extending anteriorly through the opening in the tendon III of the next anterior vertebra, inserting on the medial surface of the tendon III of the second vertebra anterior to the origin. In other words, these fibers arising from the tendon II skip one segment and insert on the second tendon III anterior to the origin.

The tendon IV also elongates longitudinally, and its ventral (posterior) part becomes separated from the rest of this tendon, attaching to the rib with the ventral part of the tendon III (Fig. 3E). Fibers arising medially and distally from this ventral part of the tendon IV attach to the almost entire lateral and ventrolateral surfaces of the next posterior rib as well as to the lateral surface of the next posterior tendon III or IV. In addition, some muscle fibers arising from the tendon V extend anteriorly ventral to the main, dorsal part of the tendon IV of the next anterior vertebra and insert on the ventral part of the tendon IV of the second anterior vertebra.

At around V12, the dorsal half of the tendon III disappears (Fig. 3E). Its ventral half, however, continues arising from the same origin as that in the more posterior region. From this level and more anteriorly, muscle fibers arising from each tendon II insert mainly on the tendon III that arises from the second or third vertebra anterior to each origin. For example, muscle fibers arising from the tendon II originating from V8, as well as those arising from the lateral surface of the prezygapophysis adjacent to the origin of this tendon, insert mainly on the tendon III arising from V6 and also on the one arising from V5.

The tendon III arising from V2 is different from the more posterior tendons III in that its origin occupies the posteroventral edge of the fused rib (*ansa costotransversaria* of Baumel and Witmer, 1993) as well as the adjacent ventrolateral aspect of the centrum of V2. On this tendon III insert muscle fibers arising from the tendons II originating from V5 and V6. Muscle fibers arising from the ventrolateral aspect of the rib of V3 and anterior part of the rib of V4 also attach to this tendon III. The tendon III arising from V1 serves as the tendon of insertion of *m. flexor colli lateralis* described below.

The tendons I and their associated muscle fibers are also present throughout the cervical region, and mainly connect successive vertebrae. The most anterior slip of this series connects the dorsal part of *ansa costotransversaria* of V2 and that of V1.

***Mm. intertransversarii* derivatives in the anterior cervical region.** My dissection of *Struthio camelus* suggests that *m. flexor colli lateralis* and *m. rectus capitis dorsalis* lying on the lateral aspect of the anterior cervical region (Fig. 2C) are considered as derivatives, or serial homologs, of *mm. intertransversarii* because the former muscles share the same (serially homologous) tendons and sites of origin and/or insertion with the latter series of muscles. The first one, *m. flexor colli lateralis*, consists of a few slips that together insert on the costal process of V1 (*processus costalis atlantis* of Baumel and Witmer, 1993) and/or the posteroventral aspect of the centrum of V1 (e.g., Boas, 1929; Zusi and Storer, 1969; Landolt and Zweers, 1985). The origins of these slips vary among birds, and include various combinations of the transverse processes, prezygapophyses, and ribs of anterior cervical vertebrae, *aponeurosis transversa*, and tendons of origin of *mm. intertransversarii* (Zusi and Storer, 1969; Zusi and Bentz, 1984; Landolt and Zweers, 1985; Zusi, 1985). The second muscle, *m. rectus capitis dorsalis*, lies anterodorsal to *m. flexor colli lateralis*, and similarly consists of slips that arise from several anterior cervical vertebrae. The origins of these slips are the lateral edges of the neural arches, lateral aspects of the postzygapophyses, anterior aspects of the ribs, and/or tendons arising from these structures (e.g., Zusi and Storer, 1969; Landolt and Zweers, 1985). These slips converge to a strong tendon that inserts on the basal tubera of the skull (*tuberculum basilare* of Baumel and Witmer, 1993).

In the *Struthio camelus* that I dissected, *m. flexor colli lateralis* arises from the following origins: tendons II arising from V6 through V3 and bone surfaces adjacent to the origins of these tendons; tendon I arising from V5; lateral surfaces of the anterior parts of ribs (*ansa costotransversaria*) of V3 and V2; and (putatively fused) intercentrum of V2 (Fig. 2C). These fibers converge to insert on V1 by a tendon (corresponding to the tendon III of *mm. intertransversarii*) that attaches to the posteroventral corner of the intercentrum (*corpus atlantis*) and ventral tip of *ansa costotransversaria* of this vertebra. In addition to muscle fibers of *m. flexor colli lateralis*, those arising from the lateral and anterior surfaces of the rib of V3 representing a part of *mm. inclusi* also attach to this tendon.

Muscle fibers of *m. rectus capitis dorsalis* in *Struthio camelus* arise from the following origins: tendons (*aponeurosis transversa*) extending between V5 and V4 and between V4 and V3; lateral surface of the prezygapophysis of V5; dorsal part of the tendon II arising from V5; lateral surfaces of the prezygapophyses and postzygapophyses, and lateral edges of the neural arches of V4 and V3; lateral aspects of the prezygapophysis, postzygapophysis, neural arch, and fused rib (*ansa costotransversaria*) of V2; lateral surface of the postzygapophysis, neural arch, and *ansa costotransversaria* of V1 (Fig. 2C). Some fibers of this muscle also arise from the tendons I arising from several anterior-most cervicals. All of these fibers converge to insert on the basal tubera by a tendon (Fig. 4A,D), through which a nerve branch extends to innervate *m. rectus capitis anterior*. Another very thin muscle slip arises from the lateral aspect of the intercentrum of V1, extends anteriorly, and inserts on the basal tubera medial to the insertion of this tendon of insertion.

Homologies of *mm. intertransversarii* and their derivatives. Based on the observations described above, homologies of the avian *mm. intertransversarii* with muscles in other diapsids are discussed here. First, for the following reasons, comparisons with the lepidosaurian and/or crocodylian conditions suggest that the tendons I, II, dorsal part of the tendon III, and muscle fibers arising from the tendon II represent the *m. longissimus* group. First, in lepidosaurs, muscle fibers of *m. longissimus* arise partially by tendons from the lateral surfaces of the prezygapophyses (Figs. 2A and 3A), just beneath the tendinous origin of *m. semispinalis* of the *m. transversospinalis* group, and extend anteriorly as described above. Although the crocodylian *m. longissimus* arises by fleshy fibers without tendons, its origin is also on the prezygapophysis (Fig. 2B), adjacent to the tendinous origin of *m. tendinoarticularis*. The latter muscle is proposed as a derivative of *m. semispinalis* (Gasc, 1981; Tsuihiji, 2005), and is considered as the homolog of the avian *m. ascendens cervicalis* (Nishi, 1938; Tsuihiji, 2005). The tendon II and its associated fibers of the avian *mm. intertransversarii* similarly arise from the prezygapophysis ventral to *m. ascendens cervicalis* (Fig. 3D,E), and I accordingly propose them as representing muscle fibers and the tendon of origin of *m. longissimus*. Second, muscles fibers of *m. longissimus* in nonavian diapsids attach to the medial surface of the tendon of insertion, which arises from the lateral surface of the prezygapophysis, proximal part of the rib, and/or posterior edge of the transverse process and extends posteriorly (Fig. 3A,B). The

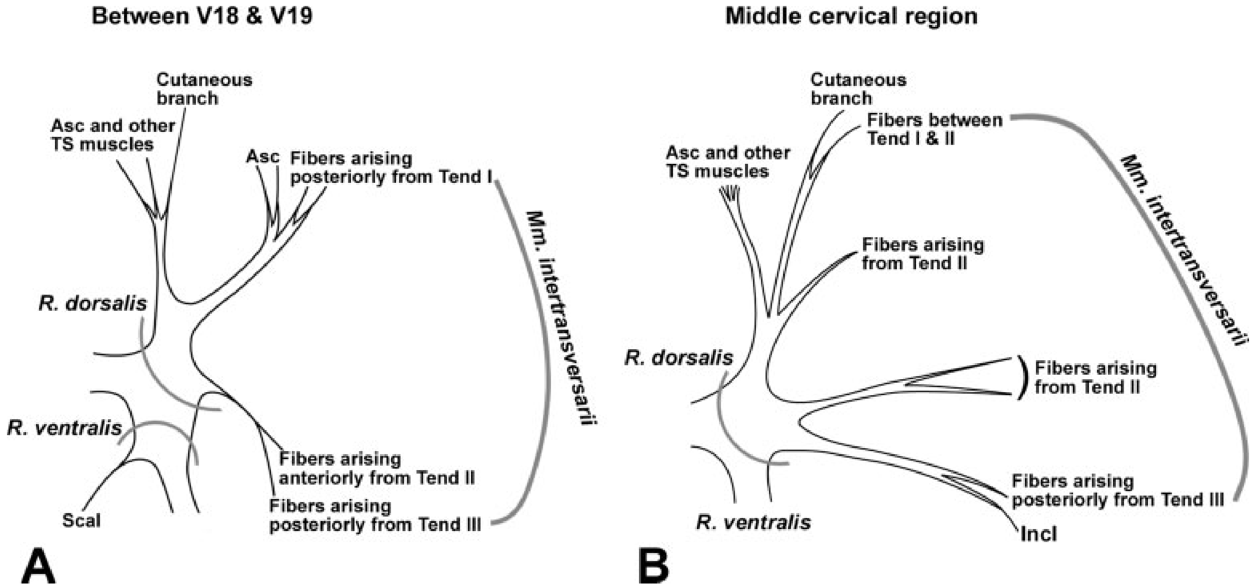

Fig. 5. Semi-schematic illustrations of the spinal nerves between V18 and V19 (**A**) and in the middle cervical region (**B**) in *Struthio camelus* (left side in anterolateral view). Branches are labeled with names of muscles they innervate. Asc, *m. ascendens cervicalis*; Inc, *mm. inclusi*; *R.*, *ramus*; Scal, *m. scalenus*; Tend I-III, tendons I-III of *mm. intertransversarii* as described in the text; TS, *transversospinalis*.

dorsal part of the tendon III of the avian *mm. intertransversarii* arises from the lateral surface of the transverse process near the prezygapophysis and proximal part of the rib (Fig. 3D), and its medial surface serves as the insertion of muscle fibers arising from the tendon II, suggesting that this part of the tendon III is the avian homolog of the tendon of insertion of *m. longissimus*.

Second, the ventral part of the tendon III of *mm. intertransversarii* arises from the posterodorsal edge of the rib (Fig. 3D,E). The tendon of *m. iliocostalis* in non-avian diapsids similarly arises from the posterior edge of the proximal part of the rib (Fig. 3A,B). This similarity in positions of attachment suggests that this part of the tendon III and muscle fibers arising from it represent the homolog of *m. iliocostalis*. As described above, these muscle fibers insert on the next posterior tendon III and/or lateral and ventrolateral surfaces of the next posterior rib. These muscle fibers and those of the *m. longissimus* homolog that arise from the tendon II "blend" with each other, and thus there is no distinct fascia separating the *m. iliocostalis* and *m. longissimus* homologs in the cervical region of birds. This is similar to the condition seen in the cervical region of crocodylians described above.

The above homology hypothesis may be further supported by the innervation patterns of these muscles. I examined such patterns in the segment between V18 and V19 as well as in the middle cervical region of an adult specimen of *Struthio camelus*. The dorsal ramus of the spinal nerve issuing between V18 and V19 consists of two major branches (Fig. 5A). The medial one, much thicker of the two, further divides into two sub-branches. One of them consists of a cutaneous branch as well as twigs innervating muscles belonging to the *m. transversospinalis* group including *m. ascendens cervicalis* while the other innervates a part of *m. ascendens cervicalis* as well as fibers arising posteriorly from the tendon I. The lateral branch of the dorsal ramus, on the other hand, divides into two twigs. One of these twigs supplies muscle fibers arising from the tendon II and extending anteriorly to insert on the tendon I as well as on the dorsal part of the tendon III while the other supplies fibers extending posteriorly from the ventral part of the tendon III. The muscle lying ventral to *mm. intertransversarii* (*m. scalenus*, or a combined form of *mm. levatores costarum* + *mm. intercostales externi*: see below) is innervated by a branch of the ventral ramus. It has generally been considered that in amniotes the *m. transversospinalis* group is innervated by the medial branch of the dorsal ramus while the *m. longissimus* and *m. iliocostalis* groups are innervated by the medial and lateral sub-branches of the lateral branch of the dorsal ramus, respectively (e.g., Nishi, 1916; Vallois, 1922; Gasc, 1981). Assuming this pattern holds true for *Struthio camelus*, *m. ascendens cervicalis* and the more medially lying muscles, as well as fibers arising posteriorly from the tendon I, that are all innervated by the medial branch of the dorsal ramus belong to the *m. transversospinalis* group while fibers extending anteriorly from the tendon II and those extending posteriorly from the ventral part of the tendon III that are innervated by the lateral branch of the dorsal ramus belong to the *m. longissimus* and *m. iliocostalis* groups, respectively.

The innervation patterns observed in the middle cervical region is slightly different from the one seen between V18 and V19 (Fig. 5B). In the middle cervical region, the dorsal ramus of the spinal nerve consists of three major branches. The first, most medial branch is the thickest among the three, and gives off three sub-branches: the first sub-branch innervates *m. ascendens cervicalis* and the more medially lying muscles, the second one includes a cutaneous branch and a twig supplying fibers connecting the tendons I and II, and the third one innervates a part of muscle fibers arising anteriorly from the tendon II. The second branch of the dorsal ramus innervates the majority of muscle fibers arising from the tendon II while the third branch divides into sub-branches innervating muscle fibers arising posteriorly from the tendon III and a part of *mm. inclusi*. The rest of *mm. inclusi* is innervated by branches of the ventral ramus. This branching pattern does not conform to the putatively general amniote pattern mentioned above. However, deviations from this pattern have also been described in non-avian diapsids (Nishi, 1938; Murakami et al., 1991). Murakami et al. (1991), for example, described that the dorsal "ramus" in the middle dorsal region of *Caiman crocodilus* consists of three separate branches innervating the *m. transversospinalis*, *m. longissimus*, and *m. iliocostalis* groups, respectively, rather than being united to form a single, common trunk as is the case with the "general" pattern; in other words, nerves supplying *m. longissimus* and *m. iliocostalis* do not branch off from the common trunk of the dorsal ramus in this crocodylian. This branching pattern of the spinal nerve in *C. crocodilus*, in which the dorsal ramus consists of the three independent branches, is very similar to that in the middle cervical region of *Struthio camelus* described here. Comparison with the crocodylian pattern would suggest that (1) *m. ascendens cervicalis* and the more medially lying muscles in *S. camelus* innervated by the first, most medial branch comprise the *m. transversospinalis* group, (2) the main part of fibers arising from the tendon II innervated by the second branch belongs to *m. longissimus* group, and (3) muscle fibers arising posteriorly from the tendon III innervated by the third branch belong to the *m. iliocostalis* group. As described above, some fibers arising from the tendon II are innervated by the medial branch of the dorsal ramus, as are fibers arising posteriorly from the tendon I in the segment between V18 and V19. This pattern might be regarded as suggesting that these muscle fibers of *mm. intertransversarii* belong to the *m. transversospinalis* group. According to Murakami et al. (1991), however, a nerve twig that arises from the nerve branch supplying the *m. transversospinalis* group innervates muscle fibers immediately lateral to s*eptum intermusculare dorsi*, or the most medial part of *m. longissimus*, in some segments in the dorsal region of *C. crocodilus*. As the muscle morphology described above rather strongly suggest that muscles fibers arising from the tendons I and II in *S. camelus* belong to the *m. longissimus* group, I here hypothesize that *C. crocodilus* and *S. camelus* share the innervation pattern of the most medial part of the *m. longissimus* group being supplied by the medial branch of the dorsal ramus.

The observation above suggests that *m. flexor colli lateralis* and *m. rectus capitis dorsalis* are anterior continuations, or serial homologs, of *mm. intertransversarii*. First, muscle fibers of *m. flexor colli lateralis* arise mainly from several tendons II and insert on the tendon III (arising from V1) as do the middle part of *mm. intertransversarii* in the more posterior region. Because muscle fibers arising from the tendons II and inserting on the tendons III are proposed above to belong to the *m. longissimus*, these fibers of *m. flexor colli lateralis* can also be considered as a part of this muscle group. Some muscle fibers of *m. flexor colli lateralis*, however, also arise from the lateral surface of a rib (*ansa costotransversaria* of V2) and insert on the tendon III. Such fibers of *mm. intertransversarii* in the more posterior region are hypothesized above to be the *m. iliocostalis* homolog. Accordingly, *m. flexor colli lateralis* is proposed here to include the *m. iliocostalis* homolog as well.

The primary origins of *m. rectus capitis dorsalis* that lies anterodorsal to *m. flexor colli lateralis* include the lateral surfaces of the prezygapophyses of V2 through V5 as well as the tendon II arising from V5. Again, these are the origins of the putative *m. longissimus* homolog in the more posterior cervical region. Accordingly, I propose that this muscle also belongs mainly to the *m. longissimus* group. Specifically, it can be homologized with *pars transversalis cervicis* of *m. longissimus capitis* in Lepidosauria and *m. longissimus capitis profundus* in Crocodylia, both of which insert on the basal tubera of the skull (Fig. 4A–C). Additionally, as is the case with *m. flexor colli lateralis*, some fibers of *m. rectus capitis dorsalis* arise from the lateral surface of a rib (*ansa costotransversaria* of V2). Therefore, this muscle can also be considered to include an *iliocostalis* component inserting on the basal tubera. The lepidosaurian *m. iliocostalis capitis* similarly insert on the basal tubera together with *pars transversalis cervicis* of *m. longissimus capitis*.

In specimens of birds examined for the present study, I did not find a *longissimus* muscle that corresponds to the lepidosaurian *m. longissimus capitis*, *pars transversalis capitis* or crocodylian *m. longissimus capitis superficialis* inserting on the paroccipital process. Accordingly, I regard the homolog of these muscles as absent in Aves.

The morphology of tendons of *mm. intertransversarii* in other birds. The number and morphology of the *mm. intertransversarii* tendons vary among avian species. *Rhea americana* (YPM 101221 and 101222) has the same number of tendons as does *Struthio camelus*, and also has the lateral and vertical parts of the tendons III that cover muscle fibers laterally as in the latter bird. In *Meleagris gallopavo* (YPM 101229), on the other hand, such parts of the tendons III are absent (Fig. 3F) except in a few, posterior-most cervical vertebrae. In addition, there appear to be more tendons present in this bird than in *S. camelus*. In the middle and posterior cervical regions of *M. gallopavo*, for example, the tendon of origin of *m. ascendens cervicalis* is wide dorsoventrally, and wraps laterally around a tendon and its associated muscle fibers that arise from the prezygapophysis of the next anterior vertebra and extend posteriorly (Fig. 3F). The latter tendon is thus similar to the tendon I in *S. camelus* with regard to its origin and direction. Ventral to this tendon, however, arises another tendon similarly extending posteriorly, below which a cutaneous branch of the spinal nerve extends laterally. In *S. camelus*, the same cutaneous branch extends ventral to the tendon I. In addition, the dorsal surface of this second, ventral tendon in *M. gallopavo* is connected with the ventral surface of the tendon of origin of *m. ascendens cervicalis* by fleshy fibers, as is the tendon I in *S. camelus*. Accordingly, I suggest that this tendon in *M. gallopavo* corresponds to the tendon I in *S. camelus*, and that the first, dorsal one is a part of the *m. ascendens cervicalis* tendon (Fig. 3F). Ventral to the tendon I and the cutaneous branch of the spinal nerve lies the tendon II, which extends anteriorly from a process on *ansa costotransversaria* as does the one in *S. camelus*. The tendon III is much shorter anteroposteriorly than that in *S. camelus*, and arises from the lateral crest of the rib, continuous dorsally with the tendon IV that arises from a posterior crest on *ansa costotransversaria* and extends posteriorly below the tendon II arising from the next posterior vertebra (Fig. 3F).

The arrangement of the *mm. intertransversarii* tendons in *Gallus gallus* (e.g., YPM 101226) is similar to the one in *Meleagris gallopavo* in that parts of tendons that laterally cover muscle fibers are lacking. According to the description by Landolt and Zweers (1985), the condition is also similar in *Anas platyrhynchos*, in which the longitudinally running, interdigitating tendons are prominent. The number of *mm. intertransversarii* tendons in *Podilymbus podiceps* as described by Zusi and Storer (1969) is greater than that in *Struthio camelus* or *M. gallopavo*. Judging from their description and figures, however, it is possible that Zusi and Storer (1969) included the tendon of origin of *m. ascendens cervicalis* as one of their *mm. intertransversarii* tendons. Otherwise, the overall morphology and arrangement of the tendons in *P. podiceps* appear to be similar to that in *M. gallopavo*.

Mm. Intercostales Externi

Each slip of *mm. intercostales externi* connects successive ribs in the dorsal and cervical regions. This series of muscles and the subvertebral muscles described in the next section are the hypaxial muscles associated with the vertebral column that are present in the diapsid cervical region.

Lepidosauria. In the dorsal and posterior cervical regions of Lepidosauria, each slip of *mm. intercostales externi* occupies an intercostal space between two successive ribs. In the dorsal region, the attachment of this series of muscles extends from the vertebral segments (vertebrocostal segments of Hoffstetter and Gasc, 1969) through the most dorsal parts of the cartilaginous sternal segments (intercostal and sternocostal segments of Hoffstetter and Gasc, 1969) of ribs. In the cervical region, the attachment of this series of muscles extends to the tips of ribs. The direction of the muscle fibers is oblique relative to the rib shafts, extending from the posteroventral to anterodorsal directions. Maurer (1896) described this series of muscles in *Sphenodon punctatus* and *Tiliqua* (“*Cyclodus*”) as consisting of deep and superficial layers. The deep layer (*m. intercostalis externus brevis*) connects two adjacent ribs while the superficial layer (*m. intercostalis externus longus*) skips one rib and connects every other rib. Carrier (1990) described that *mm. intercostales externi* in the dorsal region of *Iguana iguana* consist solely of slips connecting two adjacent ribs, the attachments of which occupy the anterior and posterior edges of the rib from the vertebrocostal articulation to just below the articulation between the vertebral and sternal segments. Although Carrier (1990) described two layers in the dorsal (upper) half of each slip, I found the morphology of this series of muscles in *I. iguana* is more complicated, with each slip consisting of several tendons and muscle fibers arising from them (Fig. 3A). According to my dissections, a dorsoventrally wide tendon arises from the anterior edge of the vertebral segment of the rib (IE1 in Fig. 3A) and serves as the origin of a muscle sheet that differentiates into two, superficial and deep layers ventrally. The insertions of both layers are on the posterior edge of the vertebral segment of the next anterior rib. The superficial layer is the broader of the two layers, and at its ventral end overlaps the proximal part of each slip of *mm. intercostales interni*, which arises from the anterior edge of the distal part of the vertebral segment and extends anteroventrally. At the head of the rib, another narrow tendon arises and extends anteriorly (IE2 in Fig. 3A). This tendon and its associated muscle fibers comprise a muscle slip that is incompletely separate from the rest of *mm. intercostales externi* and inserts on the lateral surface of the centrum posterior to the synapophysis. This slip in each vertebral segment was recognized as comprising a separate, distinct series of muscles, *mm. levatores costarum* (*m. levator costae*), in Olson (1936) and Tschanz (1986). A superficial tendon that arises from the posterolateral aspect of the prezygapophysis just dorsal to the synapophysis of the next anterior vertebra (IE3 in Fig. 3A) covers the anterodorsal corner of this slip and serves as its tendon of insertion. Ventral to this tendon, one or two thin tendons arise from the rib of this vertebra near its head and extend posteriorly (IE4 in Fig. 3A). The fibers of the *mm. levatores costarum* slip insert on these tendons as well.

Olson (1936) described *mm. intertransversarii* as a series of muscle slips that connects the successive synapophyses in *Iguana iguana*, and regarded it as a derivative of intercostal muscles. Although Tschanz (1986) also described this muscle as present in *I. iguana*, I could not recognize such a distinct series of muscles in specimens that I dissected. Based on sites of attachments described in the previous studies, I here consider *mm. intertransversarii* as merely a medial-most part of *mm. intercostales externi*, or that of *mm. levatores costarum* in some studies.

In *Varanus exanthematicus* (YPM 13318), the morphology of *mm. intercostales externi* including the tendons is similar to that in *Iguana iguana*. Unlike in *I. iguana*, however, *V. exanthematicus* has slips of this muscle series that skip one rib and insert on the second one anterior to each origin. These slips correspond to *m. intercostalis externus longus* in *Sphenodon punctatus* and *Tiliqua* described in Maurer (1896).

In the middle to anterior cervical regions of *Iguana iguana*, *mm. intercostales externi* continue to be present although the dorsoventral width of each muscle slip decreases anteriorly as ribs become shortened. From V4 through V1 that lack ribs, slips of this series of muscles are separated from one another by tendons or myosepta that arise from the synapophyses and extend posteroventrally. Each tendon rolls up around the muscle fibers, thus appearing as a cone with the apex directed anteriorly. Within each "cone," the tendinous system recognized in the dorsal and posterior cervical regions is still maintained. From the anterior edge of the rib of V5, for example, two or three tendons arise and extend anteriorly. One or two distal ones probably correspond to IE1 in the more posterior region, and the most proximal one is the origin of *mm. levatores costarum* that is also recognized more posteriorly. A tendon of insertion of *mm. levatores costarum* (IE3) is also present and extends posteriorly from the synapophysis. The ventral parts of *mm. intercostales externi* in the cervical region are closely associated with *m. longus colli* ventrally. Branches of the ventral rami of the spinal nerves extend through between these two muscles and mark their boundary.

Another muscle called *m. scalenus* has sometimes been described in the cervical region of Lepidosauria (Mivart, 1867; Hoffmann, 1890; Osawa, 1898). This muscle was described as arising from the anterior surface of a posterior cervical or anterior dorsal rib, extending anteriorly, and inserting on the synapophyses or ribs of several cervical vertebrae. As Osawa (1898) argued, however, this "*m. scalenus*" is merely the cervical parts of *mm. intercostales externi* that is just described above.

Crocodylia. Maurer (1896) described *mm. intercostales externi* in *Crocodylus niloticus* ("*Crocodilus vulgaris*") as a series of muscles that connects two adjacent ribs, occupying the intercostal space from the vertebrocostal articulation through the articulation between the intermediate and sternal (sternocostal) segments. In their detailed studies on the hypaxial musculature in *Caiman crocodilus*, Murakami (1988) and Murakami et al. (1991) divided *mm. intercostales externi* in the dorsal region into two parts, *mm. intercostales externi dorsales* and *mm. intercostales externi ventrales*, based on the innervation patterns and the sites of attachment. According to these studies, each slip of *mm. intercostales externi ventrales* connects two successive intermediate segments of the ribs and is innervated by a lateral branch of the ventral ramus, or intercostal nerve, of the spinal nerve. The second part, *mm. intercostales externi dorsales*, was described as lying between two successive vertebral segments of the ribs and innervated by branches arising from the iliocostalis nerve. Cong et al. (1998), on the other hand, described *mm. intercostales externi* in *Alligator sinensis* as being present in the presacral region posterior to V9, arising from the anterior edges of vertebral and intermediate segments of a rib, and inserting on the posterior, concave surface of the vertebral segment as well as the posterior edge of the intermediate segment of the next anterior rib. Dorsal to *mm. intercostales externi*, Cong et al. (1998) recognized another series of muscles, *mm. transversocostales*, each slip of which arises from the anterior edge of the transverse process and the adjacent anterior concavity of the medial half of the vertebral segment of the rib. The insertion of each slip was described as on the posterior edges of the next anterior transverse process and the adjacent part of the rib articulating with it. These descriptions suggest that these two muscles recognized by Cong et al. (1998) combined correspond to *mm. intercostales externi* of Maurer (1896).

In the dorsal region of *Alligator mississippiensis* that I dissected (e.g., YPM 13323), I could not recognize a separation between slips of *mm. intercostales externi* and *mm. transversocostales* that Cong et al. (1998) recognized. Instead, there is only a single muscle slip that lies immediately deep to a slip of *m. iliocostalis dorsi* and extends from the vertebrocostal articulation to almost the distal end of the vertebral segment of a rib. This slip corresponds to that of *mm. intercostales externi dorsales* in Murakami (1988) and Murakami et al. (1991). In *A. mississippiensis*, a thin fascia separates slips of *mm. intercostales externi dorsales* and *m. iliocostalis dorsi* at their proximal parts, but the separation between them becomes obscure toward the distal end of the vertebral segment of the rib. Murakami et al. (1991) also described the ventral part of *m. iliocostalis dorsi* as inseparable from the underlying slip of *mm. intercostales externi dorsales* in *Caiman crocodilus*.

Ventral to *mm. intercostales externi dorsales* lies a distinct series of muscles connecting the adjacent intermediate segments of ribs in *Alligator mississippiensis*. This series of muscle is the ventral part of *mm. intercostales externi* of Maurer (1896) and *mm. intercostales externi ventrales* of Murakami (1988) and Murakami et al. (1991). In the specimens that I dissected, this series of muscles appears not to continue into the cervical region where the intermediate (and sternal) segments of the ribs are no longer present. In the cervical region, therefore, only a single series of muscles, *mm. intercostales externi*, is present.

In the anterior dorsal through posterior cervical regions of *Alligator mississippiensis* that I dissected, the origins of each slip of *mm. intercostales externi dorsales* or *mm. intercostales externi* are the lateral surfaces of the anterior process and the adjacent part of the rib shaft, anterior surface of the area between capitular and tubercular processes of the rib, and anterior aspect of the transverse process of the vertebra (Fig. 2B). A strong tendon of origin arises from the proximal part of the anterior process of the rib and extends anterodorsally (IE1 in Fig. 3B), with its lateral and medial surfaces serving as the origins of muscle fibers. Each slip of this series of muscles inserts on the posterior aspect of the rib (rib shaft and the capitular and tubercular processes), posterior aspect of the transverse process, and lateral surface of the centrum of the next anterior vertebra by fleshy fibers and tendons. A superficial tendon of insertion arises from the posterior aspects of the transverse process and proximal end of the rib, and extends posteroventrally (IE3 in Fig. 3B). Muscle fibers insert mainly on the deep surface of this tendon, but some fibers also attach to its superficial surface. Another tendon of insertion lies deep to this tendon, also arising from the posterior aspect of the transverse process and extending posteriorly (IE5 in Fig. 3B), dorsal to the anterior end of the tendon of origin described above. As prominent vertebrocostal canals appear on V11 and more anterior vertebral segments, some fibers of *mm. intercostales externi dorsales* or *mm. intercostales externi* arising laterally from the tendon of origin (IE1) extend further anteriorly, pass through the vertebrocostal canal in front, and reach the second vertebra anterior to the origin. Murakami et al. (1991) described this condition only in the cervical region of *Caiman crocodilus*, but my observation confirmed that this condition actually appears more posteriorly in *A. mississippiensis*, coinciding with the appearance of the vertebrocostal canal in the anterior dorsal region.

In the middle to anterior cervical regions of *Alligator mississippiensis*, the general sites of origin and insertion of *mm. intercostales externi* remain the same as in the more posterior region with only small modifications. In those regions, each slip of *mm. intercostales externi* arises from the lateral surface of the anterior process of the shaft and anterior edge of the tubercular process of the rib (Fig. 2B). A strong tendon of origin also arises from the anterior process. Fibers arising from these areas as well as from the lateral surface of this tendon of origin insert on the internal surfaces of the shaft and tubercular processes of the next anterior rib. Fibers arising distally from the tendon of origin extend further anterodorsally through the vertebrocostal canal in front, pass laterally to the ventral ramus of the spinal nerve, and insert on the posterior edge of the transverse process and the lateral surface of the centrum of the second vertebra anterior to the origin (Fig. 2B). Fibers arising medially from the same tendon also attach partly to the lateral surface of the posterior part of the centrum of the second anterior vertebra, but attach mainly to the dorsal surface of the capitular process and lateral surface of the centrum of the first vertebra anterior to the origin.

A muscle called *m. scalenus* or *mm. scaleni* (e.g., Rathke, 1866; Cong et al., 1998) in Crocodylia is considered here as derived from the ventral parts of *mm. intercostales externi* in the cervical region. Because of the strong development of the anterior processes of the ribs that overlap successive rib shafts in the cervical region, such ventral parts of *mm. intercostales externi* are almost completely separated from the rest of this series of muscles. Furthermore, slips of the *m. serratus* complex (*m. serratus superficialis*, *m. serratus profundus*, and *m. levator scapulae*) arise from the lateral surfaces of the ribs between the attachments of *m. scalenus* and the rest of *mm. intercostales externi* in the cervical region (Fig. 2B), making these two parts more readily distinguishable. In *Alligator mississippiensis* that I dissected, the most posterior origin of *m. scalenus* is anterior and lateral aspects of the shaft of the rib of V9 (Fig. 2B). Immediately

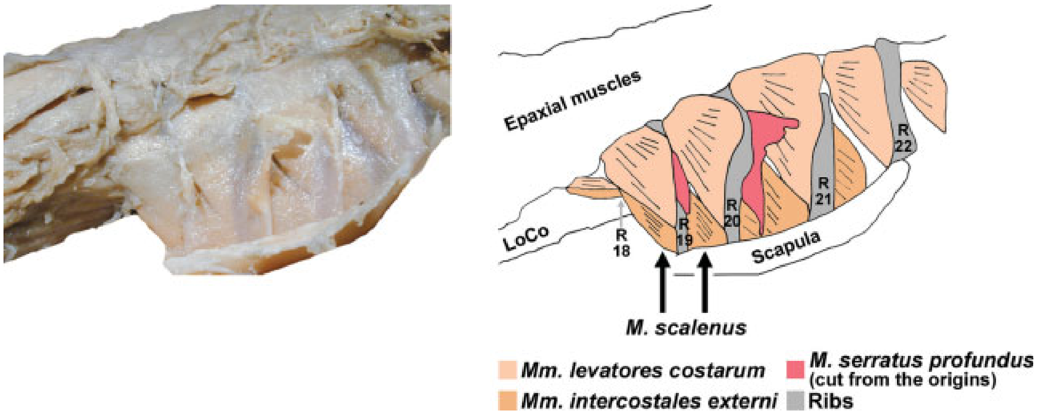

Fig. 6. Muscles connecting successive vertebral segments of ribs in the dorsal region of *Struthio camelus* (YPM 100890) in left lateral view, photograph (**A**) and semi-schematic illustration showing outlines of these muscles (**B**). The scapula is reflected laterally and *m. serratus profundus* has been severed near its origins on ribs. Note that the two slips of *m. scalenus* consist of those of *mm. levatores costarum* and *mm. intercostales externi* combined. LoCo, *m. longus colli ventralis*; R18-22, ribs of V18 through V22.

distal to the anterior process of this rib is the origin of slips of the *m. serratus* complex, and the origin of *m. scalenus* occupies the area distal to the latter. In the more anterior region, fibers of this muscle arise from the lateral and ventral aspects of the rib shafts of V8 through V3. All of these fibers extend anteriorly and insert on the tendons of insertion that attach to the posterior ends of the ribs of V8 through V2 (Fig. 2B). This muscle does not retain the strictly metameric arrangement seen in the rest of *mm. intercostales externi*. That is, fibers of this muscle arising from the rib of V9 insert not only on the tendon of insertion attaching to V8 but also on those attaching to V7 through V5. Muscle fibers arising from V8 through V3, however, insert on the tendon of insertion attaching to the rib immediately anterior to each origin. As Cong et al. (1998) described, fibers of this muscle are partially intergrown with those of *m. longus colli*. In fact, the tendons of insertion of these two muscles fuse together at their attachments to the tips of the ribs. Branches of the ventral rami of the spinal nerves extend between these two muscles.

Aves. In the dorsal region of Aves, several hypaxial muscles that connect the two adjacent vertebral segments of the ribs have been recognized. They are as follows: *mm. levatores costarum*, *m. scalenus*, *mm. intercostales externi*, and *mm. intercostales interni* (Vanden Berge and Zweers, 1993). The first three of these muscles are here considered to be the homologs of *mm. intercostales externi* of non-avian diapsids based on their morphology and innervation patterns as described below. Each slip of *mm. levatores costarum* appears triangular in lateral view, arising from the lateral surface and anterior edge of the proximal part of the rib and inserting on the lateral edge of the transverse process of the next anterior vertebra. According to Zusi and Bentz (1984) and Fedde (1987), the most anterior slip of *mm. levatores costarum* connects the first dorsal rib (defined as the most anterior rib that articulates with the sternum via a sternal segment) with the last cervical rib. Each slip of *m. scalenus*, on the other hand, arises from the anterior edge and/or lateral surface of the free (unfused to the vertebra) cervical rib and inserts on the transverse process of the next anterior vertebra. Fedde (1987) described that *m. scalenus* in *Gallus gallus* consists of two slips, corresponding to the presence of two free cervical ribs in this species, while Zusi and Bentz (1984) described only a single slip of this muscle as being present in *Eulampis jugularis* in which only a single, long, free cervical rib is present. Zusi (1985) and Vanden Berge and Zweers (1993) suggested that *mm. levatores costarum* and *m. scalenus* are serially homologous with each other, and that the latter muscle is merely the most anterior slip of the former.

The avian *mm. intercostales externi* lie distal to *mm. levatores costarum*, occupying the intercostal space. Fibers of *mm. intercostales externi* arise from the anterior edge of the vertebral segment of the rib distal/ventral to the ventral border of *mm. levatores costarum*, extend anterodorsally, and insert on the posterior edges of the vertebral segment and uncinate process of the next anterior rib (Fedde, 1987).

I observed these muscles in an embryonic *Struthio camelus* (YPM 101219). Slips of *mm. levatores costarum* and *mm. intercostales externi* in the same intercostal space are clearly separated in the middle to posterior dorsal regions with almost no overlapping between the origins of these two muscles (Fig. 6). The origin of each slip of *mm. levatores costarum* is restricted to the proximal part of the rib, occupying its lateral surface and anterior edge. The muscle fibers extend anterodorsally and insert on the posterior edges of the proximal end of the rib and distal end of the transverse process of the next anterior segment. The origin and insertion of *mm. intercostales externi* occupy shafts of vertebral segments distal to those of *mm. levatores costarum*, including areas proximal to the uncinate processes. The origin of each slip of the former muscles extends as far distally as to the level of the articulation between the vertebral and sternal segments of the rib. Muscle fibers of the proximal/dorsal part of each slip extend almost horizontally, while those of the distal/ventral part extend anterodorsally. The fibers insert on the posterior edge of the vertebral segment of the next anterior rib. In addition, some fibers arising from the distal part of the vertebral segment insert on the medial aspect of the uncinate process.

As the lengths of ribs rapidly decrease in the anterior-most dorsal region, the distinction between slips of *mm. levatores costarum* and *mm. intercostales externi* is obscured because the fibers of the both muscles similarly extend anterodorsally in this region. A narrow space is still present separating the slips of these two muscles connecting V20 and V19 (Fig. 6). The slip of *mm. levatores costarum* inserts on the posterior aspects of the transverse process and proximal part of the rib of V19 while that of *mm. intercostales externi* inserts on the more distal part of the rib of V19. Furthermore, between the insertions of these slips on the rib of V19 lies the origin of a slip of the *serratus* muscle, which makes the distinction between those two muscles clearer. The origins and insertions of the slips of *mm. levatores costarum* and *mm. intercostales externi* connecting V19 and V18 lie very close to each other (Fig. 6). However, with the aid of a dissection microscope, I could still recognize the separation between these two slips. A tendon of insertion develops on the dorsal surface of the slip of *mm. levatores costarum*, and merges with a tendon of the overlying "*m. iliocostalis*."

The slips of these muscles connecting V20 and V19 and those connecting V19 and V18 correspond to *m. scalenus* described in previous studies by Fedde (1987), Zusi and Bentz (1984), and Zusi (1985). These studies considered *mm. intercostales externi* as arising only from ribs with the sternal segments and thus are absent in the more anterior region. As described above, however, my dissection revealed that this series of muscles still coexists with *mm. levatores costarum* in this region (Fig. 6), accordingly suggesting that each slip of *m. scalenus* actually consists of slips of both *mm. levatores costarum* and *mm. intercostales externi*. Although the slip inserting on V18 is the most anterior one of *m. scalenus* as has been traditionally recognized, my dissections revealed that homologs of this muscle, or *mm. levatores costarum* and *mm. intercostales externi* combined, continue to arise from V18 and more anterior vertebrae and correspond to the series of muscles called *mm. inclusi* in the avian literature. The ribs of V18 and the more anterior vertebrae extend anteroposteriorly, rather than dorsoventrally as the more posterior ribs do. If we take such a change of the rib morphology into consideration, *mm. inclusi* are found to maintain the origins and insertions very similar to those of *mm. levatores costarum* and *mm. intercostales externi* in the more posterior region, and are accordingly considered serially homologous with the latter muscles combined. For example, the slip of *mm. inclusi* arising from V18 has its origin on the lateral aspect of the rib. This slip inserts on the V17 by a tendon (tendon IV described above) that merges dorsally with the tendon of insertion of "*m. iliocostalis*"/*mm. intertransversarii* (tendon III described above). For more detailed observations of these muscle slips in this and more anterior region, I additionally dissected adult specimens of *Struthio camelus*. In these specimens, slips of *mm. inclusi* arise from the anterior process of the rib by the tendons V and VI described above (Fig. 3D,E), as well as from the lateral and ventral surfaces of the rib by fleshy fibers, and extend anteriorly. The insertions of these muscles slips are on the medial/deep surface of the tendon IV, medial surface of the fused rib, and ventral and lateral aspects of the centrum of the next anterior vertebra (Fig. 2C). The attachment sites of this tendon IV are a ridge on the transverse process and the dorsal edge of the proximal part of the rib (Fig. 3D), and are very similar to the insertions of *mm. levatores costarum* and *mm. intercostales externi* in the dorsal region. As described above, this tendon becomes divided into two parts, dorsal (main) and ventral, in the middle cervical region, with the dorsal part attaching to the ridge on the transverse process and ventral part attaching to the distal part of the rib with the ventral part of the tendon III (Fig. 3E). At this point, therefore, *mm. inclusi* are divided into two parts, dorsal and ventral, although the separation between them is incomplete with some muscle fibers still connecting these parts. The dorsal part of this series of muscles consists of the tendons V and VI, dorsal part of the tendon IV, and muscle fibers connecting these tendons. The ventral part consists of the ventral part of the tendon IV and fibers arising from this part and inserting on the lateral and ventrolateral surfaces of the next posterior rib and lateral surface of the next posterior tendon III or IV.

Homologies of *mm. intercostales externi* in Diapsida. The morphology of *mm. intercostales externi* and its homologs is similar across diapsid clades. Details of their homologies, however, merit some discussion. First, in the dorsal region of Crocodylia, there are two series of *mm. intercostales externi* (*mm. intercostales externi dorsales* and *mm. intercostales externi ventrales*) corresponding to the presence of an additional segment (intermediate segment) of the rib that is not present in *Iguana iguana*, which has only a single series of *mm. intercostales externi*. Based on this morphology as well as topological relationships with other muscles, I here suggest that the crocodylian *mm. intercostales externi dorsales* and *mm. intercostales externi ventrales* have been differentiated from a single series of *mm. intercostales externi* like the one seen in *I. iguana,* and accordingly that those two series in Crocodylia combined are homologous with the latter series in Lepidosauria. Second, the origins and insertions of *mm. intercostales externi* in the dorsal region of non-avian diapsids suggest that this series of muscles is homologous with the avian *mm. intercostales externi* and *mm. levatores costarum* combined. Thus, "*mm. intercostales externi*" in avian and non-avian diapsids are not the same in a strict sense. In non-avian diapsids, the *mm. levatores costarum* part and the rest of *mm. intercostales externi* are not clearly differentiated except that a tendon (IE2 in Fig. 3A,B) exists between these two parts.

Second, the lepidosaurian "*m. scalenus*" is merely another name of *mm. intercostales externi* in the cervical region, while I hypothesized above that the crocodylian *m. scalenus* (e.g., Cong et al., 1998) is differentiated from the ventral parts of *mm. intercostales externi* in the cervical region. The avian *m. scalenus*, on the other hand, consists of combined slips of *mm. intercostales externi* and *mm. levatores costarum*. Therefore, the name "*m. scalenus*" that has been used in lepidosaurian, crocodylian, and avian terminologies actually does not refer to the same muscle among these clades. In addition, the avian *m. scalenus* is not serially homologous with the avian *mm. levatores costarum* only, contrary to Zusi (1985) and Vanden Berge and Zweers (1993), in a strict sense.

The serial homology between *mm. inclusi* and *mm. levatores costarum* plus *mm. intercostales externi* in Aves proposed here has not been recognized in the avian literature. However, this homology hypothesis is well-supported based not only on comparison of these muscles between the dorsal and cervical regions in birds as described above, but also on comparison of putative homologs in the cervical region between avian and non-avian diapsids. First, as described above, *mm. intercostales externi* in non-avian diapsids (including a part homologous with the avian *mm. levatores costarum*) continue from the dorsal to cervical regions. Accordingly, it may be expected that their avian homologs also continue to be present in the cervical region, rather than ceasing to exist at the cervico-dorsal boundary. Second, close similarities in the origins and insertions between the avian *mm. inclusi* and the non-avian *mm. intercostales externi* in the cervical region suggest that these muscles are homologous. Most notably, both *mm. inclusi* and the non-avian *mm. intercostales externi* arise from the anterior process of the cervical rib by tendons. Furthermore, the innervation patterns by the spinal nerve provide an additional support for this homology hypothesis. As described above, *mm. inclusi* in the middle cervical region of *Struthio camelus* are innervated by branches of the ventral ramus of the spinal nerve as well as by the third branch of the dorsal ramus that also supplies the putative homolog of *m. iliocostalis* (Fig. 5B). It is usually considered that *mm. intercostales externi* in non-avian diapsids is innervated by a branch of the ventral ramus (e.g., Gasc, 1981). In *Caiman crocodilus*, however, Murakami et al. (1991) observed that the nerve supplying *mm. intercostales externi dorsales* usually branches off from a nerve supplying *m. iliocostalis* in the dorsal region. It follows that the innervation patterns of the *mm. intercostales externi* vary among diapsid clades, but that of the avian *mm. inclusi* is still within such variation.

It is noteworthy that the avian *mm. inclusi* are incompletely divided into two parts, dorsal and ventral, by the cervical ribs in the middle through anterior cervical regions as described above. This is reminiscent of the separation between *mm. intercostales externi* and *m. scalenus* in the crocodylian cervical region. Therefore, the *mm. intercostales externi* homologs in the cervical region that are at least incompletely divided into two series of muscles appear to be an archosaurian synapomorphy not seen in Lepidosauria.

Subvertebral Layer

Lepidosauria. In *Sphenodon punctatus*, the subvertebral layer that extends into the cervical region comprises only one muscle (Osawa, 1898; Evans, 1939). Osawa (1898) called this muscle *m. longus colli* or *m. basioccipitovertebralis*, the former of which Evans (1939) also used. According to Osawa (1898), this muscle arises from the ventral and lateral surfaces of the centra of V1 through V12 as well as from the cervical and anterior dorsal ribs, extends anteriorly, and inserts on the basal tubera of the skull.

In Squamata, the subvertebral layer is differentiated into two muscles. The one lying more posteriorly and laterally inserts on the cervical ribs and/or synapophyses while the other one lying more anteriorly and medially inserts on the basal tubera. The former muscle has usually been called *m. longus colli* (e.g., Mivart, 1867; Hoffmann, 1890; Evans, 1939; Tschanz, 1986), while the latter has variously been called *m. rectus capitis anterior* (e.g., Evans, 1939; Tschanz, 1986), *m. rectus capitis anticus major* (Mivart, 1867), or *m. basioccipitocervicalis* (Hoffmann, 1890). I examined these muscles in *Iguana iguana* in detail. In this squamate, *m. longus colli* arises by fleshy fibers from the anterior edges of the centra of V7 through V5, proximal parts of the ventral surfaces of the ribs of V6 and V5, and ventral aspects of the synapophyses of V5 through V3 (Fig. 2A). It inserts on the posteroventral aspects of the synapophyses of V5 through V2, ventrolateral surface of the centrum of V2, and intercentra of V3 and V2. Although Tschanz (1986) described that large areas of the lateral surfaces of the centra serve as the attachments of this muscle, few fibers actually arise from, or insert on, these areas except for that of V2 in the specimen that I dissected in detail (YPM 13333). There are especially no fibers attaching to areas surrounding nutrient foramina of the centra. At the insertions, most fibers of this muscle share the mediolaterally broad tendons of insertion with the dorsally lying *mm. intercostales externi*. Branches of spinal nerves extend between these two muscles and mark the boundary between them as described above. Most anteriorly, muscle fibers of *m. longus colli* attach to three tendons of insertion. One of them is very thin and inserts on the lateral surface of the centrum of V3. The second one is strap-like and inserts on the lateral aspect of the intercentrum of V3. The third one is also strap-like but broader than the second one. It gives off a branch that inserts on the distal end of the synapophysis of V3, but its main part extends further anteriorly and inserts on the intercentra of V1 and V2 and synapophysis of V1.

Two slips, ventral (superficial) and dorsal (deep), are recognized in *m. rectus capitis anterior* in *Iguana iguana* (Tschanz, 1986). In the specimens that I dissected, the ventral slip is the larger of the two, and has a bipennate appearance. In this slip, muscle fibers of the lateral and medial parts converge onto the tendon of insertion, which attaches to the ventral tip of the basal tubera (Fig. 4A,B). The lateral part arises from a tubercle on the proximal part of the ventral surface of the rib of V7. From here, a tendon extends anterolaterally while giving off muscle fibers from its medial surface. These fibers extend anteromedially and attach to the lateral surface of the tendon of insertion. The medial part arises by a tendon from the anterior edge of the centrum of V7 that expands mediolaterally to make a ridge. This tendon of origin is shared by fibers of *m. longus colli*. The origin of the medial part also includes the lateral surfaces of the intercentra of V6 through V1. Some fibers also arise from small areas of the lateral surfaces of the centra of these vertebrae along their ventral margins and from ligaments connecting the successive intercentra. These fibers extend anterolaterally. Those arising from V7 through V3 converge to the medial surface of the tendon of insertion. Some fibers arising from V2 and V1 also attach partly to this tendon of insertion. The rest of the fibers arising from V2 and V1, however, inserts directly on the posterior, concave surface of the basioccipital (Fig. 4A,B). The dorsal slip of *m. rectus capitis anterior*, on the other hand, arises from the intercentra of V4 through V1 and ligaments interconnecting them, dorsal to the origins of the ventral slip (Fig. 2A). Muscle fibers converge to a strap-like tendon anteriorly, which turns dorsally along the ventral aspect of the lateral process of the neural arch of V1 and insets on a ridge or crest (*crista tuberalis* of Oelrich, 1956) of the basioccipital, dorsal to the insertion of the ventral slip (Fig. 4A,B).

Crocodylia. As in Squamata, the subvertebral layer in Crocodylia is differentiated into two muscles, one inserting on tips of the ribs and the other inserting on the basal tubera, although Frey (1988a) did not distinguish these two muscles. The former muscle is usually called *m. longus colli* (e.g., Rathke, 1866; Gasc, 1981; Cong et al., 1998) as in Squamata, although Seidel (1978) named this muscle as *m. subvertebrocostales*. The other muscle inserting on the basal tubera, on the other hand, has been variously called *m. rectus capitis anticus major* (Rathke, 1866), *m. recti capitis laterales interni* and *m. recti capitis laterales* (Hair, 1868), and *m. rectus capitis ventralis* plus *m. longus capitis* (Cong et al., 1998).

The first muscle, *m. longus colli*, arises from the lateral surfaces of the hypapophyses and ventral surfaces of the centra and ribs of the cervical and anterior dorsal vertebrae (Seidel, 1978; Frey, 1988a; Cong et al., 1998). In addition, ventral tips of hypapophyses serve as the origins of a tendon or aponeurosis, from which some fibers of this muscle also arise. From these origins, muscle fibers extend anterolaterally and insert on the tips of the cervical ribs (Seidel, 1978; Frey, 1988a; Cong et al., 1998). In *Alligator mississippiensis* that I dissected (e.g., YPM 13323), the origins of this muscle are the centra and hypapophyses of V12 through V4 and anteroventral aspects of the capitular processes of the ribs of V10 through V6 (Fig. 2B). In *A. mississippiensis*, V12 is the most posterior vertebra bearing a hypapophysis. Therefore, the extent of the origin of this muscle coincides with that of the hypapophyses along the vertebral column. A series of tendons of insertion arises successively from the muscular mass and inserts on the distal end of each rib of V8 through V1 (Fig. 2B). This series of tendons is continuous proximally with the tendons of *m. scalenus*. Some fibers also insert directly on the posterior part of the medial aspect of the rib of V1.

The second muscle, *m. rectus capitis anticus major sensu* Rathke (1866), arises from the ventral tips of the hypapophyses of V8 or V7 through V2, ventral surface of the intercentrum of V1, and medial part of the ventral surface of the rib of V1 in *Alligator mississippiensis* (Fig. 2B). A series of tendons of origin arises from the hypapophyses of V5 through V3. Some fibers also arise from the ventral surface of the tendon of *m. longus colli* as well as from the ventral surface of a fascia connecting the ventral edge of the rib of V1 and several anterior hypapophyses. The muscle inserts on the rugose margin of the basal tubera including the ventral tip of the otoccipital by a tendon and fleshy fibers (Fig. 4A,C). The tendon of insertion is sheet-like and occupies the lateral two-thirds of the entire site of insertion of this muscle. The tendinous insertion of *m. longissimus capitis profundus* is also on this rugose margin of the basal tubera, deep to the insertion of *m. rectus capitis anticus major* (Fig. 4A,C). The former, however, extends dorsally along the median crest of the basal tubera, leaving a rugosity on the lateral surface of this crest. Cong et al. (1998) distinguished the anterior and medial part of *m. rectus capitis anticus major* that arises from the hypapophysis of V2 and the intercentrum of V1 as a separate muscle, "*m. rectus capitis anterior*," in *Alligator sinensis*. In *A. mississippiensis* (e.g., YPM 13324), the common carotid artery lies on the ventral surface of this muscle and appears to mark the boundary between "*m. rectus capitis anterior*" and the rest of *m. rectus capitis anticus major*. However, dorsal to this artery, these two parts are actually continuous without a clear boundary. Some fibers of the anterior part of this muscle insert directly on the medial part of the basal tubera while the rest of this part as well as the posterior part attaches to the sheet-like tendon of insertion before inserting on the basal tubera. In *Caiman crocodilus* (YPM 14680), the morphology of *m. rectus capitis anticus major* is generally similar to that in *A. mississippiensis*. In *C. crocodilus*, however, the tendinous part is restricted to the lateral end of the entire insertion. In other words, a sheet-like tendon develops in the lateral part of the muscle, and inserts on the lateral- or dorsal-most part of the rugose margin of the basal tubera in this crocodylian. This is also the case with *Osteolaemus tetraspis* (YPM 14682). In both taxa, the sheet-like tendon of insertion of *m. rectus capitis anticus major* lies around the insertion of *m. longissimus capitis profundus*, just as in *A. mississippiensis* (Fig. 4C).

Aves. In Aves, *m. longus colli ventralis* and *m. rectus capitis ventralis* are the two major muscles comprising the subvertebral layer. In addition, innervation patterns suggest that *m. rectus capitis lateralis* also belongs to this muscle layer as described below.

A series of muscle slips comprising *m. longus colli ventralis* arises from the hypapophyses (*crista ventralis corporis* of Baumel and Witmer, 1993), carotid processes, and/or ventral aspects of the centra, and inserts on the posterior tips of the ribs and/or posterolateral process of the centra (*processus postlateralis* of Baumel and Witmer, 1993) by tendons. Fleshy slips arising from several vertebrae insert on the rib of a more anterior vertebra and comprise each unit of this muscle (e.g., Zusi and Storer, 1969; Landolt and Zweers, 1985; Zweers et al., 1987). The most posterior origin of this muscle is the hypapophysis of an anterior or middle dorsal vertebra, and the most anterior insertion is the rib of V2 or V3 (e.g., Boas, 1929; Zusi and Storer, 1969; Zusi and Bentz, 1984; Landolt and Zweers, 1985; Zusi, 1985; Zweers et al., 1987). In *Struthio camelus*, for example, this muscle arises most posteriorly from the hypapophysis of V21 and inserts most anteriorly on V2 by a tendon that merges with the tendon III of *mm. intertransversarii*.

Muscle fibers of *m. rectus capitis ventralis* arises from the ventral surface of the intercentrum of V1, hypapophysis of V2, and ventral surfaces of the several more posterior cervical vertebrae (e.g., Landolt and Zweers, 1985). Zusi and Storer (1969) noted that aponeuroses connecting successive hypapophyses also serve as the origins of this muscle in *Podilymbus podiceps* and *P. gigas*. The insertion of this muscle is the basitemporal plate, or *lamina parasphenoidalis* (e.g., Zusi and Storer, 1969; Landolt and Zweers, 1985). In *Struthio camelus* (e.g., YPM 101216), *m. rectus capitis ventralis* arises from V1 through V6 with the most anterior origin of this muscle being the ventral process of the intercentrum (*corpus atlantis*) of V1 (Fig. 2C). A fascia extends posteriorly from this process and connects it with the hypapophyses of V2 and V3. This fascia also serves as the origins of fibers of this muscle. More posteriorly, the muscle fibers arise from tendons that arise from the carotid processes of V4 through V6. This muscle inserts on the basitemporal plate, anterior to the insertion of *m. rectus capitis dorsalis* (Fig. 4A,D). In *Meleagris gallopavo* (YPM 101229), the insertion of this muscle appears to be much more extensive than that of *S. camelus*, reflecting a relatively larger basitemporal plate in the former than the latter (Fig. 4D).

The strap-like *m. rectus capitis lateralis* arises from the lateral surfaces of the hypapophyses of V2 and one or more vertebrae posterior to V2. For example, the hypapophyses of V2 through V5 serve as the origins of this muscle in *Larus marinus* and *Tetrao urogallus* while only those of V2 through V4 are the origins in *Anser domesticus* (Boas, 1929). In addition, fibers of this muscle arise from the tendon of insertion of *m. longus colli ventralis* in some taxa (e.g., *Anas platyrhynchos*: Landolt and Zweers, 1985). It inserts on the distal end of the paroccipital process by a strong tendon. In *Struthio camelus* (e.g., YPM 101216), this muscle arises mainly from the hypapophyses of V2 and V3 by tendons (Fig. 2C). In addition, the most posterior part of this muscle arises from the ventral surfaces of the tendons of *m. longus colli ventralis* and *mm. intertransversarii* that insert on the posterior tip of the rib of V3 or V4, as well as by a tendon from the small carotid process of V4. The insertion of this muscle is the ventrolateral end of the paroccipital process (Fig. 4A). In *Rhea americana*

(YPM 101221 and 101222), on the other hand, *m. rectus capitis lateralis* arises from the hypapophyses of V2 through V4 and also from the tendon of insertion of *m. longus colli ventralis* attaching to V5. The insertion of this muscle in this bird extends further dorsally along the lateral edge of the skull than that in *S. camelus* and reaches the level above the dorsal margin of the foramen magnum. In *Meleagris gallopavo*, Harvey et al. (1968) described that this muscle arises from the hypapophyses of V3 and V4. In the specimen of this bird that I dissected (YPM 101229), however, the origin of this muscle also includes the hypapophysis of V2. At the insertion, this muscle wraps around the ventrolateral end of the paroccipital process (Fig. 4A).

In addition to the muscles discussed above, *m. flexor colli medialis* that lies on the ventrolateral side of the anterior cervical region has often been regarded as belonging to the subvertebral layer (Zusi and Storer, 1969; Vanden Berge and Zweers, 1993). This muscle consists of slips that arise from the carotid processes and/or ribs and insert on the hypapophyses and/or posterior corners of the centra of more anterior vertebrae with the most anterior insertion being V2 (Zusi and Storer, 1969; Zusi and Bentz, 1984). Each slip typically skips at least one vertebra between the origin and insertion (Vanden Berge and Zweers, 1993). In *Struthio camelus* that I dissected, slips of this muscle tend to be short, arising from the ventral aspects of the ribs and centra and inserting on the hypapophyses and/or ventral aspects of the centra of more anterior vertebrae. For example, the most anterior slip of this muscle consists of muscle fibers arising from the ventromedial aspects of the anterior parts of the ribs of V4 and V3 as well as from the ventral aspect of the posterior end of the centrum of V3. It inserts on the hypapophysis of V2 by a tendon as well as on the lateral surface of the same centrum directly by fleshy fibers (Fig. 2C). These muscle fibers share their origins with the fibers of *mm. inclusi* that arise from the anterior parts of these ribs and insert on the tendons IV. The next posterior slip of *m. flexor colli medialis* arises from a ridge on the posterior end of the centrum of V4 as well as from the ventral aspect of the rib and lateral aspect of the carotid process of V5, and inserts on the ventral keel of the centrum of V3 (Fig. 2C).

Based on the sites of insertion (ventral aspects of centra), it is reasonable to hypothesize that this muscle belongs to the subvertebral layer as has previously been suggested. It is noteworthy, however, that this muscle in *Struthio camelus* arises from the ribs and partially share sites of origin with *mm. inclusi*. Accordingly, it is also possible that *m. flexor colli medialis* may instead be a derivative of *mm. inclusi* or *mm. intercostales externi*.

Homology of the subvertebral muscles in Diapsida with a comment on the crocodylian "*m. iliocostalis capitis*". All diapsids examined here except for *Sphenodon punctatus* have at least two distinct muscles in the subvertebral layer in the cervical region. Among these muscles, *m. longus colli* in non-avian diapsids and *m. longus colli ventralis* in Aves can be readily homologized across the clades based on similar origins (ventral aspects of the vertebral column in the cervical and anterior dorsal regions) and insertions (cervical ribs).

The more anteriorly lying muscles inserting on the basal tubera/basitemporal plate of the skull, the lepidosaurian *m. rectus capitis anterior*, crocodylian *m. rectus capitis anticus major*, and avian *m. rectus capitis ventralis*, have similar sites of origin and insertion. Additionally, there is strong evidence suggesting that the avian *m. rectus capitis lateralis* inserting on the paroccipital process also belongs to the subvertebral layer. First, as is the case with other subvertebral muscles, this avian muscle arises from the hypapophyses of the cervical vertebrae. Second, innervation patterns are shared by this avian muscle and subvertebral muscles inserting on the basal tubera in other diapsids. In *Gallus gallus*, for example, Watanabe (1961) described *m. rectus capitis lateralis* as being innervated by small branches arising from the ventral rami of the first through fourth spinal nerves. In addition, Webb (1957) described that the ventral branches arising from the three roots of the hypoglossal nerve innervate "the neck muscles" in *Struthio camelus* although it was not specified which particular "neck muscles" he referred to. By dissecting a specimen of *S. camelus* (YPM 101219), I confirmed that the ventral branches arising from the roots of the hypoglossal nerve (only two roots observed in this specimen) innervate the anterior part of *m. rectus capitis lateralis* from its medial surface while the dorsal branch of the posterior root of this nerve merges with that of the first spinal nerve emerging between the skull and V1, extends dorsally, and innervates *m. splenius capitis* and *m. biventer cervicis*. The avian *m. rectus capitis lateralis*, therefore, is innervated not only by ventral branches of spinal nerves as Watanabe (1961) described, but also by branches of the hypoglossal nerve. A subvertebral muscle in Aves, *m. rectus capitis ventralis*, is also described as innervated by a branch of the posterior ramus of the hypoglossal nerve (Watanabe, 1964). It has also been described that *m. rectus capitis anterior* in Lepidosauria is innervated by a branch of the hypoglossal nerve as well as by spinal nerves (Willard, 1915; Oelrich, 1956). These common innervation patterns, especially those by the hypoglossal nerve, suggest that the avian *m. rectus capitis lateralis* also belongs to the subvertebral layer. It then follows that birds have two subvertebral muscles, *m. rectus capitis ventralis*,

lis and *m. rectus capitis lateralis*, connecting anterior cervical vertebrae with the skull. The origin of *m. rectus capitis lateralis* lies dorsal to that of *m. rectus capitis ventralis* on the cervical centra in Aves (Fig. 2C). As described above, there are also two slips in *m. rectus capitis anterior* distinguished in *Iguana iguana*, with the origin of the dorsal slip similarly lying dorsal to that of the ventral slip on the cervical centra (Fig. 2A). Therefore, it is tempting to homologize the avian *m. rectus capitis lateralis* and *m. rectus capitis ventralis* with the dorsal and ventral slips of *m. rectus capitis anterior* in *I. iguana*, respectively. However, only a single slip of a subvertebral muscle inserting on the skull is present in *Sphenodon punctatus*, raising a possibility that the differentiation of the *m. rectus capitis anterior* homolog into two slips may have actually occurred independently in Aves and Squamata. Accordingly, I here only suggest that the *m. rectus capitis anterior* homolog is differentiated into two muscles, *m. rectus capitis ventralis* and *m. rectus capitis lateralis*, in Aves, and stop short of proposing the slip-to-slip homologies mentioned above between this clade and Squamata.

The crocodylian "*m. iliocostalis capitis*" of Seidel (1978), or *m. atlantimastoideus* of Fürbringer (1876), and the avian *m. rectus capitis lateralis* share similarities in their sites of insertion and topological relationships with other muscles. The former crocodylian muscle inserts on the distal (lateral) end of the paroccipital process, medial to the origin of *m. depressor mandibulae* and lateral to the insertions of *m. spinocapitis posticus* and *m. epistropheocapitis* (Fig. 4A). The avian *m. rectus capitis lateralis* similarly inserts on the distal end of the paroccipital process, between a small site of origin of *m. depressor mandibulae* and insertion of the lateral slip of *m. splenius capitis* that is considered homologous with the crocodylian *m. epistropheocapitis* by Tsuihiji (2005). These similarities suggest that the crocodylian "*m. iliocostalis capitis*" and avian *m. rectus capitis lateralis* may be homologous. This hypothesis is further supported by the innervation patterns of these muscles. Fürbringer (1876) described "*m. iliocostalis capitis*" (his *m. atlantimastoideus*) in *Alligator mississippiensis* ("*A. lucius*") as innervated by the accessory nerve, which arises from the vagus ganglion, joined by one of three branches of a nerve stem (interpreted as the second root of the hypoglossal nerve merged with the first spinal nerve) that exits from a foramen in the occiput very close to the foramen magnum.

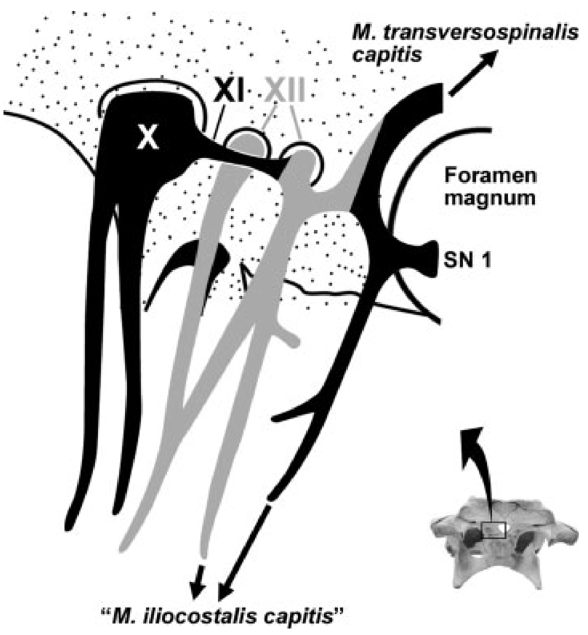

Fig. 7. Semi-schematic drawing of nerves supplying "*m. iliocostalis capitis*" *sensu* Seidel (1978) near the occipital region of *Alligator mississippiensis* (based on YPM 13321 and 13323). Note the connection among the accessory (XI), hypoglossal (XII), and fist spinal nerve (SN 1), all of which contribute to the innervation of "*m. iliocostalis capitis*." X, vagus nerve.

Fürbringer (1876) also described that the accessory nerve in *Crocodylus acutus* similarly arises from the vagus ganglion but merges with the first spinal nerve, with a branch of this merged nerve supplying "*m. iliocostalis capitis*." Fischer (1852), on the other hand, described the accessory nerve in *Crocodylus porosus* ("*C. biporcatus*") as arising from the common ganglion of the glossopharyngeal, vagus, and hypoglossal nerves and joining a branch of the first spinal nerve to innervate "*m. iliocostalis capitis*" (his *omomastoideus* muscle). Thus, the descriptions by Fürbringer (1876) and Fischer (1852) agree that the crocodylian "*m. iliocostalis capitis*" is innervated at least partially by the accessory nerve. In the *Alligator mississippiensis* specimens that I dissected (e.g., YPM 13321 and 13323), the innervation pattern of "*m. iliocostalis capitis*" is slightly different from the one described by Fürbringer (1876). In these specimens, the first spinal nerve is clearly distinct from the posterior root of the hypoglossal nerve, arising between the occiput and V1 (Fig. 7). One or two small branches that probably correspond to the accessory nerve described by Fürbringer (1876) arise from the stem of the vagus ganglion and immediately join the posterior root of the hypoglossal nerve. This merged nerve gives off a branch that innervates "*m. iliocostalis capitis*" from its medial aspect. Furthermore, another branch arising from this posterior root of the hypoglossal joins the first spinal nerve, and also innervates "*m. iliocostalis capitis*" (Fig. 7). This innervation pattern accordingly suggests that the nerves supplying "*m. iliocostalis capitis*" can be considered to have contributions from the accessory, hypoglossal, and first spinal nerves. As described above, the avian *m. rectus capitis lateralis*, as well as *m. rectus capitis ventralis* according to Watanabe (1964), is innervated by a branch of the hypoglossal nerve. This shared innervation pattern by the hypoglossal nerve, therefore, supports the hypothesis that the crocodylian "*m. iliocostalis capitis*" and avian *m. rectus capitis lateralis* are at least partially homologous with each other. This in turn means that the former crocodylian muscle is also homologous with a part of *m. rectus capitis anterior* in Squamata.

It is noteworthy, however, that the crocodylian "*m. iliocostalis capitis*" is innervated by a branch representing the accessory nerve that merges with the hypoglossal nerve as well. In Amniota, the accessory nerve is known to innervate *m. cucullaris* (e.g., Straus and Howell, 1936), which is a shoulder girdle muscle belonging to the branchiomeric musculature (see below). Therefore, this innervation pattern suggests that this crocodylian muscle also includes the *cucullaris* component, as proposed by Fürbringer (1876). This leads to a conclusion that the homology of the crocodylian "*m. iliocostalis capitis*" is quite complicated and that it consists of the both *m. rectus capitis anterior* and *m. cucullaris* components, and possibly, a contribution from *m. iliocostalis* (based on its site of origin on the rib of V1) as well.

Other Muscles Attaching to the Diapsid Occipital Region

Although not a part of the epaxial or hypaxial musculature, the morphology and attachments of the *m. cucullaris* complex and *m. depressor mandibulae* are described here because their topological relationships with several axial muscles inserting on the skull is significant in inferring homologies of the latter muscles among diapsids.

M. cucullaris complex. In *Sphenodon punctatus*, *m. cucullaris* (*m. trapezius*) is a single muscle that arises from the lateral two thirds of the clavicle and *processus clavicularis* (acromion) of the scapula, extends anterodorsally, and inserts on the posterior surfaces of the parietal and squamosal (Fürbringer, 1900). Fürbringer (1900) also described the additional insertion of this muscle as including the posterodorsal edge of the quadratojugal in one of the specimens that he examined. In the single specimen (CAS 20888) that I dissected, this muscle inserts on the parietal and squamosal between the attachments of *m. depressor mandibulae* and *m. longissimus capitis* by a thin tendon (Fig. 4A). Some fibers also insert on the fascia covering the cervical and anterior-most dorsal regions dorsally. This muscle is innervated by a branch (*ramus muscularis externus*) of the vagoaccessory nerve and branches of the fourth through sixth spinal nerves (Fürbringer, 1900).

In some squamates, *m. cucullaris* is a single muscle as in *Sphenodon punctatus* (Fürbringer, 1900). In the majority of squamates, however, this muscle splits into two, dorsal and ventral parts. Fürbringer (1876, 1900) named the dorsal part *m. capitidorsoclavicularis* and the ventral part *m. capiticleidoepisternalis* although these parts are usually called *m. trapezius* and *m. episternocleidomastoideus*, respectively, in the literature (e.g., Howell, 1936). Muscle fibers of *m. trapezius* arise from the dorsal part of the clavicle and, in some taxa, also from the adjacent area of the scapula, and insert on the parietal and/or "*os occipitale*" (Fig. 4A) as well as on the fascia of the dorsal midline of the cervical and dorsal regions up to the level of V11 to V13 (Fürbringer, 1876). This muscle is innervated by branches of the ventral rami of the third through fifth spinal nerves (*nervi thoracici anteriores* III, IV, and V of Fürbringer, 1876). The ventrally lying *m. episternocleidomastoideus* arises from the interclavicle (episternum) in most squamates, but also from the clavicle, sternum, and/or a membrane stretching between the clavicle and *processus clavicularis* of the scapula in some taxa, and inserts on the squamosal. This muscle is innervated by the same nerve branches as *m. trapezius* is, but is also supplied by *ramus muscularis externus* of the vagoaccessory nerve (Fürbringer, 1876). In *Iguana iguana, m. trapezius* and *m. episternocleidomastoideus* are closely associated with each other anteriorly, inserting together on the posterior margin of the parietal and distal end of the paroccipital process (Mivart, 1867; Fig. 4A).

In Crocodylia, Fürbringer (1876) recognized two muscles, *m. dorsoscapularis* and *m. capitisternalis*, as the *m. cucullaris* derivatives. The first muscle, *m. dorsoscapularis*, arises from the anterior edge of the proximal part of the scapula, extends dorsally, and attaches to the dorsal fascia in the midline of the posterior cervical and anterior-most dorsal regions (Fürbringer, 1876; Cong et al., 1998). It is innervated by a branch arising from the ventral ramus of the seventh spinal nerve (*nervus thoracicus anterior* VII of Fürbringer, 1876). The second muscle, *m. capitisternalis*, lies ventral to *m. dorsoscapularis*, and is divided into two parts by the rib of V1. The anterior part, *m. atlantimastoideus* (= "*m. iliocostalis capitis*" of Seidel, 1978), arises from the rib of V1 in *Alligator sinensis* (Cong et al., 1998) and from the ribs of V1 and V2 in *Crocodilus acutus* (Fürbringer, 1876), and inserts on the distal and ventral margins of the paroccipital process. As described above, Fürbringer (1876) described this part as being innervated by the accessory nerve (*ramus muscularis externus* of the vagoaccessory nerve). The posterior part, *m. sternoatlanticus*, arises from the anterior margin of the ventral surface of the sternum near the interclavicle (episternum) and inserts on the tip of the rib of V1 together with *m. levator scapulae* (Fürbringer, 1876). This posterior part of *m. capitisternalis* is innervated by a branch arising from the ventral ramus of the fifth spinal nerve (*nervus thoracicus anterior* V of Fürbringer, 1876).

In Aves, *m. cucullaris* consists of two parts. The first part, *m. cucullaris capitis* (= *m. dermotemporalis* in some studies), lies on the lateral to ventrolateral aspects of the neck, and has the insertion on the occipital region of the skull, including the squamosal, temporal membrane, or postorbital process of the frontal (Vanden Berge, 1975; Homberger and Meyers, 1989; Vanden Berge and Zweers, 1993). In *Struthio camelus* (e.g., YPM 101219), this muscle inserts on the parietal (Fig. 4A). Posteriorly, this muscle may differentiate into as many as three slips depending on the species, which are called *pars interscapularis*, *pars propatagialis*, and *pars clavicularis* (Vanden Berge and Zweers, 1993). The origins of these slips include clavicle, ligament (*membrana sternocoracoclavicularis* of Baumel and Raikow, 1993) stretching between the clavicle, coracoid, and sternum, and/or skin (Vanden Berge, 1975; Homberger and Meyers, 1989). The second part of the avian *m. cucullaris*, *m. cucullaris cervicis*, lies dorsal to *m. cucullaris capitis*, and arises from the clavicle, and extends dorsally to attach to the mid-dorsal raphe at the level of the most posterior cervical vertebrae (Vanden Berge, 1975). The accessory nerve innervates the most anterior part of *m. cucullaris capitis* while the rest of this muscle and *m. cucullaris cervicis* are innervated by cutaneous rami of several cervical spinal nerves (Fürbringer, 1902; Vanden Berge, 1975).

Mainly based on the innervation patterns, Fürbringer (1902) argued that *m. cucullaris capitis* and *m. cucullaris cervicis* in Aves are homologous with *m. capitisternalis* and *m. dorsoscapularis* in Crocodylia, respectively. The crocodylian *m. capitisternalis* was in turn homologized with *m. episternocleidomastoideus* (*m. capiticleidoepisternalis*) in Squamata (Fürbringer, 1876, 1900). It then follows that the *cucullaris* component of the crocodylian "*m. iliocostalis capitis*" of Seidel (1978) mentioned above, which is a part of *m. capitisternalis*, is homologous with the anterior part of the avian *m. cucullaris capitis* and that of *m. episternocleidomastoideus* in Squamata.

M. depressor mandibulae. In *Sphenodon punctatus*, *m. depressor mandibulae* consists of a single muscle slip that arises from the posterior edges of the parietal and squamosal (Fig. 4A) as well as the lateral surface of *ligamentum nuchae*, and inserts on the retroarticular process of the lower jaw (Haas, 1973). In Squamata, Haas (1973) described that the posterior part of this muscle tends to differentiate into a thin, independent slip called *m. cervicomandibularis* arising from the superficial fascia of the neck. In *Iguana iguana* that I dissected (e.g., YPM 13325), however, such differentiation is absent. The origin on the occiput in *I. Iguana* is the posterior edge of the parietal and distal edge of the paroccipital process (Fig. 4A).

Schumacher (1974) described *m. depressor mandibulae* in Crocodylia as consisting of two parts: the main part arises from the parietal, supraoccipital, and quadrate, and inserts on the concave, dorsal surface of the articular while the other, small part arises from a groove in the lateral surface of the squamosal and inserts on the lateral edge of the angular on the long retroarticular process. In *Alligator mississippiensis* that I dissected, the thin tendon of origin of *m. depressor mandibulae* arises from the distal edge of the paroccipital process. Muscle fibers arise both medially and laterally from this tendon. The fleshy origin of this muscle further extends medially onto a dorsoventrally thin, but mediolaterally wide, area on the posterior surface of the squamosal, just beneath the rugose area for attachment of the skin and above the insertions of the *transversospinalis* muscles, specifically *m. transversospinalis capitis* and *m. atloïdocapitis* (Fig. 4A). The fleshy origin of *m. depressor mandibulae* also includes the lateral surface of the posterior-most part of the squamosal and also the lateral surface of the tendon of insertion of "*m. iliocostalis capitis*" near its insertion on the posterior surface of the distal end of the paroccipital process.

In Aves, *m. depressor mandibulae* arises from the posterolateral part of the skull between the temporal fossa and *crista nuchalis transversa*, lateral surface of the paroccipital process, and ligaments around these structures, and inserts on the posterior fossa (*fossa caudalis* of Baumel and Witmer, 1993) on the articular of the lower jaw (Vanden Berge and Zweers, 1993). In the embryonic specimens of *Struthio camelus* (YPM 101219 and 101229), *m. depressor mandibulae* arises mainly from the posterior edge of the squamosal, but the origin extends further dorsally onto the lateral part of the posterior edge of the parietal (Fig. 4A). In addition, some fibers of this muscle also arise from the distal/ventral edge of the paroccipital process, medial to the insertion of *m. rectus capitis lateralis* (Fig. 4A). In adult specimens of *S. camelus*, on the other hand, these two origins are continuous through the posterior rim of the external auditory meatus. The insertion of this muscle is the deep posterior fossa on the articular (possibly homologous with the retroarticular process in other reptiles) that faces ventromedially, and extends further anteriorly along the ventral edge of the posterior part of the angular. In *Meleagris gallopavo* (YPM 101229), the origin of this muscle is the posterolateral edge of the skull, anterior to *crista nuchalis transversa*. The origin extends ventrally along the posterior rim of the external auditory meatus, and further occupies a bony bridge that connects the paroccipital process and basitemporal plate lateral to the parabasal fossa (Fig. 4A). It inserts on the posterior tip as well as the medial surface of the long retroarticular process.

TABLE 1. Synopsis of muscles of Lepidosauria discussed in the present study, listing their names and main origins and insertions (mainly based on the anatomy of Iguana iguana)

		Origin	Insertion
M. longissimus group			
Dorsal region	*M. longissimus dorsi*	Lateral surfaces of prezygapophyses of dorsal vertebrae	Lateral surfaces of prezygapophyses and proximal ends of ribs of dorsal vertebrae
Cervical region	*M. longissimus cervicis*	Lateral surfaces of prezygapophyses of cervical vertebrae	Lateral surfaces of prezygapophyses, posterior aspects of synapophyses, and/or proximal ends of ribs of cervical vertebrae
	M. longissimus capitis, pars transversalis capitis	Lateral process of the neural arch of V1	Distal part and ventral edge of the paroccipital process
	M. longissimus capitis, *pars transversalis cervicis*	Anterolateral surfaces of synapophyses and lateral aspects of neural arches of anterior cervical vertebrae	Basal tubera
M. iliocostalis group			
Dorsal region	*M. iliocostalis dorsi*	Posterodorsal edges of dorsal ribs	Posterodorsal edges of dorsal ribs
Cervical region	*M. iliocostalis cervicis*	Posterodorsal edges of ribs or synapophyses of cervical vertebrae	Posterodorsal edges of ribs or synapophyses of cervical vertebrae
	M. iliocostalis capitis	Lateral surface of fascia between *m. iliocostalis* and *m. longissimus*	Basal tubera
Hypaxial muscles			
	Mm. intercostales externi	Anterior edges of ribs (including proximal parts of sternal segments in the dorsal region) or synapophyses	Posterior edges of ribs (including proximal parts of sternal segments in the dorsal region), posterolateral aspects of prezygapophyses, synapophyses, and/or lateral aspects of centra
	M. longus colli[a]	Ventral aspects of centra, synapophyses, and ribs of cervical vertebrae	Ventral aspects of centra and synapophyses and lateral aspects of intercentra of cervical vertebrae
	M. rectus capitis anterior[a]	Lateral aspects of intercentra of cervical vertebrae	Basal tubera
Other muscles attaching to the occiput			
	M. trapezius[b]	Clavicle	Posterior aspect of the parietal and fascia on the dorsal midline of the neck and trunk
	M. episternocleidomastoideus[b]	Interclavicle, clavicle, and/or sternum	Posterior aspects of the parietal and/or squamosal and distal end of the paroccipital process
	M. depressor mandibulae	Posterior aspects of the parietal, squamosal, and/or paroccipital process	Retroarticular process of the lower jaw

[a] *M. longus colli* and *M. rectus capitis anterior*: form an undifferentiated, single muscle in *Sphenodon punctatus*.

[b] *M. trapezius* and *m. episternocleidomastoideus*: form an undifferentiated, single *m. cucullaris* in *Sphenodon punctatus*.

DISCUSSION

As a summary of results of the present study, synopses of the muscle discussed above are presented in Tables 1–3, and proposed homologies of these muscles are summarized in Table 4.

The most significant finding in the present study is that the avian *"m. iliocostalis"* in the dorsal region and *mm. intertransversarii* in the cervical region are composites of muscles belonging to the *m. longissimus* and *m. iliocostalis* groups. The avian "*m. iliocostalis*" is weakly developed, occupying a very small area of the lateral parts of the transverse processes and proximal parts of the vertebral segments of the ribs (Fig. 3C), meaning that the *m. longissimus* and *m. iliocostalis* groups are greatly reduced in the dorsal region of Aves. In contrast, their cervical homologs, *mm. intertransversarii*, form the principal lateral musculature of the avian neck and are well-developed. The name of "*mm. intertransversarii*" is particularly misleading because the same name has often been used to refer to just a series of short and often feebly developed segmental muscles that connects adjacent transverse processes/synapophyses in non-avian diapsids as described above. Such a series of muscles is regarded as a part of *m. longissimus* in Crocodylia (Vallois, 1922; Seidel, 1978: but see Murakami et al. (1991) and Cong et al. (1998) for different interpretations) and as a part of the hypaxial musculature in Lepidosauria (Olson, 1936). Therefore, muscles currently named "*mm.*

TABLE 2. Synopsis of muscles of Crocodylia discussed in the present study, listing their names and main origins and insertions (mainly based on the anatomy of Alligator mississippiensis)

		Origin	Insertion
M. longissimus group			
Dorsal region	*M. longissimus dorsi*	Anterior edges and dorsal surfaces of transverse processes of dorsal vertebrae	Posterior edges of transverse processes of dorsal vertebrae
Cervical region	*M. longissimus cervicis*	Lateral surfaces of prezygapophyses of cervical vertebrae; lateral surfaces of neural arches and transverse processes of posterior cervical vertebrae	Lateral surfaces of prezygapophyses and posterior edges of transverse processes of cervical vertebrae
	M. longissimus capitis superficialis	Lateral aspects of neural arches of middle to posterior cervical vertebrae	Distal end of the paroccipital process
	M. longissimus capitis profundus	Lateral aspects of neural arches and/or transverse processes of cervical vertebrae	Basal tubera
M. iliocostalis group			
Dorsal region	*M. iliocostalis dorsi*	Posterior edges and lateral surfaces of ribs and anterior edges of transverse processes of dorsal vertebrae	Posterior edges of ribs and transverse processes of dorsal vertebrae
Cervical region	*M. iliocostalis cervicis*	Posterior edges and lateral surfaces of cervical ribs	Posterior or dorsal edges of cervical ribs
Hypaxial muscles			
	Mm. intercostales externi dorsales (dorsal region) and *mm. intercostales externi* (cervical region)	Anterior edges of ribs and lateral aspects of their anterior processes	Posterior edges of ribs, posterior aspects of transverse processes, and/or lateral aspects of centra
	Mm. intercostales externi ventrales	Anterior edges of intermediate segments of ribs (in the dorsal region only)	Posterior edges of intermediate segments of ribs (in the dorsal region only)
	M. scalenus[a]	Anterior, lateral, and/or ventral aspects of cervical ribs	Posterior ends of cervical ribs
	M. longus colli	Lateral aspects of hypapophyses and centra, and capitular processes of ribs of cervical and anterior dorsal vertebrae	Posterior ends of cervical ribs
	M. rectus capitis anticus major	Tips of hypapophyses of cervical vertebrae and the intercentrum and rib of V1	Basal tubera
Other muscles attaching to the occiput			
	"*M. iliocostalis capitis*"[b]	Lateral surface of the rib of V1	Distal and ventral edges of the paroccipital process
	M. depressor mandibulae	Distal edge of the paroccipital process and posterior and lateral aspects of the squamosal	Retroarticular process of the lower jaw

[a] *M. scalenus*: differentiated from *mm. intercostales externi* in the cervical region.
[b] "*M. iliocostalis capitis*": merged form of the subvertebral, *cucullaris*, and *iliocostalis* muscles.

intertransversarii" are not homologous among Lepidosauria, Crocodylia, and Aves.

The composite nature of the avian *mm. intertransversarii* was revealed here by close examination of the morphology of the tendons, particularly those of palaeognath birds that still retain plesiomorphic structures seen in non-avian diapsids. That is, in Palaeognathae (e.g., *Struthio camelus* and *Rhea americana* in examples mentioned above), the tendons homologous with those of *m. longissimus* and *m. iliocostalis* have the lateral parts covering the muscle fibers (Fig. 3D,E), which are similar to those in Lepidosauria and Crocodylia (Fig. 3A,B). In Neognathae (e.g., *Meleagris gallopavo*, *Gallus gallus*, *Anas platyrhynchos*, and *Podilymbus podiceps* in examples mentioned above), in contrast, such parts are mostly absent and these tendons form simple, horizontally extending sheets (Fig. 3F), representing a derived characteristic not seen in Palaeognathae or other diapsids.

Homologies of muscles in the dorsal and cervical regions discussed in the present study, as well as those discussed in Tsuihiji (2005), may be reviewed in context of character evolution. As I have not established such muscle homologies between Diapsida and its extant outgroups including turtles and mammals, however, it is not possible to rigorously identify plesiomorphic conditions for Diapsida or polarities of characters at present. Therefore, this discussion should be considered as a preliminary one. First, Archosauria (= Aves + Crocodylia) is characterized by the following synapomorphies:

1. The lateral part of the *m. semispinalis* homolog is differentiated as a separate series of muscles,

TABLE 3. Synopsis of muscles of Aves discussed in the present study, listing their names and main origins and insertions (mainly based on the anatomy of Struthio camelus)

		Origin	Insertion
M. longissimus + *m. iliocostalis* groups			
Dorsal region	"*M. iliocostalis*"	Anterior edge of the ilium, lateral edges of transverse processes, and proximal parts of ribs of dorsal vertebrae	Lateral edges of transverse processes and proximal parts of ribs of dorsal vertebrae
Cervical region	*Mm. intertransversarii*	Anterior edges of transverse processes and prezygapophyses, and lateral aspects of ribs of cervical vertebrae	Lateral aspects of transverse processes and dorsal edges of ribs of cervical vertebrae
	M. flexor colli lateralis	Anterior edges of transverse processes, and lateral aspects of prezygapophyses and ribs of anterior cervical vertebrae	*Ansa costotransversaria* and intercentrum of V1
	M. rectus capitis dorsalis	Lateral aspects of prezygapophyses, postzygapophyses, neural arches, and ribs of anterior cervical vertebrae	Basal tubera
Hypaxial muscles			
	Mm. levatores costarum[a]	Anterior edges and lateral aspects of dorsal ribs	Posterior edges of ribs and distal ends of transverse processes of dorsal vertebrae
	Mm. intercostales externi[a]	Anterior edges of dorsal ribs	Posterior edges of dorsal ribs and medial aspects of their uncinate processes
	Mm. inclusi	Heads of cervical ribs	Posterior edges of transverse processes, lateral and ventral aspects of centra, and medial aspects of ribs of cervical vertebrae
	M. longus colli ventralis	Hypapophyses, carotid processes, and ventral aspects of centra of cervical and anterior dorsal vertebrae	Posterior ends of ribs and posterolateral processes of centra of cervical vertebrae
	M. flexor colli medialis	Carotid processes and ventral aspects of centra and ribs of cervical vertebrae	Carotid processes and ventral and/or lateral aspects of centra of cervical vertebrae
	M. rectus capitis ventralis	Hypapophyses or ventral aspects of centra of anterior cervical vertebrae, and the intercentrum and rib of V1	Basitemporal plate
	M. rectus capitis lateralis	Hypapophyses or ventral aspects of centra of anterior cervical vertebrae	Ventrolateral end of the paroccipital process
Other muscles attaching to the occiput			
	M. cucullaris capitis	Clavicle, *membrana sternocoracoclavicularis* and/or skin	Squamosal, parietal, temporal membrane, or postorbital process of the frontal
	M. depressor mandibulae	Posterior aspects of the squamosal and/or parietal, and distal edge of the paroccipital process	Retroarticular process or the posterior fossa of the lower jaw

[a] *Mm. levatores costarum* and *mm. intercostales externi*: these muscles arising from the free cervical rib(s) are combined and named as *m. scalenus.*

m. tendinoarticularis in Crocodylia and *mm. ascendentes* in Aves (Tsuihiji, 2005).

2. The dorsal part of the *m spinalis* homolog in the anterior cervical region is differentiated into a distinct muscle, *m. spinocapitis posticus* in Crocodylia and *m. longus colli dorsalis*, *pars cranialis* + *m. splenius anticus* in Aves (Tsuihiji, 2005: note, however, Vallois (1922) hypothesized the crocodylian *m. spinocapitis posticus* as differentiated from the suboccipital muscles. If his hypothesis turns out to be correct, this putative archosaurian synapomorphy will no longer be tenable).
3. The *mm. intercostales externi* homologs in the cervical region are at least incompletely divided into two series of muscles (dorsal and ventral parts of *mm. inclusi* in Aves and *mm. intercostales externi* and *m. scalenus* in Crocodylia).
4. The dorsal slip of the *m. cucullaris* complex, *m. dorsoscapularis* in Crocodylia and *m. cucullaris cervicis* in Aves, does not attach to the skull unlike in Lepidosauria.

Concerning the first character, *m. tendinoarticularis* appears to play a significant role in the bracing system of the dorsal region in crocodylians. Frey (1984, 1988b) argued that the vertebral column, dorsal paravertebral osteoderms, and epaxial muscles attaching to them together function as a "self-carrying bridge" for maintaining the stability and posture of the dorsal region during the high-walk and gallop in crocodylians. In the *m. trans-*

TABLE 4. Homologies of the longissimus, iliocostalis, and hypaxial muscles in extant diapsids proposed in this study

	Lepidosauria[a]	Crocodylia[b]	Aves[c]
M. longissimus group			
Dorsal region	*M. longissimus dorsi*	*M. longissimus dorsi (including mm. intertransversarii dorsales)*	Dorsal part of *"m. iliocostalis"*
Cervical region	*M. longissimus cervicis*	*M. longissimus cervicis*	Parts of *mm. intertransversarii* and *m. flexor colli lateralis*
	M. longissimus capitis, pars transversalis capitis	*M. longissimus capitis superficialis*	Absent
	M. longissimus capitis, pars transversalis cervicis	*M. longissimus capitis profundus*	Part of *m. rectus capitis dorsalis*
M. iliocostalis group			
Dorsal region	*M. iliocostalis dorsi*	*M. iliocostalis dorsi*	Ventral part of "*m. iliocostalis*"
Cervical region	*M. iliocostalis cervicis*	*M. iliocostalis cervicis*	Parts of *mm. intertransversarii* and *m. flexor colli lateralis*
	M. iliocostalis capitis	Part of "*m. iliocostalis capitis*"	Part of *m. rectus capitis dorsalis*
Hypaxial muscles			
Dorsal region	*Mm. intercostales externi*	*Mm. intercostales externi dorsales* and *ventrales*	*Mm. intercostales externi*, *mm. levatores costarum*, and *m. scalenus*
Cervical region	*Mm. intercostales externi*	*Mm. intercostales externi* and *m. scalenus*	*Mm. inclusi*
	M. rectus capitis anterior	*M.* rectus *capitis anticus major* Part of *"m. iliocostalis capitis"*	*M. rectus capitis ventralis* *M. rectus capitis lateralis*
	M. longus colli	*M. longus colli*	*M. longus colli ventralis* and *m. flexor colli medialis*

[a] Lepidosauria: terminology after Nishi (1916, modified) for epaxial muscles, and Maurer (1896) and Evans (1939) for hypaxial muscles.

[b] Crocodylia: terminology after Vallois (1922) and Seidel (1978) for epaxial muscles, and Rathke (1866) and Murakami (1988) for hypaxial muscles.

[c] Aves: terminology after Vanden Berge and Zweers (1993).

versospinalis system, *m. articulospinalis* and *m. tendinoarticularis* have their tendons attaching to these osteoderms (Frey, 1988a), and thus are an essential part of this bracing system. Gauthier (1994) suggested that the crocodylian bracing system proposed by Frey (1984, 1988b) would have already been present in the common ancestor of the extant Archosauria (as well as in its close outgroups such as *Euparkeria* and proterochampsids), based on the plesiomorphic presence of paravertebral osteoderm rows in this clade. The differentiation of the *m. tendinoarticularis*/*m. ascendentes* as an archosaurian synapomorphy (and accordingly its presence in the common ancestor of Archosauria) proposed here adds further support for Gauthier's (1994) hypothesis that this bracing system would have evolved much earlier than the origin of crocodylians, then presumably was lost toward the avian lineage.

Concerning the fourth character, a review of published accounts on diapsid outgroups reveals a complex distributional pattern of this condition on phylogeny. In turtles, Fürbringer (1874) considered *m. testoscapuloprocoracoideus* and *m. capitiplastris* homologous with *m. trapezius* (his *m. capitidorsoclavicularis*) and *m. episternocleidomastoideus* (his *m. capiticleidoepisternalis*) in Squamata, respectively. The insertion of *m. testoscapuloprocoracoideus* is on the ventral (deep) surface of the nuchal plate of the carapace (Fürbringer, 1874), and does not include the occiput unlike those of *m. trapezius* in Squamata or an undifferentiated *m. cucullaris* in *Sphenodon punctatus*. In mammals, *m. cucullaris* usually splits into two or three parts. The insertion of the dorsal-most part, *m. trapezius*, includes the occiput in both monotremes (Howell, 1937a) and most therians (Howell, 1937b). The dorsal part of the *m. cucullaris* complex (= *m. trapezius* homolog), therefore, attaches to the occiput in lepidosaurs and mammals while it lacks such an attachment in crocodylians, birds, and turtles. If turtles are the immediate outgroup of Diapsida as it has traditionally been hypothesized (e.g., Gauthier et al., 1988), the lepidosaurian condition is unique to this clade within Reptilia, representing either retention of a primitive amniote character state seen in Mammalia or an apomorphy acquired convergently with the latter clade. The phylogenetic position of turtles within Amniota, however, has been debated in the past decade (e.g., Rieppel and Reisz, 1999). One recently proposed, untraditional hypothesis based on the molecular evidence is that turtles are the extant sister clade of Archosauria or are even included within the latter clade (Zardoya and Meyer, 1998; Kumazawa and Nishida, 1999; Cao et al., 2000). If such a phylogenetic hypothesis were sustained, then the dorsal part of the *m. cucullaris* complex that does not attach to the occiput would potentially represent a synapomorphy uniting turtles, crocodylians, and birds with the lepidosaurian and mammalian conditions representing a plesiomorphy for Amniota.

The crocodylian apomorphies that are not seen in Lepidosauria or Aves are as follows:

1. The insertion of *m. iliocostalis capitis* (assuming that this muscle is actually present as a muscle merged with the *m. rectus capitis lateralis* and *m. episternocleidomastoideus* homologs) is the distal end of the paroccipital process, instead of the basal tubera.
2. The homolog of *m. rectus capitis lateralis* (part of "*m. iliocostalis capitis*") arises from the rib of V1, not from the ventral surfaces of the centra or intercentra.
3. In the dorsal region, the ventral part of *mm. intercostales externi* differentiates into a distinct *mm. intercostales externi ventrales*.

Aves is characterized by more apomorphies than is Crocodylia or Lepidosauria. They are:

1. Distinct *mm. interspinales* and tendons of *m. multifidus* are absent (Tsuihiji, 2005).
2. The origins of the *m. spinalis capitis* homolog (*m. longus colli dorsalis, pars caudalis*) extend further posteriorly to reach the posterior dorsal vertebrae (Tsuihiji, 2005).
3. The origin of the *m. obliquus capitis magnus* homolog (lateral part of *m. splenius capitis*) is restricted to the dorsal edge of the neural spine of V2 instead of occupying its lateral surface (Tsuihiji, 2005).
4. The homolog of *m. longissimus capitis*, *pars transversalis capitis* inserting on the paroccipital process is absent.
5. In the dorsal region, the *m. longissimus* and *m. iliocostalis* homologs are greatly reduced.
6. In the dorsal region, the *mm. intercostales externi* homolog is differentiated to two distinct series of muscles, *mm. levatores costarum* and "*mm. intercostales externi.*"

The first and fifth characters, reduction of several epaxial muscles, are likely correlated with the short and rigid trunk in Aves. Ritter (1995, 1996) proposed that in squamates the main role of the all three major epaxial muscle groups (including the laterally lying *m. longissimus* and *m. iliocostalis* groups) during locomotion is to provide postural stability to the trunk. Ritter (1995) and Ritter et al. (1996) further suggested that such a functional role of the epaxial muscles is a plesiomorphy for amniotes. Assuming that the main function of these epaxial muscles in birds remains the same, which is apparently the case based on data in Gatesy and Dial (1993), reduction of some of these muscles is not surprising considering that functional demands for these muscles are likely reduced in the short trunk with reduced mobility in Aves.

Lepidosauria also has the following apomorphy, and thus cannot be considered to represent entirely plesiomorphic conditions of Diapsida:

1. Part of the subvertebral layer that inserts on the paroccipital process is absent.

In fact, subvertebral muscles inserting on the paroccipital process are present in turtles (*m. atlantoexoccipitalis* and *m. epistropheosquamosus ventralis* described in Ogushi, 1913) and mammals (*m. rectus capitis lateralis brevis* and *longus* described in Nishi, 1916), suggesting that the lepidosaurian condition (loss of the insertion on the paroccipital process) is autapomorphic to this clade within Amniota.

Lastly, *m. cucullaris* in *Sphenodon punctatus* forms a single, undivided slip while this muscle is divided into two slips in mammals, turtles, most squamates, crocodylians, and birds as described above. Therefore, the apparently undifferentiated condition of *m. cucullaris* in *S. punctatus* may represent an apomorphy, not a plesiomorphy, in Diapsida.

Nomenclatural Notes

Based on the homology assessments presented above, it is obvious that names of the avian muscles are drastically different from those used for their homologs in non-avian diapsids (Table 4). Most conspicuously, the avian nomenclature does not employ a name "*longissimus*" or "*iliocostalis*" (except for "*m. iliocostalis*" in the dorsal region) and instead often uses purely descriptive names. This is partly because boundaries among the major groups of the epaxial musculature (or even the boundary between the epaxial and hypaxial musculatures in the cervical region) had not been clearly determined in birds as mentioned above. It is shown here, however, that not only can such boundaries still be recognized in the avian cervical and dorsal regions (albeit obscured in some cases), but also many muscles have their origins and/or insertions conserved between avian and non-avian diapsids. It may therefore be desirable to establish a standardized nomenclature of these muscles that is applicable for all diapsid clades. In establishing such a nomenclature, the most problematic aspect would be the selection of the terminology: among the lepidosaurian, crocodylian, and avian nomenclatures, which one should we choose for applying to the all clades? Mostly focusing on osteological characteristics, Harris (2004) recently argued that an already established standardized nomenclature such as Nomina Anatomica Avium (Baumel et al., 1993) and Nomina Anatomica Veterinaria (International Committee on Veterinary Gross Anatomical Nomenclature, 1994) should be applied to clades that are "as far as basally in their respective phylogenies" (p. 1240) so long as homologous structures are recognized. For example, he recommended applying Nomina Anatomica Avium to non-avian diapsids and discontinuing using the traditional "reptilian" nomenclature that has not been formalized. There are indeed some advantages in expanding the use of Nomina Anatomica Avium outside of Aves, especially in terms of promoting communication in the scientific community because it is published as one comprehensive and readily available volume in which terms are unambiguously defined. Concerning the cervical and dorsal axial musculature, however, applying the avian terms to other diapsids is highly problematic for the following reasons. First, based on the observations presented above, the avian cervical muscles are in general highly derived compared with non-avian counterparts. The best example is the avian (or, more precisely, neognath) *mm. intertransversarii*, each segment of which is a multipennate muscle complex consisting of complexly interdigitating tendons and associated muscle fibers. This is a highly specialized condition considering that this muscle complex is formed across the boundary between two major muscle groups, *m. longissimus* and *m. iliocostalis*, that are clearly distinct from each other not only in non-avian diapsids but also in Amniota in general (e.g., Nishi, 1916, 1938). Applying this avian name to the homologs in non-avian diapsids would therefore lead to lumping two very distinct muscles, i.e., *m. longissimus cervicis* and *m. iliocostalis cervicis*, which do not have the derived condition of forming a single muscle complex, under one name, and thus would not accurately reflect their morphology. This example demonstrates the problem of applying terminologies associated with derived anatomy to more plesiomorphic conditions. Certainly, it is true that non-avian diapsids also have their own apomorphies and thus cannot be considered to represent entirely plesiomorphic conditions of Diapsida as mentioned above. So far as the cervical muscles are concerned, however, birds tend to have more apomorphies than other diapsids, making the avian terminologies less suitable as the universal diapsid nomenclature than the lepidosaurian or crocodylian ones.

Second, the avian nomenclature for the axial musculature is markedly different not only from those of non-avian diapsids but also from those used for mammals such as those in Nomina Anatomica Veterinaria. This is because the avian nomenclature does not employ names of the major epaxial muscle groups such as "*spinalis*," "*semispinalis*," "*transversospinalis*," "*longissimus*," and "*iliocostalis*" as mentioned above while such major groups in the epaxial musculature are recognized and reflected in muscle names by the other nomenclatures. With this respect, therefore, nomenclatures for non-avian diapsids and those for mammals are fairly comparable to each other. Therefore, applying the avian names to the all diapsids (and to turtles that are phylogenetically closer to Aves than to Mammalia) would result in much more different nomenclatures of the epaxial musculature between Diapsida (or Reptilia) and Mammalia than those that would result from applying the general "reptilian" or lepidosaurian/crocodylian terms to the all diapsids including Aves. In addition, because the axial musculature divided into major, distinct groups is likely an amniote plesiomorphy that characterizes all amniote clades (e.g., Nishi, 1916, 1938), naming a muscle based on a group to which it belongs is not only reasonable but may also be helpful for future studies on the comparative anatomy and homologies of this muscle system across Amniota. With this regard, the lepidosaurian or crocodylian terms are more suitable to be adopted as the general diapsid nomenclature than the avian nomenclature is.

In conclusion, I suggest that it is not reasonable to simply apply the current avian nomenclature to other diapsids, at least for the axial (especially epaxial) musculature, contrary to Harris' (2004) argument. Instead, for nomenclatures of the axial musculature to be standardized for all diapsids, it may be desired that the current avian nomenclature be revised so that it contains information on a major group to which each muscle belongs and reflects muscle homologies across all diapsids.

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